# Extinction vulnerability in two small, chronically inbred populations of Chatham Island black robin *Petroica traversi*

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## ABSTRACT

New Zealand ecologists and wildlife managers have assumed traditionally that threatened insular endemic bird species are less susceptible to the predicted genetic consequences of declines and inbreeding. Conservation has relied on treating deterministic extinction pressures to trigger population recoveries, with few measures taken to minimise stochastic genetic threats to long-term viability. This study tested that assumption empirically by examining extinction vulnerability in two small, critically threatened Chatham Island black robin populations protected from external threats on habitat-restricted islands but not managed purposefully for genetic health. Analysis of the factors eliminating the species's original island populations indicated loss through habitat change and mammalian predation within perhaps no more than two to three decades of human contact. Loss was undoubtedly hastened by intrinsic extinction-proneness (low reproductive output, forest-interior preference, sensitivity to habitat quality, intolerance of open spaces), greater in black robins than in other *Petroica* species in New Zealand and Australia. Low productivity in ancestral survivors prevented spontaneous recovery after translocation to better habitat, requiring intensively assisted breeding to raise population sizes quickly. Strong growth in response to management did not suggest a moribund species but post-management growth rates were significantly slower. Analysis of demographic data from 1980-81 to 2001-02 showed breeding effort to be comparable in all populations but breeding failures of varying severity at different life-history stages affected natural recovery in each. The worst affected suffered from briefer adult life-spans and more severe failure late in the breeding cycle. Generally colder sub-canopy air temperatures suggested adverse environmental pressure on this population. Extant populations are highly inbred and severely depleted genetically following successive bottlenecks (prolonged historically) and recovery from a single-pair event between 1979-80 and 1982-83. At current small sizes, accumulating levels of relatedness are anomalously high. Contrary to perceptions that black robin recovery indicates normal fitness, viability was shown to be threatened by inbreeding depression expressed cumulatively in the breeding cycle as low juvenile production and survival, thus aggravating a principal vulnerability. Declines did not result during the study period and effects were limited to reproductive fitness costs in black robin fathers only. There was no evidence of harmful effects on survival probability or from maternal inbreeding but an emerging kinship effect on yearling production is possible. The restricted costs in such highly inbred populations (relative to less inbred congeners) suggest historical purging of genetic load. Work is needed to clarify this and the extent to which inbreeding could reduce responses to new extinction pressures. Recent population declines may elevate levels of inbreeding further. Genetic management is strongly recommended, including habitat expansion to maximise population sizes and prevent further cross-breeding with a sympatric congener. Management and monitoring recommendations apply valuable lessons derived from a critique of past practices. In summary, findings give qualified support to the hypothesis of reduced susceptibility to inbreeding depression in threatened insular endemic birds. Findings do not support the assumption implicit in black robin management historically and in New Zealand wildlife management practice generally that stochastic genetic threats are unimportant risks to viability.

KEY WORDS: Chatham Island black robin, *Petroica*, population, extinction, vulnerability, viability, decline, inbreeding depression, insular, endemic, genetic, translocation, bottleneck, productivity, survival, recovery, hybridisation

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*Dixie*, it's a long way from the dappled sunlight of West Woolshed, the warm nest in the old akeake and our conversations over grubs on the palm of my hand. You've been with me at my desk all these years, keeping me true to your descendants' needs. I hope I've made a difference.

*

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## 1.0 Research overview

It is an assumption implicit in New Zealand wildlife management practice that the predicted genetic consequences of unnaturally small population sizes (loss of genetic diversity and inbreeding depression; Amos and Balmford, 2001, Frankham, 2005) are unimportant to the recovery and on-going viability of threatened insular endemic bird populations. In conservation practice, the assumption is inherent in a century-long tradition of addressing the immediate deterministic causes of decline—principally introduced mammalian predators and habitat deterioration (Clout, 2001; Saunders and Norton, 2001; Wilson, 2004, 2008)—with few, if any, measures taken to anticipate or minimise potential genetic threats to population persistence (Jamieson e*t al*., 2006, 2008; Groombridge, 2007).

The safety of this assumption has important theoretical and management implications for the crucial task of safeguarding threatened species from total extinction. It contradicts seminal genetic principles of conservation biology and lies at the heart of an on-going debate between conservation ecologists and geneticists over the relative importance of genetic malfunction as an extinction-inducing factor (Frankham, 2005; Jamieson, 2007a, b). If applied uncritically in the management of unnaturally small insular or fragmented mainland populations, the assumption may result in the failure to treat genetic factors capable of compromising recovery, responsiveness to new threats or long-term persistence, even if external and other stochastic threats have been addressed (Frankham *et al*., 2002).

A small but growing body of New Zealand studies suggests that the New Zealand assumption of negligible genetic risk is not universally valid for the conservation of threatened island endemic birds (Jamieson, 2009). For both theoretical and management reasons, further empirical testing of predicted risks has been called for in free-ranging species generally (Caughley, 1994; Amos and Balmford, 2001), insular species specifically (Frankham, 1998; Elgar and Clode, 2001), and especially insofar as inbreeding depression may affect small population recovery and viability once other threats have been controlled, as is the case for many insular endemic birds under watch or management in this country (Jamieson *et al.*, 2006; Jamieson, 2007b).

The research reported in this thesis addresses the need for empirical testing by analysing extinction vulnerability in two small, geographically isolated populations of Chatham Island black robin *Petroica traversi*, a species whose dramatic recovery from the point of imminent extinction (Merton, 1990, 1992; Butler and Merton, 1992) features prominently in modern conservation lore and in the extinction literature of conservation biology.

The black robin is a small, island-dwelling member of the Australasian robins and is endemic to the Chatham Island archipelago (situated 802 km east of Banks Peninsula, New Zealand; *Figure 1.1*). It is a typical constituent of the New Zealand terrestrial avifauna, 87% of which is endemic to the New Zealand region (Wilson, 2004). Like the black robin, the vast majority of New Zealand's terrestrial birds are insular species by virtue of persistence on 700 or so outlying islands or in habitat fragments on the three major landmasses (Bell, 1991; Craig, 1991). The black robins inhabit regenerating forest remnants on Mangere Island (113 ha) and Rangatira Island (218 ha), two small outliers at the southern extremity of the species's natural range in the archipelago (Chapter Two: *Figures 2.3* and *2.4*). Both populations, one descended from the other, originate from two survivors of the species's tiny relict population (now extinct) on Little Mangere Island (8-9 ha). Despite removal from immediate extinction threats, the black robin is classified by New Zealand's Department of Conservation (DOC) as 'nationally critical'—the severest level of endangerment—because of its critically low numbers (≤ 150 adults, Massaro and Briskie, 2009; Harvey, 2009) and confinement to a fraction of its original pre-human range. The black robin's experience of range contractions, decline and small vestigial population sizes (constrained by limits on available habitat) make it a suitable analogue for threatened island endemic birds in New Zealand and world-wide.

## 1.1 Conservation genetics and extinction vulnerability in insular endemic birds

Defining and treating the factors which threaten wildlife populations with extinction are the driving mandates of conservation biology (Soulé, 1986; Caughley, 1994; Frankham *et al.*, 2002). In the main, conservation biologists agree on a number of fundamental extinction principles:

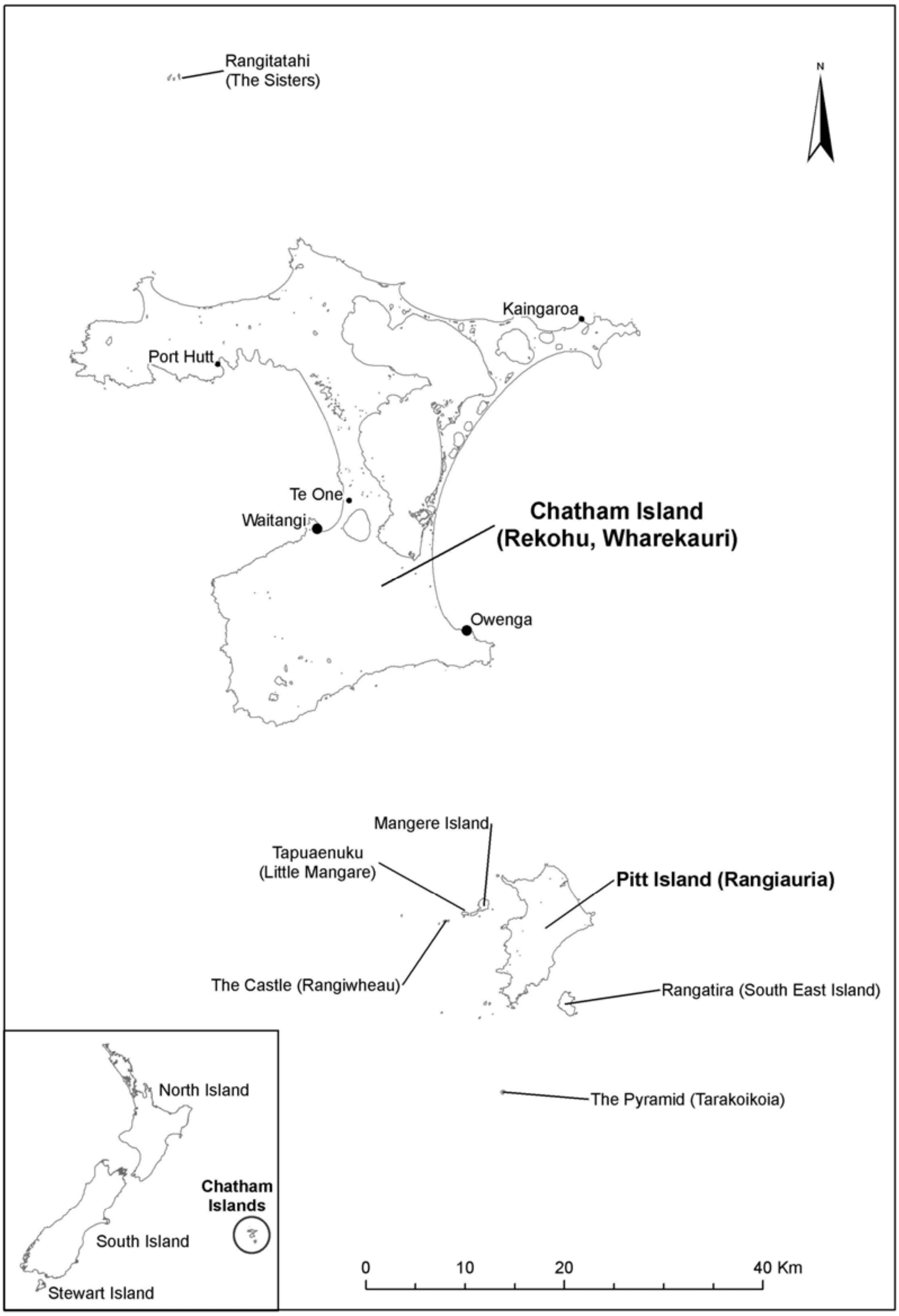

Figure 1.1 The Chatham Islands archipelago in relation to New Zealand, showing the black robin habitats referred to in this thesis (Chatham, Pitt, Rangatira, Mangere and Little Mangere Islands).

1. Deterministic pressures arising directly or indirectly from human activities (habitat loss, degradation and fragmentation, introduced predators, and over-harvesting) combine with stochastic environmental, demographic and genetic threats to increase extinction probability (Hedrick *et al.*, 1996; Jamieson, 2009).

2. Deterministic factors are the primary drivers of extinction processes (Soulé and Mills, 1998; Lande, 1999) and are rightfully the first priority for treatment because they can eliminate populations outright and quickly (Shaffer, 1981; Caughley, 1994).

3. Contractions in size erode the inherent ability of populations to cope with environmental stresses, demographic bad luck and genetic impairment—interacting stochastic pressures which amplify as numbers decrease (Caughley, 1994). Gilpin and Soulé's (1986) eloquent concept of the extinction vortex illustrates the destructive, mutually compounding feedback loops between deterministic and stochastic pressures which reduce population sizes further.

4. Even if deterministic threats are relieved or removed, adverse chance events may convey reduced populations to extinction in the short-term or may persist as threats to long-term viability (Hedrick *et al.*, 1996; Frankham, 1997; Frankham *et al.*, 2002).

Of all such pressures, the role of stochastic genetic processes in elevating extinction risk remains the least quantified and most debated, despite the prominence of conservation genetics in the evolution of conservation biology thinking (Dobson, 1999).

Conservation genetic theory anticipates that small populations of naturally outbred species will suffer two distinct forms of genetic compromise whose interacting effects increase extinction risk (Keller and Waller, 2002; Frankham, 1995, 2005). Genetic variability will be lost as the random processes of genetic drift act more aggressively in a diminishing pool of individuals to remove alleles from populations. The odds become greater as numbers fall that detrimental alleles will become fixed in all survivors. Bottlenecks, founder events and prolonged downward fluctuations in numbers increase the probability of allelic loss. Geographic or behavioural isolation will deny impoverished populations vital sources of genetic replenishment. Depletion rates are expected to be dictated by the severity of population decline and the number of generations over which a population is held at low numbers (Amos and Balmford, 2001). Loss of genetic diversity jeopardises the prospects of long-term persistence by weakening responsiveness to selection pressures and the potential to adapt to new environmental challenges (Wallis, 1994; Frankham *et al.*, 2002).

In contrast, increased rates of inbreeding, inevitable in reduced and isolated populations, lead to greater expression of homozygous semi-lethal recessive alleles in inbred individuals, reducing their fitness relative to non- or less inbred individuals (Hedrick and Kalinowski, 2000). Typically, inbreeding depression in naturally outbred species is expressed in compromised vigour, reproductive performance and survival (Frankham, 1998). Its severity is related primarily to the extent and duration of population decrease, and its effects may be felt quickly, within a few generations after population decline (Amos and Balmford, 2001). For this reason, inbreeding depression is regarded as the more immediate and potent genetic threat to population persistence (Keller and Waller, 2002; Jamieson *et al.*, 2008). Because loss of genetic variation and inbreeding depression are both negatively correlated with population size, they operate together (albeit over different timescales; Jamieson *et al.*, 2008), and are likely to be mutually reinforcing as threats to fitness at population and individual scales respectively (Frankham *et al.*, 2002).

The magnitude of extinction risk posed by these stochastic genetic processes—especially the more immediate threat of inbreeding depression—has been a controversial element in conservation biology debates (O'Grady *et al.*, 2006; Jamieson, 2007a, b). Early sceptics argued that inbreeding depression had not caused any known wild population to decline (Lande, 1988); that genetic malfunction alone had not been shown to have eliminated a species in the wild (Caughley, 1994); and that the more slowly realised costs of genetic impairment would not have time to threaten small populations in the wild before chance demographic and environmental events eliminated them (Lande, 1988, Caro and Laurenson, 1994; Craig, 1994). In New Zealand, Wallis (1994) was more circumspect, concluding that genetic threats were only a concern if gene pools were severely restricted, as was the case for many New Zealand birds. Otherwise, Wallis argued, demographic adversity was a greater threat.

In response to sceptics, geneticists have amassed theoretical, stochastic-modelling and empirical studies to support their contentions. Their studies offer evidence that reduced populations of naturally outbreeding species commonly experience inbreeding depression in the wild (Crnokrak and Roff, 1999; Hedrick and Kalinoswki, 2000), and that this can be both debilitating (Keller and Waller, 2002; Frankham *et al*., 2002; Frankham, 2005) and likely to shorten time to extinction (Brook *et al*., 2002; Spielman *et al*., 2004). Contrary to Caughley (1994), the genetic costs of small size were shown by empirical studies to be capable of eliminating declining populations outright if not reversed by introducing genes from less inbred sister populations (for example, Westemeier *et al*., 1998; Madsen *et al*., 1999, 2004). The genetic studies have convinced geneticists that stochastic genetic processes set in train by population declines will aggravate the effects of other extinction pressures (Soulé and Mills, 1998; Amos and Balmford, 2001; Frankham, 1997, 1998; Frankham *et al*., 2002; Spielman *et al*., 2004). Substantial losses of fitness are predicted if populations decline suddenly. But if recovery is rapid, natural selection is expected to remove recessive lethal alleles, reducing the potential for harm (Lande, 1999). Any recovery of fitness is likely to be partial only (Frankham *et al*., 2002). Therefore, any small inbred population with positive growth rates is expected to take longer to achieve the size of a healthy population and may respond more slowly to set-backs or longer-term changes in its environment (Wallis, 1994; Frankham *et al*., 2002). Because these deleterious effects on fitness are stochastic, they are predicted to vary in severity and expression across taxa, species, populations and environments (Hedrick and Kalinoswki, 2000; Keller and Waller, 2002).

Conservation geneticists have long recognised oceanic islands as ideal environments in which to validate stochastic genetic threats as realistic extinction risks. Aside from ready accessibility as research subjects, populations of insular vertebrates more so than their mainland relatives meet the predicted genetic risk criteria of smaller sizes, finite limits to growth, genetic structures closed by geographic isolation or limited immigration, and higher rates of inbreeding. Moreover, insular populations have usually experienced founding bottlenecks and are likely to have been isolated longer than related mainland populations (Frankham, 1998). Meta-analyses have shown genetic variability to be lower on average in insular than in continental species (Frankham, 1997, 1998) and lower in insular endemics relative to non-endemics, arguably because times since founding from mainland parent populations were longer (Frankham, 1997). Frankham (1998, 2001) also used meta-analyses to demonstrate that mean levels of inbreeding were higher in insular endemics than in insular non-endemics, and significantly higher in both relative to mainland equivalents.

On this basis, insular endemics are predicted to be amongst the most extinction-prone of species for genetic reasons (Frankham *et al.*, 2002). Disproportionate extinction rates among island bird species are often invoked to support this contention (Frankham, 1997, 1998, 2001; Frankham *et al.*, 2002). Studies documenting bird extinctions since 1600 AD have reported rates of loss and levels of endangerment among the survivors which are significantly greater than the proportion of insular species in the global avifauna (Myers, 1979; King, 1985a; b; Atkinson, 1989; Reid and Miller, 1989; Johnson and Stattersfield, 1990; Smith *et al.*, 1993). Rates of loss among insular endemics have been even higher (McDowall, 1969; Temple, 1985).

This support for genetic propositions is heavily inferential. It follows the logic that genetic factors must be implicated in insular bird extinctions because in general insular species are inherently more highly inbred and genetically depauperate. The logic understates the degree to which common evolutionary attributes of island life, such as flightlessness, predator-naivety, tameness, low reproductive rates, sedentary habits, specialist ecological requirements and restricted distributions (Bell, 1991; Wilson, 2004; Duncan and Blackburn, 2004), exaggerate extinction vulnerability in insular birds confronted with introduced predators, hostile habitat change or other unfamiliar selection pressures.

At their most insistent, conservation geneticists argue that loss of genetic variation and inbreeding depression are inevitable consequences of population declines. They conclude therefore that extinction risk will be underestimated, often radically, if these hidden stochastic threats to population persistence are ignored (Brook *et al.*, 2002; Frankham, 2005). These warnings and the weight of argument in genetic propositions are obviously and ominously at odds with the assumptions of genetic risk made commonly by managers of threatened New Zealand endemic birds.

## 1.2 The 'New Zealand cure' for threats to insular endemic birds

Conservation biologists are commonly concerned with the pressures driving small populations towards extinction. In New Zealand, extinction vulnerability is an important consideration for threatened insular bird populations recovering under conditions in which the deterministic pressures of mammalian predation and habitat deterioration have been controlled or eliminated.

Conventionally, these pervasive threats have been managed in New Zealand by translocating population survivors to threat-free islands (Craig and Veitch, 1990; Armstrong and McLean, 1995), to 'islands' of protected mainland habitat (Saunders and Norton, 2001), or by managing the threats *in situ* through pioneering advances in predator control and ecological restoration (Atkinson, 2001). Typically, translocations have been straight-forward management exercises paying little regard to theoretical genetic considerations of founder sizes, population mixing, the size of island sanctuaries or the post-liberation implications of obligatory inbreeding (Armstrong and McLean, 1995). Many translocations have been crisis-driven, one of the most notable in 1964 when wildlife managers simply moved what they could salvage at the last minute from Big South Cape Island (939 ha) after an irruption of recently arrived ship rats *Rattus rattus*. Thirty-six South Island saddlebacks *Philesturnus carcunculatus carcunculatus* were moved to two small islands (21 and 15 individuals respectively), and six Stead's bush wrens *Xenicus longipes variabilis* were moved (in vain) to one island (Nilsson, 1978; Bell, 1978e; Wilson, 2004).

After dealing with immediate deterministic threats, New Zealand wildlife managers have usually relied on spontaneous recovery in small transfer populations to counteract the hazards of environmental and demographic stochasticity they have faced. Less frequently, increases in population sizes have been engineered through active management. Increases in the numbers of populations have aimed to minimise the probability of total loss through predation or habitat changes (Diamond, 1990). For instance, descendants of the Big South Cape saddlebacks were distributed through sequential transfers to a further 18 islands, and flourished on 14 ranging in area from 6 to 270 ha (Hooson and Jamieson, 2003, 2004). The stochastic processes of genetic deterioration set in train by source-population declines, single or serial bottlenecks and elevated rates of inbreeding in populations constrained by sanctuary size are commonly neglected after the danger from deterministic threats has passed (Armstrong and McLean, 1995; Jamieson *et al*., 2006, 2008). New Zealand wildlife managers have proceeded on the assumption therefore that increasing population numbers and the numbers of populations suffices on its own as a strategy to safeguard population viability.

This assumption defines the so-called ‘common New Zealand cure’ for conserving insular endemic bird populations (Groombridge, 2007: 148). The cure’s downplaying of potential genetic threats to recovery and persistence is peculiar to New Zealand (Jamieson *et al*., 2006, 2008) and at odds with emerging consensus in conservation biology thinking that management of genetic threats should be integrated into conservation planning and practice once deterministic threats have been remedied (Hedrick *et al*., 1996; Frankham *et al*., 2002; Frankham, 2005; Jamieson *et al*., 2006, 2008; Jamieson, 2009).

The New Zealand cure has received theoretical comfort from the proposition of Craig (1991, 1994; reiterated in passing by Craig *et al*., 2000) that conservation biology’s orthodox models for conserving threatened bird populations are based on predictions of genetic risk which may hold for the large, naturally outbred, migratory populations of the continental northern hemisphere but not for insular terrestrial bird species such as those endemic to the New Zealand archipelago. Craig’s (1991, 1994) hypothesis was that New Zealand’s insular birds are less susceptible to the effects of inbreeding depression because natural populations and relict survivors of habitat loss and mammalian predators have been small and genetically isolated for many generations. Many, Craig argued, are behaviourally habituated to high levels of inbreeding through sedentary territorial habits and limited dispersal or flightlessness. Thus, the histories and social systems of New Zealand birds are expected to have exposed to natural selection the deleterious recessive alleles responsible for impaired fitness and viability.

To support this contention, Craig (1991, Table 1; 1994) cited the century-long persistence of highly inbred relict populations of New Zealand terrestrial birds at population sizes lower than 20 pairs (bellbirds *Anthornis melanura melanura* on Tiritiri Matangi Island; Campbell Island teal *Anas nesiotis* on subantarctic Dent Island, and—on Little Mangere Island—Forbes’ parakeets *Cyanoramphus forbesi* along with the ancestral black robins. Moreover, Craig (1991) noted the lack of any apparent relationship between founder sizes and the high proportion (77%) of single and sequential translocations in New Zealand resulting in self-sustaining bird populations, some founded from as few as five individuals (for example, South Island robins *P. australis* on Allports Island and Motuara Island; Flack, 1974a; see Taylor *et al*., 2005 for further empirical evidence). And, as illustrated by the Big South Cape Island saddlebacks, many translocated populations had persisted in the absence of predators and habitat stresses on very small islands as well as large (sizes and locations unspecified by Craig).

Craig's (1991, 1994) proposition of inherited resistance to genetic effects generalises for insular bird species from a handful of examples serving his argument. Geneticists are inclined to dismiss these examples—and others such as the Seychelles warbler *Acrocephalus sechellensis* (Komdeur *et al*., 1998) and the Socorro Island red-tailed hawk *Buteo jamaicensis socorroensis* (Walter, 1990)—as rare exceptions to the rule (Frankham *et al*., 2002). Nevertheless, Craig's thinking reassured most New Zealand wildlife managers and conservation ecologists that inbreeding depression and lowered genetic diversity in small insular populations will not significantly threaten their immediate or longer-term viability (Jamieson *et al*., 2006; Groombridge, 2007). Wilson (2004) has suggested that these genetic threats may be overstated as management considerations. This apparent complacency has established New Zealand's approaches to conserving island endemic birds at the heart of debates over the importance of stochastic genetic threats to small population persistence (Jamieson, *et al*., 2006; Jamieson, 2007a, b). In addition, the New Zealand cure's preoccupation with the deterministic drivers of extinction is symptomatic of Caughley's (1994) separation of 'declining-population' and 'small-population' mindsets which Caughley regarded as disabling for efforts to predict and avert further extinctions.

In stark but simple terms, the New Zealand cure was a pragmatic response to each developing crisis in the country's highly endangered avifauna (Bell, 1991; Wilson, 2004, 2008). The lack of follow-up was a pragmatic response to the next crisis. There was rarely time to theorise before or after intervention. As Groombridge (2007) remarks, the approach has established New Zealand as a world leader in the conservation of threatened insular endemic birds, but the conservation biology community is waiting to see whether the New Zealand cure will indeed ensure long-term population viability.

## 1.3 Advances in genetic studies of New Zealand insular endemic birds

In New Zealand, the establishment of threatened bird populations in natural and virtual islands of protected habitat offers ideal opportunities to test the genetic-risk implications of small capped populations without the confounding effects of other extinction pressures. The number of studies capitalising on New Zealand's wealth of such viability 'experiments' is still small but conclusions drawn so far emphasise the probability of underestimating the future viability of insular endemics if assumptions of negligible genetic risk dictate their management.

Recent predictive modelling, molecular and empirical studies have examined the genetic consequences of historical declines and range contractions, bottleneck events and recovery in source and translocated populations of North and South Island robins *Petroica* spp. (Taylor *et al.*, 2005, 2007; Jamieson *et al.*, 2007; Boessenkool *et al.*, 2007), takahe *Porphyrio hochstetteri* (Jamieson and Ryan, 2000; Jamieson *et al.*, 2003; Grueber and Jamieson, 2008), and North and South Island saddlebacks *Philesturnus* spp. (Hooson and Jamieson, 2004; Taylor *et al.*, 2005, 2007; Taylor and Jamieson, 2007, 2008). All are slow-breeding *K*-selected species, as is typical of the New Zealand terrestrial avifauna (Bell, 1991) and characteristic of southern temperate-zone passerines (Rowley and Russell, 1991). Findings have confirmed that many of New Zealand's threatened birds meet the predicted risk-criteria of lowered genetic variation (often emphatically; Jamieson *et al.*, 2006; Robertson, 2006) and elevated levels of inbreeding.

Overall, genetic drift and inbreeding intensified by prolonged persistence at low numbers appeared to account more than translocation bottlenecks for the rates of genetic depletion observed in protected island populations (Jamieson, 2009). Life-history traits limiting population growth rates (such as inherently low reproductive output) and habitat constraints on ultimate population sizes were considered to increase viability risks (Taylor *et al.*, 2005, 2007; Boessenkool *et al.*, 2007; Taylor and Jamieson, 2008), effectively by prolonging bottlenecks and retaining populations at low numbers. Higher founder numbers, faster population growth and recovery to larger population size were considered to offer better prospects of minimising the fitness and longer-term evolutionary costs of genetic depletion (Jamieson *et al.*, 2008).

Evidence that New Zealand's threatened endemic birds suffer inbreeding depression was reported in populations of ancestrally and recently inbred takahe translocated to small island sanctuaries (Jamieson and Ryan, 2000; Jamieson, *et al.*, 2003). Relative to the small relict source population in alpine Fiordland, egg infertility was higher and fledging success lower. These fitness costs were expressed differentially in inbred females and males, and seem to have arisen when removal of the birds from the ancestral inbreeding environment exposed latent genetic load (the aggregate of deleterious genes carried in the population's genome) (Jamieson and Ryan, 2000; Jamieson, *et al*., 2003). Similar environmentally dependent inbreeding depression was a possible explanation for unusually low hatch-rates in a small descendent population of the ancestrally inbred South Island saddlebacks on Motuara Island (Hooson and Jamieson, 2004). The severely habitat-limited population of North Island robins founded on Tiritiri Matangi Island showed evidence of inbreeding depression, strongly expressed in low survival rates for inbred juveniles (Jamieson *et al*., 2007). Compared with the robins, which were sourced from large, diverse mainland populations, the fitness costs of inbreeding in the small island populations of ancestrally inbred takahe were more weakly expressed, lending support to Craig's (1991, 1994) proposition that long histories of inbreeding under natural conditions lower susceptibility to its debilitating effects on fitness. Jamieson (2009) concluded from these studies that inbreeding depression of varying form and severity was probably widespread in New Zealand's small populations of threatened insular endemics. This prediction was supported by Briskie and Mackintosh's (2004) finding that hatching success correlated negatively with recent and ancestral bottleneck size and inbreeding in 22 New Zealand bird species (marine and terrestrial, including black robins).

Reviews of population-genetics research (Jamieson *et al*., 2006, 2008; Jamieson, 2009) have concluded that low genetic diversity and inbreeding depression combined to depress fitness at individual and population scales in threatened New Zealand endemic bird populations in ways which impeded rates of recovery under protected conditions. Inbreeding appeared to impose the more immediate costs on individual fitness, but its implications for population viability varied according to annual levels of inbreeding among close relatives (a function of population size), the overall incidence of inbreeding, the severity of inbreeding depression, and the life-history stages affected (Jamieson, 2009). The reviewers concluded that in general the stochastic genetic consequences of low numbers would not constitute immediate threats to viability unless other extinction drivers were operating. Then, lowered reproductive success and survival would heighten extinction probability by impairing responsiveness to population knock-downs, fluctuations and instability. On the other hand, genetic malfunction called longer-term viability into question, even if populations were recovering under protected conditions. It appeared to be most dangerous for genetically depleted, inbred populations which remained small and stable or grew only slowly (Frankham *et al*., 2002; Jamieson, 2007a; Jamieson *et al*., 2008). Average levels of inbreeding would accumulate quickly in such populations. And natural replenishment of diversity through mutation is generally expected to be too slow to restore resilience to new environmental, pathogenic or climatic selection pressures.

The New Zealand studies have begun to fill the empirical vacuum for which Craig's (1991, 1994) hypothesis of negligible genetic risk has been criticised (Jamieson *et al*., 2006). They also suggest that New Zealand ambivalence towards genetic risks may be misplaced. However, the predictions outlined above generalise for threatened New Zealand bird species from the few studies conducted so far. Broad principles of this sort require refinement through further studies, for two reasons. First, genetic risks may vary between species, populations and ecological contexts (Keller and Waller, 2002; Frankham *et al*., 2002). Second, under-resourced wildlife managers are hard-pressed to cope with the growing number of conservation crises in New Zealand (Department of Conservation and Ministry for the Environment, 2000; Wilson, 2008). As the downplaying of genetic risks in past species management has shown (Armstrong and McLean, 1995), it is intuitively difficult to divert attention and resources from the ubiquitous short-term certainty of extinction to address the distant possibility of cryptic genetic threats operating well beyond normal planning time-frames.

The authors and reviewers of the New Zealand studies acknowledge this. To preserve recovery momentum and longer-term viability from the more insidious processes of genetic impairment, they recommend precautionary genetic management of fitness and diversity in small populations, but only after the deterministic factors causing their declines have been treated (Jamieson *et al*., 2006, 2008). Jamieson (2009) suggests that mitigation of potential genetic threats should be integrated with other management considerations. If so, to make the most effective and efficient use of scarce resources, it will be highly advantageous to understand the particular genetic and non-genetic extinction vulnerabilities of recovering populations. Knowing the immediate constraints on growth rates and ultimate population sizes (for example, the critical ecological and behavioural adaptations limiting recovery or the particular life-history stages at which recovery is impeded) should minimise the potential for misdirected effort on less easily defined genetic threats. And in theory at least, managing the non-genetic constraints in order to accelerate rates of recovery will moderate the unseen genetic risks.

Genetic studies of New Zealand's threatened endemic birds have striven to improve the management of study populations while attempting to refine genetics theory. This study follows these imperatives by examining genetic and non-genetic extinction vulnerability in the two small inbred black robin populations currently under watch in the Chatham Islands archipelago.

## 1.4 Why study extinction vulnerability in the black robins?

Among New Zealand's impressive inventory of viability 'experiments' with threatened birds, there can be few more suitable or overdue than the black robin to test the assumption of minimal genetic risk to small inbred populations. The two recovered black robin populations are fitting empirical test-cases for several reasons.

First, the species has a century-long history of reduction, isolation, and inbreeding. This, and passage to recovery through a single-pair bottleneck, has exposed descendants to a perfect storm of genetic hazards. In theory, the two present-day populations should be suffering significant genetic impairment.

Second, despite their histories, both populations are deemed to be stable (Department of Conservation, 2007a) and at no particular risk from genetic malfunction (Department of Conservation, 2001a). Accordingly, no genetic management has been planned and monitoring of population health has been scaled back radically (Department of Conservation, 2001a; this study, Chapter Four). It is prudent to test the wisdom of these assumptions.

Third, much of the black robin's recovery from 1980-81 onwards was documented, primarily for operational reasons. A diverse and highly insightful demographic record of recovery accumulated as a result. The pedigrees and demographic trends discernible in the field data are shorthand for the effects of all extrinsic and intrinsic variables shaping the fates of the two populations over a period of 22 years (about 13 generations). The insights to extinction vulnerability accessible in records of this detail and duration are rarely available to conservation biologists. The black robin record has never been subjected to systematic analysis in its entirety.

Fourth, references in other studies to the apparent viability of the black robins will remain speculative until the demographic data have been analysed. Conservation ecologists have invoked the black robin's recovery and persistence as evidence that genetic threats are relatively insignificant for the conservation of New Zealand's inbred island endemic birds (Craig, 1991, 1994), while resolute conservation geneticists have argued that the black robin is a rare example of a species dodging the genetic 'bullet' (Frankham *et al*., 2002; Frankham, 2005). This study's analysis of the black robin record acknowledges the view of New Zealand conservation biologists that immunity to genetic threats has not yet been quantified adequately in the black robin populations (Wallis, 1994; Armstrong and McLean, 1995; Jamieson and Ryan, 2000; Jamieson *et al*., 2003; Briskie and Mackintosh, 2004; Wilson, 2004; Jamieson *et al*., 2006, 2008; Jamieson, 2009).

Fifth, the black robin's rescue from the uttermost brink of extinction is frequently cited as an endorsement of New Zealand conservation philosophies and methods (Diamond, 1990; Bell, 1991; Atkinson, 2001; Wilson, 2004). Lay communities at home and abroad have also been encouraged to regard the rescue as a defining conservation success for New Zealand and assurance that critically threatened species can be saved no matter how imminent extinction may be. The black robin has acquired iconic status in popular conservation literature (see for example Cemmick and Veitch, 1985; Taylor, 1993; Morris and Smith, 1988; Merton, 1990; Hutching, 2004), in television documentaries (Natural History New Zealand, 1980, 1982, 1989) and conservation media (Television New Zealand, 2009). New Zealand's reputation and credibility as a world-leader in insular bird conservation owes much to the long-term survival of the species.

## 1.5 Prior black robin research

The black robin has a history of research interest spanning seven decades, commencing with 'rediscovery' of the species in its last island refuge, Little Mangere Island, on 2 January 1938 (Fleming, 1939a, b; McEwen, 2005).

Fleming (1950a, b), Holdaway *et al*. (2001) and Miller and Lambert (2006) have made the principal contributions to the classification and taxonomy of the New Zealand *Petroica* species, proceeding variously from morphological and more recent molecular genetic analyses. The studies draw differing conclusions on black robin affinities with tomtit *P.*

*macrocephala* and robin *P. australis* congeners but all define the black robin as a determinate island endemic species within the genus.

Flack's (1976a) integrated study of black robin ecology and conservation needs, conducted on Little Mangere Island from 1971-72 to 1975-76, was the first research to address extinction issues and gives the only systematic insights to the decline of any black robin population. Black robin numbers decreased precipitously during the research programme (Chapter Three: History of Decline). Consequently, the study of black robin ecology became subordinated to the goal of designing biologically appropriate remedies to the extinction threat looming through habitat disintegration. In numerous reports and letters, Flack (1971, 1973, 1974a, b, 1976a, b, c, d, 1977) documented the processes of habitat collapse, population decline and the life-history traits accentuating the population's collapse. However, the difficult research setting and a policy of minimising disturbance denied Flack crucial insights to vital population rates under extinction pressure, especially rates of reproductive failure. The deepening crisis allowed little latitude to consider the genetic implications of decline, but in any case Flack shared the optimism of wildlife managers that the species would rebound naturally once the habitat threat was remedied (Chapter Four: Management of Extinction Threat).

Butler and Merton's (1992) account of the subsequent recovery project was written for lay as well as expert audiences. Its detailed biological, historical and social narratives elaborated significantly on Flack's groundwork. The authors described the strategy and pioneering methods used to minimise extinction risk by actively increasing the number and sizes of populations. The black robin's resilient response to this strategy (increased reproductive output, population growth and apparent resistance to avian pox) led the authors to conclude that the species was not genetically degenerate. They regarded anomalous egg-laying behaviour, through which some eggs were laid outside nest-bowls, as the sole substantive evidence of genetic malfunction. The authors did not dismiss outright the potential for genetic problems, but were confident that any such issues were inconsequential at that point. Accordingly, they identified the arrival of mammalian predators, new pathogens and habitat disasters as the most significant threats to viability. On-going quarantine of existing populations and expansion into other parts of the black robin's traditional range were the recommended means of ensuring long-term persistence. Butler and Merton's (1992) detailed insights to black robin ecology, behaviour and population growth are indispensable to my study. However, their viability conclusions drew on observation of population trends strongly shaped by management activities over ten years (1980-81 to 1989-90) and perhaps still influencing trends described cursorily in two post-management seasons (1990-91 to 1991-92). Moreover, their conviction that the black robins were genetically robust at that time may not hold for present-day viability or in the future.

Three molecular studies have clarified important aspects of genetic risk to the black robin populations. Holmes (1994), reported subsequently in Ardern and Lambert (1997), quantified present-day genetic variability in the species. The authors described levels of neutral minisatellite DNA variation too low in either population to distinguish individuals other than by sex. This unexpected finding defeated hopes of confirming black robin monogamy and closing parentage gaps in the pedigree (Chapter Four). Higher diversity in similarly bottlenecked populations of South Island robins led Ardern and Lambert (1997) to conclude that the genetic impoverishment of black robins arose from genetic drift and high rates of inbreeding during the ancestral population's long persistence at low numbers on Little Mangere Island (30-35 individuals, for at least 83 years; Chapter Three) rather than from the single-pair founding event of descendent populations. Healthy biological indicators derived from Butler and Merton (1992)—positive productivity, survival rates and population growth under management—suggested to the authors that low genetic variability did not to equate to low viability, at least under the conditions prevailing during recovery. They surmised that harmful recessive alleles had been purged historically in the closely inbred ancestral population, offering some assurance of continued unassisted survival. However, these viability predictions inferred that diversity was equally low in other more functionally significant (fitness-related) parts of the black robin genome which the study did not analyse. The fitness measures used to judge viability were largely those from the intensive management years. Ardern and Lambert were not in a position to assess how the potentially harmful effects of advanced genetic depletion and accumulating levels of inbreeding in their study populations might be realised in later generations.

Miller and Lambert (2004) examined the implications of genetic depletion for black robin immunity to pathogens. The populations were found to possess very low levels of diversity in class II B major histocompatibility complex (MHC) loci responsible for immunocompetence. Variation was significantly less than in two obligatorily inbred South Island robin populations on Motuara and Allports Islands, each founded from five individuals sourced from large, genetically diverse mainland populations (see *Section 1.2* above) and growing strongly after its translocation bottleneck. Miller and Lambert (2004) attributed the difference in diversity at MHC loci to the black robin's significantly longer ancestral bottleneck, thus agreeing with Ardern and Lambert's (1997) conclusions. Evidence of limited susceptibility to pathogens in the past (Butler and Merton, 1992) and positive population growth under natural conditions suggested to the authors that, despite depletion at MHC loci, immune function had remained adequate for pathogens commonly encountered under past conditions. Immunity under changed conditions or to new pathogens was considered to be less certain.

Ma and Lambert's (1997b) assessment of multilocus minisatellite DNA markers in the two black robin populations was intended to improve detection of future black robin cross-breeding with sympatric Chatham Island tomtits *P. macrocephala chathamensis* by profiling of suspected hybrid genotypes. Their molecular analyses reiterated Ardern and Lambert's (1997) findings of low genetic variation and discovered comparable depletion in the small tomtit population on Mangere Island. The study revealed unsuspected introgression on Mangere Island and confirmed hybrid fertility, thus quantifying an underestimated threat to the genetic integrity and long-term viability of both parent populations. My analysis of hybridisation events and predisposing factors (Chapter Eight: Hybridisation) examines the implications of Ma and Lambert's (1997b) findings for the persistence of the black robin genotype in the stressful habitat conditions in parts of both black robin islands.

Inbreeding effects were first investigated by Mallinson (1992) whose dissertation research looked for correlations between individual inbreeding coefficients, reproductive success (eggs laid, hatch-rate, fledge-rate, offspring reaching independence, juveniles recruited) and survival in the two black robin populations on Mangere and Rangatira Islands between 1980-81 and 1991-92. This timely study was hindered by omissions and inconsistencies in the raw productivity and pedigree data which required Mallinson to make potentially confounding assumptions in order to construct coherent datasets. No significant inbreeding effect was detected in any of the life-history parameters measured. Mallinson concluded therefore that observed variations in breeding performance and survival were not inevitable consequences of inbreeding in the black robin populations. As with previous studies, analyses were able to examine only short-term sequences of demographic data in which management effects (direct or shadow) may have masked evidence of inbreeding depression.

None of the authors of these genetic studies suggested that genetic depletion and inbreeding would remain inconsequential for longer-term viability in the black robin populations. The general weight of their conclusions suggested, however, that fitness and resilience had not been significantly affected by genetic problems during the first 12 years of recovery from the single-pair bottleneck. The threat posed by hybridisation with sympatric tomtits was the exception. Craig's (1991, 1994) proposition of reduced susceptibility to genetic risks appears to be supported by these studies, notwithstanding the fact that there are no healthy black robin populations surviving to indicate how far fitness and recovery rates might have been compromised. This is a common impediment to assessing genetic risk in threatened New Zealand species (Wallis, 1994).

My study is in a better position to assess whether the conclusions drawn in prior research and their implications for management are sound or premature. It conducts the first systematic analysis of the black robin demographic data accumulated during the recovery project. The data have been checked rigorously to avoid the problems faced by past researchers. Most importantly, the data sequences are longer and span the 12-year period in which black robin population dynamics operated without interference by conservation management. These last insights were unavailable to earlier studies. Finally, my study addresses potential genetic threats to population persistence alongside analysis of other extrinsic and intrinsic extinction factors.

## 1.6 Thesis objectives

This study pursues fundamental management and theoretical imperatives of conservation biology—that is, to define and minimise extinction vulnerability in threatened relict or fragmented wildlife populations surviving in natural environments. By analysing extinction vulnerability in the small closed black robin populations on Mangere and Rangatira Islands, it addresses two closely related questions central to conservation of threatened insular endemic bird species in New Zealand and overseas.

The first question is theoretical. Does Craig's (1991, 1994) hypothesis that insular endemic birds are less susceptible to inbreeding depression hold for all small populations of insular endemics currently protected from other threats to survival?

The theoretical issue considered here relates to the prediction of conservation geneticists that short- and longer-term viability in small, isolated, obligatorily inbred wildlife populations will inevitably be compromised by stochastic genetic threats even after the deterministic causes of decline have been treated and population growth has reduced exposure to stochastic demographic and environmental threats. Craig's counter-hypothesis is that viability in such populations is not compromised unduly by the genetic consequences of reduction and decline.

The second question relates to appropriate management of viability in threatened insular endemic bird populations. Is the assumption of negligible genetic risk implied in the New Zealand 'cure' a sound basis on which to manage recovering populations? In other words, is their persistence guaranteed simply by treating the deterministic causes of decline and raising population sizes to the carrying-capacities of their habitat sanctuaries?

To evaluate these questions, my study analyses the detailed demographic record of recovery in the black robin populations to assess potential threats to persistence. Specifically, the study asks:

- which extrinsic and intrinsic factors were responsible for historical declines in black robin populations, and which appear to increase extinction vulnerability in descendent populations?
- did growth trends vary in the recovering populations and which demographic variables appear to have influenced trends negatively?
- are those demographic variables sufficiently correlated with levels of inbreeding in the populations to suggest that future viability will be compromised by further inbreeding?
- was management of extinction threats to past and present black robin populations typical of New Zealand conservation practice, and what lessons discernible from this management can be applied to improve prospects of long-term persistence in present and future populations?

In addition to assessing the theoretical issues posed by this study, my aim in clarifying extinction vulnerability in the black robin populations is to strengthen their management and monitoring regimes. Similarly threatened species are expected to benefit from pursuing these objectives.

## 1.7 Thesis structure

My research questions are addressed in six analytical chapters whose lines of inquiry build towards assessment of the genetic questions prompting this study.

The chapters bring a range of scientific perspectives to bear on the research questions. They combine natural historian with quantitative biological perspectives, along with elements of historical and social research disciplines, to explore the black robin questions as informatively as possible. This integration recognises that conservation biology generally and black robin conservation specifically are fundamentally biological and social undertakings.

In **Chapter Two: Black Robin Biology**, I introduce the black robin as a research subject and summarise key biological features which characterise it as an island endemic bird species. This chapter adds to or amends existing knowledge (Flack, 1976a; Butler and Merton, 1992; Higgins and Peter, 2002) by reporting new biological information obtained over longer periods of observation and under natural conditions. The chapter concludes by comparing black robin life-history traits with island and mainland congeners in New Zealand and Australia. This comparison is useful in identifying the particular biological attributes of the black robin which increase sensitivity to extinction pressures.

**Chapter Three: History of Black Robin Decline** combines an historical narrative with analysis to examine the deterministic and stochastic causes of decline, and probable extinction intervals, in the each of the black robin's original island populations in the Chathams archipelago. This is the first island-by-island analysis of extinction factors and timing for the black robins (or any other bird of the Chatham Islands). It attempts to define how the black robin's evolutionary adaptations to island life may have exaggerated the lethal force of deterministic extinction pressures. The chapter examines the key features of the only decline documented by conservation biologists (that is, the near-extinction of the ancestral population on Little Mangere Island and its translocated remnant on Mangere Island). This analysis conveys the study to the threshold of intensive conservation management in 1980-81. Findings are intended to increase awareness of the black robin's vulnerability to new or renewed threats. Finally, the chapter examines a previously unexplored dimension in the black robin story—the conviction shared by many Pitt Islanders that black robins survived until the mid-20th century on Pitt Island in the presence of extinction factors which had eliminated them swiftly from other islands. Examining the conflicting bodies of biological and local knowledge helps to consolidate conclusions reached in the chapter about historical causes of decline.

**Chapter Four: Management of Extinction Threat** examines the conservation measures taken to avert black robin extinction. This overview is the first to critique the recovery project from its beginnings on Little Mangere Island until the present. Its aim is to identify key principles and motivations shaping the tactics employed to rescue the black robins. My review examines the degree to which black robin conservation measures were consistent with conventional practice in New Zealand to minimise extinction vulnerability in insular bird species. The chapter also explains the ways in which commonly overlooked external factors (institutional imperatives and arrangements, logistical and resource issues) influenced the choices made by black robin managers and the effectiveness of their work. The valuable lessons learned during this protracted conservation effort have not been documented previously. In the course of this critique, I am able to explain the nature and quality of the records and demographic data available to my study.

**Chapter Five: Data Collation and Verification** describes the types and sources of demographic data exploited by my study and the processes I have followed to prepare the data for analysis. This is a brief account only of systematic collation and verification methods. It explains the efforts necessary to preserve the empirical value of raw field data which varied extensively in quality and quantity.

**Chapter Six: Population Trends After 1980** defines the growth trajectories and underlying demographic trends in the black robin populations on Mangere and Rangatira Islands after intensive management commenced in 1980-81. The chapter examines the variations in productivity, survival and behaviour which appear to have limited population growth and raise questions about on-going viability. The chapter analyses for the first time new demographic data from the post-management period (1990-91 to 2001-02) which give a truer indication of black robin viability under natural conditions. A preliminary study of potential environmental influences on demographic trends is reported also.

**Chapter Seven: Was Inbreeding A Problem?** quantifies the levels of inbreeding in the recovered black robin populations and assesses whether these levels are sufficiently correlated with the demographic variables limiting population recovery to be suggestive of genetic threats to viability. In addition to testing the theoretical and management assumptions underpinning New Zealand conservation practice, findings from these analyses are intended to guide the management and research recommendations made at the conclusion of my study.

**Chapter Eight: Hybridisation** assesses what can be learned from past black robin x tomtit hybridisation events. Latter-day black robin managers are generally unfamiliar and therefore unprepared to deal with this potential threat to the genetic integrity of black robin and tomtit populations. The chapter reviews the history of cross-breeding in order to identify predisposing factors and the risk of recurrence. Although the cross-breeding has been reported in conservation biology literature, the nature and circumstances of events are not widely known. My findings add to the small body of empirical evidence that hybridisation is a significant extinction threat in its own right. Conclusions from the chapter are designed to benefit management of similarly at-risk wildlife populations.

**Chapter Nine: Conclusions** summarises my study's key findings on black robin extinction vulnerability and assesses what these imply for the genetic and management assumptions outlined in this chapter.

**Chapter Ten: Management Recommendations** offers a series of recommendations intended to ensure that black robins in the first instance and similarly threatened insular endemic species are managed appropriately to maximise their prospects of long-term persistence and evolutionary resilience. I suggest refinements to current management strategies and make proposals for appropriate monitoring to reduce extinction vulnerability.

# CHAPTER TWO
# BLACK ROBIN BIOLOGY

## 2.0 Introduction

The Chatham Island black robin is probably the best known of the New Zealand *Petroica* and the best known New Zealand passerine, yet elements of its biology remain inadequately defined. Behaviour, vital rates and population dynamics under natural (unmanaged) conditions have received scarce attention in popular or peer-reviewed literature. The uncertainties limit ability to interpret the demographic record of the species reliably for research and management purposes. Predictive modelling of population trends is also hindered by limited quantifying of life-history characteristics, with potentially adverse consequences for black robin conservation.

Early first-hand biological accounts of the species were few and spare (Travers, 1871; Travers and Travers, 1872; Fleming, 1939b) principally because ornithologists and collectors of the time had difficulty accessing black robin habitats or loitering there once ashore. Vicarious accounts of the time were even more parsimonious (for example, Hutton, 1872; Forbes, 1893; Buller, 1890, 1894a). Mid-20th century descriptions dwelled principally on behavioural and morphological features pertinent to black robin phylogeny, drawing extensively on the skins and notes of earlier observers (Fleming, 1950a, b).

Knowledge improved significantly after 1971-72 when first biological inquiry began as a pre-cursor to conserving the species (Flack, 1971, 1973, 1974a, 1976d, 1979). Knowledge advanced significantly during intensive conservation management between 1980-81 and 1989-90. Despite sustained annual contact, however, a true picture of black robin biology could not emerge because key vital rates associated with breeding and survival were manipulated to avert extinction. The information acquired during this latter period has been described in both popular and scientific literature. Butler and Merton (1992) give a fulsome but informal biological description in the course of explaining how the species was saved. Much of their detail forms the basis of the most comprehensive formal description in Higgins and Peter (2002).

In addition to describing the character of black robin habitats, this chapter gives a summarising account of the species's biology, dwelling on aspects which help to explain population trends and extinction vulnerability. A more exhaustive account is unrealistic given that the underlying data were not acquired through systematic study but as a by-product of conservation management. Even so, my description refines existing knowledge in two ways. First, it draws on a much longer view of the black robins, from 1980-81 until 2008-09. Second and more importantly, it incorporates data from the 12 years during which black robin population dynamics were closely observed but not actively managed (1990-91 to 2001-02). These data yield fresh insights to black robin biology under natural conditions.

This biological summary generalises across all populations and leaves analysis of behavioural and demographic differences at the population scale to later chapters in the thesis (particularly Chapter Six: Population Trends After 1980). Unless otherwise specified, I rely on observations made in breeding seasons from 1980-81 until comprehensive monitoring of each population ceased (1998-99 on Rangatira Island and 2001-02 on Mangere). Particular emphasis is given to post-management seasons from 1990-91 to 2001-02. Longevity data are drawn from the current sample-monitoring phase of management on both islands (2002-03 until 2008-09; see Chapter Four: Management of Extinction Threat).

The methods used to gather, collate and verify biological data from these periods are summarised in Chapter Four (Management of Extinction Threat) and Chapter Five (Data Collation and Verification). The explanations given in these chapters emphasise the empirical basis for this biological account. For example, nest success was determined in almost every instance from field observation and did not require sample-based or inferential modelling.

The chapter concludes by assessing what is known of black robin biology and reproductive output relative to temperate-zone *Petroica* species in the New Zealand and Australian regions. In so doing, the chapter addresses an evident shortage of biological and life-history information on indigenous *Petroica* species specifically and passerines generally (Rowley and Russell, 1991). My assessment supports propositions that the life-histories of southern hemisphere passerines differ significantly from those of phylogenetically related passerines in the northern hemisphere. And it throws important light on ecological and behavioural adaptations which accentuate extinction vulnerability in the black robins.

In what follows, the term ‘nestling’ is preferred over the more ambiguous ‘chick’ and refers to hatchlings brooded until fledging. ‘Fledglings’ have left the nest but remain dependent on parental care. ‘Juvenile’ and ‘independant’ are preferred over Flack’s (1976a) term ‘immature’ and refer to fledglings which are nutritionally independent of parents and fully self-sufficient.

## 2.1 Origins and taxonomy

Black robins *Petroica (Miro) traversi* (Buller 1872; Order: *Passeriformes*; Family: *Petroicidae*, Australasian robins) are small, confiding, exclusively insectivorous passerines endemic to the Chatham Islands archipelago, 802 km east of Banks Peninsula, New Zealand (*Figure 1.1*; see Appendix One for a brief summary of archipelago topography, climate and flora). The *Petroica* genus is Australian in origin but Australo-Papuan and Pacific in distribution (Miller and Lambert, 2006).

Figure 2.1 [Left] Chatham Island black robin in characteristic hunched posture, Woolshed Bush, Rangatira Island, June 2006 *Photo: D. Houston*

[Right] Colour-banded black robin male, Woolshed Bush, Rangatira Island, September 2006 *Photo: K-J Wilson*

Recent estimates of time-of-arrival in New Zealand and the Chatham Islands follow Fleming’s (1950a, b) initial contention—based on morphological and behavioural characters—that black robins are descended from ancestral *Petroica* stock which migrated eastwards from the Australian continent in the earlier of two petroicid invasions, probably towards the end of the Pliocene period. The first invasion is considered to have established the robins in New Zealand; the second introduced the smaller tomtits, from which was derived a sympatric congener of the black robin, the Chatham Island tomtit *P. macrocephala chathamensis* (*Figure 2.2*).

Figure 2.2 [Left] Adult male Chatham Island tomtit (Woolshed Bush, Rangatira Island) and [right] adult female (Top Bush, Rangatira Island). *Photos: E. Kennedy*

Recent molecular analyses provide some evidence in support of the differentiated invasion hypothesis, though an indication that New Zealand's robins and tomtits also form a monophyletic cluster distinct from Australian species argues for a common time of arrival (Miller and Lambert, 2006).

Since arrival, dispersal and radiation has been more significant than in other naturalised species, giving rise historically to on-going debate over taxonomy. The principal features of this debate are summarised in Butler and Merton (1992: 5-7, 14-15) and more latterly in Miller and Lambert (2006). The division of species and subspecies has been particularly problematic, yet throughout the debate morphological and molecular perspectives after the mid-20th century have distinguished the black robin as a species among the New Zealand members of the genus.

Fleming's (1950a, b) comprehensive revision on the basis of morphology and behaviour distinguished the black robin as a robin species distinct from three robin sub-species in the sub-genus *Miro* (North Island robin, *Petroica australis longipes*; South Island robin *P. a. australis*; Stewart Island robin *P. a. rakiura*). Five tomtit sub-species were proposed by Fleming (North Island tomtit *P. macrocephala toitoi*; South Island tomtit *P. m. macrocephala*; Chatham Island tomtit *P. m. chathamensis*; Auckland Island tomtit *P. m. marrineri*; Snares Island tomtit *P. m. dannefaerdi*).

Latterly, Holdaway *et al*. (2001) have elevated all forms of robins and tomtits to full species alongside the black robin (thus one of seven *Petroica* species—three robins and four tomtits—extant on the main islands of New Zealand and its principal outlying groups). Morphological similarities with the South Island tomtit retained the Chatham Island tomtit as a sub-species. Miller and Lambert (2006) acknowledge the morphological distinctions between tomtits but contend on the basis of molecular analyses that sub-specific status is sufficient for all five forms. This study follows the robin and tomtit nomenclature proposed by Miller and Lambert (2006: Table 4), placing black robins among eight representatives of the *Petroica* genus in the New Zealand region (three robins and five tomtits).

Miller and Lambert's analyses question prevailing views of black robin provenance. Mitochondrial DNA markers align them more closely with the tomtits than with the ancestral robins, a finding which contradicts observed morphological and behavioural similarities to robins (Fleming, 1950a, b; McLean *et al*., 1994). Vocalisations share the characteristics of other *Petroica* species, particularly the 'down-scale' call, but black robin song is quieter, shorter and less complex than the New Zealand robin song and lacks the 'warbling' of the tomtits (Hay, 1975; Flack 1976a). Reconciliation of conflicting evidence for molecular and morphological affinities may help to explain the timing of the black robin's arrival in the Chatham archipelago (Miller and Lambert, 2006).

## 2.2 Morphology

Black robins are distinctively melanic and sexually monomorphic in appearance. Sexes in all age-classes are a uniform dull black, the juveniles discernible only by softer plumage and barely visible pale streaking on the head and body. Adult plumage does not vary seasonally or with age. The bright yellow soles characteristic of the *Petroica* genus and visible in black robins collected by the early ornithologists (Fleming, 1950b) were lost prior to the early 1970s and are now a dull brown or flesh colour (Flack, 1976a, 1977).

The species has been isolated on the Chatham Islands archipelago long enough to have evolved form and plumage unique among the New Zealand robins (Fleming 1950a, b). They are intermediate in size, tarsus length and wing dimensions between mainland robins and tomtits. Body shape appears shorter and rounder than the mainland *Petroica* through the black robin's habit of holding its large head hunched close to its body. Stance on long thin legs is usually upright and alert (*Figure 2.1*).

Morphological characters have not often been measured systematically. The surprisingly few measurements taken in the field (many opportunistically) indicate that characters vary within and between the sexes and adult and juvenile age-classes. The differences are small and indistinguishable to casual observation. Variations in means are more subtle, but on average, juvenile and adult females possess shorter wings, tails and bills than adult males (Table 2.1). Overlaps in character measures are frequent so that, coupled with the small sample sizes, measurements are not infallible indicators of age-class or sex. Breeding behaviour is the most dependable guide to the latter in the field.

Black robin wings are broad, rounded and short (more so on average in females).[1] The adult tail is only slightly longer on average in males. The bill is slender, black, short and encircled at its base by the bristles typical of other New Zealand robins. Tarsus length is comparable in males and females of all age-classes (Table 2.1).[2]

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[1] Fleming (1939b) gives a wing-length range of 82.0 - 86.0 mm ($\bar{x}$ = 84.0 mm) but the four unsexed birds measured may have been collected skins. Fleming (1950b: 144) gives wing-lengths for males and females (male, n = 11, range 81.0 - 86.0 mm, $\bar{x}$ = 82.6 mm; female, n = 10, range 79.0 - 85.0 mm, $\bar{x}$ = 81.4 mm) but it is unclear how Fleming verified the sex of the specimens he measured (they may have been sexed by dissection at the original time of skinning). McLean *et al.* (1994: Table 1) combined Fleming's wing-length measures to arrive at a mean of 82.0 mm.

[2] Flack (1976a) gives significantly longer mean tarsus lengths for known-sex adult males (32.0 mm, n = 7) and adult females (31.1 mm, n = 8) on Little Mangere Island. The differences probably arise from using alternative points of measurement (Flack does not declare his method) but arguably later measurements may reflect morphological changes resulting from the single-pair bottleneck of 1979-80 to 1982-83 (Chapter Three: History of Decline).

Adult males are generally heavier than females but the relatively few data gathered in the field indicate that their weight ranges overlap. Heather and Robertson (1996) give average weights for males as 25 g and females 22 g. Unsexed juveniles and adults bled for DNA analyses in late summer ranged from 20 – 25.5 g ($\overline{x}$ = 23 g; Ardern *et al.,* 1994). All-season multi-year data gleaned for this study from disparate records of field work on Mangere and Rangatira Islands give the mean male weight as 23.5 g (n = 24; range 20.5 – 25.7 g) and the female mean as 22.3 g (n = 16; range 20 – 25.3 g). Flack (1976a) recorded slightly higher mean all-season weights for adults in the ancestral black robin population on Little Mangere Island (male $\overline{x}$ = 24.4 g; female $\overline{x}$ = 22.7 g).

Male and female nestling weights differ also. In broods of known-sex nest-siblings (brood n = 40; summer, 1980-81 to 1998-99), male nestlings were on average 2.2 g heavier (range -1 g to 6.5 g) than females at banding age (14-16 days after hatching). In all broods, known-sex nestling weights for males and females overlapped closely (males: 20.5 – 33 g; females: 20 - 31.3 g).

Few data exist for adult weight variations throughout the year. Flack (1976a: Table 6) reports that mean weights for adult females on Little Mangere Island varied by less than 1 g (summer $\overline{x}$ = 23 g; autumn and winter $\overline{x}$ = 22.3 g) but males differed by almost 2 g (summer $\overline{x}$ = 25.5 g; autumn and winter $\overline{x}$ = 23.6 g). Weights were highest in summer and lowest in winter.

## 2.3 Distribution

Prior to human contact, black robins were believed to be distributed throughout the Chatham Islands archipelago (Fleming, 1939b, reporting local knowledge), on the islands possessing forest (Chatham, Pitt, Little Mangere, Mangere and Rangatira Islands). They are now confined to the two largest of the vegetated outliers in the group—Mangere Island (113 ha) and Rangatira (South-East) Island (218 ha) (see Chapter Three for a detailed assessment of historical range and contractions).

On Rangatira Island, black robins occupy two large habitat complexes known informally as the Woolshed Bush and the Top Bush (*Figure 2.3*). On Mangere Island, the black robins inhabit a recovering forest remnant known to field-workers as Robin Bush (*Figure 2.4*).

Table 2.1 Wing length (carpal to longest primary), tail length and bill length (forehead feather-line to tip of upper mandible) of known-sex black robins. Wing, bill and tarsus measurements from Rangatira Island (March 1992; Holmes, 1992); tail measurements from Little Mangere Island (1972-1976; Flack, 1976a).

| | Wing length (mm) | | | Tail length (mm) | | | Bill length (mm) | | | Tarsus length (mm) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | Mean | Range | *n* | Mean | Range | *n* | Mean | Range | *n* | Mean | Range |
| **Adult** | | | | | | | | | | | | |
| Male | 15 | 81.2 | 79-84 | 6 | 66 | 65-69 | 13 | 15.2 | 13.0 - 16.9 | 15 | 28.5 | 27.3 - 29.0 |
| Female | 7 | 77.9 | 77-79 | 8 | 64 | 61-66 | 7 | 14.9 | 13.8 - 16.2 | 7 | 28.0 | 26.8 - 29.2 |
| **Juvenile** | | | | | | | | | | | | |
| Male | 3 | 80.3 | 80-81 | | | | 4 | 15.8 | 14.0 - 16.7 | 3 | 29.0 | 28.7 - 29.1 |
| Female | 2 | 76.5 | 75-78 | | | | 1 | 14.7 | - | 2 | 28.0 | 26.7 - 29.2 |
| Unknown | 3 | 76.3 | 75-78 | | | | 3 | 15.8 | 13.8 - 17.6 | 3 | 26.8 | 25.6 -28.2 |

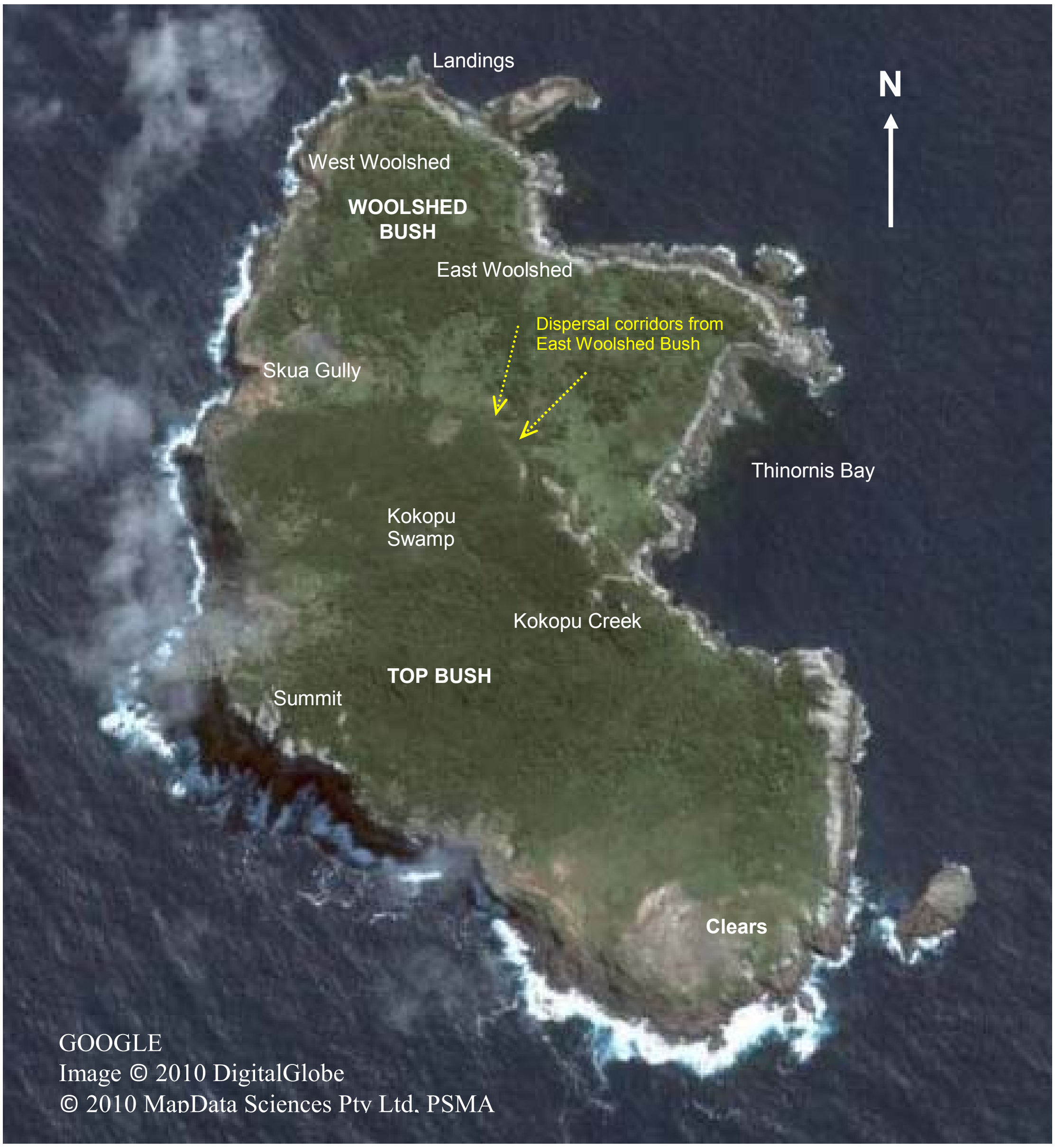

Figure 2.3 Rangatira (South East) Island (218 ha) showing the principal black robin habitats, Woolshed Bush and Top Bush, and other sites named in the text.

*Source: Google ™ Earth*

Field observations since March 1972 in the differing habitat complexes on Little Mangere, Mangere, Rangatira and (more recently) Pitt Islands affirm that the black robins are forest-dwellers capable of breeding successfully in deep-forest interiors and at dense forest-edges alike.

In the larger continuous tracts of habitat on Rangatira Island where the choices made by black robins are most evident, territory density tends to be greater at the forest-edge (for observations on present-day territory disposition, see Kennedy and Wilson, 2005). Forest margins are not as permeable for black robins as they are for the sympatric Chatham Island tomtits. The black robins do not favour shrubland vegetation outside forest perimeters and are generally disadvantaged if attempting to breed in scattered vegetation (Flack, 1974b, 1976a).

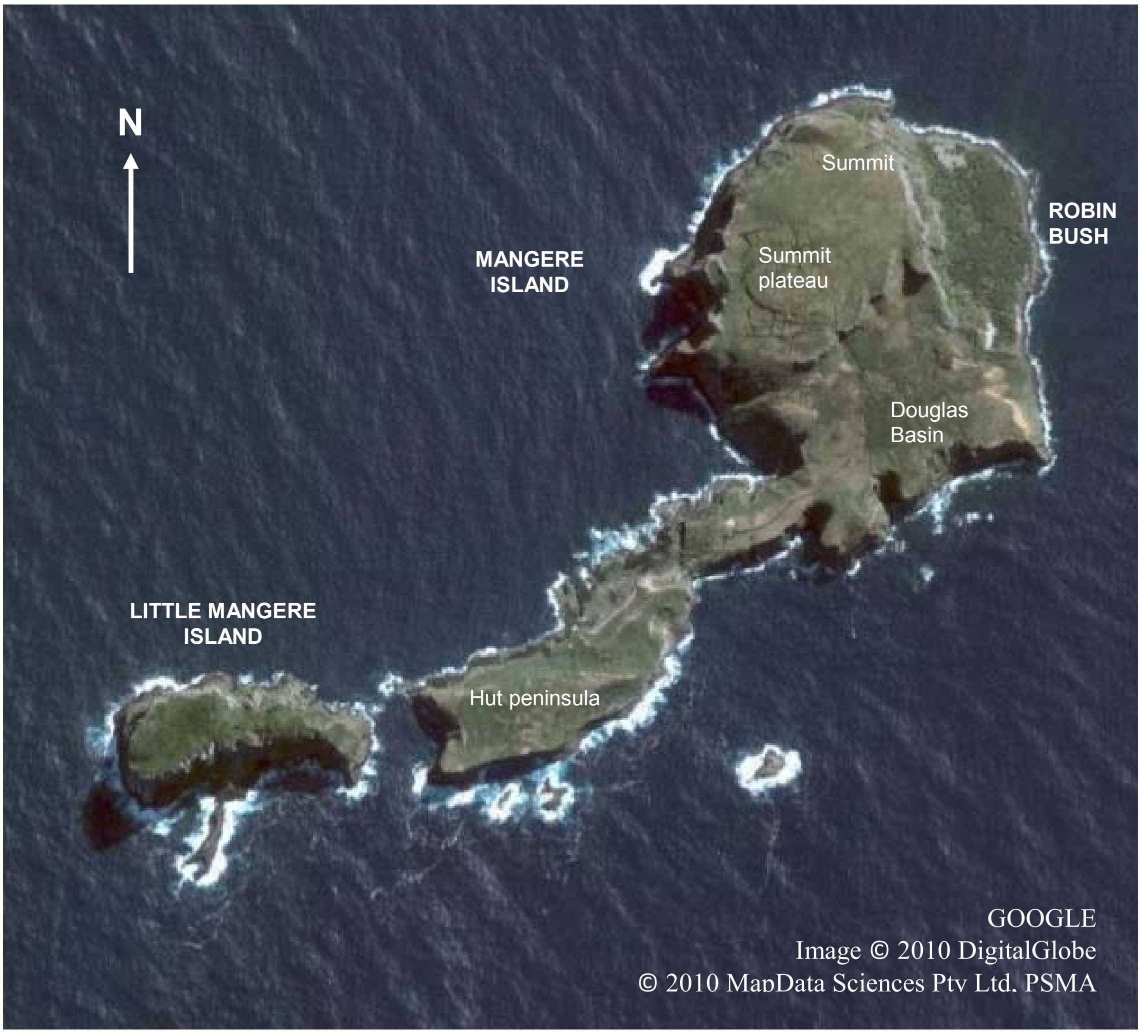

Figure 2.4 Mangere Island (113 ha) showing the principal black robin habitat, Robin Bush; Little Mangere Island (8-9 ha, plateau area), and other sites named in the text.

*Source: Google ™ Earth*

The preference for forest rather than open habitat suggests that historically the black robins were widespread on Chatham and Pitt Islands wherever contiguous tracts of taller woody vegetation occurred. The generally impenetrable character of this vegetation (Travers, 1868) may not have hindered their distribution but its varied composition may have influenced local densities.

## 2.4 Present-day habitat character

The two tracts of forest habitat on Rangatira Island differ markedly in character, topography and aspect. The Woolshed Bush comprises a complex of disaggregated forest remnants distributed across approximately 26 ha [3] of a flat low-lying marine terrace in the northern third of the island (*Figure 2.3*). This broad terrace (of Pleistocene origin; Adams *et al.*, 1988) inclines southwards towards the centre of the island and slopes in a gentle gradient down to the sheltered eastern coastline. Continuous forest cover has regenerated on the central and western parts of the terrace. Connectivity between the very scattered forest remnants to the east has improved through natural regeneration of woody cover since black robins were reintroduced to the island in 1983-84. Though the Woolshed Bush faces north and is sheltered from the prevailing salt-laden southerly winds, gales from the west (relatively common) and east (rare but destructive if storm-force) can create very cold conditions in the forest interior.

In contrast, the significantly larger Top Bush habitat comprises an almost unbroken expanse of forest (c. 84 ha) mantling the southern two-thirds of Rangatira Island (*Figure 2.3*). The northern perimeter of this forest extends over a second smaller marine terrace (about 80-100 metres above sea-level.) overlooking the Woolshed Bush. Behind this relatively sheltered plain, the island rises steeply south-westwards to a height of 224 metres. The elevated western and south-western margins of the habitat culminate in precipitous cliffs which receive the brunt of prevailing winds. Ramparts of lower stature on the opposite north-eastern perimeter deflect easterly winds. The majority of the forest descends, often steeply, towards the south. Much of its complex topography is defined by the contours of the island's only water-course (an ephemeral stream known informally as Kokopu

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[3] Cartographic (plan-view) measurements are used here, generated from polygons drawn around the relevant bush perimeters in Google™ Earth satellite images of each island. Topographic measurements would give a truer (greater) area but Google™ Earth's underlying contour data are at too coarse a scale for reliable calculations.

Creek). The Top Bush culminates in flat, low-lying areas of regenerating akeake *Olearia traversii* forest which is advancing over the northern margins of the 'Clears'. Akeake, a multi-stemmed tree daisy, is a robust ever-green coloniser of exposed forest edges and open spaces. On the highly eroded, very exposed Clears, scattered akeake trunks indicate the presence historically of a stunted forest of 3.7 – 7 metres in height (Atkinson, 2003), destroyed when livestock breached the windward edges of the vegetation (Ritchie, 1970).

Robin Bush on Mangere Island (*Figure 2.4*) is distributed across approximately 7.9 ha of boulder debris-field below towering cliffs. The field descends steeply to the island's eastern coastline. The forest is generally of lower stature than on Rangatira Island and noteworthy for the number and longevity of mature akeake trees (Kennedy and Wilson, 2005). This forest is regenerating from the small remnant of original bush which survived the farming era (Ritchie 1970). It receives limited winter sunshine and is subject to destructive rock-falls from the cliffs above (Merton, 1992; pers. obs.). Continual disturbance of this sort is probably responsible for the dominance of akeake in the bush (Atkinson, 2003).

When the black robins were reintroduced from Little Mangere Island in 1976-77, the forest was scattered over 4.7 ha (Flack, 1977).[4] The canopy has since closed over significant areas of the debris-field and, as on Rangatira Island, the forest perimeters are expanding naturally. This process is being actively augmented by a long-running revegetation programme (Atkinson, 2003). Exposure from the south has moderated as a result. Despite the regeneration and canopy closure, parts of the bush retain a conspicuously patchy character.

### *2.4.1 Vegetation type*

The present-day forest communities of Mangere and Rangatira Islands are structurally and floristically less diverse than those elsewhere in the island group. A small body of historical evidence examined by this study suggests closer similarities in the past but sheds little light on the original pre-human character of the bush. If differing naturally from the original unmodified forest communities on the larger landmasses (Chatham and Pitt Islands),

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[4] 1.7 ha of tree cover distributed in patches over an area of 4.7 ha by 1976-77, according to Flack (1977); about 5 ha according to Atkinson (2003). The area was reduced to 4.2 ha in the winter of 1979 by a massive rock-fall (Butler and Merton, 1992, correcting Cox and Merton, 1980) which may have accounted for the loss of two experienced black robin breeders at a critical time near the point of extinction (see Chapter Three: *Section 3.7*).

the bush habitats occupied by black robins today would not have been familiar to the vast majority of black robins in the pre-human archipelago. The degree to which the historical and present-day habitats of Rangatira and Mangere Islands differ and are typical of pre-human habitats is discussed in Appendix One.

The two extant black robin populations on Mangere and Rangatira Islands occupy forest habitat of simple structure and modest stature. On Rangatira Island, the forest canopy (up to 15 metres, Roberts *et al.*, 2007) comprises akeake and ribbonwood *Plagianthus chathamicus*, a deciduous species whose straight stems, simple branch structure and smooth bark offer black robins fewer nest cavities and foraging opportunities. Matipo *Myrsine chathamica,* karamu *Coprosma chathamica* and, to a lesser extent, ngaio *Myoporum laetum* also compete for canopy space. The climbing vine *Muehlenbeckia australis* is abundant on the bush edge where it smothers seral vegetation and trees but deflects winds from the forest interiors during summer. The vine's dense leafy walls increase black robin densities by augmenting nest-site and foraging opportunities (Flack, 1976a) but because it is deciduous, *Muehlenbeckia* is ineffective as shelter during winter.

The canopy in Mangere Island's smaller forest remnant, Robin Bush, reaches a height in places of 10-12 metres and comprises largely akeake and ribbonwood. *Muehlenbeckia* mantles bush-edge vegetation and outliers as it does on Rangatira Island. Unlike Rangatira Island where the forest is refreshed through relatively rapid rates of canopy collapse and recovery—owing to storms and the burrowing activities of oceanic petrels (Roberts, 2004)—the forest structure and cover in Robin Bush appears to be relatively stable. Forest floors and substrates differ. Rangatira Island possesses broad expanses of deep soil, many on relatively level or gently undulating gradients. Most areas of forest floor are accessible to abundant oceanic petrels (seven species, all burrow-breeders; Nilsson *et al*., 1994; West and Nilsson, 1994). In contrast, the Robin Bush forest grows among massive angular boulders (up to house-size) among which soil does not accumulate so extensively and is not so readily 'ploughed' by petrels.

Sub-canopy vegetation on both islands varies locally in character and density. It comprises mahoe *Melicytus chathamicus*, matipo (a significant source of nesting cavities for the black robins), kawakawa *Macropiper excelsum*, and supplejack *Rhipogonum scandens,* a climbing liane. Hoho *Pseudopanax chathamicus* is also present in parts of the Rangatira

Island forest and is becoming more common, especially as seedlings on bush perimeters (pers. obs.).

The forests occupied by black robins today are regenerating from stressed and simplified conditions induced by 19th- and 20th-century farming activities on both islands (see Roberts *et al*., 2007 for analysis of change on Rangatira Island; see also Chapter Three). In the interior of Woolshed Bush where black robins are currently most numerous, ribbonwood is succeeding senescent akeake, the only canopy species of note to survive the farming years (Bell, 1953). In the process, a simple monotypic structure is emerging under which sub-canopy conditions have become more open and exposed (pers. obs.). The changes have coincided with, but may not be directly related to, signs of a decline in the number of black robin territories (Kennedy and Wilson, 2005). The increasing stature of sub-canopy vegetation in both the Top Bush and Robin Bush seems likely to result in more open, exposed and arguably colder black robin habitat there too (Kennedy and Wilson, 2005). In the past 30 years, canopy composition does not appear to have altered significantly in Robin Bush, though photographic comparisons with images taken in 1976-77 (Veitch, 1982) show a marked increase in canopy area. Canopy composition in the Top Bush on Rangatira Island appears to casual observation to be comparatively stable but there are few suitable historical images available for comparison.

Despite centuries of human contact, rodent species have not established on either Mangere or Rangatira Island. Accordingly, invertebrate communities are conspicuously more diverse and abundant than elsewhere in the archipelago. The islands are currently free of the exotic mammalian predators present elsewhere in the archipelago (see below). Predatory buff wekas *Gallirallus australis hectori*—introduced to Chatham Island from New Zealand in 1905 (Bell, 1996), and to Pitt Island in the early 1960s (Ken Lanauze Snr, pers. comm.)—are also absent. The Australasian harrier *Circus approximans* and the introduced European starling *Sturnus vulgaris* breed, roost and forage on both islands. Both are occasional predators of black robins and their nest contents (Butler and Merton, 1992).

## 2.5 Habitat occupancy

By habit, adult black robins are sedentary (Flack, 1976a, 1977) and occupy all-purpose territories. Observations under both managed and natural conditions show that most paired adults and established bachelors remain in or near their territories throughout the year. Within and between seasons, adult females may also remain in or on the perimeter of territories after mates perish.

Patterns of black robin distribution within the habitats and territory sizes on Mangere and Rangatira Islands were not measured systematically during the study period. The highest recorded density of breeding pairs under natural (unmanaged) conditions during full-population monitoring was in Robin Bush (2.53 pairs $ha^{-1}$, 1998-99; mean area available $pair^{-1}$ = 0.4 ha).[5] Breeding pair numbers were highest in 1998-99 on Rangatira Island (Woolshed Bush: 1.58 pairs $ha^{-1}$; mean available area $pair^{-1}$ = 0.63 ha). In the more lightly populated Top Bush, breeding density peaked in 1998-99 at 0.2 pairs $ha^{-1}$ (mean available area $pair^{-1}$ = 5.6 ha, much of it undefended).

Under natural conditions between 1990-91 and 2001-02, movements within and between habitats were made predominantly by juveniles. On Rangatira Island, the majority of movements between the Woolshed Bush and Top Bush were made via forest corridors (*Figure 2.3*) and by female juveniles (see Chapter Six: *Section 6.3*). Movements by juveniles and unmated adults alike appeared to be random rather than related to population density and often resulted in individuals settling far from natal territories. Movement occurred typically towards the end of the breeding season (January-March) or during the ensuing winter. Migrants had usually settled in a new territory by early spring (September).

The black robin's powers of flight are limited but although reluctant to venture beyond forest perimeters, individuals may make strong flights across open country occasionally (Flack, 1976a). It is probable (but not certain) that individuals dispersed intermittently across the 260 metres of ocean between Little Mangere and Mangere Islands when both islands were forested, so that historically black robins on these two islands may have constituted a single population genetically. Broader expanses of water appear to be insurmountable barriers to dispersal for present-day black robins.

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[5] These densities exclude unmated adults holding territory and do not refer to actual territory sizes. Based on cartographic area (see Footnote 3, *Section 2.4*).

In contrast, open terrestrial spaces appear to hold no fears for site-attached individuals 'homing' to established territories. During the cross-fostering seasons (1980-81 to 1989-90), match-making managers on Rangatira Island attempted to relocate unmated males to the Top Bush from Woolshed Bush. The males always returned to their original territories within hours or a day at most, some evidently crossing a large expanse of grassland known for good reason as Skua Gully (Butler and Merton, 1992; Chapter Four). The possibility of inter-island homing cannot be ruled out but the evidence for this is circumstantial. Two uniquely colour-banded adult males transferred to nearby Pitt Island (narrowest point of crossing, 2.2 km; direct line from point-of-release in Caravan Bush, 6 km) were reported back on Rangatira Island in September 2004 (Fastier, 2005; Kennedy and Wilson, 2005). However, neither individual was seen a second time despite intensive searching, and both were reported originally in proximity to local black robins with similar colour-band combinations.[6]

## 2.6 Foraging

The foraging niche, ecology and behaviour of black robins closely resemble those of sympatric Chatham Island tomtits (McLean *et al.,* 1994; Powlesland *et al*., 2001). Black robins are not known to eat fruits or seeds as the tomtits and mainland congeners do (Powlesland *et al*., 2000; Higgins and Peter, 2002), nor do they possess the food-caching habit typical of the New Zealand robins (Fleming, 1950b; Powlesland, 1980). Like the Chatham Island tomtits, black robins forage diurnally for invertebrates in ground litter, tree crevices and sub-canopy vegetation. Crepuscular foraging on nocturnally active prey has also been recorded (New Zealand Wildlife Service, 1983).

Black robins forage close to the ground more often than close under the canopy (Flack, 1976a), and spend more time than tomtits foraging on the ground and on trees (McLean *et. al.* 1994). Ground prey is captured by pouncing from low branches, raking vegetation on the ground or through hopping excursions across the forest floor. Frequent short flights are taken for insects in foliage or on tree-trunks and branches (Higgins and Peter, 2002). Tak-

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[6] One was transferred as a putative juvenile. Despite having no fixed territory on Rangatira Island, it was reported to be 'home' within six months of transfer. The other, a five-year-old site-attached male, had been transferred two years earlier and had held territory with a mate on Pitt Island. Its return 'home' within eight months of its last sighting on Pitt Island seems highly improbable.

ing insect prey on the wing was observed on Little Mangere Island where ground prey was depauperate (Flack, 1976a) but has seldom been observed in the richer prey environments of today's habitats. Unlike the tomtits, black robins forage very rarely beyond the forest interior or in open spaces, a behavioural constraint which limits the available prey area and obliges them to forage over greater distances if living in smaller or narrower tracts of forest (Flack, 1974b, 1976a).

Prey size and type have not been quantified systematically (Wilson and Kennedy, 2008) and few observers have noted what is being caught and consumed when reporting breeding activity. Incidental field data exist for feeding frequency at the nest but systematic observations of frequency are scarce. Marris (1988) reported feeding visits to fledglings and nestlings averaging one every 3.5 minutes over two 12-hour periods, but this visit rate was affected by observer presence and supplementary-feeding. On Mangere and Rangatira Islands, where invertebrate diversity and abundance have not been modified by introduced mammalian pests, diet is highly varied. Natural prey comprises many winged and flightless invertebrate taxa and most life-stages (pupae, larvae, adult)—spiders, beetles, bugs, weta, worms, flies, moths, aphids, cockroaches and caterpillars (Flack, 1976a, Higgins and Peter, 2002; Kennedy, 2006). Large natural prey can be taken; adult black robins can subdue (and consume) cave wetas *Novoplectron serratum* and *Talitropsis megatibia* up to 20 mm in body length, after removing legs and antennae by violent flicking and dashing against logs (pers. obs.). Black robins readily consume the larvae of cultivated mealworms *Tenebrio molitor* and waxmoths *Galleria mellanella* used commonly to aid census work and for supplementary-feeding after 1987-88 (Kennedy, 2010).

On Pitt Island, where introduced mice *Mus musculus*, pigs *Sus scrofa* and weka have severely depleted insect life, especially ground-dwelling species (Rowan Emberson, pers comm.), the versatile prey preferences of black robins appear sufficient to sustain the effort of raising nestlings on predominantly arboreal prey (Kennedy, 2006), but poor rates of breeding success (Chapter Four) hint at nutritional inadequacy. Observations on Mangere and Rangatira Islands indicate that black robins do not favour blow-flies (Family: Calliphoridae), the ubiquitous black carabid beetles (Family: Carabidae) and some species of caterpillar, particularly of the seasonally abundant noctuid or owlet moth *Homohadena fortis* (John Dugdale, pers. comm; Wilson and Kennedy, 2008).

## 2.7 Life-span

Black robins are capable of living up to 14 years of age but life-spans longer than 12 years are exceptional (< 1% of those hatched between 1980-81 and 2001-02). Life-expectancy can vary significantly between populations but not between sexes. Contrary to Mallinson (1992), the field data available to this study indicate that on average black robins achieving adulthood under natural conditions survive to four years (see Chapter Six: Table 6.17). Population-scale variations in average life-expectancy are examined later in this thesis.

## 2.8 Breeding

### *2.8.1 Breeding age*

Contrary to Merton (1983c) and Higgins and Peter (2002), sexual maturity is achieved in both sexes in the season following fledging. Late-season juveniles can breed in their first adult season at less than 12 months of age. The majority of black robins surviving ≥ one year first pair and breed as yearlings under natural conditions (see Chapter Six: Table 6.16). Higher proportions of females breed, and produce independent offspring, at year one (Table 2.2). Both sexes can raise viable offspring at very advanced ages (≤ 12 years; this study).

Table 2.2 Percentage by sex of black robin recruits known to have first paired and bred as yearlings under natural conditions on Mangere and Rangatira Islands (black robins hatched between 1990-91 and 2001-02). *N* for each productivity class is the total qualifying. Recruitment is defined as ultimately producing eggs (males, n = 192; females, n = 181).

| | Males | | Females | |
|---|---|---|---|---|
| Known at year one to have | *n* | % | *n* | % |
| Paired | 187 | 68.4 | 169 | 85.8 |
| Laid eggs | 172 | 58.1 | 158 | 72.2 |
| Produced juvenile(s) | 145 | 40.7 | 124 | 53.2 |
| Produced juvenile(s) at first attempt | 85 | 69.4 | 73 | 89.0 |

The ages at which females first produced juveniles between 1990-91 and 1998-99 give a mean generation time under natural conditions of 1.7 years.

### *2.8.2 Breeding system*

Breeding in the black robin's patriarchal social system is territorially based. During breeding, both sexes defend territories (pers. obs.) and, as in the South Island robin (Flack, 1979), the male response to conspecific and tomtit intruders alike is usually the more immediate and aggressive. During the balance of the year, responses to intruders tend to be less aggressive. If resident males die during breeding, experienced females may remain alone in the territory or on the perimeter until breeding ceases or a new mate is found. Typically, paired males and females associate outside the breeding season (Butler and Merton, 1992). Territory fidelity is strong between years and linked predominantly to survival of the occupying male (pers. obs., collated data).

Males attract mates to territories through individually distinctive song and court approaching females through pursuit flights and gifts of prey items. Males subsequently monopolise the food supply in order to subjugate receptive females, and harry them relentlessly to induce egg-laying, incubation and renesting. Harassment of the female commonly includes feather-wrenching, severe cases of which can visibly deplete her dorsal plumage. Food monopoly and harassment diminishes only when both adults are required to provision their nestlings and fledglings (pers. obs.).

Black robins are socially and sexually monogamous. On very rare occasions, males were observed attempting to breed simultaneously with two females, but breeding always failed (pers. obs.). Concurrent polyandry has not been recorded. As in some other *Petroica* species (for example, North Island robin, Armstrong *et al.*, 2000; Powlesland *et al.*, 2000; and Australia's red-capped robin *P. goodenovii*, Dowling, 2003), sequential polyandry has been observed but only rarely. In 1998-99, for instance, three older females on Rangatira Island deserted their mates mid-brood or after fledging and paired with another male. All three deserted males fledged and raised their offspring alone (collated data). The reasons for the three desertions were not clear but the very low incidence of such desertions does not suggest that sequential polyandry is a strategy to maximise individual reproductive output.

As with many monogamous species, pair-fidelity within and between years is strong but not absolute (Butler and Merton, 1992). Data from this study agree with Merton (1992) that young breeders are more inclined to switch mates. Of 14 females deserting pairings after laying (5% of all females reaching breeding age), ten were one or two years old (both management phases, this study). Eight deserted after breeding failure. Commonly, new pair bonds are formed locally but in unmanaged seasons, young females on Rangatira Island were observed to move far from the old territory before pairing again (for example, from the Woolshed Bush to the Top Bush). Females of any age may switch mates between seasons, even if the original male is still alive. Contrary to Higgins and Peter (2002), it is difficult to define the extent of divorce by males because they are much less inclined to abandon a territory. Even in the event of successive breeding failures, life-long pairings are not uncommon and stable pairings of shorter duration are frequent between seasons. The longest recorded pairing under natural conditions endured into a ninth season before the female died (Mangere Island, 1991-92 to 1999-00). The location and identity of paired adults may be predicted with reasonable assurance from year to year once the pair-bond has been consummated through breeding (successful or otherwise).

Rates of promiscuity (if any) have not been quantified in black robin populations, despite the duration and intensity of field observations. For this reason, the paternity of offspring cannot be assigned with absolute confidence to the social male. The determination of extra-pair paternity (EPP) through molecular analyses is frustrated by the anomalously low genetic diversity of black robins (Ardern and Lambert, 1997; Ma and Lambert, 1997a). This is also the case for intraspecific brood parasitism (ISBP). Between 1980-81 and 2001-02, the extremely low incidence (n = 5) of black robin clutches in excess of the accepted maximum of three eggs suggests that an ISBP habit is highly unlikely. The five anomalously large clutches are believed to have resulted from the territorial female laying eggs alongside a previous undetected clutch in the same nest. Analysis of EPP and ISBP in New Zealand robins also implies a very low probability of infidelity and egg-dumping (Holmes, 1994; see also Ardern *et al.*, 1997a; Taylor *et al.*, 2008, and Jamieson, 2009, for confirmation of genetic monogamy in North Island and South Island robins). The probability of EPP and ISBP in black robins is made lower still by the aggressive eviction of black robin trespassers from breeding territories, the strength of female-female hostility, and the durability of pair-bonds.

Contrary to Higgins and Peter (2002), instances of black robin hybridisation have been recorded. Three black robin females bred with sympatric tomtits in various seasons between 1980-81 and 1998-99. Managers intervened to prevent another apparent cross-pairing (Butler and Merton, 1992) and other cross-pairings were suspected on Mangere Island (pers. obs.). No black robin males are known to have cross-bred. For a detailed assessment of hybridisation events, see Chapter Eight (Hybridisation).

### *2.8.3 Nesting*

Like the Chatham Island tomtit, black robins are hollow- and cavity-nesters. Females select nest-sites in hollow tree-trunks, branches, in dense mantles of *Muehlenbeckia* or even (rarely) in rock cavities. Concealment from extant avian predators such as harriers and brown skuas *Catharacta skua lonnbergi* is usually good in such sites. However, more so than appears to be the case for the tomtits (Powlesland *et al*., 2000), nests can also be built in sites exposed to weather, nocturnal petrel-strikes or predatory starlings (for example, in the hollow tops of decaying matipo stumps which are common in the forest interior on Rangatira Island). Females will also build in highly unstable sites such as rotten tree-trunks. Nest-sites may range from ground level to the upper strata of the forest, though sites in or near the crown structures of trees are uncommon. Sites easily accessible to observers (one to three metres above ground level) are frequent (pers. obs) and most are ≤ 10 metres above ground (Nilsson *et al*., 1994). Females will also use artificial nest-boxes. Unlike other insular congeners (Snares Island tomtit, McLean and Miskelly, 1988; Auckland Island tomtit, Fleming, 1985), no black robin nests have been found in the open or in vegetation and human-made structures outside forest cover.

Typically, females chose new sites for successive nests, though a few experienced females re-used familiar nest cavities in successive seasons after 1990-91. Re-use of cavities in the same season (and use of the same nest) has been observed on only five occasions between 1990-91 and 2001-02, which is less than 0.46 % of the 1070 clutches laid (Chapter Six: Table 6.14). The preference for new nests and sites imposes a time-cost on breeding and presumably an additional energy cost. Nests are built by females alone, typically in short episodes of frantic activity over three to four days (pers. obs.). As with the South Island robin (Powlesland, 1983), building activity decreases as the nest nears completion (so much so at times that observers may often believe the partially prepared nest to be abandoned). On occasions, several nests may be started before one is completed. Nest material is collected from the ground (feathers, leaves, moss, twigs) and from standing vegetation (decaying tree fibre, cobwebs). Nest composition varies little on Mangere and Rangatira Islands. A base is formed from coarse materials (tree fibre, large leaf skeletons, small twigs bound with cobwebs), within which a second-stage bowl is built comprising moss, strands of soft ribbonwood fibre, small leaf skeletons. The final nest-bowl is a deep open cup lined with moss and copious feathers from petrels and terrestrial birds. A very late black robin nest on Pitt Island containing a 12-day-old nestling (12 February 2006) contained no feather-lining at all, perhaps because suitable feathers were unobtainable locally (Kennedy, 2006).[7]

### 2.8.4 *Breeding cycle*

A successful breeding cycle (nest-building to independent offspring) takes approximately 90 days depending on the intervals between nest completion and egg-laying, the number of eggs laid and the time taken to raise offspring to independence. Females may renest if successful, and cycles can overlap if renesting commences after the previous brood fledges. Relaying intervals recorded on Rangatira Island for 18 renesting females in the 1990-91, 1997-98 and 1998-99 seasons averaged 12.6 days (range, 4 - 28 days). Females may begin construction of new nests as soon as four days after breeding failure (Butler and Merton, 1992). Desertion of a failed clutch can take as long as 41 days (two females, Rangatira Island, 1996-97) and 45 days (one female, Rangatira Island, 1991-92). Desertion after ≤ 10 days after the due hatch-date is more usual.

First eggs may be laid almost immediately upon completion of the nest but delays are more usual, sometimes of ten days or more (this study).[8] Eggs are laid on consecutive days or very occasionally longer (Butler and Merton, 1992). The few shorter or longer intervals

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[7] On Little Mangere Island, a nest believed by Fleming (1939b: 507) to be a black robin's also contained few feathers ('[the nest] was fairly bulky, with a small cup neatly lined with a few feathers'). But this was early January, at or near the end of breeding, and the nest may have lacked feathers because it had already served its purpose.

[8] Daily observations during the nest-building phase were uncommon between 1990-91 and 2001-02 so that the precise intervals between nest-completion and the laying of first eggs were not quantified systematically. The data available for Woolshed Bush and Top Bush pairs in 1990-91 indicates a mean delay of 6.12 days (n = 16, range, 3 - 11 days), but this is a rough guide only.

recorded under natural conditions probably result from unreliable or intermittent observations. Incubation, by the female alone, generally begins on the laying of the final egg and lasts 18 days (this study, confirming Butler and Merton, 1992). The incubation period did not vary with successive changes in management regimes. As with South Island robins (Powlesland, 1983), a female may continue to incubate if her mate dies but a clutch will be abandoned if the female dies.

Usually, all eggs hatch within 24 hours. Only the female broods the nestlings but both parents feed them. The transition to feeding nestlings is typically the stage at which yearling males fail in their parental duties.[9]

There is no evidence of obligate brood reduction or siblicide.

Intervals to fledging vary, perhaps in accordance with environmental conditions and parental experience. On average, nestlings fledge 22 days after hatching (range 19 - 25 days; collated data) and typically all nest-siblings fledge during the same day. Fledglings are altricial and fed by both parents which often but not always divide the brood amongst themselves and retain the division. At first, some fledglings may roost on the ground briefly but thereafter siblings tend to remain together above ground close to nest sites until flight improves and they begin to wander independently. Fledglings straying too far into neighbouring territories are at risk of abandonment and starvation. In at least two observed instances after 1990-91, a stray fledgling was fed by an unrelated breeding adult in a neighbouring territory (male and female respectively, each neglecting its own fledgling; collated data). Fledglings in maternal care are also at risk of starvation she renests before they are sufficiently advanced towards independence. Fathers do not automatically shun fledglings abandoned by renesting mates nor do they automatically abandon fledglings after the second brood hatches (pers. obs.). But many fledglings die of starvation at these times.

The independence threshold is difficult to discern precisely and intervals vary greatly because fledglings differ in their willingness to become independent. Data from non-management seasons indicate that independence is rarely achieved at fewer than 35 days after fledging (contrary to Nilsson *et al.,* 1994), and intervals of up to 60 days have been

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[9] Historically a cue for extra vigilance at nests during management seasons (pers. obs.).

recorded (this study). Butler and Merton (1992) reported 40 to 65 days for the intensive management seasons. Juveniles may linger in or near the territory during the balance of their natal season and will beg for food from any adult, even if nutritionally independent. Others disperse significant distances almost immediately (a common reason for assumptions by observers that they have died). Parents do not tolerate offspring in the territory once they are independent. Thus, offspring do not help with parenting or territory defence. No other forms of co-operative breeding (creching, parenting of other pairs' young) have been observed.

### *2.8.5 Timing of egg-laying*

The seasonal onset of egg-laying is unsynchronised and experienced pairs may not lay first. Females commence nest-site prospecting and nest-building in or about the last week of September. Eggs may be laid as early as the first week of October. The earliest recorded date for the commencement of a clutch is 1 October (estimate based on count-back from fledging date, Mangere Island, 1992-93). First-egg laying peaks in the last week of October (*Figure 2.5*). Laying can be deferred in some years by up to four weeks for reasons which have not been clarified but may relate to climatic conditions or food availability.

Egg-laying rarely extends beyond mid January, by which time breeding adults are retiring to moult. The latest recorded clutch in any season was commenced on 27 January 1997 (Top Bush, Rangatira Island). A clutch estimated to have commenced on 18-19 January 1992 (Woolshed Bush, Rangatira Island) is the latest known to have produced offspring surviving to adulthood (fledging date c. 28-29 February 1992; collated data).

Most first clutches are laid in late October and November but some pairs may not commence egg-laying until December (*Figure 2.6*).

These egg-laying intervals are more extended than the very short period of egg-laying reported in the food-stressed ancestral population on Little Mangere Island between 1973-74 and 1975-76 (minimum, about one month, late October to mid-November; maximum ≤ 56 days, mid-October to mid-December; Flack, 1976a).

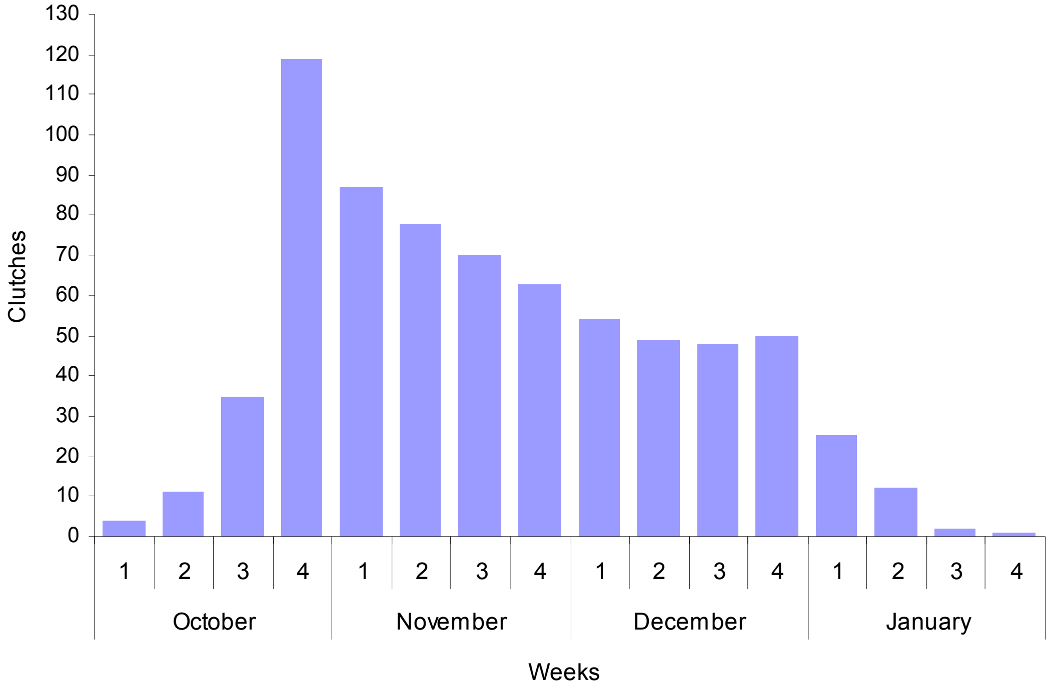

Figure 2.5 Weeks in which first eggs were laid in all clutches (n = 757) under natural conditions in the two black robin populations on Mangere and Rangatira Islands, 1990-91 to 1998-99. Weeks measured in seven-day increments (1-7, 8-14 etc), except for the last week which represents the balance of days remaining in each month. Data are from observed and estimated dates of first-egg laying.

Most pairs attempt to nest once only during a season (51.5% of all pairs breeding between 1990-91 and 1998-99; collated data). Fewer pairs make second and third attempts after successful first nesting (41.4% and 6.6% of pairs respectively in the unmanaged seasons). Second attempts may succeed also, but no successful third attempts were observed under natural conditions. Three females laid four clutches in a season, each with their original mate, but only one of these 12 breeding attempts succeeded in producing juveniles. One further female failed with four clutches in a season, having switched mates for the last. Overall between 1990-91 and 2001-02, each pair laid 1.54 clutches on average (*Section 2.11*: Table 2.5).

### *2.8.6 Clutch sizes*

Flack (1976a) reported two-egg clutches only in known nests of the ancestral population on Little Mangere Island (1972-73 to 1975-76) but on Rangatira and Mangere Islands, clutches comprise one to three eggs. The majority contain two eggs (74.1% of 996 clutches of verified size laid between 1980-81 and 2001-02). The remainder comprised a single egg (9.5%) or three eggs (16.4%). Mean clutch size is 2.02 eggs (all populations combined, 1990-91 to 2001-02; Table 2.5).

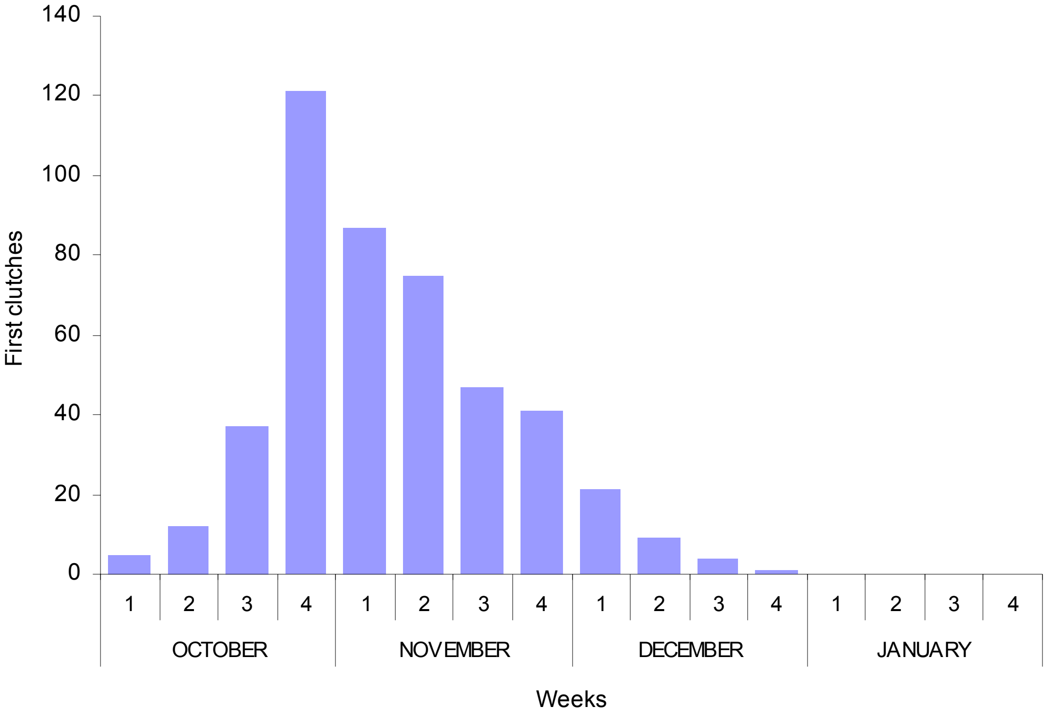

Figure 2.6 Weeks in which black robin pairs laid first clutches under natural conditions in the two populations on Mangere and Rangatira Islands, 1990-91 to 1998-99. Weeks measured in seven-day increments (1-7, 8-14 etc), except for the last week which represents the balance of days remaining in each month. Data are from observed and estimated dates of first-egg laying in all first clutches.

### *2.8.7 Mean reproductive output under natural conditions*

Productivity differed between populations (see Chapter Six for analysis of historical variations). Across all seasons in the Mangere and Rangatira Island populations combined, annual average output per pair was 1.86 nestlings, 1.37 fledglings and 1.13 juveniles. Juveniles surviving ≥ one year averaged 0.81 pair$^{-1}$ year$^{-1}$ (Table 2.5).

Of all eggs laid between 1990-91 and 2001-02, 60.0% hatched. After egg mortality is taken into account, the hatch-rate for eggs incubated full-term was 74.8%. Of nestlings produced, 73.4% fledged and 60.8% survived to independence (82.9% of fledglings). Across all unmanaged seasons, 71.5 % of juveniles achieved adulthood (Table 2.5).

Nest success in both populations combined (measured as the proportion of nests producing one or more juveniles) was 50.4% between 1990-91 and 2001-02. The lowest measure of nest success in any one year was recorded in the Top Bush (19.0%, 1995-96), and the highest was on Mangere Island (85.7%, 1992-93).

### *2.8.8 Maximum numbers of juveniles raised*

Black robins (including individuals of either sex bereaved or deserted by mates) are capable of raising all clutch-siblings to independence (maximum, three; collated data). Under natural conditions, the majority of successful breeding pairs raised a total of one or two juveniles season$^{-1}$ from all their breeding attempts (46.6% and 42.5% respectively of all pairs monitored, 1990-91 to 2001-02). Significantly fewer (7.9%) raised three juveniles season$^{-1}$, and four is the maximum raised in a single season (3.0% of all pairs). The maximum number of broods a pair can raise to independence in any unmanaged season appears to be two (15.6% of total successful pairs, 1990-91 to 2001-02) but most pairs raise only one brood (84.4% of successful pairs; *Section 2.11*: Table 2.4).

## 2.9 Mortality

### *2.9.1 Potential causes*

The causes of black robin mortality are numerous and have not been quantified systematically. In field records for the study period, the cause of mortality is frequently a matter for speculation. Explaining egg-failures, the disappearance of birds between observations and the cause of injuries in those found dead proved particularly problematic for field-workers. For this reason, it is not possible to distinguish natural mortality (infirmity, poor parenting, infertility, pair-bond failure, old age, intraspecific aggression) from losses—confirmed or otherwise—associated with predation (starlings, harriers), nest evictions by Chatham Island red-crowned parakeets *Cyanoramphus novaezelandiae chathamensis* (Melanie Massaro, pers. comm.) or multiple forms of misadventure (disease; mite infestations; entanglement in nest material, vegetation or cobwebs; exposure to poor weather; nest-site collapse; nocturnal petrel-strikes; straying from parent care; accidents in the nest).

### *2.9.2 Loss rates*

On average during seasons of no conservation management, 16.3% of all eggs laid were lost to factors unrelated to fertility or fitness (that is, through predation and misadventure). This rate of loss includes ‘rimshots’ (eggs laid on or over nest-rims). The incidence of rimshots varied annually after 1984-85 when the phenomenon was first observed in the Top Bush on Rangatira Island. At its most severe, 20.4% of all eggs laid in a single season were rimshots (1989-90, all populations combined). Under natural conditions, rimshot frequency averaged 4.2% annually, significantly less than during intensive management seasons (12.9%). The reasons for the difference may be attributable in part to under-reporting through failure to detect some rimshots during the post-management seasons.[10]

The mean annual proportion of full-term eggs failing to hatch during non-management seasons was 25.2% across both populations. Infertility was not measured systematically during these seasons, and I have treated many field diagnoses of egg failures as likely to be unreliable.[11]

Mortality in all hatched black robins was highest in pre-yearlings (56.1% of all those hatched between 1990-91 and 2001-02 inclusive). Mean annual nestlings mortality was 25.9% (all populations combined). Of those surviving to fledge, 17.6% perished on average before achieving independence. Juvenile mortality was higher: on average 29% perished annually before achieving adulthood at year one. Mean annual mortality of adults within seasons was higher for females (9.7%) than for males (7.3%) under natural condi-

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[10] During the intensive management phase, detection and management of every egg was imperative to maximise nest productivity. During the post-management seasons, nest inspections no longer needed to be so thorough.

[11] Normally, failed eggs (if retrieved at all) were broken open but relatively few observers were practised enough to determine cause of death through casual inspection, especially if egg contents were in advanced states of decay. For this study, I checked diagnoses reported for candled eggs in field records for 1992-93 against Massey University’s expert pathology for the same eggs (Cork, 1993). The eggs had been candled to preserve them for the later *post mortem* analyses. Many of the field predictions of infertility proved to be incorrect.

tions. Between-season (winter) mortality in breeding-age adults was more severe—16.1% of males and 15.5% of females were lost on average.

As black robins grew older, overall mortality rates increased only slightly until year nine, after which mortality increased sharply (*Figure 2.7*).

## 2.10 Sex ratios

Under natural conditions between 1990-91 and 2001-02, tertiary (breeding-age) sex ratios fluctuated seasonally in each population (these ratios are calculated from pre-breeding censuses on a 'head-count' basis, as appropriate for monogamous mating systems; Mills, 2007).

Large imbalances among unmated individuals were unusual and short-lived. On Mangere Island, for example, spare females outnumbered spare males nine to four in 1993-94 but by the following season this bias had eased to four females to two males (see Chapter Eight: *Figure 8.4*).

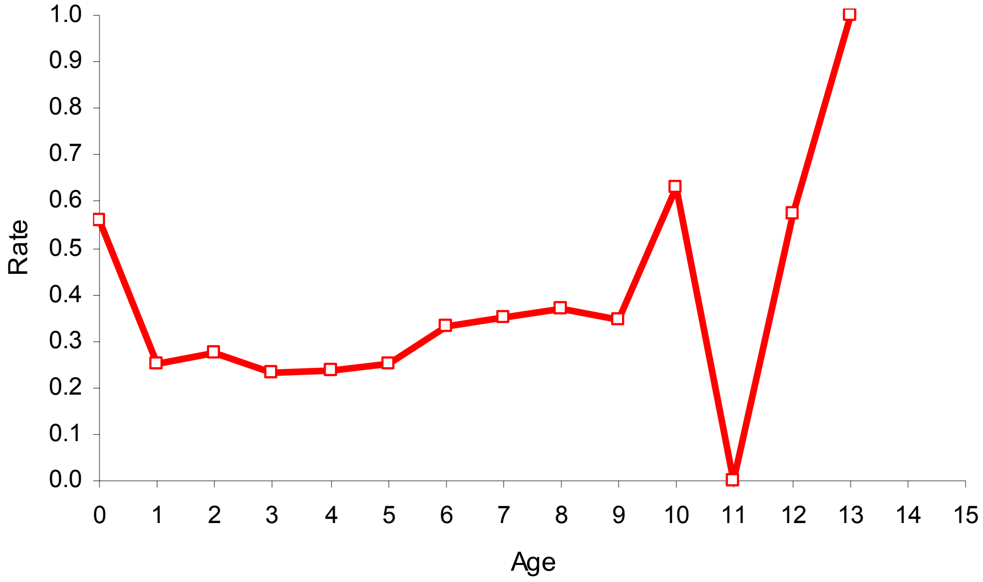

Figure 2.7 Mortality rates at each age for black robins (both sexes combined) hatched in the two populations on Mangere and Rangatira Islands during non-management seasons, 1990-91 to 2001-02 (n = 1354). None died at year 11.

Among the unmated breeding-age birds in the Top Bush on Rangatira Island, females outnumbered males in six of nine non-management seasons (female-to-male ratio $\bar{x}$ = 1.01, range 0.82 – 1.2; 1990-91 to 1998-99). On Mangere Island, seasonal male surpluses were evident in six of twelve seasons (female-to-male ratio $\bar{x}$ = 0.97, range 0.71 – 1.5; see *Figure 8.4*). Spare breeding-age females in the Woolshed Bush were always outnumbered by males in the nine non-management seasons between 1990-91 and 1998-99 (female-to-male ratio $\bar{x}$ = 0.84, range 0.73 – 0.93).

## 2.11 Comparison with New Zealand and Australian congeners

Black robin life-history information invites comparison with the traits and breeding of the 12 other *Petroica* species in the temperate regions of New Zealand and Australia (Tables 2.3 to 2.7). To what extent does the black robin differ from its relatives in both regions? It is the most immediately threatened of the south temperate *Petroica* (Higgins and Peter, 2002; Department of Conservation, 2007a), suggesting the probability of one or more critical vulnerabilities.

Interspecific comparisons of the *Petroica* are troubled by a lack of basic biological and life-history information for many of the 12 congeners. In studies for which information is available, authors quantify demographic variables in different ways (Rowley and Russell, 1991). Few studies are long enough to explore longevity and longer-term trends in survivorship. And few span the entire breeding season to gauge reproductive success in terms of juvenile production and survival, defaulting instead to the demographically less informative measure of fledgling output (Russell, 2000). The ecologies of widely distributed species are subject to dislocating spatial and temporal variations between populations. The black robin is a rare exception on all such counts. The effects of introduced predators on nesting success and mortality rates complicate comparisons within and between species on both sides of the Tasman. In mainland New Zealand, few undisturbed populations of predator-naïve robins and tomtits are available for study. In what follows, therefore, I have gleaned what is capable of comparison from a diverse range of studies in diverse ecological contexts.

The black robin's social and breeding systems are more typical of New Zealand than Australian congeners, though the regional points of difference are few. Like its New Zealand relatives, black robins are predominantly socially and sexually monogamous, breeding is strongly territorially based, and pair-bonds tend to endure, often until one of a pair dies. Most Australian *Petroica* are believed to be monogamous too but little is known of fidelity in species such as the pink robin *P. rodinogaster* and rose robin *P. rosea* (Higgins and Peter, 2002). Molecular analyses have detected high rates of extra-pair paternity in the red-capped robin (Dowling *et al*., 2003). Like all other New Zealand *Petroica*, black robins are sedentary. Mated and single black robin adults remain in or near their territories throughout the year. In contrast, seasonal nomadism is a feature of several Australian species. The flame robin *P. phoenicea* (Robinson, 1990b), red-capped robin (Dowling, 2003) and rose robin (Higgins and Peter, 2002) relinquish territories and disperse to varying extents from breeding habitats between seasons. Co-operative breeding, a reproductive strategy common among southern hemisphere passerines (Woinarski, 1985), is unknown in any of the regional *Petroica*. With the observed exception of one scarlet robin population at Nimmitabel (south-eastern New South Wales, Robinson, 1990b) and the Snares Island tomtit (McLean and Miskelly, 1988), all of the species are multi-brooded (capable of fledging more than one brood in a season).

### *2.11.1 Habitat requirements*

The black robin inhabited a variety of tall woody vegetation types in the pre-human Chathams archipelago. This is consistent with the habitat preferences of congeners in both regions (Higgins and Peter, 2002). But unlike all New Zealand and Australian *Petroica* relatives, the black robin is more obviously a closed-canopy, forest-interior specialist in its breeding and foraging habits. North Island robins translocated to fragmented habitats on Tiritiri Matangi Island appear to be similarly constrained (Armstrong *et al*., 2000) but this may be an artefact of altered forest cover on the island. As a result, breeding-site choices and foraging areas are more limited for the black robins than for congeners behaviourally tolerant of open spaces. Unlike New Zealand and Australian relatives, black robin juveniles and adults appear to possess neither the powers nor the instinct for long-distance dispersal outside forest margins or over open country or water. The ancestral population's decline in Little Mangere Island's contracting and disintegrating forest cover, assisted by the high rates of breeding failure observed in marginal habitats (Flack, 1976a, 1977; see also Chapters Three, Four and Six), suggest that this specialised forest-interior habit makes black robins are more sensitive than *Petroica* relatives to reduction in the extent and quality of forest cover.

### *2.11.2 Longevity and survivorship*

Black robin longevity and survivorship are very well understood but almost nothing is known of life-spans in the other regional congeners, especially in New Zealand (Table 2.3). What few data exist for other *Petroica* species suggest that black robin longevity (mean and absolute) in the two small recovering populations may not be exceptional, and is certainly not a liability. Annual survivorship exceeds the few rates recorded or estimated for Australian species, all of which co-exist with native and introduced predators.

Similar rates of survivorship in black robin males and females of breeding age do not suggest partitioned breeding effort. Both sexes appear to bear equivalent reproductive costs. This may not be true of red-capped robins in Terrick Terrick National Park, a higher proportion of whose females disappeared after each of two seasons (Table 2.3). However, this imbalance may result from undetected dispersals from the study site (Dowling, 2003).

### *2.11.3 Breeding densities*

McLean and Miskelly (1988) observe that in addition to slow breeding strategies, insular terrestrial bird species usually breed at higher densities than their mainland equivalents. Predation pressure (natural or otherwise) on almost all mainland and some insular populations complicates assessment of relative *Petroica* densities. The few New Zealand and Australian comparisons I have been able to make in Tables 2.4 and 2.6 support McLean and Miskelly’s observation.

On small islands which are free of introduced mammalian predators and in which birds are rarely affected by native avian predators, three New Zealand *Petroica* species (including the black robin) breed at the highest reported densities for southern temperate-zone *Petroica*. South Island tomtits achieve densities of five pairs ha$^{-1}$ on Little Solander Island (4 ha) and the Snares Island tomtit study population (9.6 ha) breeds at 2.7 pairs ha$^{-1}$ (McLean and Miskelly, 1988).

Table 2.3 Longevity (in whole years) and mean annual rates of adult survivorship in *Petroica* species of the temperate New Zealand and Australian regions. Asterisks (*) denote values for unspecified sex(es). **Red** values indicate data from predator-free environments; **black** values indicate data from predator-affected populations. Blank fields indicate absence of data.

| | Longevity<br>Maximum age (mean) | | Survivorship<br>Annual average (%) | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| **New Zealand** | | | | |
| Black robin [1]<br>*P. traversi* | 14 (4.2) | 13 (3.7) | 83.9 | 84.5 |
| North Island robin<br>*P. longipes* | | | | |
| South Island robin<br>*P. australis* | | | * 38.6 [2], * 70 [8] | |
| North Island tomtit<br>*P. macrocephala toitoi* | | | | |
| South Island tomtit<br>*P. m. macrocephala* | | | | |
| Chatham Island tomtit<br>*P. m. chathamensis* | | | | |
| Snares Island tomtit<br>*P. m. dannefaerdi* | | | | |
| Auckland Island tomtit<br>*P. m marrineri* | | | | |
| **Australia** | | | | |
| Flame robin<br>*P. phoenicea* | | | * 70 - 75 [7] | |
| Scarlet robin<br>*P. multicolor* | | >10 [3] | * 70 - 75 [7]<br>* 70.9 [4] | |
| Rose robin<br>*P. rosea* | | > 9 [3] | | |
| Pink robin<br>*P. rodinogaster* | | | | |
| Red-capped robin<br>*P. goodenovii* | *>5 [3], >3 [5] | > 3 [5] | 62.5, 45 [5], * 79 [6] | 31, 41.9 [5] |

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[1] Means for birds hatched in post-management years and achieving adulthood (year one; data from this study)

[2] Kowhai Bush, Kaikoura (Powlesland, 1983)

[3] Australian Bird and Bat Banding Scheme (ABBBS)

[4] Norfolk Island (Major, 1989)

[5] Ages for ten males, three females in Terrick Terrick National Park, Victoria; survival rates for two consecutive years, potentially affected by dispersal from study site (Dowling, 2003)

[6] New South Wales; extrapolation allowing for the diminishing effect of emigration on observed survival (Major and Gowing, 2002)

[7] Nimmitabel, New South Wales (Robinson, 1990a, cited in Robinson, 1990b)

[8] Kowhai Bush, Kaikoura (Flack, 1979)

Table 2.4 Breeding biology of insular and mainland *Petroica* congeners in the New Zealand region. Values are colour-coded **red** to signify data from habitats free of introduced mammalian predators**; black** to indicate data from habitats in which predators have not been controlled, and **blue** to signify data from habitats in which some or all introduced predators have been controlled. Descriptions of breeding-season length differ in most sources; lengths given here are approximate. Blank fields indicate absence of data.

| | | | **Tomtit** | | | | | **Robin** | |
|---|---|---|---|---|---|---|---|---|---|
| | | **Black robin**<br>*P. traversi* | **Snares Island**<br>*P. m .dannefaerdi* | **Chatham Island**<br>*P. m. chathamensis* | **Auckland Island**<br>*P. m. marrineri* | **North Island**<br>*P. m. toitoi* | **South Island**<br>*P. m. macrocephala* | **North Island**<br>*P. longipes* | **South Island**<br>*P. australis* |
| Breeding season—nest-building to last young independent (earliest to latest recorded, all years) | Weeks<br>wk / 4 | 27<br>4/4 Sep – 4/4 Mar | 14<br>3/4 Oct –3/4 Jan [2] | 16<br>2/4 Sep – 4/4 Jan [3] | c.18<br>2/4 Sep – Jan [4] | 23<br>1/4 Oct – 1/4 Mar [5] | 25<br>2/4 Sep - 4/4 Feb [7] | 30<br>1/4 Sep – 4/4 Mar [8, 15] | ≥ 32 [10, 11]<br>1/4 Aug – 2/4 Mar [10] |
| Egg-laying period—first eggs laid to last eggs laid (earliest to latest recorded, all years) | Weeks<br>wk / 4 | 17<br>1/4 Oct – 4/4 Jan | 7<br>3/4 Oct –1/4 Dec [2] | 8<br>3/4 Oct-2/4 Dec [2] | | | | 18<br>1/4 Sep – 1/4 Jan [8] | 23<br>1/4 Aug – 1/4 Jan [10] |
| Egg-laying period—first clutches, earliest to latest, all years (mean annual period (days), n of seasons) | Weeks<br>wk / 4 | 13 ($\bar{x}$ = 45, 9)<br>1/4 Oct – 4/4 Dec | | | | | | 15<br>1/4 Sep – 2/4 Dec [8] | |
| Sexual maturity | Year | 1 ♂; 1 ♀ | | | | | | | 8-12 mnths, ♂ ♀ [12] |
| Renest if successful (max. successful attempts in a season) | | Yes (2) | No [2] | Yes (2) [3] | | Yes | Yes | Yes | Yes |
| Breeding density | Pairs ha$^{-1}$ | 0.2 – 2.53 | 2.7 [2] | | | 0.4-1.08 [2], <0.25 [13] | 5.0 [2], 0.63 [7], 0.53 [14] | | |
| Breeding cycle (nest-building to independence) | Days | 83-94 | 79-86 [2] | 65-73 [2, 3] | | | c.37 [7] | ~ 49 [15] | |
| Incubation period (mean) | Days | 18 (18.0) | 18-20 [1, 2] | 17-18 [3] | | 14-16 [6] | 15-17 [7] | 18-20 [15] | c.19 [10], c.18 [12] |
| Nestling period—range (mean) | Days | 19-25 (c.22) | 17-22 [1] | 16-19 [2], 17-21 (18.8) [3] | | 17-20 [5] | 17-20 [7] | 20-22 [15] | 20-26 [12] |
| Fledging to independence interval— range (mean) | Days | 35-60 (c.42) | 21-35 [1, 2] | c. 25 [3] | | c. 21 [5] | 18-23 [7] | 32-49 (c.35) [8] | 24-50 [10] |
| Clutch sizes (usual number of eggs) | *n* | 1-3 (2) | 3 [1], 2-3 (3) [2] | 3-4 [2], 2-4 [3] | 3 [4] | 3-5 [5], 3-6 [6] | 3-6 [7] | 2-3 [8], 2-3 (2) [15] | 2-4 [10, 12] |
| Nest attempts (with eggs laid) pair$^{-1}$ yr$^{-1}$— majority (max) | *n* | 1 (4) | 1 (2, 1 pair) [2] | | | | | 2 (4) [8], 3 (5) [15] | 3-6 [12] |
| Total broods hatched pair$^{-1}$ year$^{-1}$ — majority (max) | *n* | 1 (3) | 1 (1) [2] | | | 4 (5) [5], 3 (5) [6] | (3) [7] | | 3 (4) [12] |
| Total broods fledged pair$^{-1}$ year$^{-1}$ —majority (max) | *n* | 1 (2) | 1 (1) [2] | ≤ 2 [2] | ≤ 2 [4] | (3) [5] | ≤ 3 [7] | 3 [8] | 3 [10], 4 [11] |
| Total broods independent pair$^{-1}$ year$^{-1}$ —majority (max) | *n* | 1 (2) | | | | | | | |
| Total eggs produced pair$^{-1}$ year$^{-1}$ — majority (max) | *n* | 2 (10; 1 pair) | (3) [2] | | | | | | |
| Total nestlings produced pair$^{-1}$ year$^{-1}$ — majority (max) | *n* | 2 (7; 1 pair) | | | | | | | |
| Total fledglings produced pair$^{-1}$ year$^{-1}$ — majority (max) | *n* | 1 (5; 2 pairs) | (3) [2] | (8) [2] | (6) [4] | | (15) | 2 (6, n = 1) [8] | |
| Total juveniles produced pair$^{-1}$ year$^{-1}$ — majority (max) | *n* | 1 (4; 11 pairs) | | | | | | | |
| Study duration (number of seasons reported) | | 9 RGT 12 MGR | 1 [1, 2] | 1 [2], 8 [3] | | 1 [5] | 2 [7] | 7 [8], 1 [9], 2 [15] | 2 [10], 1 [11], 7 [12] |
| SOURCES | | Black robin data from this study | [1] Best (1975)<br>[2] McLean and Miskelly (1988)<br>[3] Powlesland *et al*. (2001)<br>[4] Fleming (1985) | | [5] Knegtmans and Powlesland (1999)<br>[6] OSNZ Nest Record Scheme<br>[7] Kearton (1979)<br>[8] Armstrong *et al*. (2000) | | [9] Powlesland *et al*. (1999)<br>[10] Powlesland (1983)<br>[11] Etheridge and Powlesland (2001)<br>[12] Flack (1979) | [13] Kikkawa (1960)<br>[14] Kikkawa (1966)<br>[15] Powlesland *et al*. (2000) | |

Table 2.5 Comparison of black robin reproductive performance with insular and mainland *Petroica* congeners in the New Zealand region. Black robin breeding effort is measured for all full-scale monitoring seasons combined under natural (unmanaged) conditions on Mangere and Rangatira Islands, 1990-91 to 2001-02. Values are colour-coded **red** to signify data from habitats free of introduced mammalian predators**; black** to indicate data from habitats in which predators have not been controlled, and **blue** to signify data from habitats in which some or all introduced predators have been controlled. Blank fields indicate absence of data.

| | | | **Tomtit** | | | | | **Robin** | |
|---|---|---|---|---|---|---|---|---|---|
| | | **Black robin** *P. traversi* | **Snares Island** *P. m .dannefaerdi* | **Chatham Island** *P. m. chathamensis* | **Auckland Island** *P. m. marrineri* | **North Island** *P. m. toitoi* | **South Island** *P. m. macrocephala* | **North Island** *P. longipes* | **South Island** *P. australis* |
| Clutch numbers pair $^{-1}$ year $^{-1}$ | $\bar{x}$ | 1.54 | | | | | | 1.92[8], 3.1[14] | 4.1[10], 3.1[12] |
| Eggs laid pair $^{-1}$ year $^{-1}$ | $\bar{x}$ | 3.11 | | | | | | | |
| Mean clutch size year $^{-1}$ | $\bar{x}$ | 2.02 | 2.83[2] | 3.3[2], 3.13[3] | 3.0[4] | 4.15[5], 4.1[6] | 4.0[6], 2.75[7] | 2.33[8], 2.60[14] | 2.7[10] |
| Nestlings hatched per clutch year $^{-1}$ | $\bar{x}$ | 1.21 | 2.52[2] | | | 4.0[5] | 4.0[6] | | |
| Nestlings hatched pair $^{-1}$ year $^{-1}$ | $\bar{x}$ | 1.86 | | | | | | | |
| Fledglings pair $^{-1}$ year $^{-1}$ | $\bar{x}$ | 1.37 | | | | | | 2.48 (3.5)[8], 3.8[14] | 2.1-2.9[10], 3.0[11], 5.9[12] |
| Fledglings per clutch year $^{-1}$ | $\bar{x}$ | 0.89 | | | | 3.3[5] | 4.1[6] | | |
| Juveniles pair $^{-1}$ year $^{-1}$ | $\bar{x}$ | 1.13 | | | | | | | |
| Juveniles per clutch year $^{-1}$ | $\bar{x}$ | 0.73 | | | | | | | |
| Juveniles surviving ≥ 1 year pair $^{-1}$ year $^{-1}$ | $\bar{x}$ | 0.81 | | | | | | | |
| Nestlings produced per egg laid year $^{-1}$ | $\bar{x}$ | 0.60 | 0.68[2] | 0.83[3] | | | | | |
| Fledglings produced egg laid year $^{-1}$ | $\bar{x}$ | 0.44 | | | | | | | 0.27[10] |
| Juveniles produced per egg laid year $^{-1}$ | $\bar{x}$ | 0.36 | | | | | | | |
| Yearlings produced per egg laid year $^{-1}$ | $\bar{x}$ | 0.26 | | | | | | | |
| Proportion hatched of all eggs laid | % | 60.0 | 87.0[1] | 83.5[3] | | | | | 63.0[10] |
| Proportion hatched of all eggs fully incubated | % | 74.8 | | | | | | 85.0[8] | 91.0[13] |
| Proportion all eggs laid resulting in fledglings | % | 44.0 | 55.6[1] | | | | | | 89.3[12] |
| Proportion of all nestlings fledged | % | 73.4 | 63.9[1] | | | | | | 42.0[10] |
| Proportion all clutches producing ≥ 1 fledgling | % | 57.8 | 97.0[2] | 93.0[3] | | 73.3[5], 45 4[6] | | 51.0 (71.0)[8], 67.0[9] | |
| Proportion all fledglings reaching independence | % | 82.9 | | | | | | | |
| Proportion all eggs laid resulting in juveniles | % | 36.5 | | | | | | | |
| Proportion all clutches producing ≥ 1 juvenile | % | 50.4 | | | | | 31.3[6] | 89.0[14] | |
| Proportion of all juveniles living ≥ 1 year | % | 71.5 | | | | | | | |
| Study duration (number of seasons reported) | | 9 RGT 12 MGR | 1[1, 2] | 1[2], 8[3] | | 1[5] | 2[6], 7[7] | 2[3], 7[8], 1[9] | 2[10], 6[11], 1[12] |

SOURCES

Black robin data from this study

[1] Best (1975)
[2] McLean and Miskelly (1988)
[3] Powlesland *et al.* (2001)
[4] Fleming (1985)
[5] Knegtmans and Powlesland (1999)
[6] Kearton (1979)
[7] Flack (1979)
[8] Armstrong *et al.* (2000) (blue) = losses to avian predators ignored
[9] Powlesland *et al.* (1999)
[10] Powlesland (1983)
[11] Flack (1976d)
[12] Etheridge and Powlesland (2001)
[13] Mackintosh and Briskie (2005)
[14] Powlesland *et al.* (2000)

Table 2.6 Breeding biology of black robins and insular and mainland *Petroica* species in the Australian region. Black robin breeding parameters are measured for all seasons combined under unmanaged conditions on Mangere and Rangatira Islands, 1990-91 to 2001-02. Values are colour-coded **red** to signify data from habitats free of introduced mammalian predators**,** and **black** to indicate data from habitats in which predators have not been controlled. Data vary regionally for the Australian *Petroica* species; values given here are the best available from the regional sources cited. Blank fields indicate absence of data.

| | | **Black robin**<br>*P. traversi* | **Flame robin**<br>*P. phoenicea* | **Scarlet robin**<br>*P. multicolor* | **Rose robin**<br>*P. rosea* | **Pink robin**<br>*P. rodinogaster* | **Red-capped robin**<br>*P. goodenovii* |
|---|---|---|---|---|---|---|---|
| Breeding season—nest-building to last young independent (earliest to latest recorded, all years) | Weeks<br>wk / 4 | 27<br>4/4 Sep – 4/4 Mar | 23<br>2/4 Sep –3/4 Feb [1] | 28<br>2/4 Aug –3/4 Feb [1] | 35<br>1/4 Aug - 4/4 Mar | Sep – Mar [11] | Late Jun – early Feb [11]<br>26 (2/4 Aug - c. 2/4 Feb) [16] |
| Egg-laying period—first eggs laid to last eggs laid (earliest to latest recorded, all years) | Weeks<br>wk / 4 | 17<br>1/4 Oct – 4/4 Jan | 18<br>3/4 Sep – 3/4 Jan [1] | 22<br>3/4 Aug – 3/4 Jan [1] | Sep – Jan [6, 8] | (All range) late Nov – late Jan<br>(Tas) late Sep – mid Jan | (All range) late Jun – mid Jan [11] |
| Egg-laying period—first clutches, earliest to latest, all years (mean annual period (days), n of seasons) | Weeks<br>wk / 4 | 13 ($\bar{x}$ = 45, 9)<br>1/4 Oct – 4/4 Dec | 7 ($\bar{x}$ = 32, 2)<br>3/4 Sep – 1/4 Nov [1] | 8 ($\bar{x}$ = 45, 2)<br>4/4 Aug – 3/4 Oct [1] | | | |
| Sexual maturity | Year | 1 ♂; 1 ♀ | 1 ♂; ♀ unspecified [1, 9] | 1 ♂; ♀ unspecified [1, 7] | | | 1 ♂; 1 ♀ [16] |
| Renest if successful (max. successful attempts in a season) | | Yes (2) | Yes (2) [1] | No [1], Yes [2] | | | Yes (4) [6, 13] |
| Breeding density | Pairs $ha^{-1}$ | 0.2 – 2.53 | 0.03 – 0.04 [1] | 0.06 – 0.07 [1] | | | |
| Breeding cycle (nest-building to independence) | Days | 83-94 | | | | | |
| Incubation period (mean) | Days | 18 (18.0) | 16-19 (16.8) [1], 15-17 (15.4) [6] | 14-18 (16.2) [1] | 15-16 [6], 12-14 [9] | | 12-16 (13.5) [6], 14 [15], 13-14 [16] |
| Nestling period—range (mean) | Days | 19-25 (c.22) | 15-20 (17.3) [1], 14-18 (16.3) [6] | 17 [1] | | 16 [6] | 12-17 (14) [6], 11-16 (12.5) [15],<br>13-15 (14) [16] |
| Fledging to independence interval— range (mean) | Days | 35-60 (c.42) | 21-37 [6] | | | | c. 21-27 [16] |
| Clutch sizes (usual number of eggs) | *n* | 1-3 (2) | 2-3 (3) [1, 4], 2-4 (3) [5] | 3 [1], 1-4, (3) [3], 2-4 (2) [7] | 2-3 (3) [6, 10] | 1-4 (3) [6] | 1-4 (2-3) [6, 14], 1-3 (2) [16] |
| Nest attempts (with eggs laid) pair $^{-1}$ yr $^{-1}$— majority (max) | *n* | 1 (4) | (5) [1] | (5) [1] | | | (10) [6] |
| Total broods hatched pair $^{-1}$ year $^{-1}$ — majority (max) | *n* | 1 (3) | | | | | |
| Total broods fledged pair $^{-1}$ year $^{-1}$ —majority (max) | *n* | 1 (2) | 1 (2) [1], (3) | (1) [1], (3) [10] | (3) [10] | | (4) [13], (2) [14], 1 (3) [16] |
| Total broods independent pair $^{-1}$ year $^{-1}$ —majority (max) | *n* | 1 (2) | | | | | |
| Total eggs produced pair $^{-1}$ year $^{-1}$ — majority (max) | *n* | 2 (10; 1 pair only) | | | | | |
| Total nestlings produced pair $^{-1}$ year $^{-1}$ — majority (max) | *n* | 2 (7; 1 pair only) | | | | | |
| Total fledglings produced pair $^{-1}$ year $^{-1}$ — majority (max) | *n* | 1 (5; 2 pairs only) | | | | | (5) [16] |
| Total juveniles produced pair $^{-1}$ year $^{-1}$ — majority (max) | *n* | 1 (4; 11 pairs) | | | | | (5) [16] |
| Study duration (number of seasons reported) | | 9 RGT 12 MGR | 2 [1] | 2 [1], 1 [7] | | | 2 [15, 16] |

SOURCES

Black robin data are from this study

[1] Robinson (1990b)
[2] Robinson (1997)
[3] Masters and Milhinch (1974)
[4] Birds Australia Nest Record Scheme (NRS) (VIC)
[5] NRS (TAS)
[6] NRS (throughout entire Australian range)
[7] Major (1989)
[8] Morris *et al.* (1981)
[9] Howe (1928)
[10] Howe (1932)
[11] Higgins and Peter (2002)
[12] Whitlock (1909)
[13] Sanders (1914)
[14] Leach (1928)
[15] Coventry (1988)
[16] Dowling (2003)

Table 2.7 Comparison of black robin reproductive performance with insular and mainland *Petroica* species in the Australian region. Black robin breeding is measured for all seasons combined under unmanaged conditions on Mangere and Rangatira Islands, 1990-91 to 2001-02. Values are colour-coded **red** to signify data from habitats free of introduced mammalian predators**,** and **black** to indicate data from habitats in which predators have not been controlled. Blank fields indicate absence of data.

| | | **Black robin**<br>*P. traversi* | **Flame Robin**<br>*P. phoenicea* | **Scarlet robin**<br>*P. multicolor* | **Rose robin**<br>*P. rosea* | **Pink robin**<br>*P. rodinogaster* | **Red-capped robin**<br>*P. goodenovii* |
|---|---|---|---|---|---|---|---|
| Clutch numbers pair $^{-1}$ year$^{-1}$ | $\bar{x}$ | 1.54 | 2.03 [1] | 2.64 [1], 2.7 [5] | | | |
| Eggs laid pair $^{-1}$ year$^{-1}$ | $\bar{x}$ | 3.11 | | | | | 4.39 [16] |
| Mean clutch size pair $^{-1}$ year$^{-1}$ | $\bar{x}$ | 2.02 | 2.97 [1], 2.96 [4], 3 [5] | 3 [1], 2.7 [6] | | 2.92 [6] | 2.1 [16] |
| Nestlings hatched per clutch year$^{-1}$ | $\bar{x}$ | 1.21 | ≥ 0.65 [1], 1.16 [6] | 1.47 [1], 1.64 [6] | | | c.1.07 [16] |
| Nestlings hatched pair $^{-1}$ year$^{-1}$ | $\bar{x}$ | 1.86 | | | | | 2.74 [16] |
| Fledglings pair $^{-1}$ year$^{-1}$ | $\bar{x}$ | 1.37 | 1.20 [1] | 0.39 [1] | | | 1.20 [15], 1.60 [16] |
| Fledglings per clutch year$^{-1}$ | $\bar{x}$ | 0.89 | 0.25 [1], 0.73 [6] | 1.0 [1], ≥ 0.36 [7] | | | 0.84 [6], 1.4 [15], c. 0.62 [16] |
| Juveniles pair $^{-1}$ year$^{-1}$ | $\bar{x}$ | 1.13 | | | | | 1.45 [16] |
| Juveniles per clutch year$^{-1}$ | $\bar{x}$ | 0.73 | | | | | c. 0.57 [16] |
| Juveniles surviving ≥ 1 year pair $^{-1}$ year$^{-1}$ | $\bar{x}$ | 0.81 | | | | | |
| Nestlings produced per egg laid year $^{-1}$ | $\bar{x}$ | 0.60 | 0.64 [1], 0.40 [6] | 0.49 [1], 0.64 [6] | | | 0.62 [16] |
| Fledglings produced per egg laid year $^{-1}$ | $\bar{x}$ | 0.44 | 0.22 [1], 0.25 [6] | 0.08 [1] | | | 0.36 [16] |
| Juveniles produced per egg laid year $^{-1}$ | $\bar{x}$ | 0.36 | | | | | 0.33 [16] |
| Yearlings produced per egg laid year $^{-1}$ | $\bar{x}$ | 0.26 | | | | | |
| Proportion hatched of all eggs laid | % | 60.0 | 64.0 [1] | 48.7 [1] | | 65.4 [6] | 66.2 [6], 62.4 [16] |
| Proportion hatched of all eggs fully incubated | % | 74.8 | | | | | |
| Proportion all eggs laid resulting in fledglings | % | 44.0 | 22.2 [1] | 7.8 [1] | | | 36.5 [6, 16] |
| Proportion of all nestlings fledged | % | 73.4 | 34.7 [1] | 16.0 [1] | | | 58.4 [16] |
| Proportion all clutches producing ≥ 1 fledgling | % | 57.8 | 25.0 [1], 40.6 – 62.2 [6] | 60.0 [6] | | 45.5 [6] | 51.5 [6], 62.4 [16] |
| Proportion all fledglings reaching independence | % | 82.9 | | 50.0 [7] | | | 90.7 [16] |
| Proportion all eggs laid resulting in juveniles | % | 36.5 | | | | | 33.1 [16] |
| Proportion all clutches producing ≥ 1 juvenile | % | 50.4 | | | | | 34.0 [16] |
| Proportion of all juveniles living ≥ 1 year | % | 71.5 | | | | | |
| Study duration (number of seasons reported) | | 9 RGT 12 MGR | 2 [1] | 2 [1], 1 [7] | | | 2 [15, 16] |

SOURCES

Black robin data are from this study

[1] Robinson (1990b)
[2] Robinson (1997)
[3] Masters and Milhinch (1974)
[4] Birds Australia Nest Record Scheme (NRS) (VIC)
[5] NRS (TAS)
[6] NRS (throughout entire Australian range)
[7] Major (1989)
[8] Morris *et al*. (1981)
[9] Howe (1928)
[10] Howe (1932)
[11] Higgins and Peter (2002)
[12] Whitlock (1909)
[13] Sanders (1914)
[14] Leach (1928)
[15] Coventry (1988)
[16] Dowling (2003)

These densities represent natural (presumably stable) states, whereas the recorded peak density of 2.53 pairs ha$^{-1}$ for black robins on Mangere Island (Robin Bush, 7.9 ha) is best treated as intermediate, since the population was rebuilding from very low numbers in a slowly recovering fragment of forest habitat. This qualification applies also to the maximum recorded densities on Rangatira Island (Woolshed Bush, 26 ha; 1.58 pairs ha$^{-1}$). The substantially lower peak density of 0.2 pairs ha$^{-1}$ in the larger 84-hectare Top Bush forest on Rangatira Island (*Figure 2.4*) appears to be a function of other limiting factors and not symptomatic of densities expected in larger habitats. The Top Bush may be sub-optimal habitat for black robins (see Chapter Six) and a further indication of sensitivity to habitat type. Unexplained post-peak declines in both black robin populations (Chapter Six) have reduced breeding-pair densities but census data do not permit reliable assessments of pair numbers today.

The density maxima reported for predator-affected *Petroica* species are conspicuously lower (Table 2.6), especially among the Australian robins which evolved in the presence of native avian, marsupial and reptilian predators (Trevelyan and Read, 1989) and are now preyed upon by introduced mammalian predators. At the 300-hectare Nimmitabel study site, nomadic flame robins and resident scarlet robins achieved densities of 0.04 pairs ha$^{-1}$ and 0.07 pairs ha$^{-1}$ respectively (Robinson, 1990b).

Data for predated robins and tomtits on the New Zealand mainland vary considerably between populations but indicate higher overall breeding densities despite all species being predator-naïve (Table 2.4). For example, South Island tomtits bred in Banks Pensinsula habitats at 0.63 pairs ha$^{-1}$ (Kearton, 1979), and Kikkawa (1966) estimated a mean of 0.53 pairs ha$^{-1}$ over 14 widely distributed South Island populations (range 0.14-0.88 pairs ha$^{-1}$). The breeding densities of North and South Island robin populations have not been quantified in studies.

Explaining these differences is beyond the scope of this study. What is noteworthy, however, is that black robin populations have been able to sustain themselves, and grow, at historical densities as low as 1.32 and 1.37 pairs ha$^{-1}$ (Mangere and Rangatira Islands respectively) at the start of natural recovery in 1990-91 (19 pairs in the Woolshed Bush; six pairs on Mangere Island; Chapter Six: Table 6.8). At its peak, the Top Bush density of 0.2 pairs ha$^{-1}$ was clearly insufficient to support population growth under natural conditions (Chapter Six). In contrast, the congeners whose pair distributions are reported have persisted at lower densities in the presence of predators and regardless of their evolutionary histories. This is true also of the sympatric Chatham Island tomtit which persisted in Chatham Islands habitats long after introduced mammalian predators extirpated black robins (Chapter Three).

### *2.11.4 Sexual maturity*

Black robins do not differ from regional congeners in the ability of both sexes to breed as yearlings (Tables 2.4 and 2.6) but few studies indicate whether first-year adults in other *Petroica* species are as successful as black robins in producing juveniles at their first attempt (Chapter Six: Table 6.16).

In the predator-affected population of South Island robins at Kowhai Bush (Kaikoura), female yearlings were significantly less likely than older females to fledge offspring, in part because nestlings were preyed upon more frequently (for undisclosed reasons; Powlesland, 1983). Other studies do not distinguish breeding success by age-class. The high success rates of black robin yearlings may reflect the fact that the recovering study populations had yet to reach the carrying-capacities of their habitats, thus offering yearlings opportunities to claim breeding space and resources.

### *2.11.5 Breeding intervals*

Breeding-season duration in Australian and New Zealand *Petroica* species varies inter- and intraspecifically, frustrating ready comparison. Studies also use differing parameters to measure duration (time-to-fledging versus time-to-independence intervals, for instance). Few report or give enough data to calculate average season-length.

Taking the recorded interval across all seasons from the earliest recorded nest-building to the latest offspring independence), all New Zealand and Australian robins are capable of breeding over six months or longer (Tables 2.4 and 2.6; *Figure 2.8*). New Zealand's tomtits confine their breeding to fewer months overall, especially the insular tomtits on the Snares, Chathams and Auckland Islands which may breed over three to four months only (Table 2.4).

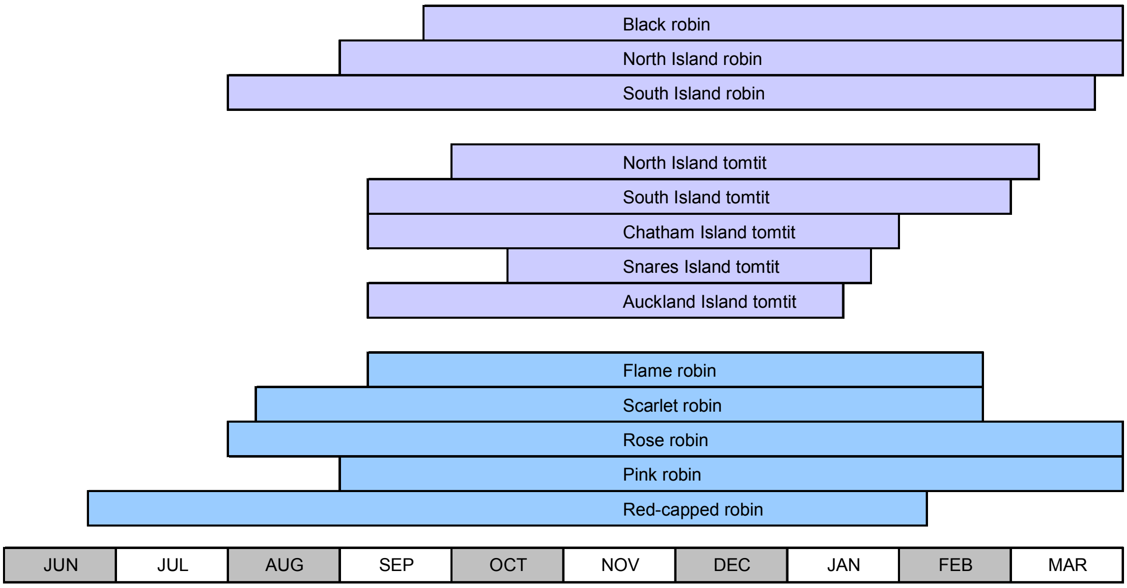

Figure 2.8 Maximum span of months over which temperate-zone *Petroica* species of New Zealand and Australia are reported to breed. Intervals are based on the earliest recorded start to nest-building to the latest reported independence of offspring over all years studied. Months have been divided into quarters for comparative purposes.

Maximum season lengths give only a rudimentary basis for comparison, since the merging of data from multi-year studies inflates estimates, as does the ‘clumping’ of data from temporally and spatially varying populations. Breeding-cycle intervals give more precise points of comparison.

The black robin, New Zealand robins and insular tomtits incubate for similar periods whose means lie between 17-20 days (Table 2.4). The briefer incubation intervals of the North and South Island tomtits (14-17 days; Table 2.4) are closer to those of Australian species. Australian incubation intervals range on average from 13.5 days (red-capped robin) to 16.8 days (flame robin; Table 2.6). Nestling periods are also briefer overall in the Australian *Petroica*. Black robin females brood nestlings for periods close to those of their New Zealand equivalents (range 19-26 days for all). This is slightly longer than the tomtits on the Snares and Chatham Islands (17-22 days). However, black robin fledglings remain dependent on their parents for longer than is the case in any other *Petroica* species for which fledging-to-independence intervals have been estimated (Table 2.4). On the basis of current information, therefore, black robins have the longest breeding cycle (nest-building to independence: 83-94 days) of the New Zealand and Australian *Petroica* congeners.

The black robin lays first clutches later than any of the other robins (first week of October at the earliest) but like the others may sometimes start final clutches in January. Potentially, the lack of a food-caching habit denies the black robin the advantage of an earlier start to breeding. Food-caching is typical of the New Zealand robins (Fleming, 1950b), but none of the studies cited in Higgins and Peter (2002) makes mention of the habit in their Australian equivalents. As Powlesland (1980) suggests of South Island robins, food-hoarding might have allowed black robin males to provision females on the nest at times of low prey availability during the cooler months and shorter days prior to October.

### *2.11.6 Seasonal reproductive output*

The black robin is multi-brooded, as are all the south temperate *Petroica* species. The black robin's shortened breeding season and long breeding cycle restricts the maximum number of broods fledged per pair to two per season, in common with the insular tomtits (Snares Island tomtit, one). Most black robin pairs succeed in fledging only one brood per season. The longer seasons and shorter breeding cycles allow the pairs of other robins in both regions and New Zealand's mainland tomtits to fledge up to three or four broods per season.

Black robin breeding effort in its predator-free habitats tend to be lower overall than for their New Zealand congeners, some of which (the mainland robins and tomtits) exceed black robin performance despite losses to introduced predators. Clutch sizes are invariably small (one to three eggs) and thus have less room to vary than the larger clutches of other *Petroica*. Even so, clutch sizes are relatively invariable in all of the regional *Petroica*. The black robin's mean annual clutch size of 2.02 eggs (Table 2.5) is the lowest observed for both New Zealand and Australian species. Only the red-capped robin's clutch size is similar (2.1 eggs).

Mean brood size is low as a result (1.21 nestlings per clutch), compared with means of 4.0 nestlings for North Island and South Island tomtits. On average, each black robin clutch produces 0.89 fledglings, substantially fewer than the means of 3.3 and 4.1 for North Island and South Island tomtit clutches respectively. By this measure, the black robin's modest fledgling output lies between the minimum and maximum reported averages for Australian robins (Table 2.7)—0.25 fledglings per clutch in the flame robin (Robinson, 1990b) and 1.4 in the red-capped robin (Coventry, 1988).

Data are scarce for annual rates of production per pair in New Zealand and Australian congeners. Based on the few measures reported for fledglings, mean annual reproductive output in black robins (1.37 $\text{pair}^{-1}$ $\text{year}^{-1}$) is very low relative to North Island robins protected from mammalian predators on Tiritiri Matangi Island (2.48 $\text{pair}^{-1}$ $\text{year}^{-1}$; Armstrong *et al.*, 2000) and South Island robins under predator-controlled conditions in the Nelson Lakes region (5.9 $\text{pair}^{-1}$ $\text{year}^{-1}$, Etheridge and Powlesland, 2001). These New Zealand comparisons imply that black robin productivity in other per-pair measures (nestlings, juveniles, and juveniles living ≥ one year) may also be much lower. The modest output for most black robin pairs of one brood per season supports this prediction.

Mean annual fledgling output by robin pairs in Australia (Table 2.7) is lower than for all reported New Zealand species. Output ranges from 0.39 fledglings $\text{pair}^{-1}$ $\text{year}^{-1}$ in the scarlet robin (Robinson, 1990b) to 1.6 $\text{pair}^{-1}$ $\text{year}^{-1}$ in the red-capped robin (Dowling, 2003). The average rate of fledgling production by black robins (1.37 $\text{pair}^{-1}$ $\text{year}^{-1}$) lies within this range. It is the only New Zealand *Petroica* known to do so.

### *2.11.7 Nesting success*

Black robin hatching success (60.0% of all eggs laid in the two populations) is the lowest reported for predator-free *Petroica* populations in New Zealand (Table 2.5). It remains lowest when corrected for the effect of egg mortality (74.8% of all eggs incubated full-term). Success at later life-stages in the breeding cycle appears to be markedly lower too when measured as the overall proportions of eggs or clutches resulting in fledglings and juveniles. Only the proportion of fledglings produced per clutch in the small translocated population of North Island robins on Tiritiri Matangi Island (51.0%) is worse than the black robin's (57.8%), but exceeds it when corrected for the effects of anomalous exposure to avian predators, especially the introduced Indian myna *Acridotheres tristis* (Armstrong *et al.*, 2000).

Data are lacking on overall rates of hatching, fledgling, independence and juvenile survival in mainland New Zealand *Petroica*. Other than the proportions of eggs hatching overall, little more is known for island congeners. Predator-free tomtit populations in the Chatham and Snares Islands hatch higher proportions of eggs laid (83.5% and 87.0% respectively) than were recorded for the black robins under natural conditions (60.0%). The black robin's overall fledging rate (73.4% of all nestlings hatched) was higher than that of the Snares Island tomtit (63.9%) but the latter's rate is derived from one season only (Best, 1975).

The very useful measure of mean nestling, fledgling and juvenile output per-egg is rarely reported in New Zealand studies. The only mean available (for sympatric Chatham Island tomtits, 0.83 nestlings egg$^{-1}$ year$^{-1}$) exceeds the black robin's rate of production (0.60 nestlings egg$^{-1}$ year$^{-1}$).

Despite considerable variation in population data, Australian studies reveal that nesting success in flame, scarlet, pink and red-capped robins is generally lower than that of New Zealand relatives. Only the black robin's success rates come closest to those of the Australians. The proportions of eggs resulting in nestlings range from 48.7% in one population of scarlet robins (Robinson, 1990b) to 66.2% in red-capped robin populations Australia-wide (Birds Australia Nest Record Scheme). This range fits hatching outcomes for black robins (60.0%) and predator-affected South Island robins at Kowhai Bush (63.0%; Powlesland, 1983). Thereafter, the proportions of Australian eggs producing fledglings and juveniles can only be compared with those of black robins, which are greater (Table 2.7). These relativities are reflected in egg outcomes. On average, black robins are slightly less proficient at converting eggs into nestlings (0.60 nestlings per egg, as opposed to maximum ratios of 0.62 to 0.64 for populations of flame, scarlet and red-capped robins) but do better at producing fledglings and juveniles. Egg-ratio data for other New Zealand *Petroica* are lacking, except for the Chatham Island tomtits on Rangatira Island which managed 0.83 nestlings per egg in one season (Powlesland *et al*,. 2001).

### *2.11.8 Summary*

The behaviour and breeding ecology of black robins fit the pattern of distinctive life-history characters in the Corvida species of the southern hemisphere's temperate regions.

Relative to the temperate northern hemisphere's Passerida species whose obviously differing life-histories have been the customary bench-marks for comparison (Rowley and Russell, 1991; Franklin and Wilson, 2003), south temperate passerines tend towards stable, frequently sedentary populations, long adult life-spans and high rates of annual survivorship, long breeding seasons, and multiple small clutches. Breeding is characterised as a result by extended parental investments in few offspring and low reproductive output over many breeding seasons (Woinarski, 1985; Yom-Tov, 1987; Rowley and Russell, 1991; Dowling, 2003; Russell *et al*., 2004). These attributes distinguish the 'slow' breeding strategy of south temperate birds from the abbreviated breeding patterns of Passerida in the northern hemisphere. There, the life-spans of adults and pair-bonds are generally shorter and the laying single (or a few) large, sometimes variable clutches appears to be an evolutionary response to shorter, climatically compressed breeding seasons (Rowley, 1983; Rowley and Russell, 1991; Russell *et al*., 2004).

My study has not set out to explore the specific environmental or phylogenetic bases for these 'southern' attributes in the black robins. It is plausible to suppose, however, that they are evolutionary adaptations to the stable habitats of the Chatham Islands archipelago, the lack of seasonal climatic extremes, year-round food supply and the reduced resource and recruitment opportunities within populations whose resident, long-lived breeders saturate available habitat. These are variables thought to explain the life-histories of endemic passerines of the temperate southern regions generally (Ashmole, 1963; Skutch, 1967; Woinarski, 1985; Yom-Tov, 1987; Robinson, 1990b; Rowley and Russell, 1991; Russell, 2000). Relative freedom from nest predation cannot be discounted as a factor also. It distinguishes the insular endemic passerines of New Zealand as a whole from those of Australia whose life-histories and breeding strategies are conditioned by evolutionary exposure to native predators (Trevelyan and Read, 1989; Dowling, 2003).

Like the other members of the *Petroica* genus in the temperate zones of New Zealand and Australia, the life-history traits of black robins are typical of *K*-selected species. Long isolation in the Chatham Islands and specialist adaptations to local forest environments, most of relatively small area, appear to have resulted in a higher degree of *K*-selection than in mainland relatives on both sides of the Tasman. The few available insights to the insular tomtits of the subantarctic Snares and Auckland Islands suggest that they may be *K*-selected to a similar degree. Even so, the black robin possesses several characteristics which seem likely to have favoured the survival of *Petroica* relatives in more hostile environments.

Adult longevity and rates of survivorship are consistent with trends for passerines of the temperate southern hemisphere generally, a higher proportion of which survive at mean annual rates exceeding 70% relative to the shorter-lived Passerida of continental Europe and North America (Rowley and Russell, 1991). As with southern *Petroica* congeners, the longer life-span of black robin adults serves its slow breeding strategy by preserving breeding experience in populations. In the black robins, enduring pair-bonds may help to realise this benefit. In turn, the lower seasonal reproductive effort has the potential to prolong life-spans.

The black robin's breeding is characterised by the long nesting seasons and longer breeding intervals observed in *Petroica* congeners and temperate southern passerines generally (Russell, 2000; Russell *et al.*, 2004). These patterns are longer from those of northern hemisphere birds (Franklin & Wilson, 2003). The extended breeding regimes of southern birds are predicted to improve the survival probability of juveniles by producing fewer of them but investing more effort in their care (Martin, 1996). Few comparable data on juvenile output have been reported for *Petroica* congeners, but the high proportions of juveniles surviving to breeding age in the two expanding black robin populations (71.5% overall; 0.81 $pair^{-1}$ $year^{-1}$; Table 2.5) support the hypothesis of pay-offs in juvenile production. The black robin rates are significantly higher than Russell's (2000) means of 37.4% for 34 southern passerines and 27.6% for 22 northern birds.

Although in other respects (early sexual maturity, success as yearling breeders, small clutch sizes, multiple-brooding), black robin breeding mirrors that of its *Petroica* relatives and other southern passerines, reproductive output is low relative to mainland New Zealand congeners, including those subjected to unnatural rates of nest predation. The output of chronically predated Australian relatives tends to be lower still, yet all predated relatives in both regions have persisted (albeit at very low breeding densities for the Australian species). In contrast, the black robin has demonstrated an inherent inability to cope with predators and unfamiliar forms of habitat change. Later chapters in this thesis explore the features of these changes and their implications for black robin survival.

Anomalously small clutch sizes point to a decisive source of vulnerability. Its potentially disabling consequences for gross reproductive output are evidently realised by modest success only at later life-stages in the breeding cycle, relative to other New Zealand *Petroica* (Table 2.5). The black robin's unusually prolonged breeding cycle restricts brood-raising potential to no more than two (one for most pairs) in the abbreviated Chathams breeding season, a constraint reflected in the lowest reported clutch-laying effort (1.54 pair$^{-1}$ year$^{-1}$) of all south temperate *Petroica* (Tables 2.5 and 2.7).

Vulnerability is increased further by the species's specialist forest-dwelling and foraging habits, exclusively insectivorous diet (*Section 2.6*) and conspicuously limited powers of migration—all factors which suggest narrower viability thresholds for the small insular black robin populations. By implication, the factors favouring survival of mainland New Zealand *Petroica* appear to be their higher rates of reproductive output and comparatively more generalist habits. Further demographic studies of suitable duration and insight are needed to confirm this.

Taken together, the black robin's life-history traits and breeding effort were sufficient to sustain populations in benign pre-human habitats and under the conditions prevailing between 1990-91 and 2001-02 when population sizes grew naturally on Rangatira and Mangere Islands (Chapter Six). However, the small clutches characteristic of the slow breeding strategists in the southern hemisphere do not allow for large variations in size to compensate for losses through disaster or set-back. Only the number of nests can be increased, and that number is a function of breeding intervals, season length and resources (Rowley and Russell, 1991).

In the chapter which follows, I examine the interplay of life-history characteristics and changes in the Chathams environment which exposed the particular evolutionary vulnerabilities of the black robin.

# CHAPTER THREE
# HISTORY OF BLACK ROBIN DECLINE

> ‘There were other birds but I have forgotten what they were like.’
>
> Surveyor S. Percy Smith
> *The Chatham Island Survey, 1868-69*

## 3.0 Introduction

This chapter examines the factors responsible for the historical decline and extinction of black robin populations in the Chatham Islands archipelago.

The loss of black robin populations from the larger islands of the archipelago was not witnessed by European naturalists or ornithologists. Only the final stages of decline—in the species’s last tiny population on Little Mangere Island—were recorded by latter-day researchers. They observed the black robin’s descent to and passage through its most recent bottleneck—in this case, of a single productive breeding pair. Through these fortuitously timed observations, understanding of the species’s subsequent recovery under management has been informed by knowledge of survivor family-lines and by first-hand experience of the stochastic pressures inducing the population’s final collapse. These valuable insights are rarely available to conservation managers under pressure to avert the extinction of critically endangered populations in the wild. But the extinction pressures witnessed on Little Mangere Island do not wholly explain the declines and final extirpation of black robin populations elsewhere.

In this chapter, I combine knowledge of the black robin’s biological vulnerabilities (outlined in the previous chapter) with historical evidence of changes in the Chatham Islands environment to show that the black robins were progressively eliminated from their island habitats as an unintended consequence of human presence and activities. Using the modest body of historical evidence, much of it inferential and very widely dispersed in formal and anecdotal sources, the chapter illustrates the diversity of deterministic pressures which conveyed black robins to the brink of total extinction. And, as much as historical sources and latter-day paleontological research allow, it identifies the timing and specific deterministic causes of extirpation in each island habitat. These extinction pressures have not been investigated closely until now. Investigation prepares this study for more detailed analysis of the dynamics of black robin recovery in the course of and following conservation management.

### 3.1 Pre-human distribution and densities

As is often the case with critically small populations at risk of extinction, biologists and conservation managers are not able to refer to an undisturbed black robin population in intact habitat to understand what constitutes natural distributions and densities. No such populations have survived human colonisation of the Chathams archipelago. The information crucial to the design of ecologically appropriate management must be inferred from black robin behaviour in the disturbed and simplified habitats they occupy today.

No specific insights into pre-human distributions and densities are available from early European accounts of Chatham Islands flora and fauna (Dieffenbach, 1841; Travers 1868; Travers, 1871; Travers and Travers, 1872; Forbes, 1893; Cockayne, 1901, Smith, 1916) and later interpolations (Hutton, 1872; Buller, 1888, 1890, 1894a, b). Rothschild (1907) said merely that the species was originally very common in the Chatham Islands and disappeared from Chatham Island long ago. Fleming (1939b) reported local knowledge that black robins originally inhabited the major islands of the Chathams archipelago. Fossil and archaeological deposits assist but do not complete the picture. Deposits are plentiful on Chatham Island and have been found on Pitt and Mangere Islands (Tennyson and Millener, 1994). But other islands in the group lack suitable natural repositories (caves, sand dunes, wetlands; Millener, 1999) or have not yet been examined thoroughly. Rangatira Island is singularly poor in fossil sites (Alan Tennyson, pers. comm.). No evidence of a pre-human black robin population has yet been discovered on this island (Butler and Merton, 1992).

### 3.2 Chatham Island *Rekohu* (90040 ha)

Skeletal material confirms that black robins were present on Chatham Island before human arrival. Millener (1999) reports that black robin bones were common until at least 1150 yr BP at all levels in a limestone cave deposit he examined on the shoreline of Te Whanga Lagoon. No complete specimens have been recovered from the island at any time. A

‘Chatham Island’ specimen from Henry H. Travers’s second collecting expedition to the Chathams in July–August 1871 (reported as Dominion Museum number A.264 in Fleming, 1950b: 144, Table 11) is almost certainly a mislabelled specimen from Mangere Island (Tennyson and Bartle, 2008). It was no longer considered possible to collect the species from Chatham Island by 1871 (Travers, 1871; Travers and Travers, 1872; Fleming, 1939b).

No indications of pre-human density on Chatham Island have survived. Natural distribution is similarly obscure but easier to infer. The first European naturalists reported significant tracts of bush on the island, interspersed with numerous, often broad areas of wetland. In the mid-1800s, a low forest ‘varying in width from a mile or more down to one or two hundred yards’ encircled almost all the coastline (Seed, 1861).[12] Travers (1868) and Cockayne (1901) took these areas of bush and evidence of an original old-age forest elsewhere to suggest an extensive pre-human forest cover in the lower-lying northern and central regions of the island. If correct, their conclusions indicate that the black robins should have been widespread in these parts of Chatham Island. The diversity of forest types, topography and geology hints at local variations in abundance.

Stratigraphic studies of dune and soil profiles indicate extensive coastal and near-shore forests inhabited by abundant terrestrial bird species historically and currently sympatric with black robins (Millener, 1999). On the higher, more exposed southern tablelands—a vast area of higher rainfall and more ‘quaking bog(s)’ (Cockayne, 1901: 248)—black robins may only have flourished on drier interstitial ridges or areas of elevated ground. The bush was dominated by tarahinau *Drachophyllum arboretum*, a signature species of cold, poorly drained soil conditions (Amanda Baird, pers. comm.). Patterns of black robin distribution today indicate that this is a forest-type deficient in shelter and nesting cavities suitable for the species. No black robins are known to have bred or held territory in the only habitat in which tarahinau and black robins coincide today (the modest remnant of mature tarahinau forest at the southern extremity of Rangatira Island).

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[12] Travers (1868: 176) is more generous, giving the bush ‘a depth of two or three miles [forming] a fringe round a large portion of the island, and partly along the seashore… the whole so interwoven with our old friend the supple-jack, as to be almost impenetrable.’ This gives the impression of forest well suited to black robins.

The timing of extirpation from Chatham Island cannot be determined precisely. In this respect, Fleming's (1939b: 508) statement that the black robin was present 'in very early days' is unhelpful. What can be said is that coincident with the timing of other bird extinctions in the Chathams (Millener, 1999), extirpation followed the arrival of Moriori from New Zealand 450-500 years ago (McFadgen, 1994; King, 1989).[13] These first-wave colonists brought with them the partially arboreal Polynesian rat (kiore) *Rattus exulans* (Matisoo-Smith *et. al.,* 1999; Atkinson and Towns, 2001). The kiore remained the sole novel mammalian predator of birds, reptiles and invertebrates in the archipelago for at least 300 years, until the first major influx of Europeans (sealers, whalers and settlers) in the second and third decades of the 19th century.

Kiore are adept ground-hunters and doubtless compounded the difficulties for black robins from the outset by depleting invertebrate-prey biomass and diversity (Towns *et al*., 1997; Holdaway, 1999, Atkinson and Towns, 2001). But direct predation of eggs and nestlings could be expected to expose the black robin's principal biological vulnerability—its low reproductive output (Chapter Two). Kiore are significant predators at the nests of mainland New Zealand *Petroica* (Flack and Lloyd, 1978). Black robin body mass, behaviour and habitat fit the species readily within the rat's predatory potential. As a bird of the lower forest strata, black robins nest well within the vertical foraging range of kiore (>10 metres; Cuvier, Kapiti and Little Barrier Islands, Lovegrove, 1996). Cavity- and hollow-nesting—effective as a form of concealment from traditional avian predators—is ineffective in protecting nests from scenting rats (Brown, 1997). Black robin eggs (length, 22 mm) and nestlings (≤ 33 g) fall within kiore prey-size and weight ranges (eggs, ≤ 55-60 mm, Atkinson, 1978; Holdaway, 1999; nestlings, ≤ 60 g; Lovegrove, 1996).

Predation of juveniles and adults is less certain. Atkinson (1978) surmises that the kiore—smallest of the three introduced *Rattus* species—is less effective at attacking passerines. Evidence of adult predation in other New Zealand *Petroica* is also scarce. The black robin possesses the quick flight responses of a fly-catcher, which appear to have minimised losses to mammalian predation of adult South Island robins at Kowhai Bush, even at the nest (Flack, 1973, 1976d; Moors, 1976).

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[13] Holdaway (1999) places the date of human arrival 200 years earlier, nearer to 1350 AD.

On Chatham Island, predation of nesting or roosting adults was probably confined to periods when kiore densities were very high—during the initial irruption for instance—or later when periodically high densities coincided with shortfalls in alternative prey. Fledglings and juveniles roosting on or near the ground would have been more at risk.

Early sexual maturity and long adult life-spans in black robins have the potential to offset the effects of unnaturally high rates of reproductive failure but kiore pressure on the species's modest reproductive output may have overwhelmed this advantage, starving populations of recruitment. In contrast, the higher reproductive output of Chatham Island tomtits appears sufficient to have deferred their extirpation on Chatham Island until at least the mid-20th century (Powlesland *et al.*, 2001).

Kiore alone are likely to have eliminated the black robins from Chatham Island, and the time-to-extirpation may not have been protracted. The island's black robin populations may have been overwhelmed in the first rat irruption since the super-abundance of invertebrate prey and small ground-nesting petrels would have sustained extremely high densities of kiore after arrival. In the absence of other rodents, kiore thrive periodically at very high densities (> 96 individuals ha$^{-1}$) in both forest and grasslands in island contexts (Craig and Moller, 1978; Holdaway, 1999). How long black robins persisted is a matter for speculation. Bones recovered at very low frequency at the sites of excavated Moriori middens (Point Durham; Marshall *et al.*, 1987) suggest a period of overlap with kiore but the dating of the sites is too problematic to define the interval, when it occurred or when the black robin bones were deposited (Fiona Petchey, pers. comm.).

There is no evidence that the species persisted on Chatham Island until the 19th century. The earliest European descriptions of the island's biota often lacked informative references to land birds of any kind and none mentions black robins. In the course of his lengthy botanical account, Dieffenbach (1841: 207) is no more specific than a fleeting reference to the 'three or four, small insectivorous birds' he recorded on the island at the time of his visit in 1840.[14] He does not list black robins in his later account of the New Zealand bird

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[14] Dieffenbach was also unable to find kiore, though perhaps he could not distinguish them from the Norway rats *Rattus norvegicus* which were evidently very abundant by 1840. Travers (1871: 66) knew from the Moriori of 'the probable existence of a native rat' but could not find a specimen in 1863-64.

fauna (Dieffenbach, 1843). Nor does Henry Travers (1868) list them among the terrestrial bird species persisting on Chatham Island in the presence of plentiful wild cats *Felis catus*, mice and Norway rats in 1863-64. Informal newspaper accounts of visits to the island are similarly silent. An article from 1866 refers only to tomtits being seen during a walk through bush and grassland (*A Cruise to the Chatham Islands*, West Coast Times, 17 August 1866).[15] It seems reasonable to assume then that the existence of black robins on Chatham Island had long passed from human memory, so that Travers (1871: 65) was able to claim, upon encountering them for the first time on Mangere Island in September 1871, that the species was 'new to our fauna'.

If severely depleted black robin populations had lingered until the time of earliest European contact, their fates were sealed by new guilds of browsers and predators introduced in the first decades of the 19th century. The second wave of human immigrants, the European sealers, whalers, agriculturalists and missionaries introduced sheep *Ovis aries*, cattle *Bos taurus*, pigs, goats *Capra hircus*, horses *Equus cabalus*, dogs *Canis familiaris* and a suite of mammalian predators: cats (c.1800), hedgehogs *Erinaceus europaeus*, Norway rats (c. 1830), mice (c.1850s),[16] and the most lethal of the rats, the ship rat, an arboreal specialist which arrived after 1890 (all putative arrival dates from Holdaway, 1999: Table 1). The island's complement of introduced animals has since been augmented by predatory Australian brush-tailed possums *Trichosurus vulpecula* (introduced in 1911; Pracy, 1962; King, 1990) and buff weka (introduced in 1905; Oliver, 1955; Bell, 1996). Together with the broad-scale clearance of forest cover for farming, the Chatham Island environment remains hostile to black robins.

## 3.3 Pitt Island *Rangiauria* (6325 ha)

Black robins inhabited Pitt Island though the fossil evidence of their presence is still rare. The scarcity of evidence is not an indication of original abundance (Alan Tennyson, pers. comm.). Small passerine bones collected at Motutapu Point, Paremata Cove and northwest Pitt Island in 2002 have yet to be identified reliably as belonging to black robins (Brian Gill, pers. comm.). The 1871 museum specimens labelled "Pitt's Island" in Fleming

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[15] http://paperspast.natlib.govt.nz/1866

[16] Searle *et al*. (2008) suggest, without supporting evidence, that mice first arrived in cargo landed on Chatham Island in 1853 from the wreck of the English barque *Randolph*.

(1950b: 144, Table 11) are considered to be from Mangere Island (Tennyson and Bartle, 2008), since Travers does not mention collecting black robins from any other location (Travers and Travers, 1872).

The black robins almost certainly persisted into the 19th century on Pitt Island. The timing of local extinction cannot be determined accurately but declines in black robin density are likely to have been deferred until after the time of European contact in the first two decades of the 1800s. Moriori both visited and populated Pitt Island at various times prior to that (Travers, 1868; Smith, 1916; Richards, 1990) but kiore are not known to have survived the sea journey from Chatham Island (Holdaway, 1999). Inference suggests then that the black robins survived through centuries of Moriori contact until Europeans significantly modified the vegetation cover of the island and introduced the cats which had become feral and common by 1863-64 (Travers, 1868).

The processes of disintegration in the Pitt Island bush were probably set in train when European livestock were introduced. Pigs may have been liberated prior to 1831, either by sealers or whalers (Bill Carter, pers comm.), or by the unspecified inhabitants of Pitt Island noted in December of that year by Captain John Biscoe, master of the sealing vessel *Tula* (Richards, 1982). Broad-scale changes to the bush were inevitable after Frederick Hunt imported domestic pigs in 1842 or 1843 to generate income from provisioning American whaling and merchant ships with pork, potatoes and other vegetables (Richards, 1990).

After Hunt imported English grass-seed in 1847-48 and converted both bush and his own gardens to pasturage, sheep followed in growing numbers, then cattle. By his own admission, Hunt had overstocked the island by the mid-1860s. At this time, his sheep, horses and cattle were running in the home paddocks and the island's open grasslands. At least one other settler (Apitia Punga, son of Rangiapitea) was farming 150 sheep at Glory by 1863 (Bill Carter, pers. comm.). Pigs had become well established in the bush by this time too and were 'excellent ploughmen, rooting up the fern in all directions' (Richards, 1990, Chapter XIII). They had 'greatly destroyed' the island's undergrowth by July and August 1871, preventing Henry Travers from obtaining worthwhile specimens of ferns and other increasingly rare plants (Travers, 1871: 65).

It is difficult to judge precisely how pervasively or decisively the effects of these and other settlers' livestock had compromised the black robin's habitat by this period. Photographs of Pitt Island c.1888 show fragmenting bush cover, open understorey, forest wind-throw and erosion (see Appendix Three: *Figures 3B* and *3C*; see also photographs of devastated nikau palm groves in Walls *et al*., 2000: 42). Unquestionably, reduction in the quality and extent of habitat available to black robins would have weakened their capacity to cope with the additional costs of predation by cats.

Historical sources give few clues to the origins and timing of cat arrival on the island. Future developments in molecular science may be more informative. Cats may have reached Pitt Island as early as 1827 when the sealing brig *Glory* went aground and was run ashore on the island's south-east coast in the bay which now bears her name. Some of the crew returned to New Zealand in open longboats (Prickett, 2008), but others, perhaps with the ship's cats, were left behind with stores and cargo depoted on the island (Richards, 1982). Along with sealers, itinerant convicts and deserters from whaling vessels, Moriori fleeing the newly arrived Maori inhabited the island prior to Frederick Hunt's settling there in October 1842 (Richards, 1982). Any of these may have brought cats for companionship, as may Hunt himself or Bill the Clerk, another European who settled briefly at Glory Bay prior to 1844 (Richards, 1990).

Cat presence had already been documented on Rangatira Island (see *Section 3.4* following) from which an unruly gang of shore-whalers subsisting there in 1840 launched occasional raids on Pitt Island for supplies (Bill Carter, pers. comm.). It seems unlikely that the cats originated from a second shipwreck at Flower Pot in 1859 (the *Franklin*, an American whaler) given the interval necessary for feral cats to have become numerous by the time of Travers's visit in 1863-64. But the crews of the many American whaling and trading vessels provisioning at Flower Pot and befriended by the Hunt family in the previous decades (Richards, 1982, 1990) may have gifted cats to the young Hunt children. Notwithstanding all of these possibilities, Frederick Hunt's silence on the existence of black robins hints at an earlier rather than later date for cat arrival. Travers (1868) trusted Hunt as a source of bird information. His apparent failure to tell Travers of so distinctive a species as the black robins suggests that he had no knowledge of them. Perhaps they had been extirpated before he took up residence on the island in 1842.

Travers gives the first published evidence of cat presence on Pitt Island and the first date at which we can infer that the black robin is locally extinct. As a keen collector of rare plant and animal species, Travers visited Hunt for a week in October 1863 and returned in November for a stay of several months. He made the island his expedition base 'in consequence of its offering greater advantages as a collecting ground' (Travers, 1868: 176). At this time, Travers says, Pitt Island was completely covered in bush apart from 250 acres of farm clearings at Flower Pot, now the island's main settlement. He makes no comment on the condition of the bush but laments the lack of land birds which he attributes to the effects of wild cats—'…it is rare to meet with any [land birds] at all during a whole day's walk in the bush' (Travers, 1868: 178).

Travers (1868: 178) lists land birds still extant on Pitt and Chatham Islands ('a large Kite, the Pigeon, the Tui or Parson Bird (*Prosthemadera Novae Zelandiae*), the Pukeko (*Porphyrio melanotus*), the Parakeet (*Platycercus, Sp.*), the Fan-tail (*Rhipidura*), the Lark, and a small Titmouse,[17] all identical with the birds of the same genera found on New Zealand'). This list is not exhaustive—it does not mention tomtits (still to be seen on Chatham Island, see *Section 3.2* above), nor does it include the Chatham Island bellbird *Anthornis melanocephala* which was still on Pitt Island in the 1880s (Buller, 1894b; Fleming, 1939b, quoting Robert Paynter, a Pitt Islander). Crucially, the list makes no mention of black robins, an omission giving another strong indication that this distinctive species was not yet known to naturalists, or was not on Pitt Island to be seen if indeed naturalists had heard of it. None had visited Mangere Island yet, and that is where the species was probably confined by 1863-64. Although Moriori, Maori and a few sealers must have landed on Mangere Island, Travers (1868) makes no mention of information received from them.

Feral cats were evidently very numerous on Pitt Island four years after Travers's visit. While surveying the island in 1868, S. Percy Smith (later Surveyor-General of New Zealand) observed a 'great number running wild' and their devastation of what he supposed to be storm-grounded 'terns' (probably storm petrels) on the forested peninsula at Tarawhenua Point (Drummond, 1910b; see Appendix Two).

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[17] The 'Titmouse' is the silver-eye *Zosterops lateralis*, not the tomtit as its name suggests (W. T. L Travers, 1872:215, reporting his son H.H.T). Henry Travers (1868: 178) reports Frederick Hunt's claim that the 'titmouse' arrived in the Chatham Islands soon after disastrous 'Black Thursday' fires in Australia (1851).

No other mammalian predators appear to have been present at this time. Norway and ship rats did not persist on the island if they ever reached it, and mice are the only rodents present today. The scant early literature hints that mice were introduced after the cats (a curious reversal of convention) but their time of arrival is undocumented. Holdaway (1999) estimates accidental introduction to Chatham Island in the 1850s (see also footnote 16). Since mice and seed are customary travel companions, Frederick Hunt's importation of grass-seed and his cultivated farm-holding of 'English grasses' (Travers, 1868: 173) are strongly suggestive of mouse arrival well before 1863. But Travers (1868: 178) is careful in his wording to say that 'English mice' were only on Chatham Island at this date. Robertson, a surveyor working on Pitt Island in 1883, states that 'on Pitt's Island, there were originally no rats or mice…' (cited in Richards 1990: 102). This ambiguous observation hints at arrival by 1883 but is more likely in my view to mean that rodents were naturally absent from the island. Current Pitt Islander lore indicates that mice did not arrive until after 1900, when a 'pregnant mouse was observed to escape from a bag of flour unloaded from the ship' (prior to 1903, Bill Carter, pers. comm.).[18]

Whichever of the post-1863 founder dates is accepted, mice appear to have arrived too late to be implicated in the black robin's decline. Despite the uncertainty over the timing of cat arrival, cats were conspicuous enough in 1863-64 to suggest that they alone could have been the ultimate deterministic cause of black robin extirpation from Pitt Island. The decline was no doubt hastened by feral and domestic livestock whose unrestrained browsing in the bush would have induced progressively more sub-optimal conditions. The speed with which cats eliminated black robins from Mangere Island (see *Section 3.5* following) indicates that extirpation from Pitt Island may have been relatively rapid. The island is larger, the bush more complex, and allowance must be made for lag-time while cat numbers increased to lethal densities after the founder event. Whether cats arrived in 1827 or after

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[18] Robert Gregory-Hunt, a Pitt Islander, recalls hearing of the mouse arrival after asking his father James Sidney White when Pitt Island's large spiders had disappeared (the spiders *Dolomedes shauinslandi* are still found on rodent-free Rangatira and the two Mangere Islands). His father described the mouse jumping out of a newly arrived box of flour when it was opened in the family home. It escaped despite the concerted efforts of the family and visitors to kill it. The mouse was assumed to be pregnant because after a period of about two years in which there was no sign of it or others, a mouse irruption occurred on Pitt Island, sustained no doubt by the abundance of grass-seed and invertebrates. Robert understands that his father was about 12 years old at the time, but this would place mouse arrival at about 1912 to 1914 (Bill Carter, pers. comm.).

the time of European settlement, it seems likely that the black robins had been eliminated well before Travers's visit in 1863-64. By 1871, Travers asserts that he had 'only found [the black robins] at Mangare Island' (Travers and Travers, 1872: 216).

In their tradition of heritage stories, Pitt Islanders hold fast to the conviction that black robins persisted on Pitt Island for at least another 65 years after this date. As recorded by Aikman (2002), Pitt Islander Sam Gregory-Hunt recounts that, as a 14-year-old youth home from secondary school in New Zealand in summer 1938-39, he saw '15-16 black robins' in an isolated patch of native bush ('about one acre' in area) at Paremata Cove, west of Flower Pot on Pitt Island's north coast (*Figure 3A*, Appendix Three). The birds disappeared after the bush was burned accidentally in efforts to clear adjacent 'sand-grass'[19] for a fence-line, and that was the last time he saw black robins on the island. Kenneth Lanauze, Gregory-Hunt's nephew, remembers this story clearly, knows the location of the bush referred to, and recalls that two other islanders engaged in farming activities at that time claimed to have seen black robins in bush elsewhere on Pitt Island (Kenneth Lanauze, pers. comm.; see Appendix Three for details). Support for the Pitt Islanders' conviction that black robins survived beyond the time of Travers's visits (1868; Travers and Travers, 1872) comes from a passing reference in Buller (1890) and an earlier Pitt Islander's account of black robins and their breeding behaviour given in a natural-history newspaper column of 1909 (Drummond, 1909; see Appendix Three for discussion).

The biological case for extirpation before 1863-64 is persuasive. It seems unlikely that black robins could have survived long in the presence of cats alone (and later in combination with mice), especially if their forest habitats had also been accessible to livestock and feral browsers. On the other hand, the anecdotal evidence of persistence cannot be discounted entirely. It is not easily corroborated but unless an open-mind is kept, it will not receive the attention it warrants as a compelling subject of inquiry.

Widespread loss of forest cover and the introduction of numerous animals followed the populating of Pitt Island and its energetic conversion to a predominantly pastoral farming landscape. In addition to mice and cats, livestock (pigs, cattle, sheep, horses, goats; some

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[19] Marram grass *Ammophilia areanaria* was imported to Pitt Island from Chatham Island by Frederick Hunt in the 1880s (Bill Carter, pers. comm.).

now feral) and weka (established in the early 1960s, Ken Lanauze Snr, pers. comm.) have reduced Pitt Island's forest remnants to states inhospitable to black robins. Recent attempts to reintroduce black robins to a semi-protected forest reserve (40 ha) have failed, for reasons which have yet to be clarified (see Chapter Four and Chapter Six: Population Trends After 1980; see also Kennedy, 2006).

### 3.4 South East Island *Rangatira* (218 ha)

Black robins are assumed to have populated Rangatira Island (Butler and Merton, 1992), and Fleming's (1939b: 508) 'larger islands' comment leaves that possibility open too, but I have found no anecdotal, naturalist or physical evidence to confirm their presence prior to human contact. For a remarkable length of time after European arrival, the island's biota and condition escaped documentation by naturalists who visited the Chatham Islands but failed for various reasons to land on Rangatira Island itself (Dieffenbach, 1841; Buller in 1855, Travers, 1868; Travers and Travers, 1872; Forbes, 1893; Cockayne, 1901; Archey and Lindsay, 1924). The island is also depauperate in fossil-deposit sites such as sandy substrates, rock overhangs and fissures. Its acidic soil is expected to have dissolved fragile bones (Alan Tennyson, pers. comm.). If the black robins were naturally absent, the gap in distribution is difficult to explain.

Black robin extirpation from Rangatira Island lacks obvious explanations. The absence of introduced mammalian predators today indicates that predation was unlikely to be a factor. A large black cat was said to have surprised pig-hunters on the island in November 1831 (Richards, 1982, citing the master of the sealing vessel *Tula*),[20] but this is the only reference in the historical or recent literature to cats on the island. There is no evidence of other mammalian predator introductions. Common starlings, predators of black robin eggs and nestlings and competitors for nest cavities today (see Chapter Six), could not have been implicated since they were not introduced to the Chatham Islands until 1881 (Long, 1981; Holmes, 1984).

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[20] In the ship's log, Captain John Biscoe of the *Tula* does not specify Rangatira Island as the site at which his men were hunting pigs but other locality details relating to the Cornwallis Islands (known variously, according to source, as Pitt, Mangere, Little Mangere and Rangatira Islands) indicate strongly that that is where the cat was encountered.

In addition to cause, the timing of disappearance from Rangatira Island is also obscure. Without exception, all early European accounts of Chatham Islands species and their distribution are silent on the question of black robin presence (Travers, 1868; Travers, 1871; Travers and Travers, 1872; Hutton, 1872; Forbes, 1893; Buller, 1894a; Kirk, 1895; Rothschild, 1907). If present originally, the black robins had disappeared by 1871 when Travers understood that they were confined to Mangere Island (Travers and Travers, 1872).[21] Evidently, Henry Palmer did not encounter any when collecting red-crowned parakeets in September 1890 (Tennyson and Bartle, 2008), because no comment to that effect is made in the literature of the time. Nor did W. Hawkins, a resident bird collector thoroughly familiar with the Chathams, when collecting Chatham Island petrels *Pterodroma axillaris* in May 1892 (Buller, 1894a). The silence in all sources implies loss before European occupation of the island (about or prior to 1836 when a sealing gang was living there; Richards, 1982) or between that time and the initial exploratory surveys of the Chathams by ornithologists and bird collectors (1863-64 onwards).

What little evidence is available from the literature and local anecdote points to progressive deterioration in the area and quality of forest cover on Rangatira Island as the cause of black robin extirpation. Except for the scale and precipitating causes, this explanation shares strong similarities with the black robin's decline on Little Mangere Island (*Section 3.6*). The chronology of fatal change is unknown but is most plausibly associated with European contact. Moriori journeyed to Pitt Island's outliers for seasonally available food resources (Shand, 1894) but the absence of kopi groves, found commonly near Moriori camps and settlements on Pitt and Chatham Islands, suggests that they did not stay permanently on Rangatira Island (Roberts *et al*., 2007). The scarcity of water on the island may have discouraged settlement too. There is no reported evidence of Moriori fires or other forms of disturbance which might have affected the island's original forest cover. If any existed, it has been disguised or obliterated by the profound changes following the intro-

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[21] Travers does not say how he arrived at this understanding. He did not reach Rangatira Island on his first visit (Travers, 1868) and makes no mention of landing there on his second visit, even though the opportunity may have presented itself through Frederick Hunt's interest in the island's livestock at that time. Both Travers (1868) himself and Drummond (1910a, reporting Travers on the subject of his 1871 visit to Mangere Island) indicate quite clearly that Travers was guided by local knowledge in his pursuit of rare bird specimens. If Hunt himself or his family had seen black robins on Rangatira Island, they evidently did not tell Travers during his two visits to Pitt Island in summer 1863-64 and winter 1871.

duction of European livestock (pigs before 1831) and more deliberate farming practices in 1840.

Between 1840 and 1871, pastoral farming on Rangatira Island was episodic and beset with reversals which resulted in livestock being abandoned to run wild on the island. Contrary to Ritchie (1970), farming commenced on a structured basis as a supplement to sealing in 1840 when William Reeve introduced more pigs and potatoes to provision whaling vessels. Fifty merino sheep were introduced in March 1841. Goats were liberated in this period too (Richards, 1982), though their purpose and ownership is unclear. By 1845, sheep numbers are estimated to have risen to about 300 (Bill Carter, pers. comm.) but many were removed in that year following eviction of the Europeans by Maori claimants to the island. Remaining sheep and the goats were abandoned to Frederick Hunt who, followed by his son-in-law Matthew Gregory and son William Hunt, assumed nominal absentee ownership of them. The livestock remained largely untended until William died in 1892.

No record of farm-management activities during the 1840-1871 period has survived. It is not possible to determine therefore how rapidly and severely the quality of forest habitat declined in these three decades. If black robins were not to be found in this large habitat by 1871, then evidently the changes were sufficient to have fatally compromised population viability. During the first five years of farming, the island's grasslands were probably burned regularly to induce regrowth, as was conventional practice (Bill Carter, pers. comm.). Hunt and his relatives may have burned the grasslands after 1845 but there is no evidence to indicate that they did so. Some felling of forest cover was inevitable to increase pasturage and provide construction materials (yards, fences, buildings) but throughout the 30-year period, the goats no doubt served the broader-scale objective of clearing forest by browsing woody vegetation (shrub and low tree cover). The goats remained until shot out by Tom McClurg between 1913 and 1915. At times of food stress (summer droughts, winter), shrub and tree seedlings would have been browsed heavily.

Twentieth-century observers documented the nature of the changes set in train by these practices. Fleming (1939c: 8) alluded to a significantly fragmented forest cover on the warmer woolshed flats, the absence of understorey, and grasslands and meadows '200 feet' a.s.l. in which shore plovers *Thinornis novaeseelandiae* were breeding. Bell (1953) documented very extensive forest die-back, wind-throw, loss of the forest-edge ecotone, retreat of forest perimeters, canopy collapse and self-perpetuating processes of desiccation in the forest interior. By 1961, the understorey in the island's Top Bush was so open that New Zealand Wildlife Service hunters pursuing the last 14 sheep could run unimpeded through the forest (Ian Hogarth, pers. comm.).

Loss of the wind-deflecting vegetation gradient at the forest-edge was arguably the most ominous of the changes for the black robins. Climatic conditions would probably have deteriorated under whatever forest cover remained. Processes of understorey loss and forest collapse would follow naturally, hastened by browsing pressure. Without the shelter of a forest edge, black robin adults and young alike would have experienced unnaturally elevated rates of mortality during the harsh winter months, the period in which greatest mortality is recorded today (Chapter Two: *Section 2.9.2*). Fragmentation of forest cover coupled with the loss of understorey no doubt reduced the area of forest suitable for breeding. Optimal nest-sites probably became less common, increasing the rates of breeding failure by exposing nests to weather and disturbance by arriving and departing petrels. Competition with tomtits for food and nest-sites is likely to have increased. As the forest assumed a canopy-only character unfitted for a lower-stratum forest-interior specialist such as the black robin, prey availability would have diminished, with predictable consequences for the energy costs of foraging and breeding.

These predictions draw on observations of habitat collapse on Little Mangere Island (*Section 3.6*). But a small body of inferential evidence on Rangatira Island suggests that the processes of habitat change might hardly have been far enough advanced or pervasive to eliminate the black robins between 1840 and 1871.

First, Bill Carter (pers. comm.) considers it likely that sheep and goat numbers remained quite low for some time after 1845. Certainly, if forest still covered much of the island, grazing opportunities would have been limited. The scarcity of fresh water on the island probably placed a significant constraint on stock numbers. Clearly, the bush interior had not become so dry that moist-dependent plants were jeopardised. On the sheltered woolshed flats where extensive loss of forest cover indicates that much of the grazing was concentrated, mature tree-ferns were still sufficiently abundant in the early 1900s to supply the cladding and fencing for Tom McClurg's woolshed (Appendix One: *Figure 1A*).

Second, other forest bird species were not eliminated. Even under the more severely depleted conditions of the early 20th century, tomtits, Chatham Island warblers *Gerygone albofrontata* and Chatham Island fantails *Rhipidura fuliginosa penitus* were evident and at times abundant (Fleming, 1939b; Bell, 1953, Dawson, 1954). However, the presence or abundance of these species is not a wholly convincing indication that changes in forest character had been minimal. None of these species is dependent on intact, closed-forest habitat. All possess the powers of flight which make them more likely than black robins to recolonise the island. The tomtit's reproductive output gives that species an advantage over the black robin (see Chapter Two). Intriguingly, Ma and Lambert (1997b) offer evidence from molecular analyses that Rangatira Island tomtits have passed through one or several periods of critically low numbers historically (see also Chapter Eight: Hybridisation).[22] Perhaps this was such period.

Finally, early and mid-20th century photographs of Rangatira Island show glimpses of an extensive canopy cover surviving in the Top Bush (Fleming, 1939a, c; Roberts, 2004). Despite Hogarth's recollections of a devastated understorey at the end of the farming era, it is difficult to believe that the cumulative effects of the mid-19th century's more modest pastoral activities could have eliminated black robins from all corners of this vast area of forest before 1871. Perhaps they did not and surviving robins were overlooked by any individuals advising Travers in 1871.[23] Analyses of latter-day demographic data reported later in this study (Chapter Six) indicate that if a remnant of the black robin population was indeed confined to the Top Bush in 1871, its persistence was doubtful. Under improved, regenerating conditions between 1990-91 and 1998-99, the natural reproductive output of black robins in the Top Bush was insufficient to sustain their numbers. Juvenile production and survival were lower than in the Woolshed Bush. The resident population was reliant on constant replenishment through dispersal from the woolshed flats. These latter-day findings raise the intriguing possibility that the effects of farming between 1840 and 1871 only needed to compromise black robin reproduction and longevity on the lower northern terraces of Rangatira Island to threaten the viability of the entire population.

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[22] This evidence comes from analysis of blood taken from the descendants of tomtits reintroduced to Mangere Island from Rangatira Island in April 1989 (Merton, 1989).

[23] Latter-day observers found it very difficult to locate human-habituated black robins in the Top Bush after the species was reintroduced to the island in 1983-84 (pers. obs.).

If my reasoning is correct, the elimination of black robins from Rangatira Island before 1871 is noteworthy for two things. First, it is attributable to a single extinction-inducing factor—in this case, environmental stress originating from detrimental changes to the character of the island's forests. The severity of this stress cannot be determined from available historical sources, but relative to the very poor condition to which pastoral farming had reduced the forests by the mid-20th century (Bell, 1953), it was probably modest. Second, the interval to local extirpation may have been very brief—perhaps no more than 30 years. Loss in so short a period supports the conclusion that the black robin's extinction vulnerability derives ultimately from its low reproductive potential and the threat that poses to persistence when recruitment does not keep pace with mortality. The species's inability to produce juveniles in compromised habitat was amply demonstrated later on Little Mangere Island (*Section 3.6*). Low reproductive output could be expected to threaten population viability on Rangatira Island when the species's other vulnerability—its specialist forest-interior habit—was exposed by reduction in the area and quality of the island's bush cover.

The brief time to extirpation under conditions of habitat stress alone raises valid questions about how long before 1863 black robins had been eliminated from Pitt Island where extinction pressures (habitat disintegration and cats) worked in combination. If the interval was 30 years or fewer, it was not unique to Rangatira Island. The population on Mangere Island was lost within a comparable period of unfamiliar changes.

## 3.5 Mangere Island *Mangare* (113 ha)

Mangere Island is the first of the original pre-human habitats in which the black robin's presence and extirpation interval were documented in published literature. Travers collected the first specimens there in September 1871 (Travers, 1871; Travers and Travers, 1872) during a weather-bound stay of 12 days, 11 more than intended (Drummond, 1910a). At this time, the black robin 'was not uncommon'. The island itself appears to have become the last predator-free refuge of significant area for other terrestrial bird species declining or eliminated elsewhere in the archipelago. In addition to the black robin, Travers found parea *Hemiphagus chathamensis*, bellbirds, tomtits, fernbirds *Bowdleria rufescens*, Chatham Island snipe *Coenocorypha pusilla*, Forbes's parakeets, Chatham Island red-crowned parakeets, shore plover and the naturally rare (thus highly prized) Chatham Island rail *Rallus modestus*.

This assemblage of birds, the relative abundance of most, and the numerous Procellariformes listed by Travers at the same time, suggest an unmodified terrestrial environment. In fact, the processes of habitat destruction had already been set in train (see below). Travers reported that Mangere Island was 'nearly covered in a low, rigid scrub' (Travers and Travers, 1872: 213). As described by an anonymous correspondent[24] in a contemporary newspaper column (Chatham Island Sketches—Pitt's Island, *Hawke's Bay Herald*, 3 November 1868),[25] this vegetation—'so impervious that it is somewhat difficult to force a passage through'—was confined to the lower reaches of the island. The top of the island was 'thickly studded over with trees of large growth, interspersed with scrub.' Everywhere, passage was hindered by petrel burrows so deep and numerous that a visitor 'at every other step…will sink to his knees in loose soil…'. Evidence of old-age akeake trunks littering the grasslands at all altitudes on the island today (see Ritchie, 1970: *Figure 6*; Bell, 1974) indicate that Travers and the article's author were describing a low-stature, wind-shorn bush, the most continuous tracts of which may have been located on the exposed peninsula adjacent to Little Mangere Island. From the fallen tree trunks, Atkinson (2003) assessed a canopy height of 3.7 – 7.0 metres in places where akeake grew.

Curiously, Travers makes no mention at this time of the rabbits and goats which were 'in large numbers' on the island during his visit (Travers, quoted four decades after his visit in Drummond, 1910a). Frederick Hunt is said by W. Hawkins (letter to W. Buller, August 1893; British Natural History Museum, TM/1/6/9) to have liberated these animals, apparently after securing grazing rights to the island from its Maori claimants. The rabbits may have been come from Tasmanian whalers in the 1850s and were liberated on Mangere Island (and Rabbit Island; *Figure 3A*) because Hunt did not want them on Pitt Island (Bill Carter, pers. comm.).

The precise dates of liberation for these browsers are undocumented but the anonymous newspaper correspondent of 1868 refers to 'a numerous colony of goats and rabbits in-

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[24] Believed by Richards and Carter (2009) to be John Amery who also ghost-wrote Frederick Hunt's 'autobiography' (Richards, 1990).

[25] http://paperspast.natlib.govt.nz/1868

creas[ing] and multiply[ing]', which hints at introduction long enough beforehand for the animals to have become numerous by that date. These browsers were the vanguard for sheep (11 merino ewes and a ram; Bill Carter, pers. comm.) introduced in or before 1890 by William Pepper of Pitt Island under a grazing lease obtained from Hunt. According to Travers (Drummond, 1910a), the rabbits were so abundant that Pepper released cats to destroy them, apparently because they were exhausting the grazing potential of the island (Forbes, 1893; Drummond, 1910a). The fate of the goats is undocumented.

Pepper probably obtained his cats from Pitt Island, the source nearest to hand. Bill Carter (pers. comm.) considers that he liberated them on Mangere Island no earlier than 1888 and no later than 1890, but there is equivocal evidence of an earlier date. A report of Henry Palmer, one of Rothschild's collectors (The Naturalist, *Otago Witness*, 27 November 1890), [26] implies that cats were already numerous in 1890—'…through the depredations of cats, the [rare] birds are being reduced wholesale'. The article does not say that Palmer was referring specifically to Mangere Island but the reference to cats, an 1890 photograph of Palmer on the island (Miskelly, 2008) and the black robin specimens obtained there (see below) suggests that that is where he was 'very successful in his mission [of obtaining] two rare specimens of birds'.[27] Assuming that Pepper did not liberate great numbers of cats, a lag-time of years would be necessary for numbers to have increased, even allowing for the year-round abundance of rabbit prey.

The black robins were still on Mangere Island in 1890 when Palmer collected black robin specimens there (Rothschild, 1907). Thereafter, it is necessary to read carefully from what is *not* said in published sources to estimate how long the doomed black robin population persisted after the cats arrived. W. Hawkins, the diligent commercial collector writing to Walter Buller on 6 September 1892, makes no mention of black robin extinction when recording the strenuous efforts a colleague made nightly over two months to obtain a Chatham Island rail specimen from the island (Buller papers, Alexander Turnbull Library, MS-Papers-0048-22). Hawkins also wrote to H. O. Forbes of rediscovering the rail but evidently made no reference to black robin demise in that letter either, because Forbes does

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[26] http://www.paperspast.natlib.govt.nz/cgi-bin/1890

[27] Clarification cannot be obtained from Palmer's Chatham Islands correspondence. A letter dated 1896 archived in the British Natural History Museum at Tring (Ref. TM/1/19/12) indicates that Palmer's letters were destroyed soon after his visit to the Chathams.

not report it. Forbes reports the black robins as extant (Forbes, 1893), no doubt on the basis of his own collecting visit to the Chathams in 1892.[28] He is also in receipt of black robin specimens from both Mangere and Little Mangere Islands but he does not specify the collector or collection date. It appears however that publication of Forbes's paper (October 1893) overran the news from Hawkins that the black robins were no longer obtainable on Mangere Island. In August 1893, Hawkins advised Buller by letter that the black robin was 'gone' (British Natural History Museum, Archive ref. TM/1/6/9; Buller, 1894a).[29]

If gone between late 1892 and early 1893, the black robin population on Mangere Island appears to have been eliminated in fewer than five years of cat arrival, assuming cat liberation between 1888 and 1890. The population had probably been reduced in size and viability by the effects on habitat quality of goat and rabbit browsing over two or more decades. Goats had no doubt opened the bush edge and interior to chilling winds. The 1890 photograph of Palmer shows him sitting, apparently on the ridge above the present hut, in open, grazed, disintegrating bush among the debris of fallen akeake trees and branches. Pastoral management by Pepper may have accelerated habitat decline but no record of his activities has survived. Buller (1905) refers to the burning and active clearance of forest to plant grasses on the island, but it is not clear if he is alluding to the period prior to 1893 or after. In all probability, Pepper burned the island's existing grasslands to induce regrowth. Fire may have encroached on the forest, especially in dry conditions and high winds but according to Bill Carter, the Chathams bush cannot be burned effectively unless the standing timber has first been felled and dried. No evidence exists to indicate that Pepper did this, in which case the goats, rabbits and wind alone were probably the principal agents of black robin decline prior to cat arrival.

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[28] Contrary to Butler and Merton (1992: 1), I can find no reference in Forbes (1893) or elsewhere to indicate that Forbes himself collected specimens from Little Mangere Island in January 1892.

[29] Forbes (1893: 525) quotes Hawkins as saying that the cliffs of Little Mangere Island had collapsed, making it 'terribly difficult' to obtain specimens there. This and other oblique references point to Hawkins being the collector of Forbes's black robin specimens from that island. However, even if Hawkins had not visited the island but had engaged locals to collect birds from the top of the island for him, as Fleming suggests (1939b: 383), it is difficult to explain how he could be so sure that the black robin was 'gone' (implying extinction). He may have assumed that cats had also reached Little Mangere Island. Or maybe the locals had misled him to avoid further hazardous (and perhaps underpaid) excursions to the top of the island on his behalf.

Extirpation from Mangere Island followed the pattern of loss from Pitt Island in which the interacting processes of habitat decline and mammalian predation each obscured the other's effects. Ultimately, it was the cats which delivered the *coup de grâce* to black robin populations whose vital rates of recruitment and mortality had doubtless been compromised by habitat reduction. The capacity of vegetation change alone to undermine population viability—merely inferred from events on Rangatira Island—is demonstrated explicitly in the decline of the black robins in their last island refuge.

## 3.6 Little Mangere Island *Tapuaenuku* (8-9 ha)

The black robin populations on Mangere and Little Mangere Islands were probably linked by occasional exchanges of individuals across the narrow ocean gap between the two islands (about 260 metres from historic bush-edge to bush-edge). After elimination from the larger part of this combined area—most likely between late 1892 and early 1893—the black robins were reduced abruptly to a vestigial population in the compact, wind-shorn forest on the 200-metre heights of Little Mangere Island. The species persisted in this tiny habitat until 1976-77 when the seven remaining individuals were transferred to Mangere Island (see below, and Chapter Four). Over the final six years in this refuge (1971-72 to 1976-77), the small, obligatorily inbred population was conveyed swiftly towards extinction by the destabilising effects of forest degeneration which lowered productivity and increased mortality rates. Regular visits to study black robin biology and conservation needs in each of these years yielded important demographic insights to the extinction process, and to those extrinsic (environmental) and intrinsic (demographic) features which were no doubt instrumental in the species's extirpation from all other island habitats.

### *3.6.1 Timing of habitat collapse*

The processes of bush deterioration on Little Mangere Island and their consequences for the island's small black robin population were documented but observers of the time could not agree on the precise timing and causes of the habitat's collapse.

Nineteenth-century naturalists and bird collectors left no record of forest character and extent on Little Mangere Island, and only a little can be read from the observations of the first ornithologists to land with more benign intentions in the next century. Charles Fleming, Graham Turbott and Alan Wotherspoon spent approximately three hours ashore over midday on 2 January 1938, more than two of them devoted to the fearful climb and descent (Turbott, 1938; McEwen, 2005). Under pressure of time to gather information on island biota of all kinds (Turbott, pers. comm.), the party did not explore the full extent of the bush on the plateau. Fleming (1939a: 383) observed that the forest occupied by the black robins and Forbes' parakeets comprised 'barely an acre of virgin tangled vine and bush on its summit, wherein the birds find refuge'. Turbott (1938) described the mainly low, scrub-like character of the vegetation elsewhere—generally lower than shoulder height (Turbott, pers. comm.)—and the scarcity of cover in which it was possible to walk upright.

Twenty-nine years later, Merton and two others landed by helicopter to make a two-day survey of the island's birdlife (2-3 September 1968). The party noted that the area of tall forest available to black robins on the island's summit amounted to about one acre of tall bush (Merton, 1969; Ritchie, 1970). Their visit made apparent for the first time the threat posed to the species's survival by ecological change on the island (Merton, 1969). The party was unpleasantly surprised to find that a large area of vegetation on the island's summit (about half a hectare; Butler and Merton, 1992) had been cleared to allow helicopter landings so that harvesters could gather *titi* (sooty shearwaters *Puffinus griseus* and other petrels). Broad areas of scrub and *Muehlenbeckia* cover nearby had been heavily trampled and broken down (Merton, pers. comm.).[30] The helicopter pad made the island easily accessible where previously the difficulty in scaling the cliffs had limited *titi* harvesting. Fleming's (1939a, b) confidence in the island's impregnability as an ecological safeguard had been misplaced.

No ornithological visits were made after September 1968 until late March 1972 when Dr Douglas Flack of the New Zealand Wildlife Service began his study of black robin biology. Thereafter, until removal of the seven surviving black robins to Mangere Island in 1976-77, Flack's research teams, botanists and wildlife managers monitored deterioration in the bush cover during 12 visits of varying duration (Table 3.1; see Chapter Four for additional details). During Flack's first visit on 29-30 March 1972, the fragmented and de-

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[30] The wording in Merton (1969: 4-5) indicates that the helicopter pad had been cut in April or May 1968. It was '25 yards square' and sited close to the tallest forest on the island. The island plateau was strewn with beer bottles and other rubbish. According to Pitt Islanders, the culprits were New Zealand cray-fishermen from Bluff. They and companion birders had dug up burrows to take about 2000 *titi* that season.

generating condition of bush remnants prompted immediate concern (Flack, 1973, 1974a, b, 1976b).

Atkinson *et al.* (1973) and Flack (1976a) assessed the bush condition systematically while attempting to define the black robin's habitat needs. Mature akeake trees, judged by Flack to be the original canopy species, had died along with matipo trees which appeared by their growth to have succeeded the akeake quite some time beforehand. Living and standing-dead matipo trees substantially covered in *Muehlenbeckia* vines formed the majority of the bush cover available to the black robins (Flack, 1976a). Regeneration of both akeake and matipo was minimal within and outside the standing bush perimeters. Fragmentation of the bush cover over significant areas of the plateau had opened the bush interiors to wind and weather (Atkinson *et al.*, 1973; Rod Morris, pers. comm.). Atkinson *et al.* (1973) noted that only three of the ten black robin territories at that time possessed vegetation in stable condition. These territories offered relatively good shelter from all but the strongest of winds (Flack, 1976a). Sea-facing vegetation was in rapid retreat. In six of the ten territories, the area of habitat available to the birds was decreasing on one or more margins.

Atkinson *et al*. (1973) judged that the processes of habitat collapse had commenced at least three decades beforehand (that is, at or after the time of Fleming's visit in 1938) and, without remedy, would culminate in a low, woody successional scrubland unsuited to the black robin's needs. Flack (1976a, 1977) treated decayed and moribund root systems in the eroding soil at the coastal edges of the plateau as evidence of a formerly healthy closed-canopy forest covering an area of 8-9 ha 50 years previously. He concluded that more than 50% of that area had already become or was in the process of converting to open habitat (Flack, 1976c). In his judgment, the island's vegetation changes had been gradual in the first half of the 20th century and had gathered momentum in the latter half. By 1976, the total area of forest fragments available to the black robins amounted to 3.9 ha, supplemented by 2.2 ha of scattered vegetation in which nesting might be possible (Flack, 1976a). Applying contour information to aerial photographs, Flack calculated that the largest tract of closed canopy bush (5-10 metres high) was barely one hectare in area. Understorey vegetation was conspicuously absent and the ground was bare of both leaf litter and herbaceous plants (Flack, 1974a, b, 1976a).

The 1938 observations of Fleming (1939a, b) and Turbott (1938) offer incidental support for early onset of the decline. Beyond Fleming's reference to virgin bush (presumed to mean unaffected by human activities), both remarked on the small area of tall forest, the noteworthy *Muehlenbeckia* vine, the lack of undergrowth under any of the taller scrub and trees, and petrel burrowing of such extraordinary density that the team plunged knee-deep into the soil 'with every step' (Fleming, 1939b: 507).

How far habitat deterioration had advanced after 1938 cannot be determined from Merton (1969). The personal recollections of the 1968 party members are more informative, as are Flack's (1976b) allusions to their impressions (see below). Merton (pers. comm.) believes that the conditions he observed in 1968 were not as bad or the forest as open as Flack found them in March 1972. John Kendrick (pers comm.) recalls the *Muehlenbeckia* vine being everywhere, collapsing the bush under its weight. But although the extent of tall forest was limited, there were still good areas of bush cover 'over head-height'. In the three years after 1968, the cover had evidently become more severely fragmented and degraded (Flack, 1973, 1974a, b).

The reasons for the sudden deterioration are unclear. The helicopter pad has often been cited (see for instance Cemmick and Veitch, 1985; Hutching, 2004) and has assumed apocryphal significance in the black robin story, more than may be justified by its direct effects on habitat quality (Rowley Taylor, pers. comm.).

Merton (pers. comm.) considers that the clearing breached the vegetation gradient at the edge of the taller bush, permitting wind to penetrate and securing for *Muehlenbeckia* vines an unnatural advantage through access to the deep spoils within. But this may have been a localised effect only and not the cause of the widespread deterioration in bush cover. Atkinson *et al.* (1973) did not mention the clearing at all in their assessment of forest collapse, causes and remedies.

More probably, the helicopter pad aggravated the existing processes of collapse by allowing *titi* harvesters easy access to the island's plateau during the three seasons after 1968. The damage done by birding parties to soil structure and vegetation cover over wide areas was amply evident in 1968 (Merton, 1969). This damage may have been enough to trigger rapid deterioration in a habitat already predisposed to collapse through decades of shearwater stress.

### *3.6.2 Causes of decline in habitat quality*

Indirectly, the helicopter pad served the black robin's interests by acting as a catalyst for efforts to purchase the island from its Maori owners (Merton, 1969; Butler and Merton, 1992). These efforts were ultimately unrewarded. The intrusions and their apparent effects also prompted much closer assessment of the black robin's biology and viability (Flack, 1971).

The research programme which followed identified the smothering effects of the prevalent *Muehlenbeckia* (Fleming's 'tangled vine') and the destructive effects of extremely abundant, heavy-bodied sooty shearwaters [31, 32] as the two principal causes of forest disintegration. The relative importance of these two factors was disputed by black robin researchers and managers but both sides of the argument agreed that conditions of unusual climatic stress had accelerated the rate of bush collapse. The damage wrought by consecutive years of severe summer droughts, such as occurred between 1972-73 and 1973-74, and a series of intensive dry (low humidity) salt-laden storms was evident in the extensive dieback of foliage on the island (Atkinson *et al*., 1973; Flack, 1976a). The extensive deep-soil burrowing of the shearwaters increased the drought-prone-ness of the island's soils (Atkinson

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[31] Alluding to the views of Brian Bell and other Wildlife Service colleagues, Flack (1976a) suggests that hostile changes in the shearwater's breeding habitats elsewhere in the Chathams were responsible for their overwhelming numbers on Little Mangere Island. If so, displacement has not resulted in super-abundant shearwater densities on predator-free Rangatira Island (Nilsson *et al*., 1994; West and Nilsson, 1994), or on neighbouring Mangere Island now that it is free of introduced predators. The latter appears to have had higher shearwater densities historically (see 3.4 above—the reference to walking difficulties in the 1860s), but perhaps the complete absence of bush cover over most of the island since the early 1900s exposes the shearwaters unduly to avian predators (skuas and harriers). In contrast, Flack (1976a) observed that the geological character of Little Mangere Island favoured the shearwaters with powerful up-draughts from the vertical cliffs and very short journeys to take-off points—attributes not possessed by other islands in the vicinity.

[32] At least 60,000 pairs, considerably more than the number of burrows available, judging from the great number of eggs laid on the surface (Flack, 1976c). According to Flack (1976a: Table 2), burrow density for sooty shearwaters on Little Mangere Island ($\bar{x}$ = 102 per 100 square metres) exceeded any cited for five southern *titi* islands of comparable size around Stewart Island. The Little Mangere Island density is a little less than those found in *Poa* meadows (1.9 per $m^2$) and *Olearia* forest (1.2 per $m^2$) by Warham and Wilson (1982) on the larger Snares Islands.

*et al.,* 1973). Their nocturnal traffic polished the soil surface and swept it clear of leaf litter, reducing moisture retention and seed germination. Tree seedlings were dislodged everywhere except in small isolated areas. The moisture and leaf-litter deficits created scarcities of ground invertebrates crucial for black robin breeding and survival (Flack, 1976d). Many palatable insect groups were barely represented or unavailable to the birds during summer (Flack, 1976a, c). Modest winter improvements in soil texture, ground litter and invertebrate biomass were swept away again when the shearwaters returned to breed each year. The installation of wire-netting petrel-exclosures in 1973-74 and later seasons demonstrated that natural regeneration would be rapid in the absence of the shearwaters (Flack, 1976a, d).

Researchers and managers became deeply divided over the role of *Muehlenbeckia* in the bush's decline, especially when decreasing black robin numbers made it critical to address the correct cause of habitat collapse swiftly. Merton (1969) had made no special mention of *Muehlenbeckia* but was convinced by 1976 that the vine was the principal problem. He argued that its smothering growth stifled regeneration through light deprivation and through wind-sail effects which killed the tall trees by destabilising their root systems ('the trees rocked backwards and forwards in the wind'; Merton, pers. comm.).

In a letter to colleagues, Flack (1976b) rejected these propositions, citing old-age vine growth as evidence that *Muehlenbeckia* was an original component of the habitat and therefore not naturally destructive. He regarded its apparently aggressive mantling of low vegetation and trees, both living and dead, as a symptom rather than the cause of senescent forest cover. In his judgment, dead and dying trees dominated the bush because the shearwaters had suppressed the processes of forest replenishment for some time.

The issue was part of a larger debate on *Muehlenbeckia* threats to forest recovery on Rangatira and Mangere Islands following complete removal of their livestock (1961 and 1968 respectively). The vine had encroached swiftly on the bush edges, light-wells and replantings (Veitch, 1982). It remains a conspicuous and contentious feature of black robin habitat today (Roberts *et al.* 2006; pers. obs.). Observations of black robin nest-site choices and territory disposition at the forest edges (Chapter Two) suggest that *Muehlenbeckia* was a mixed blessing on Little Mangere Island. The destabilising effects of shearwater burrowing on soil and root systems accentuated the vine's harmful properties, but on balance, Flack's (1976a, b) position was probably correct. Without the sheltering and foraging benefits of *Muehlenbeckia*, the black robins might not have survived in the degenerating, open habitat otherwise available to them.

Because the black robins did not use the expanding areas of open woody vegetation, the progressive contraction in suitable forest habitat on so small an island had measurable reducing effects on territory disposition, quality and numbers (Flack, 1974a, b). Through the loss of continuous bush cover, pairs occupied isolated territories which lacked the multiple points of connection and boundary negotiation possible in the forest habitats of mainland *Petroica* (Flack, 1976a). The changes are certain to have imposed higher energy costs, especially during the critical summer periods of nesting and parenting.

Under contracting bush cover devoid of ground litter, foraging ranges and opportunities would have narrowed, obliging birds to make longer foraging journeys. This was an effect observed in the very fragmented Caravan Bush on Pitt Island where, in 2006, black robins flew long circuitous routes through bush corridors rather than crossing clearings on foraging trips (Kennedy, 2006). On Little Mangere Island, the conditions reducing prey availability also undermined the reliability of food supply (Flack, 1976a). The modest winter recovery of ground invertebrates may have averted a higher rate of winter mortality, but conversely the sheltering benefits of the deciduous *Muehlenbeckia* were lost during these harsh months. The stresses resulted in high mortality rates and lowered reproductive output (Flack, 1974b, 1976a, d, 1977), with predictable consequences for population viability and size.

The growing environmental pressures were aggravated by the presence of exotic bird species, especially blackbirds *Turdus merula* and dunnocks *Prunella modularis*. The latter were common on Little Mangere Island in the 1970s, apparently because conditions were improving for them on neighbouring Mangere Island (Flack, 1976a). Both exotics competed with the black robins for diminishing nest-site opportunities and—especially the dunnock, a ground-foraging specialist (Heather and Robertson, 1996)—for invertebrate prey in the lower strata of the bush (Flack, 1976a). Reports of the period make no mention of starlings on the island, though these were very common on Mangere Island in 1968 (Merton, 1969).

### *3.6.3 Population decline*

Knowledge of black robin's decline towards total extinction, first on Little Mangere Island and later on Mangere Island (see *Section 3.7* below), is book-ended by Fleming's observations in January 1938 and first conservation management in 1980-81. With one notable exception, the decline has been treated merely as a prefatory narrative in published accounts of the species's subsequent recovery. Butler and Merton (1992) offer the fullest published record of the decline but their summary is troubled by incomplete and contradictory data in the official reports of research on Little Mangere Island between 1971-72 and 1975-76.

To analyse the intrinsic (demographic) features of the decline, I have attempted to rectify the uncertainties through recourse to the primary field sources. Other than the diaries of Morris (1973, 1975, 1976, 1977a) and field-books of Hay (1975), however, few such sources have been available. Douglas Flack has not permitted me to consult his field diaries and workbooks, and by a dismaying accident of timing, Warwick Brown, his long-term field assistant, had burned all his field notebooks ten days before I sought permission to look at them. A definitive demographic analysis of the decline is unachievable in a data vacuum of this nature. Therefore, the following description of the population's decline is reconstructed from secondary sources in the public domain, from the small number of official field and summarising progress reports from those years, from the recollections of participating field-workers and associates, and from Flack's incomplete black robin monograph (1976a).[33]

The data conveyed through these diverse sources are incomplete and often ambiguous, resulting in a conservative picture of annual productivity and mortality. Against this, only rudimentary comparisons can be drawn with the detailed demographic data recorded after active conservation management commenced in 1980-81.

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[33] This is the only paper in which Flack attempted to document his research findings for the period 1971-72 to 1975-76. Unfortunately, copies of the draft manuscript still extant in the public domain are missing maps and tables essential to systematic analysis of the population's decline. Hand-written notations and marginalia imply that important corrections were still to be made.

### 3.6.4 Original population size

The size of the black robin population originally isolated on Little Mangere Island after 1893 is undocumented. Flack (1976a, 1977) concluded from the area of soil-covering on the island (8-9 ha, topographic; 5.2 ha cartographic[34]) that the former closed bush had naturally supported 20-30 pairs, considerably more than the six pairs and four bachelors (ten territories) counted definitively in October 1973 (Flack, 1974a, b, 1976a). The correct measure of historical abundance may lie between Merton's (1986, 1990) unsupported predictions of no more than 30 individuals at any one time and densities observed in present-day habitats.

Merton's estimate of $\leq$ 30 black robins allows for a historical density of 5.7 birds ha$^{-1}$ cartographic (3.75 ha$^{-1}$ topographic). Unlike Flack (1973, 1976a, 1979) who referred to a predator-reduced South Island robin population (Kowhai Bush, Kaikoura) for typical *Petroica* densities, Merton was basing his estimate on rising black robin densities on predator-free Mangere and Rangatira Islands prior to 1990 (Butler and Merton, 1992). These densities increased further after 1990 (see Chapter Six), achieving a pre-breeding peak in 1999-2000 of 6.8 bird ha$^{-1}$ and 4.0 territories ha$^{-1}$ (cartographic) in the Robin Bush on Mangere Island (7.9 ha), the habitat most comparable in size and insularity to Little Mangere Island (see Chapter Six: Table 6.3 for census count). Extrapolation from this peak Robin Bush density suggests a maximum population on Little Mangere Island (5.2 ha cartographic) of 35 black robins occupying 20 territories. This may be the upper limit of historical population size because Little Mangere Island's carrying capacity was probably the lower of the two habitats through greater exposure to winds from all directions, climatic pressures (storms, drought, lower mean seasonal temperatures), vegetation constraints and the more linear configuration of the habitat.

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[34] Flack used aerial photos, contour data and on-the-ground measurements to arrive at his topographic estimate of 8-9 ha for the original (pre-decline) forest cover on Little Mangere Island. As the basis for converting his estimate to cartographic area (the only measure feasible elsewhere), I have drawn plan-view polygons around the edge of the island's plateau in Google™ Earth satellite images, following Flack's (1976a) use of cliff-edge soil-cover to define the original bush perimeter. To correct for probable underestimate in the use of polygons, I have calculated the ratio of topographic to cartographic area using the lower range of Flack's topographic estimate (8 ha).

The cartographic densities of 3.8 birds ha$^{-1}$ and 2.5 territories ha$^{-1}$ (2.6 birds ha$^{-1}$ and 1.64 territories ha$^{-1}$ topographic) observed in 1973-74 in Flack's 6.1 ha of forest and scrub-cover remaining on Little Mangere Island were lower than pre-decline estimates of population size. In equating to a 19th-century population of about 20 black robins and 13 territories, they offer a possible measure of the degree to which habitat deterioration had already reduced the population to an unnaturally low density.

### *3.6.5 Decline in black robin abundance*

Fleming (1939b) was the first observer to quantify black robin abundance numerically. In the belief that the species's confiding nature gave him a truer indication of numbers, Fleming determined from the birds seen everywhere along the crest of the island that the population on the plateau comprised about 12 pairs. Having seen black robins in a cliff-side territory traversed on the climb up from the landing, he made further allowance for cliff territories assumed to exist beyond view, arriving at a total estimated population of (minimum) 20 and (maximum) 35 pairs (Table 3.1). Later experience of counting colour-banded black robins convinced Flack (1976a) that Fleming could not have avoided double-counting of unmarked birds in 1938. Adults moulting reclusively in early January and highly mobile, gregarious young of the year would have complicated Fleming's estimate. Flack (1976a) also established that no more than one cliff territory was likely to have existed at Fleming's time or at any time during that century.

Three subsequent counts also over-estimated numbers. A one-hour visit in late November 1961 was too brief to test Fleming's conclusions (Bell and Hogarth, 1962; Hogarth, pers. comm.). Merton (1969) attempted the first whole-island census of the population on 3 September 1968. This was essentially a pre-breeding survey capable of yielding a more ecologically prudent indication of population size and status. Walking line-abreast, the survey team of three counted 30 robins on the plateau, from whose distribution they extrapolated a total of about 17 pairs. Allowance was made for up to eight more pairs believed to inhabit inaccessible cliff ledges. The total of 17 pairs for the plateau alone was treated in retrospect as an over-estimate resulting from double-counting (Butler and Merton, 1992; Merton, pers. comm.). Multiple-counting difficulties also troubled Flack's estimated minimum of 26 black robins in late March 1972 (Butler and Merton, 1992), despite the benefits of having colour-marked nine adults and juveniles with unique combinations (Flack, 1974a, 1976a). In hindsight, Flack (1977) gave the likely number at 1968 as fewer than 20. Inference from his post-breeding count in January 1973 (18-20 birds, Flack, 1974a) suggests that this was close to the likely number in March 1972 also.[35]

Between late-January 1973 and September 1976, 11 further research visits of short duration plotted annual reductions in population size, pair numbers and territory configuration (Tables 3.1 and 3.2). Estimates of adult numbers were not accurate until all adults were finally colour-banded in February 1975 (the penultimate season of the research programme). The timing of visits (spring and late summer or autumn) also deprived researchers of opportunities to follow breeding attempts and fledgling fates, omissions which perpetuated uncertainties about annual juvenile production and survival. Even so, deterioration in the habitat's carrying-capacity was amply expressed in the post-breeding population declines of about 60% over four successive seasons (from no more than 20 individuals in early February 1973 to seven in September 1976). Known pre-breeding numbers declined by 56% between October 1973 and September 1976 (Tables 3.1 and 3.2).

The hostile changes in habitat quality exerted pressure on the population's reproductive potential in a number of ways. Despite no evident sex-bias in juvenile production (Table 3.2), the population developed a pronounced male skew (Tables 3.2 and 3.4) caused apparently by the poor habitat selecting more heavily against females (Flack, 1976a, 1977). Breeding was successful in only five of the ten recognised territories on the island, in part because males in small, isolated territories failed to attract females.

Food stress delayed the onset of egg-laying and abbreviated the season, shortening the potential for renesting. Egg-laying periods varied from approximately 30 to 56 days during the last three research seasons, considerably less than the interval between earliest and latest recorded egg-laying in superior habitats on Mangere and Rangatira Islands (about 120 days; Chapter Two: *Figures 2.5* and *2.6*; Chapter Six). The short breeding season also limited the period within which offspring could be raised and resulted in higher mortality rates

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[35] As knowledge of the black robin situation improved on Little Mangere Island, numbers reported at the time of the early surveys were often revised several times (without comment) in the multi-year summaries of later years. Confusion is also created by figures reported in many sources which did not differentiate between pre- or post-breeding totals. No final statement of annual population sizes was ever published for the censuses between 1968-69 and 1975-76.

in late offspring (Flack, 1976a). Food stress increased adult mortality during summers (Table 3.4; Flack, 1974b, 1976a) and was deemed responsible—along with the suspicion of inbreeding depression—for the failure of productivity to improve when larger territories became available on the death of occupants (Flack, 1976a). Recruitment to the breeding population was almost completely extinguished by the high mortality rate of juveniles (Flack, 1974b, 1977), all of which perished in the climatically taxing periods of winter and early spring (Flack, 1976d). Most of the juveniles dying during these periods were produced in bush of inferior quality or had been marginalised there over winter (Flack, 1976a).

Flack's research showed that habitat and resource stresses had conveyed the shrinking population below a critical viability threshold. The rudimentary productivity data acquired from 1973-74 until 1975-76 indicated that the population's reproductive output had been about 1.7 juveniles year$^{-1}$, which equated to 0.36 juveniles pair$^{-1}$ year$^{-1}$ (Table 3.3). Juvenile survival over the same period was 0.7 year$^{-1}$ (0.14 pair$^{-1}$ year$^{-1}$). This output no longer compensated for the elevated rates of mortality in adults and offspring alike. These mortality rates were higher than those recorded by Flack in predator-free and predator-reduced New Zealand robin populations in island and mainland habitats (Flack, 1973, 1976a, d, 1979).

Only three of the 10-12 juveniles thought to have been produced between 1971-72 and 1975-76 survived to breeding age. Only one (the legendary *Old Blue*) may have bred successfully within that period, though there is reason to doubt that she did so (Table 3.3).[36] Up to 16 adults perished after research commenced in March 1972. At least nine of the 11 dying in the final three seasons (1973-74 and 1975-76) were experienced breeders (Table 3.4). Eight of these 11 adults died during summer (Table 3.4). As the population became smaller, each death—especially of the numerically disadvantaged adult females—deprived it of progressively greater proportions of its reproductive potential.

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[36] Merton (1986) and Butler and Merton (1992) say that only one of the juveniles produced during this period bred successfully. This would be true of *Old Blue* if success is measured by the two fledglings she is known to have produced in 1973-74. There is some doubt that she raised these two offspring to independence (see Footnote 37), and too much doubt exists over breeding in later seasons to be certain that *Old Blue* raised any other offspring to independence prior to 1979-80.

The relentless rate of decrease witnessed after March 1972 suggests that the population's viability had been fatally compromised, or brought to the point of fatal compromise, before that date. A slow approach to the critical threshold is inferred from Flack's proposition of gradual habitat decline over more than half a century, a proposition supported perhaps by Fleming's observations on habitat character and petrel abundance in January 1938. Then, a growing proportion of the black robins encountered may have been occupying territories in transition to sub-optimal quality or destined to become so. The population's persistence may already have become unduly reliant on the reproductive potential of the small number of breeders occupying the few forest remnants described by Fleming (1939b) and Turbott (1938). Their genes were likely to become dominant. At some stage between 1937-38 and 1971-72, the pool of productive breeders appears to have become unnaturally small, since it was during this time that genetic serendipity deprived the species of its distinctive 'bright yellow' foot-pads (Fleming, 1950b: 143; Flack, 1976a, 1977).

At whatever time viability became irretrievably compromised, the population's decline was hastened by the black robin's inability to adapt behaviourally to an unfamiliar environment increasingly devoid of forest cover. The species's foraging niche at or near ground-level jeopardized viability through the seasonal shortfalls in ground invertebrate prey noted by Flack (1974b, 1976a, c, d). The high rate of summer mortality in adults suggests that the black robin's broad invertebrate prey preferences were not versatile enough to compensate for the severity of ground-food shortages during the breeding seasons.

Under these stressful circumstances, low reproductive rates arising from the short breeding season, small clutch sizes (no more than two eggs; Flack, 1976a), declining pair numbers and low rates of offspring survival proved to be fatally disadvantageous to population persistence.

As numbers fell year-by-year, only the longevity of survivors—fortuitous in so small and stressed a population—sustained the species until the courageous decision was taken to intervene. This advantage remained crucial until the ranks of ageing breeders on Mangere Island were first joined under better conditions by increasing numbers of their offspring, then swelled with many more under intensive management of breeding (Chapter Six).

Table 3.1 Black robin numbers, territories and pairs reported on Little Mangere and Mangere Islands between January 1938 and March 1977. Totals given between 1938 and March 1972 (inclusive) are regarded as over-estimates.

| **Visit Date** | **Numbers** | **Territories (Breeding)** | **Principal sources** |
|---|---|---|---|
| 2 January 1938 | 20-35 pairs | 20-35 | Fleming, 1939b |
| Late November 1961 | No change | unknown | Bell and Hogarth, 1962; Hogarth, pers. comm.; Butler and Merton, 1992 |
| 2–3 September 1968 | ≤ 25 pairs | ≤ 25 | Merton, 1969; Flack, 1971 |
| 29–30 March 1972 | ~26 | unknown | Butler and Merton, 1992 |
| 29 January – 3 February 1973 | 18-20 | 10 (7-8) | Flack, 1973, 1974a, 1976a |
| 7–14 October 1973 | 16 | 10 (6) | Flack, 1974a, 1976a; Atkinson *et al.*, 1973; Butler and Merton, 1992; Rod Hay, pers. comm. |
| 25 November – 1 December 1973 | 14 | | Morris, 1973; Butler and Merton, 1992 |
| 16–24 January 1974 | 18 | | Rod Hay, pers. comm; Butler and Merton, 1992 |
| 13 and 22 April 1974 | 14 | | Morris, 1973; Flack 1974a, b, 1976a; Butler and Merton, 1992 |
| 10–19 November 1974 | 11 | 7 (4) | Butler and Merton, 1992 |
| 9–13 February 1975 | 11 | | Butler and Merton, 1992 |
| 8–12 November 1975 | 9 | 5 (4) | Morris, 1975 |
| 23–29 January 1976 | 12 | | Flack, 1976a, c |
| 28 May – 8 June 1976 | 8 | | Flack, 1976a, Butler and Merton, 1992 |
| 16–21 September 1976 | 7 | 3 (2) | Morris, 1976, 1977b; Flack, 1976a; Butler and Merton, 1992 |
| March 1977 [MANGERE ISLAND] | 7 | | Billing, 1977; Morris, 1977a, b, c; Bell, 1978a; Butler and Merton, 1992 |

Table 3.2 Number and age-class of black robins known to be alive at the beginning and end of each season on Little Mangere Island (1971-72 to 1976-77) and Mangere Island (1976-77 to 1979-80). An asterisk (*) indicates unknown age-classes (adult, yearling, juvenile).

| | Start of season | | | | | End of season | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Male | | Female | | | Male | | Female | | |
| **Season** | **Adult** | **Yearling** | **Adult** | **Yearling** | **Unknown** | **Adult** | **Juvenile** | **Adult** | **Juvenile** | **Unknown** |
| **LITTLE MANGERE** | | | | | | | | | | |
| 1971-72 | No observations | | | | | At least 9 females * and 8 males * (4-6 juveniles) | | | | |
| 1972-73 | No observations | | | | | 5 females * and 5 males * ( ≥ 1 juvenile), 3-4 other territories | | | | |
| 1973-74 | 10 * | | 6 * | | | 7 | 1 | 5 | 1 | |
| 1974-75 | 7 | | 4 | | | 5 | 1 | 4 | 1 | |
| 1975-76 | 4 | 1 | 4 | | | 5 | | 2 | 1 | |
| 1976-77 | 5 | | 1 | 1 | | All black robins transferred to Mangere Island by season's end | | | | |
| **MANGERE** | Three males and two females moved to Mangere Island, 17-21 September 1976. Two males followed on 15 March 1977. | | | | | | | | | |
| 1976-77 | 3 | | 1 | 1 | | 4 | | 2 | 1 | |
| 1977-78 | 4 | | 2 | 1 | | 3 | 2 | 2 | | |
| 1978-79 | 3 | 2 | 2 | | | 5 | | 2 | 1 | |
| 1979-80 | 3 | | 1 | 1 | | 3 | | 2 | 1 | |

Table 3.3 Annual reproductive output in the black robin ancestral population on Little Mangere Island (1971-72 to 1975-76) and the post-transfer population on Mangere Island (1976-77 to 1979-80). Data are drawn directly or through inference from summarising sources and are incomplete. Blank fields indicate no available data. Totals in **red** are minimum values, some inferred from other values.

| | **Pairs** | | **Clutches** | **Eggs** | | | **Nestlings** | | **Fledglings** | | **Juveniles** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Season** | ***n*** | **Effective** | ***n*** | **Laid** | **IFT** | **FTH** | **Hatched** | **Lost** | **Fledged** | **Lost** | **Produced** | **Lived ≥ 1 year** |
| 1971-72 | No observations until 29-30 March 1972 | | | | | | | | | | 4-6 | 1 F (*Old Blue*, *) |
| 1972-73 | 7-8 | 1 | | | | | | | 1 | | 1 | 0 |
| 1973-74 | 6 | 2 | 6 | 10 | 10 | | | | 8 | 6 | 2 | 0 |
| 1974-75 | 4 | 2 | 4 | 6 | 6 | | 6 | | 4 | | 2 | 1 male |
| 1975-76 | 4 | 1 | 4 | 8 | 8 | 5 | 3 | | 3 | 2 | 1 | 1 female [BF, *] |
| | 3 males, 2 females moved to Mangere Island, 17-21 September 1976; 2 males followed on 15 March 1977 | | | | | | | | | | | |
| 1976-77 | 2 | 1 | 2 | 5 | 5 | 3 | 2 | 1 | 1 | | 1 | 1 female [BF, *] |
| 1977-78 | 3 | 2 | 6 | 6 | | | 2 | | 2 | | 2 | 2 males [BF, 1 *] |
| 1978-79 | 2 | 1 | 1 | 1 | | | 1 | | 1 | | 1 | 1 female [BF] |
| 1979-80 | 2 | 1 | 2 | 3 | 3 | 1 | 2 | 1 | 1 | | 1 | 1 female [OB] |

| | | |
|---|---|---|
| NOTES | Effective | Succeeded in producing one or more juveniles |
| | IFT | Incubated full-term |
| | FTH | Failed to hatch |
| | * | Ultimately bred successfully |
| | OB | *Old Blue* maternal line (see *Section 3.7* below) |
| | BF | *Blow-Out Female* maternal line |

Table 3.4 Annual mortality by season and age-class in the ancestral black robin population on Little Mangere Island (1971-72 to 1975-76) and Mangere Island (1976-77 to 1979-80). Figures in square brackets [ ] denote ages. Ages in **red** denote a known or probable experienced breeder.

| | Adult | | | | | Juvenile | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Male | | Female | | | Male | | Female | |
| | *n* pre-breed | Summer | Winter | Summer | Winter | *n* produced | Summer | Winter | Summer | Winter |
| 1971-72 | Not known | | | | | 4-6 | 3-5 lost during summer and winter | | | |
| 1972-73 | Not known | ≥ 5 of unknown age lost over winter | | | | At least 1 | 1 (sex unknown) lost over winter | | | |
| 1973-74 | 16 (10 M, 6 F) | 3 [≤ **2**, **2**, 3] | | 1 [≤ **3**] | 1 [≤ **3**] | 1 male, 1 female[1] | | 1 | | 1 |
| 1974-75 | 11 (7 M, 4 F) | 2 [≤ **2**, **3**] | 1 [≤ 2] | | | 1 male, 1 female[2] | | | | 1 |
| 1975-76 | 9 (5 M, 4 F) | | | 2 [≤ **3**, **4**] | 1 [≤ **3**] | 3 (at least 1 female)[3] | 2 (sex unknown) lost over winter | | | |
| | Three males, two females moved to Mangere Island, 17-21 September 1976. Two males followed on 15 March 1977 | | | | | | | | | |
| 1976-77 | 7 (5 M, 2 F) | 1 [≤ **4**] | | | | 1 female[4] | | | | |
| 1977-78 | 7 (4 M, 3 F) | 1 [≤ **6**] | | 1 [**1**] | | 2 males[4] | | | | |
| 1978-79 | 7 (5 M, 2 F) | | 2 [≤ **8**; 1] | | 1 [**3**] | 1 female[4] | | | | |
| 1979-80 | 5 (3 M, 2 F) | | | | 1 [≤ **8**] | 1 female[4] | | | | |

NOTES

[1] 1973-74—at least six fledglings appear to have died before achieving independence

[2] 1974-75—one known nestling presumed to have fledged; died during the season

[3] 1975-76—the surviving juvenile was a female; two known fledglings died before achieving independence

[4] 1976-77 to 1979-80—almost nothing known of reproductive effort

## 3.7 Mangere Island, 1976-77 to 1979-80

Seven black robins—five adult males, one adult female and a yearling female—survived the 1976 winter on Little Mangere Island. Only two young black robins were of known age (Table 3.5). Between 17 and 21 September 1976, both females were moved with three males to the smaller, regenerating Robin Bush on Mangere Island and bred there in the season ahead.

Table 3.5 Age and sex of survivors in the ancestral black robin population on Little Mangere Island, September 1976. All were transferred to Mangere Island in the 1976-77 season. Ages given as years-of-age (that is, *Old Blue* was at least five years old when transferred).

| Name | Sex | Band number | Age at transfer | Natal year | Transferred |
|---|---|---|---|---|---|
| Old White * | M | B-35348 | 2 | 1974-75 | 17 Sep 1976 |
| Old Blue * | F | B-11384 | ≥ 5 | Probably 1971-72 | 18 Sep 1976 |
| Red Yellow * † | M | B-31201 | ≥ 6 | Prior to 1971-72 | 18 Sep 1976 |
| Blow-Out Female II * † | F | B-36481 | 1 | 1975-76 | 21 Sep 1976 |
| Helipad Male †† | M | B-35343 | ≥ 4 | In or prior to 1972-73 | 21 Sep 1976 |
| Cliff Male * † | M | B-35345 | ≥ 5 | In or prior to 1971-72 | 15 Mar 1977 |
| Ridge Male * † | M | B-35479 | ≥ 5 | In or prior to 1971-72 | 15 Mar 1977 |

NOTES
* Bred successfully on Mangere Island
† Died before the 1980-81 season
†† Died before 1980-81without breeding

The two males left behind on Little Mangere Island were transferred to Mangere Island on 15 March 1977 (Morris, 1977a, b, c). It was at least 83 years since black robin extirpation from the island.

Though related through shared ancestors in the tiny Little Mangere Island population, the two surviving females, *Blow-Out Female* and *Old Blue,* had no parents in common and represented separate maternal family-lines on Mangere Island. After transfer, the *Blow-Out Female* line persisted in two daughters (*Gauntlet*, 1976-77; *Old Green*, 1978-79) and one grand-daughter (*Gunner*) reared in 1980-81. All but *Gunner* bred successfully, contributing four of the five juveniles produced in the post-transfer population prior to 1980-81. The line produced five juveniles in total (the three females named above and two males) before terminating on the sudden death *Old Green* in November 1986 (the last surviving female, assumed killed by starlings at her nest on Rangatira Island; Butler and Merton, 1992). The line would have contributed nothing further to the species's future were it not for the providential survival and nine-year longevity of the *Blow-Out Female*'s grandson, *Old Yellow* (raised in 1977-78 by *Gauntlet*, in her only year of adult life). Total extinction of the species was averted by the mate choice of this male.

*Old Yellow* mated with the seven-year-old *Old Blue* in 1978-79 and remained paired with her until the time of her death aged 12 years in December 1983. The pair-bond effected a convergence of the two maternal lines and realised the second line's productive potential, perhaps for the first time.[37] The pairing occurred just in time. Though the *Blow-Out Female* line had done most to sustain black robin numbers in the first four years after transfer, it was destined to produce no successful breeders after 1978-79. From this point, the fate of the species depended entirely on *Old Blue*'s productivity. *Old Blue* and *Old Yellow* were not successful at first, but produced a single female juvenile (*Red*) in 1979-80, the only surviving offspring of the year (Cox and Merton, 1980; Bell, 1980a). *Red* remained unmated in the next season—there were no males to spare—and died in the following winter (1981).

Had conservation managers not intervened in 1980-81 to boost the reproductive output of the population's two breeding pairs through obligatory renesting and cross-fostering, it is doubtful that *Old Blue* and *Old Yellow*'s natural productivity would have preserved the species from extinction. Intervention averted this looming catastrophe but could do nothing to avoid the *Old Blue-Old Yellow* bottleneck. All black robins in the Mangere Island population and sister population on Rangatira Island are therefore descendants of the *Old*

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[37] Between 1972-73 (when first observed as a yearling breeder) and 1978-79, *Old Blue* was not confirmed as having produced any juveniles (Table 3.3). Butler and Merton (1992) assume—perhaps on the basis of field notes I have not seen—that two juveniles roaming in the vicinity of *Old Blue's* breeding territory in 1973-74 were her progeny. My reading of Flack's (1976a: 29-30) wording suggests that these juveniles were produced by the neighbouring *Western* female. Neither juvenile survived the winter of 1974. The uncertainties frustrating productivity analyses for these seasons would have been minimised if reports of that period had routinely referred to individuals by their colour-band combinations and territory names together.

*Blue* line and have received from *Old Yellow* the genetic inheritance of the *Blow-Out Female* line.

It is not possible to determine the scale, reasons or timing of reproductive failure in the tiny Mangere Island population after 1976-77. Optimistic of natural recovery, a management policy of minimal disturbance was followed which resulted in minimal information on breeding attempts over the following four seasons (Table 3.3). Numbers and survival were monitored during fleeting early- and late-season visits, some timed early enough to acquire fragmentary evidence of longer egg-laying periods in the better habitat (Bell, 1977a, b, c, d, 1978a, b, c, d, 1979, 1980a, b; Billing, 1977; Morris, 1977a, b, c; Wright, 1978; Russ, 1979; Fisher, 1979; Cox and Merton, 1980). The population did not increase as hoped. Five juveniles were produced and survived between 1976-77 and 1979-80 (1.25 year$^{-1}$, which equated to 0.55 pair$^{-1}$ year$^{-1}$, nearly quadruple the survival rate in the five seasons prior to transfer; Table 3.3). But this was only just sufficient to offset the mortality of ageing adults (Table 3.4).

As a result, the size of the pre-breeding population remained unchanged until 1979-80 (n = 7; Table 3.2). Pairs became isolated in large territories (Russ, 1979; Butler and Merton, 1992), minimizing the likelihood of stimulatory interaction between males during the breeding season. The male bias persisted. Pair numbers fluctuated annually between two and three (Table 3.3). Three of the four seasons commenced with just two females, the most experienced of which (*Old Blue*) had a long history of breeding failure. It was questionable how long chance would favour this modest stability in such perilously low numbers.

Productivity finally failed to compensate for adult losses after 1978-79. Mortality over the winter of 1979 accounted for the only productive breeders remaining—the four-year-old matriarch *Blow-Out Female* and *Red Yellow* (at least eight years old), her mate of the 1978-79 season, and possibly her father.[38] Their deaths might have been associated with a massive rock-fall destroying about 0.5 ha of the bush between autumn and spring visits

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[38] *Red Yellow*'s consistently successful breeding in the Western territory on Little Mangere Island (Flack, 1976a) was likely to have contributed crucially to the ancestral population's persistence after 1971-72. Breeding data are too imprecise to confirm whether he fathered the *Blow-Out Female* but the only other qualifying male is less likely to have done so (this study).

(Butler and Merton, 1992). The pair's yearling son perished also, unmated for lack of a spare female. The losses reduced the population to five and shifted the burden of breeding to two pairings yet to demonstrate that they could breed successfully. Only the juvenile female *Red* was produced that season, but the death over winter of the sole bachelor (*Cliff Male*), her potential mate, deprived the population of her breeding potential.

Cross-breeding commenced under extreme urgency in 1980-81 with the pre-breeding population reduced to two adult males and three adult females (Butler and Merton, 1992; see Chapters Four and Six).

## 3.8 Conclusions

The history of the black robin's extirpation from each of its historical island habitats traces the familiar pattern of retreat to small populations lingering in marginal refugia, the course taken by many plants and animals driven towards extinction by human activities (Olson, 1989). Loss of each discrete black robin population is also symptomatic of the perils faced by forest-dwelling bird species in particular (King, 1985b) and by the island endemic birds that comprise such a prominent proportion of recent global bird extinctions (Myers, 1979; King, 1985a, b; Atkinson, 1989). Extirpation from the extensive habitats of Chatham Island (90040 ha) is proof that ample abundance alone is no safeguard for locally adapted, slow-breeding *K*-selected species confronted by sudden hostile changes in their environments.

The late 20th-century observations made on Little Mangere and Mangere Islands give partial but crucial insights to the ways in which anthropogenic change might fatally have compromised the viability of black robin populations lost unobserved elsewhere in the island group. Inferences made possible by these insights compensate for the paucity or complete lack of information in historical sources.

Directly and indirectly, human activities in the Chatham Island archipelago exerted reducing pressures on all of the black robin's historical populations. Regardless of their size, all declined independently towards local extinction at different times. These pressures culminated over six seasons in unrelenting contractions in the size of the last vestigial population on Little Mangere Island, conveying the black robin to the brink of functional extinction before intensive boosting of reproductive output on Mangere Island after 1980-81 averted loss of the entire species.

The five black robin populations succumbed to differing extinction pressures, some apparently operating singly rather than through synergistic interaction with others. On Rangatira and Little Mangere Islands, habitat loss was the principal (and seemingly only) form of change inducing population collapse. Predation alone seems likely to have accounted for the large population on Chatham Island—if so, adding this species to the grim inventories of local insular extinctions attributable to kiore (Atkinson, 1978, 1985; Holdaway, 1999; Towns *et al.*, 2006). Gradual changes in forest structure following Moriori settlement might have become contributed but this assumes that kiore did not eliminate the species first, within years or a decade of the pioneering rat irruption. In contrast, we can be more certain that mammalian predation compounded the difficulties of habitat deterioration for the original Mangere Island population. The short three- to five-year interval between the introduction of cats (presumably a small number only) and black robin extinction implies that the two to three decades of goat and rabbit browsing had already undermined population stability. The mutually compounding costs of habitat deterioration and cat predation on Pitt Island may simply have differed in relative scale, assessment of which requires better knowledge of when the cats arrived.

The Little Mangere Island experience revealed explicitly the nature of habitat changes lethal to black robin survival. Although the initial agent of habitat change (sooty shearwaters) differed from the introduced browsers on Pitt, Rangatira and Mangere Islands, habitat structure and quality suffered comparable forms of disintegration. Fragmentation, opening up and simplifying of naturally closed, sheltering forests probably resulted in the harmful changes to prey availability and abundance, contractions in foraging ranges, and reductions in territory numbers and quality observed on Little Mangere Island. Harsher forest-interior climates and higher energy costs must surely have followed. On Little Mangere Island, the effects of habitat deterioration were expressed in fatally high rates of reproductive failure, breeding-season mortality in adults and winter mortality of juveniles, all of which culminated in the population's decline.

Isolation on geographically discrete islands gave populations no assurance of immunity to habitat change. The effects of ecological disturbance elsewhere in the archipelago could migrate through familiar ecological associates such as sooty shearwaters (perhaps deprived of breeding space elsewhere), or through the movements of introduced starlings, dunnocks and blackbirds, strongly flighted competitors for space and resources. Today's black robin populations are still exposed to the threats of disease, competition, predation and habitat change through these vectors.

Regardless of extinction pressures (habitat change, predation, or both), extirpation intervals for most populations appear to have been relatively brief and shorter perhaps than the 15-33 years I have postulated for Rangatira (c.1840-1871), Pitt (1827-1842 or 1863) and Mangere Islands (c.1860-1893). The intervals give a crude measure of the degree to which evolution in the challenging Chathams environment did not equip the black robin with the requisite biological tolerances to cope with or adapt to change. Its tolerances were significantly more slender than those of the sympatric *Petroica* congener, the Chatham Island tomtit, which narrowly survived the period of human colonisation and the growing diversity of threats, but no doubt similar to those of the other extinct insular sympatrics whose biologies are not known—the Chatham Island bellbird, fernbird and rail.

The advantages of longevity delaying extirpation of the Little Mangere and new Mangere Island populations were clearly outweighed by the species's particular biological vulnerabilities. As witnessed in those populations, the black robin's naturally low rates of productivity—an artefact of late, short breeding seasons, long (c.90-day) rearing intervals, small clutch sizes and, more often than not, single broods (Chapter Two)—penalised capacity to replace adults and offspring lost at unnaturally high rates through resource and climate stresses. Those rates would have been higher still under pressure from cat or kiore predation. As was evident on Little Mangere Island, the species's specialist ground-foraging habit was debilitating during summer ground-prey shortages. In fragmenting habitat conditions, intolerance of open spaces reduced territory opportunities and foraging ranges within them. Strong territorial instincts appear to have aggravated the shortage of cover by forcing less dominant males into sub-optimal bush margins where pairing and breeding was unsuccessful. Settlement opportunities for dispersing juveniles were similarly compromised, no doubt contributing to the unsustainable rates of winter mortality. Under such conditions, limited social interaction with neighbours may have subdued the stimulus to breed. Poor flight and aversion to open spaces doubtless prevented recolonising of vacated habitats and would certainly have prevented inter-island replenishment.

On Little Mangere Island, the habitat changes appear to have selected against females, in part perhaps because the black robin's long breeding intervals imposed greater energy demands on them (Chapter Two). On Chatham and Pitt Islands, kiore and cat predation at the nest may also have selected against the females whose exclusive duty it is to incubate and brood. However, very low rates of adult mortality at the nests of South Island robins suggest that mammalian predation accounted mostly for the contents of black robin nests (Flack, 1973, 1976d; Flack and Lloyd, 1978), thus compromising recruitment potential. If, as the male-skew on Little Mangere Island suggests, habitat disintegration was prejudicial to female survival, historical black robin populations may have comprised males only in their terminal stages of decline.

The courses taken towards extinction by the vestigial population on Little Mangere and its descendent population on Mangere Island support the prediction that isolated populations reduced to arbitrarily small sizes by deterministic pressures have demographic thresholds below which they become exposed to lethal combinations of threat from stochastic factors (Lande, 1988, 1999; Brooks *et al.*, 2002). The declines on Little Mangere and Mangere Islands illustrate the working of extinction-vortex pressures through which the mutually compounding effects of environmental and demographic misfortune drive numbers even lower (Gilpin and Soulé, 1986). Reduced, fragmented and destabilised by habitat loss and predation, the largest populations in the black robin's range seem certain to have been captured within similar vortices.

On Little Mangere and Mangere Islands, demographic chance began to play a disproportionately greater role in determining population fates. Chance favoured the populations through the fortuitous survival and pairing of key breeders (*Old Yellow* and *Old Blue*, for instance), but also deprived the tiny Mangere Island population of all experienced breeders simultaneously. Reproductive potential was wasted when by chance potential breeders became separated in habitat fragments or there were no suitable mates at the right time. On both islands, variations in individual breeding performance which are normally averaged out in larger populations (Caughley, 1994; Lande 1999) became progressively more hazardous to population viability as numbers decreased. As indicated by *Old Blue*'s long history of unsuccessful breeding, strong pair-fidelity in black robins could be a liability in such circumstances. Unproductive pairings were likely to endure even if better mates were available. Diminishing mate options may also have matched the few experienced females with young or yearling males less likely than older experienced males to possess crucial parenting skills (Chapter Two).

The fate of the relocated Mangere Island population is especially illuminating. It shows clearly that the intrinsic risks of small population size can be lethal on their own if overwhelming deterministic pressures such as predation or sudden catastrophic loss of habitat have not first eliminated a population outright. The failure of the tiny population to increase in size naturally once removed to Mangere Island's stable environment confirms Gilpin and Soulé's (1986) prediction that populations exposed to stochastic threats may be irrecoverable even if the deterministic causes of collapse are remedied. Unfortunately, the policy of minimal management has denied us close insights to the life-history factors at play, but pre- and post-breeding head-counts between 1976-77 and 1979-80 suggest that demographic stochasticity would ultimately have delivered the *coup de grâce* had conservation managers not intervened to raise the population's size rapidly after 1980-81.

Elimination of the black robins throughout their historical range is consistent with the prediction that the short-term effects of environmental and demographic adversity will extinguish isolated populations before the harmful genetic implications of small size are realized (Caughley, 1994, Lande, 1999; Dobson, 1999). With the possible exception of the Chatham Island population whose survival interval after kiore arrival is simply not known, all populations were eliminated quickly, allowing little time for the potential fitness costs of inbreeding depression and genetic drift to weigh in. Persistence at very low numbers and the obligatory inbreeding which ensued over at least 83 years on Little Mangere Island contributed more significantly perhaps than the intervening *Old Blue-Old Yellow* bottleneck to the severe depletion of genetic diversity evident in today's black robin populations (Ardern and Lambert, 1997). But the steep rate of collapse over the population's last five years is more obviously suggestive of punishing habitat pressures rather than compromised fitness. How significantly genetic depletion contributed to the rate of decline and the failure to rebound naturally on Mangere Island was not quantified at the time and can only be inferred now from the demographic histories of today's recovered populations. This question is examined in Chapter Seven (Was Inbreeding A Problem?).

# CHAPTER FOUR
# MANAGEMENT OF EXTINCTION THREAT

## 4.0 Introduction

This chapter summarises and critiques the conservation measures employed by New Zealand wildlife managers between 1971-72 and 2007-08 to avoid total extinction of the black robins and return them to important parts of their natural range. The summary is the first to review black robin management in its entirety. Given the context, it cannot boast the detail of earlier histories, the fullest and most illuminating of which is Butler and Merton's (1992) description of events up until 1991-92. The longer view given here draws together information contained in a wide variety of documents, especially departmental instructions, summary reports, letters and e-mails or in black robin field records and hut logbooks. Some of these sources are held in public archives but none is published. Where possible, I have also referred to the field notebooks and personal diaries of project participants and project associates. I have made strenuous efforts to obtain copies of most records but some no longer exist, have not been placed at the disposal of my study or have become too widely dispersed to trace. Where documentary evidence is not available, I have drawn on the memories of the relevant wildlife managers or on my own recollections. The latter span 30 years of direct involvement in or close connection with the black robin recovery programme (1977-78 until present).

The summary benefits this study in several ways. First, it explains the ecological and institutional contexts in which black robin recovery was pursued. The directions taken to manage extinction risk in the black robin populations were often dictated by non-ecological factors operating in the working environments of successive conservation teams. Resource constraints were the most influential factor. In this chapter, I illustrate the inauspicious effects of such pressures on black robin management and the consequences for retrospective analysis of the data accumulating throughout the programme.

Second, the narrative explains that the species's recovery was accomplished through four distinct phases of management, each reflecting shifts in conservation imperatives. These shifts resulted in varying degrees of contact with the populations. In describing these phases, my intention is show how well or poorly the differing levels of contact served management of extinction risk. In the process, the summary explains the origins of the field data analysed by this study and the reasons for their variable coverage and quality.

Third, the summary sets the scene for Chapter Seven (Was Inbreeding A Problem?). It reveals the degree to which black robin conservation was small-population management as Caughley's (1994) declining population paradigm defines it. That is, management preoccupied with unnaturally small population size as a product of deterministic extinction pressures. Early conservation managers were justifiably concerned about the critical decline in black robin numbers and the external threat (habitat collapse) driving them lower. The remedy dictated by these concerns (remove the threat and increase population sizes) followed, if in fact it did not entrench, the New Zealand 'cure' as conventional conservation practice in this country to salvage critically threatened vertebrate species from extinction (Diamond, 1990; Atkinson, 1990, 2001; Wilson, 2004). As I have explained in Chapter One (Research Themes), this long-standing strategy has tended to treat the intrinsic risks of small population size—greater vulnerability to stochastic genetic threats—as secondary or inconsequential threats to viability (Caughley, 1994; Armstrong and McLean, 1995; Jamieson *et al.*, 2006). Black robin recovery placed its faith in eliminating the ecological pressures and raising population sizes quickly as insurance against any such viability problems. This optimism persists in the operative Black Robin Recovery Plan (Department of Conservation, 2001a) which makes no mention of stochastic genetic threats or precautionary management of them. Chapter Seven examines the wisdom in this optimism, especially as it might suffice as an on-going strategy to maintain the mid- and long-term viability of tomorrow's small, habitat-limited black robin populations.

Finally, this summary defines the black robin recovery project as an empirical test-case for the proposition that New Zealand's reduced and fragmented populations of terrestrial bird species, especially those on outlying islands, are inherently less susceptible to inbreeding depression (Craig, 1991, 1994; Craig *et al.*, 2000). As I have outlined in Chapter One, this proposition rests on the assumption that prolonged high rates of inbreeding in New Zealand's naturally small, isolated and largely sedentary bird populations would already have exposed to natural selection the deleterious recessive alleles responsible for inbreeding depression. The growing evidence that this may not be the case for all threatened insular endemic bird populations in all ecological contexts (Jamieson *et al.*, 2006; Jamieson 2009) argues for empirical testing of the assumption. As this chapter shows, the black robin offers a generally very detailed record of population recovery in which the emergence of viability problems is likely to be unobscured precisely because conservation management did not attempt to address them directly.

## 4.1 Management phases

Conservation of the black robins proceeded in four management phases:

1. 1971-72 until 1979-80: the *initial* phase of biological inquiry in the black robin's last surviving population on Little Mangere Island. During this nine-year period, the population declined towards total extinction. The phase was marked by the now-famous transfer in 1976-77 of the last seven individuals from Little Mangere Island's disintegrating forest fragment to a small, modified but regenerating tract of forest on neighbouring Mangere Island.

2. 1980-81 until 1989-90: the *intensive management* phase during which wildlife managers intervened to increase population sizes by boosting black robin productivity on Mangere Island (throughout the period) and on Rangatira Island (1983-84 until 1989-90). This phase commenced when it was apparent that, without human intervention, natural rates of productivity could not compensate for annual rates of adult and juvenile mortality in the tiny post-transfer population. This was the period of actively assisted population recovery.

3. 1990-91 until 2001-02: the *full-population* (or *post-management*) monitoring phase which followed the end of active intervention. During this phase, each black robin population was observed as intensively as resources would allow to determine whether it could continue to increase in size without further help. This 12-year phase marked the period of natural population recovery.

4. 2002-03 until present: the *sample-* (or *index-*) *monitoring* phase during which monitoring was reduced in intensity, scale and precision. Annual assessment of population trends relied on pre- and post-breeding walk-through surveys of abundance in defined population sectors and on monitoring of productivity in a smaller subset of the popula-

tion. During this period, attempts to establish a third black robin population on Pitt Island failed (2002-03 to 2005-06).

## 4.2 Initial Phase—Research and rescue: 1971-72 until 1979-80

As outlined in Chapter Three (History of Decline), systematic observation of the black robins commenced on Little Mangere Island on 29-30 March 1972, after breeding had ceased for season. From the outset, observations served management aimed at increasing the numbers and range of the species (Flack, 1971), an over-arching goal which guided all subsequent management. The initial objective of visits was to study black robin ecology and determine the status and composition of the vestigial population. Between March 1972 and the initial transfer of five individuals to Mangere Island in September 1976, 12 sets of observations were made, usually at the beginning and end of breeding seasons (Chapter Three: Table 3.1). Within the limits imposed by the timing of visits and the hesitant colour-banding programme, observers also monitored annual trends in population structure and size through head-counts of adults and offspring surviving during each period of contact (Flack, 1977). The number and identity of breeding pairs, the production of juveniles, and rates of recruitment and mortality were also assessed, with degrees of accuracy varying seasonally.

Other than the use of locally available invertebrates to attract birds and the marking of individuals with unique colour-band combinations, observers did not interfere with the black robins or manipulate their behaviour in any way. Colour-banding commenced during the inaugural visit in March 1972 and helped to define population size more accurately (Chapter Three: *Section 3.6.5*). In the four seasons which followed, 20 black robins were banded, five of them verified juveniles (Department of Conservation non-gamebird banding schedules, 1972-1975). Banding proceeded fitfully for the first three seasons. Local conditions reduced the effectiveness of capture techniques (clap-trapping, mist-netting), so that it was not until February 1975, near the near the end of the study project, that observers succeeded in marking the whole population (by then, 11 individuals). Banding experiences on Little Mangere Island informed the practices used later on Mangere and Rangatira Islands.

Observations proceeded in parallel with vigorous between-season debates on management options for the species, coupled with pilot studies of management alternatives on the New

Zealand mainland using the South Island robin (Flack, 1971, 1973, 1976d, 1977, 1979). This larger congener was then thought to be the most suitable ecological analogue and 'test-bed' but experience in later management phases demonstrated that the sympatric Chatham Island tomtit closer at hand would have been more appropriate. To obtain insights to black robin life-history, the ecology of South Island robins and their interactions with sympatric yellow-breasted (South Island) tomtits were also studied at this time (Flack, 1971, 1973, 1974a, b, 1976a, d). Unlike the debates and experimental work elsewhere, field observations on Little Mangere Island adopted a wait-and-see approach based on optimism that the population contractions witnessed in each successive season would correct themselves in the next. This optimism was ultimately dashed.

The continuing decline in black robin numbers threatened to deprive the population of its few experienced breeders after the 1974-75 season (Butler and Merton, 1992). Managers responded with a two-pronged strategy. First, the population on Little Mangere Island was to be increased *in situ* by improving habitat area and quality (Flack, 1976d, 1977). Second, the decision was taken to found a new population on adjacent Mangere Island at the end of the 1975-76 season. Initially, managers planned to transfer up to three unmated black robins deemed to be least important to the ancestral population (Flack, 1976c, 1977).

In the context of declining black robin numbers, the longer-term strategy of habitat enhancement seems ill-founded but it addressed two problems plainly visible to observers. Forest cover and quality on Little Mangere Island had been deteriorating year-by-year (Chapter Three: *Section 3.6.1*). And contrary to expectations, black robins remaining in the diminishing population were not occupying newly vacated territories, arguably because resource opportunities had diminished there (Flack 1976a, 1977). Managers anticipated that nurturing the habitat's natural regenerative processes would augment resource opportunities in the territories and trigger the hoped-for recovery. Habitat restoration acted also as insurance against failure of the transfer strategy over which—far from being optimistic—managers had long been suffering agonies of doubt (Morris, 1973; Flack, 1971, 1974b, 1977).

Large wire enclosures installed in black robin territories in 1973-74 had shown that forest cover would regenerate if the surface and burrowing activities of sooty shearwaters could be moderated (Flack, 1974a, b, 1976a, d, f). Saturation deployment of seedling enclosures was considered, along with supplementary-feeding of the black robins and the wholesale removal of Little Mangere Island's estimated 60,000 pairs of shearwaters (Flack, 1976c, d). None of these options was adopted.

To improve conditions further for the black robins, the tomtit population of Little Mangere Island (five adults) was culled (Butler and Merton, 1992). Earlier observations of aggressive interactions between the species had prompted fears that the black robins might be unable to compete successfully for resources and nest sites (Flack, 1976a, c, d, f). Mangere Island's tomtit population (19 individuals) was also culled ahead of the transfer (Flack, 1976c, f), eliminating the one species which would later prove crucial to black robin conservation on that island. In November 1973, planting commenced in Mangere Island's extensive grasslands to augment the meagre forest cover surviving the farming era. Estimates of plant numbers vary. Between 1974-75 and 1978-79, 150,000 – 160,000 akeake trees, 30,000 *Hebe dieffenbachii* and 4000 shelter-belt flaxes *Phormium* 'Chathams' were planted (Veitch, 1982; Amanda Baird, pers. comm., September 2008). Restoration was not expected to provide suitable habitat on Mangere Island for up to ten years (Flack, 1977), and long lead-times were anticipated for habitat improvement on Little Mangere Island (Atkinson *et al.*, 1973).

Alarming contraction in the number of black robins overran this two-pronged strategy. All seven individuals remaining were moved to Mangere Island in the 1976-77 season (Chapter Three: *Section 3.7*).

In the three seasons following the transfer, the wait-and-see management policy was resumed despite the extremely tenuous position of the species and cogent arguments for modest forms of intervention to increase productivity. Morris (1977c: 8) expressed dismay at the prospect of 'leaving the robins to it', arguing instead for supplementary-feeding and the installation of nest-boxes, measures which would later contribute significantly to black robin recovery. Cox and Merton (1980) recommended that the saturation density of other insectivorous passerines in Mangere Island's threadbare habitat (dunnocks, starlings, Chatham Island warblers, silvereyes, blackbirds) be reduced each autumn to relieve resource stress. This last recommendation was not implemented.

Between 1976-77 and 1979-80, monitoring of black robin breeding and survival often coincided with other work on Mangere Island but the timing of visits seldom allowed conclusive quantifying of breeding outcomes. Observers strove to colour-band each season's juveniles but by delaying this until after independence, they could not know precisely how many offspring had been produced originally. Apart from banding, a policy of minimal interference was adopted, conditioned by optimism that the black robin numbers would rebound naturally in the better habitat.

Midway through the 1979-80 season, it was apparent that numbers were unlikely to rise in response to the improved conditions and food availability. The population had declined by then to five individuals, and only one of the two pairs was productive (Table 3.2). The recommendation was made formally to address the population's inadequate reproductive output through direct intervention (Cox and Merton, 1980). The Little Mangere and Mangere Island populations had produced on average one yearling per year since 1971-72 (Table 3.3). Under the better conditions on Mangere Island, the population produced only 1.25 yearlings per year, insufficient to compensate for adult mortality (Table 3.3). It was proposed to induce black robin pairs to renest by removing first-clutch eggs to another sympatric species for fostering (Recommendation 4, Cox and Merton, 1980). In the absence of the culled tomtits, the most promising foster species was considered to be the ubiquitous Chatham Island warbler. Fostering was to be conducted *in situ* following generic principles derived from captive-rearing practice (Butler and Merton, 1992). These proposals were implemented under extreme urgency in 1980-81.

The forms of management adopted during this initial phase of contact with the species focused on ecological extinction pressures (habitat deterioration). This was justifiable given the critically low numbers of black robins, the limited knowledge of their biology and the uncertainty about their ability to cope with highly intrusive management. The logical remedies were to remove the threat from the population (improve habitat conditions on Little Mangere Island), and then to remove the population from the threat (transfer to Mangere Island). However, these strategies failed to achieve the initial research and management goals of increasing abundance and range because black robin numbers were also influenced by the stochastic demographic risks of small population size. Optimism that removal to better habitat would guarantee recovery was symptomatic of the degree to which this stochastic threat was underestimated.

During this initial management period, a variety of factors and decisions affected the quality and quantity of demographic data acquired. Inevitably, access to and from the precipitous heights of Little Mangere Island had been dictated by weather, which also curtailed work on the island. Operational requirements elsewhere often determined the time available for observations. Life alongside the black robins in their inhospitable refuge was physically and logistically taxing (Flack, 1976c). As a result, contact was unduly brief by later standards, varying in duration from just a few hours to 11 days ($\bar{x}$ = 5 days). The timing of visits did not always coincide with the peak of breeding activity. Observers were seldom able to determine the fate of breeding attempts or the precise causes of mortality in eggs, young and adults. The parentage of the few roaming juveniles encountered was frequently a matter for speculation. Uncertainties about the age and identity of individuals were created by the inability to mark the whole population, a problem aggravated by the decision to colour-band offspring at the juvenile stage only. This policy complicated contemporary assessments of relatedness and adult age structure. Finally, as black robin numbers decreased, observations grew progressively less intrusive to minimise disturbance. This had predictable consequences for first, understanding of black robin breeding ecology; second, assessment of the bird's tolerance to intervention, and third, the depth and precision of demographic data acquired.

Scarce data on individual longevity, productivity and relatedness in this ancestral population hinder analyses of decline during this period. Limited knowledge of parentage has also obliged me to rely on underestimates of inbreeding and kinship coefficients in the black robin pedigree to assess inbreeding effects on population recovery (Chapter Seven). My attempts to define individual life-histories have also been frustrated by the generalising and contradictory accounts provided by the secondary sources available (see for example the conflicting summaries of Flack, 1974a, 1976a, and Butler and Merton, 1992). Black robin management had yet to evolve a culture of systematic reporting which included detailed annual tabulation of survival, the fates of individual breeding attempts and seasonal productivity. Only Morris (1973) provided a list in which the pairs of one season (1973-74) were identified by their colour-band combinations. However, despite the knowledge gaps created by justifiable concern to minimise disturbance, the demographic information gathered prior to the 1976-77 transfer was significantly more detailed and insightful than afterwards. The intrinsic factors predisposing black robins to decline—short breeding seasons, low reproductive success and high mortality among adults and juveniles (Flack, 1974b, 1976d, 1977)—were fundamentally understood.

The stand-off policy adopted on Mangere Island after the 1976-77 transfer obliged managers to accept pre- and post-breeding census counts as the sole quantitative measure of population viability. The policy permitted few insights to reproductive effort. When the timing of visits allowed, managers investigated nests which were easily accessible but did not intrude on others which required more disturbance to find. As on Little Mangere Island, information on clutches or brood fates remained undetermined more often than not. The ability to predict population declines was limited therefore by knowing little about the causes and extent of breeding failures. This information might have quickened responses to the stalled black robin recovery and strengthened vigilance for inbreeding depression. Observations were not close enough to acquire basic biological information about incubation and fledging intervals, or the time to independence (Butler and Merton, 1992).

However, post-transfer observations on Mangere Island made significant advances for black robin conservation. The entire species remained colour-banded, consolidating the foundation for a near-complete genealogical record spanning another two decades. This investment served management needs of the time but is now a critically important asset for assessments of extinction vulnerability (Chapter Six: Population Trends After 1980, and Chapter Seven). Monitoring the activities and pairings of each black robin was just sufficient to document the productivity of the two female breeding lines remaining in the tiny population (Chapter Three: *Section 3.7*). Relatively accurate estimates of hatching or fledging dates were made for the few juveniles banded. Rates of mortality prompted thinking about the threats posed to young and adults alike by avian predators, especially starlings (Butler and Merton, 1992). Systematic mapping of territories and nest sites began. The following management phase improved radically on these advances.

## 4.3 Phase Two—Intensive management: 1980-81 until 1989-90

Active intervention in black robin breeding commenced in September 1980 and marked the beginning of the resurgence in numbers. Managers then had at their disposal five of the six black robins alive at the end of the previous season (two adult pairs and a yearling female). Full-scale intervention concluded ten seasons later at the end of the 1989-90 season when 113 individuals were known to be alive (Chapter Six, Table 6.3).

This period of management is defined by the goals and operational requirements of the cross-fostering programme whose principal aim was to raise black robin numbers rapidly by boosting annual productivity. This was the only pragmatic option at that time, but at the outset, managers were convinced that the crisis was induced wholly by external factors and not in any way by genetic degeneracy in the species. Raising population numbers quickly was regarded therefore as the best means of achieving a full recovery of the species (Merton, 1980).

By obligatory renesting, females were forced to lay more than their usual one clutch per year (Butler and Merton, 1992). Cross-fostering necessitated the founding of a larger sister population on Rangatira Island and the regular transfer of birds between the two populations, thus satisfying the ancillary aim of extending the species's range. These forms of management were extremely effective (Chapter Six) but could not avert the bottleneck event which defines the beginning of the black robin's recovery. The death of the eight-year-old female *Old Green* in November 1986 terminated both her breeding line and its unrealised potential to cultivate genetic diversity in black robin populations (Chapter Three: *Section 3.7*). From this point, management was obliged to work solely with the descendants of the founder pairing of *Old Blue* and *Old Yellow*.

Cross-fostering commenced with the two first clutches laid in the 1980-81 season (10 and 15 October). Before placing the first eggs in warbler nests, managers experimented to assure themselves that both species would tolerate disturbance at the nest and the interruption of normal nesting routines. Pilot trials used the eggs and nestlings of other possible foster species (silvereyes and dunnocks). The techniques and innovations developed during this season informed the fostering practices used until 1989-90. In later years, experimentation preceded commitment to any new measure if time and contingencies allowed.

Despite the overlap with black robin diet and concurrent breeding, the warblers proved unsuitable as a foster species. In the 1980-81 and 1981-82 seasons, 11 warbler pairs received eggs (in one instance, nestlings) from seven of the 12 black robin clutches laid but none succeeded in raising broods beyond 11 days. Evidence suggested that malnutrition through problems with food type rather than quantity was the most common cause of nestling mortality (Butler and Merton, 1992). In 1981-82, warblers were relegated to temporary egg-holding duties and were permitted to brood black robin nestlings for no longer than seven days (Merton, 1981). Fostering to tomtit pairs on Rangatira Island was trialled successfully. The three black robin nestlings transferred to the island in 1981-82 were raised throughout by tomtits and returned to Mangere Island as juveniles in accordance with restrictive conditions imposed by the government agency then administering Rangatira Island.

In spite of the losses in warbler nests during the first two seasons, cross-fostering demonstrated its value. By compelling black robin females to lay additional clutches, productivity climbed to an annual average of 2.25 juveniles pair$^{-1}$ (this study). The time between clutches was compressed, improving survival prospects for second-clutch offspring.

On the threshold of the 1982-83 season, black robin managers were confident of having perfected the necessary cross-fostering techniques (Merton, 1982). A series of proposals was made which set the pattern for cross-fostering and other forms of management over the next seven seasons. The use of warbler pairs was discontinued entirely. Black robin eggs and nestlings were to be fostered instead to tomtit pairs on Rangatira Island despite the risks associated with the uncomfortable 15 km ocean journeys between islands by fishing boat (weather, timing, and the handling of fragile mobile incubators). As a matter of policy, it was decided to exploit productive potential further by transferring second clutches to Rangatira Island. Third clutches (if any) were to be retained for rearing by black robins to ensure pair stability (Merton, 1983b). This last decision was providential for the management of later mal-imprinting problems (Chapter Eight: Hybridisation). Along with the practice of transferring nestlings back to black robin nests for fledging, this last measure had the potential to preserve pair bonds from any effects of multiple nesting ‘failures’.

The need to establish a second black robin population on Rangatira Island was apparent by the end of the 1981-82 season. The fostering potential of Mangere Island’s few black robin pairs was limited and the precautionary culling of tomtits in 1976-77 had deprived Mangere Island of its only alternative foster species. Reintroduction of black robins to Rangatira Island could capitalise on the fostering potential of the largest tomtit population in the

Chathams archipelago. Aside from the safety in having a second geographically discrete black robin population, there were three additional benefits. The scale and frequency of inter-island transfers could be reduced; counter-productive congestion in Mangere Island's tiny 4.5 ha habitat could be avoided, and (eventually) two discrete black robin 'breeding-lines' could be created (Merton, 1982, 1983b).

The nucleus of Rangatira Island's adult population was a pair of two-year-old black robins with breeding experience, moved from Mangere Island in January 1983. Two further adults followed in June 1983. They and their offspring flourished under intensive management so that by the mid-1980s, the Rangatira Island population had become the focal point of conservation efforts. The small Mangere Island population became principally a centre for harvestable production.

Inter-island transfers were indispensable to this period of management. Fifty-three eggs (36.8% of eggs laid) and four nestlings were transferred from Mangere Island to black robin and tomtit foster-nests on Rangatira Island by the end of the cross-fostering project. Eight juveniles and 11 adults were also moved (Chapter Six: Table 6.2). Movements from Rangatira Island were much less frequent and were usually intended to sustain the Mangere Island population itself (two eggs, eight nestlings, five juveniles and seven adults).

Transfers served other purposes. To maximise seasonal productivity early in the project, managers ensured that proven breeders were mated by moving individuals to correct periodic sex-ratio imbalances. Conversely, individuals were transferred to break unproductive pair-bonds. The founder female *Old Blue* was (literally) a casualty of this last practice in November 1983 when retired to Rangatira Island in her 13th year of life. The option was also available to break pairings between closely related individuals (Merton, 1983b). Established breeding pairs were not moved, a policy retained until the 2002-03 season transfers of black robins from Rangatira Island to Pitt Island (Aikman and Thompson, 2003; see Chapter Four: *Section 4.5*).

While Mangere Island remained tomtit-free, black robins known or suspected to have become mal-imprinted on tomtit foster-parents could be sent there to reduce the risk of cross-breeding (Chapter Eight). Mal-imprinting was first suspected in 1981-82 (Butler and Merton, 1992), prompting a precautionary policy of returning all tomtit-fostered black robins to Mangere Island, and establishing on Rangatira Island only black robins which had been fledged and raised by their own kind (Merton, 1982). In practice, this policy proved difficult to implement. While black robin numbers were very low, managing the risk of extinction took precedence over the lesser risk of cross-breeding. The policy of returning fostered individuals to Mangere Island lapsed and fears of cross-breeding were eventually realised (Chapter Eight).

The operational requirements of cross-fostering grew considerably with each successive season's increase in the number of black robin breeding pairs. From the outset, five cross-fostering prerequisites increased the complexity of management: (1) the requirement to synchronise breeding in both black robin and potential foster pairs; (2) the renesting of black robins and tomtits whose chosen nest was sited inconveniently for cross-fostering; (3) the synchronising of (ideally) up to six foster pairs for each clutch of black robin eggs; (4) the careful manipulation of nest contents in donor, recipient and back-up pairs to ensure that egg or nestling transfers were reversible in the event of desertion or failure; and (5) the necessity to return nestlings to black robin pairs before fledging in order to minimise the risk of mal-imprinting. A sixth humanitarian constraint was adopted as a matter of pride. Displaced tomtit eggs and nestlings were themselves redistributed whenever possible to suitable foster nests (pers. obs.).[39] These operational complexities were exacerbated significantly by inconvenient variations in the timing and numbers of tomtits breeding on Rangatira Island in many seasons.

The synchronising of tomtit pairs anticipated fostering contingencies which might jeopardise the safety of precious black robin eggs and nestlings (nest desertion, pair-bond failure, inadequate feeding at the nest). Several synchronising techniques were used: removal of inappropriately timed or poorly sited nests during construction, the use of plastic eggs to prolong incubation or to preserve a female's commitment to a nest, and the cold-storage of un-incubated eggs (Butler and Merton, 1992).

Cross-fostering activity commenced each season by locating all paired black robins and assessing their breeding status. All black robins had been conditioned from the late nes-

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[39] Even so, 99 tomtit eggs were collected from Rangatira Island during the cross-fostering seasons. The eggs included those deserted, failing to hatch or sacrificed (Powlesland *et al.*, 2001).

tling stage to associate hand-clapping with food hand-outs. Birds approaching observers on these cues were called ‘friendly’. Tomtit foster pairs were generally conditioned as adults (and continued to respond in later years even if not used again for cross-breeding). Thereafter, pairs and nests were located by feeding the males of both species and following them to their mates. Unmated black robins, fledglings and juveniles were monitored in the same way. Breeding pairs were fed regularly to bring nesting forward and to ensure an adequate supply of food to nestlings and fledglings. Black robin solo-parents received special attention. Initially, supplementary-feeding relied on locally sourced invertebrates but eventually, when black robin numbers overwhelmed the inefficient food-gathering capacities of field-workers, commercially cultivated *Tenebrio molitor* larvae were substituted (Kennedy, 2010. Black robins and tomtits accepted these unfamiliar larvae with alacrity.

Nest-boxes were trialled first in the 1980-81 season to supplement Mangere Island’s limited range of natural nest cavities, and were in widespread use on both islands by 1983-84. Nest-boxes offered important advantages. They increased nest-site options in habitats occupied by other hollow- and cavity-nesting passerines (dunnocks, starlings, blackbirds). Black robin and tomtit nests were moved into boxes after egg-laying to protect their clutches, broods and females from starling predation and nocturnal petrel-strikes. Both species accepted nest transfers readily. Once nests were installed and incubation had resumed, the boxes themselves were moved to sites appropriate for easy access and safe manipulation of contents. To minimise disease and parasite threats to black robin nestlings, the nest-box design was modified so that recycled fumigated nests could be exchanged for old ones at regular intervals. In addition to protecting their fragile contents, nest-boxes improved management efficiency and knowledge-gathering. These benefits outweighed the costs of nest desertion or egg loss through handling accidents, the incidence of which was low and well within limits tolerated by managers of the time. Rooves and plastic mesh were installed over natural nests to protect them *in situ* from weather, predation and petrels.

Cross-fostering continued unabated in both populations until the end of 1988-89, a season in which 25 breeding pairs (55 clutches) had been managed on both islands. Fostering to black robin nests ended in 1989-90. By then, managers felt able to manipulate breeding to forestall egg-laying late in the season, thereby minimising the higher rates of mortality in late-season fledglings (Merton, 1987). Management of so many fostered eggs and nestlings was an extraordinarily complex undertaking, demanding constant surveillance of foster pairs and back-ups in case of failures, and the continual evolution of contingency plans. The growing numbers of experienced black robin pairs relieved the pressure when cross-fostering approached or exceeded the finite limits of tomtit numbers.

In April 1989, managers reintroduced tomtits to Mangere Island from Rangatira Island (Merton, 1989, Grant, 1989), confident that the island's black robin population (n = 14) could compete successfully for space and resources in the limited habitat available in the Robin Bush. The risk of cross-breeding was considered to have passed when the last of the mal-imprinted black robins had been lost from the population through natural attrition (Chapter Eight). The liberation succeeded in founding a new tomtit population on the island after an absence of 11 years.

In 1988-89, managers sought assurance that the black robins could cope naturally by experimenting with differing degrees of productivity enhancement. Pairs on both islands were divided into three groups comprising equal numbers of experienced and inexperienced breeders. Productivity in two groups (one subjected to conventional cross-breeding and supplementary-feeding, the other to nest protection only) was compared with that of the third, undisturbed control group (Merton, 1988). The experiment's sample sizes were small and unruly (black robins deserted pairings in one group to form pairings in another). Even so, the trial revealed that production of juveniles by unmanaged pairs was approximately half that of fully managed pairs (Butler and Merton, 1992). Despite the reductions in output, the increase in total numbers during the season (38.9%) was within the range of annual increases over the preceding four years (18.8 - 45.8%; this study). Ironically, this encouraging result fuelled mounting criticism within the newly constituted Department of Conservation (DOC) that the cross-fostering effort was excessive and unjustified (Butler and Merton, 1992).

At the end of the 1988-89 season, when total post-breeding numbers stood at 95 (81 on Rangatira Island, 14 on Mangere Island; Table 6.3), black robin managers agreed to halt all cross-fostering and other forms of intervention. In their place, a comprehensive monitoring regime was proposed. The intention was to eliminate all forms of disturbance to gain a true measure of natural population trends. Of necessity, the new project sanctioned the individual colour-banding of birds and the use of food hand-outs to trace them. Supplementary-feeding was discontinued. The old habits proved hard to break, however, especially when managers witnessed the construction of doomed nests, nest-mite irruptions, the wastage of eggs and nestlings, or the demise of black robins through preventable accident or misadventure, all which would have been remedied previously. The inaugural monitoring season (1989-90) was not completely free of intervention. ‘Rimshots’ (eggs laid on nest rims, the perplexing phenomenon first detected in 1984-85; Chapter Two: Black Robin Biology, and Chapter Six) were returned to incubation, often producing fledglings which technically should not have survived. Some deserted eggs were salvaged and fostered to other black robin pairs. A few nest sites were protected and mite-infestations in some nests were treated with insecticides. At least one female solo-parent received supplementary-feeding assistance. These residual forms of intervention were discontinued in later seasons but because they had complicated assessment of black robin viability in this season, the three-year monitoring programme was restarted from 1990-91.

The cross-fostering programme had been labour- and time-intensive but the conservation efforts of this period averted total extinction of the species. Numbers had been raised over ten breeding seasons from five individuals in September 1980 to 93 in October 1990. Annual productivity averaged 1.88 juveniles pair$^{-1}$ season$^{-1}$ (this study). The two sister-populations consolidated during this period were closely linked genetically through inter-island transfers, but these were about to cease, closing each population to gene flow and the risk of disease or other threats migrating from one to the other.

Management of extinction risk benefited from continuity in both leadership and field staff, and from the near-continuous contact with the populations throughout most or all of each breeding season. The continuity resulted in such intimate knowledge of the populations, and of the individual black robins themselves, that critical problems could be anticipated or detected before they became insurmountable. Managers learned where to find important breeders and could anticipate their behaviour. The mal-imprinting issue arising from early cross-fostering practices was corrected promptly before hybridisation threatened project outcomes because managers were alert for signs of abnormal behaviour, were there to detect them and were equipped with the necessary knowledge to respond appropriately.

Although lapses occurred, the data gathered as a by-product of management between 1980-81 and 1989-90 set a very high standard for precision, detail and recording practice.

Knowledge of black robin biology advanced step-wise through what amounted to the first in-depth study of ecology and behaviour. Visits made to the islands during the programme's first winters extended this knowledge and reinforced for managers the harsh nature of the conditions endured by black robins between seasons (pers. obs.).

Explicit management imperatives of full-population census (prior to and after each breeding season) and careful attention to each black robin's breeding preserved the integrity of the genealogical record founded at the initial transfer from Little Mangere Island in 1976-77. With very few exceptions, all breeding attempts were monitored, the vast majority from beginning to end. The outcomes of occasional late-season broods might remain unknown when observers departed the islands, but offspring surviving in the next season gave valuable clues. Clutch numbers and sizes were recorded, and where possible the fertility of eggs was assessed before and after failure. Every black robin was uniquely colour-marked while in the company of parents (usually as 10- to 19-day-old nestlings or at the next convenient opportunity), made 'friendly' and located repeatedly throughout each breeding season to determine mates and fate. The causes of mortality at all life-stages were considered more fully though not always conclusively (Chapter Six).

Data collection practices developed during this phase introduced habits adopted as standard practice in the following management phase. To avoid confusion and the inevitable transcription errors, managers referred to all black robins by given names rather than by names relating to localities or colour-band combinations. Rudimentary field log-books were introduced from 1981-82 in which summary diaries of each day's black robin events were kept alongside other biological and social accounts of island life. Demographic and narrative detail varied considerably according to the literacy, mood and maturity of observers. The breeding of each pair was tracked systematically for the first time and was plotted schematically on charts by the end of the period. Daily tick-charts of black robin sightings made their first appearance as a means of tracking survival and disappearances (the latter were investigated). Annual and multi-season black robin data were tabulated consistently for the first time. All of these practices were responses to the exigencies of cross-fostering but became instrumental in shaping a culture of black robin management which insisted on acuity and quality in both the record and labour of the recovery programme. Expectations of this sort were severely tested by the institutional circumstances of the next management phase (*Section 4.4*).

During this period, managers had concluded from early successes with multiple-clutching that black robin fitness and resilience had not been affected significantly by inbreeding in the ancestral population (Merton, 1980). They were aware that inbreeding after the *Old Blue – Old Yellow* bottleneck might threaten viability in the long-term (Merton, 1983b) and remained alert for signs of inbreeding depression in the early seasons when pairings between closely related individuals were unavoidable in such a small population. The establishment of the second population on Rangatira Island gave some latitude to separate closely related individuals but it is not clear from the records how often this option was invoked specifically as an avoidance measure. Fears that inbreeding depression might be a problem began to recede when all 16 eggs laid by two brother-sister pairs in 1983-84 proved to be fertile (Merton, 1983a; Butler and Merton, 1992). High rates of egg fertility (90%), egg hatchability (80%) and juvenile survival to year one (70%) reported for an undisclosed period were taken to indicate the absence of harmful inbreeding effects (Butler and Merton, 1992). These rates agree with my estimates for 1980-81 to 1989-90—80.9% hatch-rate of eggs incubated to full-term; 71.7% survival of juveniles to adulthood (Chapter Six: Table 6.13). The laying of eggs on nest rims was the only behavioural abnormality to raise suspicions (Butler and Merton, 1992), and this was managed by returning the rim-shots to incubation.

At the conclusion of successful intensive management, geneticists were invited to assess the genetic status of both populations (Don Merton, pers. comm.). Benchmark profiling of variability between individuals and populations was sought, along with advice on potential problems ahead. This research was conducted during the post-management phase (Chapter One: *Section 1.5*). In general, however, concerns about inbreeding depression were afterthoughts which had little effect on the design and direction of the recovery programme.

## 4.4 Phase Three—Post-management monitoring: 1990-91 until 2001-02

Post-intervention monitoring aimed to assess whether the two black robin populations were capable of sustaining themselves naturally, without further management (Kennedy, 1993a). As a minimum, monitoring was expected to yield authoritative pre- and post-breeding estimates of abundance. It was immediately apparent however that this could not be achieved unless every individual was uniquely colour-banded and made ‘friendly’. This objective was pursued diligently for the most part, thereby continuing the genealogical record. In addition, caution argued for preserving continuity in the knowledge of productivity inherited from the cross-fostering years. This was felt to be indispensable for interpreting emerging trends and highly advantageous should remedial action be necessary to correct population declines. As with the data gathered during the initial phase of management (1971-72 to 1979-80), observations in this new phase recorded black robin behaviour largely unmodified by management actions, though in considerably greater detail.

Essentially, monitoring teams followed the routines of the past, this time with their hands firmly in their pockets. Monitoring was scaled back from the intensity of the cross-fostering years, but—at least in the earlier seasons—observers remained in the field for the duration of breeding. They visited all black robin pairs and unmated individuals at two- to five-day intervals (more frequently close to hatching or fledging dates). The project aimed to colour-band all individuals, account for each one throughout the season, record all pairings and follow all breeding attempts to their conclusions. The timing of mortality at all life-stages was documented as closely as possible, and comments were made on possible causes. As during the management phase, incidental information was gathered on dispersal and distribution, habitat occupancy, predation, evidence of disease and physical abnormalities, unusual or aberrant behaviour, climatic conditions (through daily maximum-minimum temperature readings), habitat changes and interactions with other species. Much of this was narrative comment.

Initially, three breeding seasons were to be monitored but because the false start in 1988-89 did not give a true indication of population trends, a fourth season was added (1993-94). Responsibility for planning of the monitoring project fell to the newly established Black Robin Recovery Group, a small group of black robin specialists from within and outside DOC. The group first met in September 1991 and had compiled the first formal multi-year recovery plan for the species by October 1993. This made the case to continue full-population monitoring on both islands until a third viable population was established, preferably within the species's natural range (Kennedy, 1993a). Ultimately, the founding of a third population on nearby Pitt Island (the preferred option) was hindered by the failure of DOC to secure from the Pitt Island community consent to eradicate feral pigs, weka, cats and mice, the first three of which were highly valued locally (see for example Walls *et al.*, 2000). Therefore, the monitoring project continued after 1993-94 and persisted until 1998-99 on Rangatira Island and 2001-02 on Mangere Island.

From the outset, the project drew criticism from under-resourced managers of other threatened species in the Chathams region. On an annual basis, black robin managers were urged to curtail the duration and intensity of field work, especially by reducing the frequency of visits to territories and the intensity of productivity monitoring. In response to these pressures, managers experimented reluctantly with episodic monitoring of the smaller Mangere Island population. Between 1990-91 and 1992-93 (inclusive), brief visits to the island were timed to coincide with the onset of breeding, its conclusion and the anticipated banding dates for nestlings in-between. This experiment was a return to the approaches taken to monitoring on Little Mangere and Mangere Islands prior to 1980-81. It yielded such patently inadequate information on black robin numbers, pairings, breeding attempts (some of which were missed altogether), productivity and survival that the original monitoring regime was reinstated in 1993-94. Though well-intentioned, these cost-saving measures opened the largest breaches in the black robin pedigree. Undetected cross-breeding events laid the foundations for another entirely unexpected extinction crisis in the years ahead (Chapter Eight).

In this stressful operating climate, project leaders persevered with full-population monitoring (Department of Conservation, 1995, 1996a; Kennedy, 1996a). Once in the field, observers strove to preserve monitoring quality and intensity through an unspoken policy of persisting with business as usual. Relatively detailed demographic data was acquired from both populations. The Rangatira Island pedigree remained almost wholly intact. Business as usual yielded valuable dividends for black robin conservation. Aside from detecting the development of a potentially calamitous black robin x tomtit hybrid swarm on Mangere Island, the prolonged and detailed data sequences allowed more detailed tracking of demographic trends. In addition, important research into inbreeding effects and levels of genetic diversity in the black robin populations (Mallinson, 1992; Ardern and Lambert, 1997; Ma and Lambert, 1997b) was strengthened by the knowledge of life-histories and familial relationships. Among other benefits of a lengthening overview, monitoring experience accumulated. This ensured that lessons of the past were applied, avoiding costly repetition of mistakes, misjudgements and misinterpretations.

To cope with rising population sizes and associated increases in the volume of data, tracking and recording methods were refined. Field information was cross-checked on a daily basis so that errors could be rectified immediately, if necessary through a return visit to the territory of interest. The goal was to account for the fate of every egg laid in a season. Breeding progress was tracked on large wall-charts so that nest or territory inspections on key dates were not missed (egg-laying, hatching, banding of nestlings, fledging). Breeding observations and commentaries on behaviour were recorded for each pair in log-books which centralised information. The activities of unmated birds were followed in the same way. Daily ‘roll-call’ charts were essential means of alerting observers to the unexplained absences of adults or offspring. The practice of summarising daily work activity and weather conditions in hut logs continued from the cross-fostering era.

Understandably, the operational demands of monitoring escalated significantly as population sizes increased season by season. Following the growing numbers of itinerant juveniles was particularly taxing. At the same time, however, the institutional arrangements of DOC weakened capacity to meet these demands. Internal arrangements were largely out-of-step with the particular demands and contingent nature of wildlife management (Kennedy and Perkins, 2000; Kennedy, 2003). The supply of experienced black robin observers dried up, compelling project leaders to fall back on unqualified staff and volunteers who lacked the experience or intuition necessary to interpret and anticipate black robin behaviour. Field work often commenced late to save funds and concluded prematurely to comply with DOC’s inflexible administrative calendar. As a result, reliable pre- and post-breeding censuses could not be conducted and late fledglings could not be made ‘friendly’ for tracing in the following spring (Kennedy, 1994a, b). Recovery planning for the following season was almost always obliged to proceed on incomplete understanding of the season in progress.

For these reasons, the demographic data of the monitoring years were more variable in quality and coverage than the data gathered previously. For example, the fertility of eggs which failed to hatch was not routinely checked nor did field-workers always check for rimshots during nest inspections. Important information on the causes and timing of mortality or the disappearance of eggs, nestlings and fledglings was lost when visits to nests and territories became less frequent in the latter part of the monitoring phase. Little more was learned about nest predation or the species responsible for it, and the incidence of overlooked nests (and therefore of juveniles of uncertain parentage) increased as populations expanded. Black robins on population peripheries were increasingly neglected, especially by inexperienced observers not as attuned to the need to search for them or as adept at doing so. With the notable exceptions of Atkinson (2003) and Roberts (2004), habitat character and quality was not quantified systematically on either island. As a result, understanding of successional changes in forest structure and their implications for black robin viability remains largely anecdotal.

Under extreme resource stress in late 1997, the Black Robin Recovery Group sought advice from DOC scientists, conservation associates and external conservation biologists on the wisdom of continuing with full-population monitoring (Kennedy, 1997). I have not been able to locate the responses on official files, but the balance of opinion shared the views of Hay (1998) who favoured monitoring of lesser intensity while acknowledging the value of what had been achieved. To support their recommendations for reduced effort, most respondents alluded to the positive growth trajectories in the two black robin populations. In the meantime, full-scale monitoring continued on both islands in the 1997-98 season. By 1998-99, the programme had passed in its entirety to fresh but inexperienced hands through another administrative restructuring of DOC. In addition to a rushed operational hand-over, the new institutional arrangements favoured stricter local autonomy (Kennedy, 2003). As a result, the incoming project leaders found themselves obliged to proceed without meaningful access (then and on-going) to the long-term experience of the previous programme leaders and observers. Unfamiliar with the long-standing conventions of monitoring, well-meaning new-comers disturbed the demographic record by intervening in breeding, in particular by salvaging rimshots (Thurley, 1999). In the same season, the first in a succession of commercial wildlife contractors was engaged to conduct the fieldwork. This practice of ‘out-sourcing’ black robin management compensated for the chronic shortage of internal skills but ultimately it weakened management continuity and institutional familiarity with the populations.

At the conclusion of breeding in March 1999, 199 robins were judged to be alive on Rangatira Island (54 breeding pairs) and 71 were alive on Mangere Island (20 breeding pairs)—the highest number of black robins in existence for more than a century (Tables 6.5 and 6.10). This proved to be the final season of full-population monitoring on Rangatira Island. Three seasons later when full-scale monitoring ceased on Mangere Island, post-breeding numbers there had dipped to 63 robins (17 breeding pairs).

Management during this phase relied on close-order monitoring of populations as the simplest way to detect new ecological threats and harmful trends (Kennedy, 1993a). Given that monitoring was the only management tool adopted, managers were inclined to protect its quality and coverage from the effects of chronic resource shortages by treating the data-gathering and the data themselves as the principal objects of interest. This was clearly beneficial in that it preserved close contact with the populations and a demographic record capable of interrogation for viability threats. However, the habit discouraged critical assessment of which population parameters were the best to monitor. For this reason, and because positive growth trends in both populations did not argue for doing so (Hay, 1998), the field data were not analysed systematically between seasons. Instead, data were simply collated and subjected to summary analysis only, often in rudimentary end-of-season reports to the Recovery Group (see for example, Kennedy, 1996a; Bell, 1998). Few reports attempted to fit what had been observed to longer-term views.

The recovery strategy for this period acknowledged the possibility of inbreeding depression as justification for monitoring but stipulated no specific measures to minimise it (Kennedy, 1993a). Intervening to manage any such threat would have contradicted the primary goal of monitoring, which was to measure wholly undisturbed population trends. In practice, field observers remained alert for signs of physical or behavioural abnormalities which might suggest inbreeding depression. Otherwise, the programme relied principally on a change in population sizes to signal more serious problems. By this relatively crude numbers-watching measure, subtle fitness-related declines in productivity and survival measures were likely to be hidden by the volume of data accumulating. There was assurance taken that at least high quality data were accumulating, putting ‘money in the bank’ for unforeseen contingencies. Reduced sensitivity to inbreeding risks was also vindicated by investigations of black robin genetics which concluded that inbreeding depression and the anomalously low genetic diversity in the black robin genotype showed no apparent effects on the vital rates of either population (Chapter One; Mallinson, 1992; Holmes, 1994; Ardern and Lambert, 1997).

The policy of preserving the level of demographic detail inherited from the cross-fostering era resulted in monitoring which exceeded the standards and expectations of similar projects elsewhere in New Zealand, even for other critically threatened species on the same islands (Forbes’ parakeets, Chatham Island petrel, New Zealand shore plover). The project was heavily criticised for this despite having detected serious threats such as hybridisation on Mangere Island (Chapter Eight) which monitoring of reduced intensity had missed. The single-species focus was regarded as out-of-step with new ecosystem-scale management imperatives (Department of Conservation, 1996b). Other critically threatened species in the region competed for its resources, their shortages aggravated by difficulties with biodiversity funding inequities nationally (Department of Conservation, 1997; Kennedy and Perkins, 2000). These pressures prevailed in the next management phase when monitoring was radically reduced in intensity.

## 4.5 Phase Four—Sample-monitoring: 1999-2000 until present

The new managers assuming full responsibility for black robin recovery in 1998-99 were predisposed to reducing monitoring intensity. In September 1998, prior to the onset of breeding, they conducted population-indexing trials on Rangatira Island to assess the feasibility of alternative, less labour-intensive monitoring techniques. Internal reviews questioned the value and cost-effectiveness of full-population monitoring. Hay (1999:1) concluded that monitoring had contributed little to management of the species—'intensive monitoring has been the management'. At the end of the 1998-99 season, the Recovery Group was confident that the two populations were secure enough with numbers at 254 (O'Connor, 1999) [40] to reduce monitoring intensity (Department of Conservation, 2001a).

The new managers were mindful of the risks in abandoning full-population perspectives. The debate preceding the decision to reduce monitoring considered the many ways in which index-monitoring might disadvantage correction of future problems. Concerns were expressed about ability to detect declines quickly, to detect hybridisation, to select the right founders for new populations or to find 'unfriendly' black robins. Experienced observers warned that thorough familiarity with the populations (including the 20-year-long genealogical record) could never be recovered once contact was interrupted or minimised (Department of Conservation, 1999). There was a risk that the knowledge lost through less intensive monitoring would be critical to defining the factors at play if negative trends developed (Kennedy, 1999). The failure to analyse earlier data deprived the debate of insights to which vital rates might account for future population changes. No agreement was

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[40] The post-breeding total was actually 270 (see Chapter Six: Table 6.3)

reached on which population parameters should be measured by index-monitoring regimes.

Despite these concerns and warnings that the ‘friendliness’ of the black robins was a complication likely to inflate population estimates (Hay, 1999), the Recovery Group endorsed Hay’s (1999) recommendation that distance-sampling be adopted immediately (Department of Conservation, 1999). To test the accuracy of distance-sampling, its estimates of population size on Mangere Island were to be tested and calibrated against censuses conducted during a further season of full-population monitoring. Full-scale monitoring was to cease on Rangatira Island but breeding pairs in a standardised area of habitat (easily accessible tracts of West Woolshed Bush) were to be monitored annually to obtain measures of productivity, pair stability and the ratio of paired to unmated birds (Department of Conservation, 1999).

The new monitoring strategy was formalised in a revised recovery plan (Department of Conservation, 2001a) which retained the long-standing focus on disease and ecological threats to extant populations and the goal of founding more populations in the region. Pitt Island was still the preferred site for a third population but the plan also favoured returning black robins to Little Mangere Island, despite acknowledging that this population would always be small. The genetic ramifications of such an inbred population were not mentioned. The plan required all black robin populations to be stable and self-sustaining. It set a minimum of 250 adults (in total) as its viability benchmark. Genetic concerns raised in the earlier plan (Kennedy, 1993a) were dropped.

Distance-sampling was abandoned on both islands after one season’s trial (1999-2000). When run in parallel with full-scale monitoring which required a ‘friendly’ population, index-counts on Mangere Island gave significant over-estimates of population size (Thurley, 2000). The natural inclination of black robins to approach observers also did not suit the monitoring technique in which distance from observers at the initial sighting was a fundamental criterion (Hilary Aikman, pers. comm.). Mark-resighting was adopted instead, a method capitalising on the black robin’s confiding behaviour. The new method was calibrated against head-counts from further full-population monitoring on Mangere Island in 2000-01 and 2001-02.

From 2000-01, both populations were monitored through mark-resighting surveys prior to and after breeding (in some seasons, at only one of these times). Surveys were supplemented by recording incidental black robin sightings. Assessment of breeding pairs and nesting attempts in the sample area on Rangatira Island was discontinued after hostile weather conditions obliged observers to cancel their pre-breeding visit in spring 2006 (Department of Conservation, 2007b). Following a split decision (Kerry-Jayne Wilson, pers comm.), the Recovery Group dispensed entirely with full-population monitoring on Mangere Island at the end of the 2001-02 season. As a result of these decisions, understanding of population trends on both islands deteriorated markedly.

Analyses of survey data using a range of mark-resighting estimators in Program NOREMARK yielded varying measures of population size (sometimes outside the known sizes), requiring on-going adjustment of survey methodology (see Pryde, 2003, for a discussion of the methodology). The precision of estimates proved sensitive to a number of survey variables (for example, the number of banded individuals in the populations, the conspicuousness of birds at different times in the season, the number of surveys and the validity of sightings). Inaccurate sightings of banded black robins contributed to the uncertainty in estimates by over-counting the number of individuals seen (individuals sighted once might be recorded again as another). These inaccuracies were common in some seasons (Houston, 2008b) and appeared to arise from the mis-reading or mis-recording of band combinations by observers of varying skill or obliged by inflexible time-frames to survey in poor conditions. In addition, erroneous sightings of black robins known to be dead or obviously out of territory were accepted unknowingly or uncritically by novice observers unfamiliar with the populations (Kennedy, 2007a, 2007d; Houston 2008b). Difficulties were compounded by the use of easily confused band colours (a practice avoided in the past) and an unusually high incidence of colour-band failure (losses, or fracture and slippage resulting in obscured or inverted combinations), the causes of which have not yet been determined. Managers did not begin systematic replacement of missing or faulty colours until the 2007-08 season.

These monitoring problems were first quantified in 2006-07 during my collation of survival data for this study. Correction of the errors drew on my longer-term familiarity with the black robin populations (Kennedy, 2007b, 2007c). Successive project leaders in the index-monitoring period had only short-term familiarity and were largely unaware of these troubling inaccuracies or their effects. The corrected mark-resighting data are to be subjected to revised NOREMARK analyses (Dave Houston, pers. comm., August 2008) but these have yet to be conducted (Moira Pryde, pers. comm.).

Loss of familiarity was an inevitable consequence of index-monitoring but institutional pressures amplified its severity. During this time, continuity suffered from high rates of staff turn-over and disproportionate numbers of inexperienced observers. Visits to the two black robin islands were fleeting and tightly constrained in their objectives. Black robin surveys confined themselves to strictly prescribed quantitative measures of population size. Despite genuine interest in doing their best for the species, contractors were under pressure to confine themselves to narrow contractual obligations (pers. obs.).

The mark-resighting method concentrated surveys and other contact with the black robins to restricted areas of the two islands.[41] Thus censuses did not detect the disappearance of birds from substantial areas of habitat elsewhere on Rangatira Island, especially in the Top Bush (Chapter Six: *Section 6.2.3*). The contraction in range was first noticed during microclimate research conducted as part of this study (Kennedy and Wilson, 2005). Suspicions of reduced numbers overall were reported at the same time. Although acknowledging that numbers 'seemed excessively depleted' (Department of Conservation, 2005: 1), the Recovery Group declined Kennedy and Wilson's (2005) recommendation that a one-off full-population head-count be conducted to assess the status of the Rangatira Island population. The Group felt that mark-resighting analyses showed insufficient evidence of a decline to warrant the census (Hilary Aikman, pers comm.).

Island-wide censuses were eventually conducted on Rangatira Island two seasons later, in 2007-08 and 2008-09, after further acknowledgement of lower than usual black robin numbers on both islands (Leseberg, 2007; Department of Conservation, 2007b). The first head-count on Mangere Island was conducted in March 2009 (Harvey, 2009). These free-ranging head-count surveys have yielded the most informative insights to population trends during the index-monitoring period. I have described the declines and head-count censuses in greater detail in Chapter Six.

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[41] On Mangere Island, the main tracks in the Robin Bush interior but not the bush perimeters or contiguous habitat beyond; on Rangatira Island, the principal tracks of the Woolshed Bush interior and major eastern outliers.

During this period, attempts were made to establish the long-awaited third black robin population on Pitt Island (Kennedy, 1993a; Department of Conservation, 2001a). It is possible that transfers of black robins from Rangatira Island were partly or wholly responsible for the suspected population decline there (Kennedy and Wilson, 2005). Too little is known of the population's condition at the time of the transfers to draw firm conclusions.

Thirty-four adult and juvenile robins were transferred to the Ellen Elizabeth Preece Conservation Covenant (Caravan Bush) between 2002-03 and 2003-04 (Aikman and Thompson, 2003; Collen, 2004; Charteris, 2004a, b; Lewis, 2004; Bester, 2005; Aikman, 2005). The new habitat comprised a 40 ha tract of mixed broad-leaf coastal forest modified historically by browsing and separated from contiguous forest by a three metre-high protective fence designed to exclude cats, wekas, and pigs but not mice.

Birds were transferred on two occasions, drawing from the more numerous and accessible Woolshed Bush sub-population (Table 4.1). In order to ensure an even sex ratio, established pairs were targeted for the first transfer in September 2002 (Aikman and Thompson, 2003), but contrary to Collen (2004), difficulties with capture resulted in the transfer of only three recognised pairs (14 birds in total, aged from one to seven years). A fourth resident pairing was terminated with the transfer of the male. None of the transferred birds survived longer than six months. Mortality was attributed to dispersal from the protected area and to storms which followed the releases (Aikman and Thompson, 2003; Collen, 2004) but these were assumptions only. Although several individuals had dispersed to bush immediately adjacent to the reserve (at least one was recaptured and returned), there was no evidence to suggest that dispersal and storms accounted for all of the losses.

A second larger transfer was made in February 2004. Twenty black robins judged to be non-site-attached juveniles were moved. The switch from adults was intended to minimise impacts on the Woolshed Bush breeding population (Collen, 2004). The Recovery Group aimed to establish at least three breeding pairs on Pitt Island (Department of Conservation, 2004). By spring 2004-05, only eight of the 20 black robins could be found, and two pairs had formed (Charteris, 2004b). To meet the target of three pairs, managers transferred two adults from Mangere Island in October 2004 (Charteris, 2004b; Lewis, 2004), separating the male and female from their mates in the process. Two Mangere Island females followed later to correct sex imbalances created by ongoing mortality (Fastier, 2006). To be sure of their sex, the two females were taken from established pairings.

No steps were taken to assess the effects of these transfers on either source population. Managers assumed that both would recover naturally from the losses and were confident that the mark-resighting survey regime would signal any adverse change. More precise means of detecting change were unavailable after full-population censuses had ceased but managers had historical benchmarks at their disposal. The 14 adult robins removed in September 2002 represented 12.5% of the pre-breeding total in the Woolshed Bush (n = 112) at the last full-scale census in spring 1998 (Table 6.3). The 20 juveniles represented 38.5% of the number of Rangatira Island juveniles counted (n = 52) in autumn 1999 (Appendix Four: Table 4B).

Table 4.1 Black robins transferred to Caravan Bush from Mangere and Rangatira Islands between September 2002 and September 2005. Juvenile sexes are based on relative weights if not confirmed by behaviour, breeding or later dissection.

| | Adults | | | Juveniles | | Unknown |
|---|---|---|---|---|---|---|
| | Male | Female | Pairs | Male | Female | Sex |
| **Rangatira Island** | | | | | | |
| 25-26 September 2002 | 6 | 4 | 3 | | | 4 |
| 18-26 February 2004 | | | | 12 | 6 | 2 |
| **Mangere Island** | | | | | | |
| 17 October 2004 | 1 | 1 | | | | |
| 3 September 2005 | | 2 | | | | |

The few records available to me indicate that post-liberation monitoring on Pitt Island detected at least six breeding attempts between September 2002 and February 2006 (Table 4.2). Only one attempt appears to have produced a fledgling. Breeding failures were attributed to the loss of a parent, suspected predation and unexplained injuries to offspring. Information on other brood failures is lacking in reports.

Table 4.2 Breeding attempts reported in Caravan Bush (Pitt Island) after the transfer of 38 black robins from Rangatira and Mangere Islands between September 2002 and September 2005.

| | Pairs | Clutches | Eggs | Nestlings | Fledged | Cause of failure |
|---|---|---|---|---|---|---|
| 2002-03 | 1 | 2 | 4 | 3 | | First nestling predated (?) and failed egg infertile; 2 nestlings deserted after death of parent (Aikman and Thompson, 2003) |
| 2003-04 | 0 | | | | | |
| 2004-05 | 2 | 2 | | ≥ 1 | 1 | First clutch fate unknown; fledgling dead with traumatic injuries to leg (Lewis, 2004; Bester, 2005; Aikman, 2005) |
| 2005-06 | 1 | 2 | | 2 | | First nestling dead with traumatic injuries to leg and thorax (Aikman, 2005). Second nestling last reported alive at 12 days of age (Kennedy, 2006) |

Despite changes in the timing of transfers, supplementary-feeding and the shift from hard- to soft-releases, black robin numbers dwindled rapidly after each liberation. Only three of the 37 robins eventually released from the holding aviary were found dead. The remainder disappeared without trace, often soon after release. Observations and *post mortem* tests showed that avian pox, other viral and bacterial infections, and nematode infestations were problems for the adults (Collen, 2004; Charteris 2004a; Lewis, 2004; Bester, 2005; Department of Conservation, 2005). Managers attempted to treat these problems by administering antibiotics and worm-drenches injected into *Tenebrio* larvae (Department of Conservation, 2005).

To safeguard source populations from the further potentially harmful transfers planned for Pitt Island and other islands (Star Keys, Little Mangere Island; Department of Conservation, 2005), Kennedy and Wilson (2005) recommended intensive management of the transfer survivors on Pitt Island, surmising that they may possess inherent ability to cope with the local conditions. Proposals for nest manipulations, renesting of brooding females and (if necessary) cross-fostering reminded managers that they had at their disposal intervention techniques which had been highly effective during the extinction crisis of 1980-81. The Recovery Group did not act on the intervention proposals and opted instead to persist with transfers which were the more affordable option (Department of Conservation, 2005).

The subsequent decisions to move four individuals from Mangere Island disagreed with Kennedy and Wilson's (2005) recommendation that the black robins on this island should be left undisturbed as a reference population.

Transfers to Pitt Island were suspended in 2006-07 and were to be resumed only if the last founder female survived into 2007-08 (Department of Conservation, 2007b). She did but disappeared some time after November 2007 (Leseberg, 2008). The Recovery Group elected to defer a decision on the alternative of returning black robins to Little Mangere Island (Merton, 2008a), preferring to wait until the viability of the Mangere and Rangatira Island populations had been clarified (Department of Conservation, 2008). To date, no formal review of the Pitt Island translocation experiment has been commissioned.

During this management phase, monitoring of the Mangere and Rangatira Island populations retained the long-standing pre-occupation with abundance as the indicator of viability. The imprecise instruments of index-monitoring used to measure abundance were less likely than the full-scale monitoring method they replaced to detect the signs of inbreeding depression. They have not left a useful demographic record or pedigree in which signs of depression can be read in hindsight.

Although resource constraints dictated the final choice to reduce monitoring intensity, the decision signalled confidence first-and-foremost that the black robin populations were stable and likely to remain viable in the long-term. This confidence was maintained despite evidence of declines and problems with the means of verifying them. The reduced monitoring effort also reflected rigorous new institutional expectations of efficiency, measurable, cost-effective outputs and short-term, tightly goal-directed investment of resources. These were imperatives of the so-called 'Bach Model' (Kennedy, 2003) with which black robin managers were obliged to comply in their planning and management decisions, field practices, staffing policies and work programmes. Coupled with reliance on a succession of external contractors to conduct the field work, these limiting factors resulted in loss of contact with the populations which severely undermined sensitivity to trends.

The black robin management culture inherited from previous phases was lost through high rates of staff turn-over. Lacking continuity and peer-review, management did not recognise the need to remedy lapses in the consistency and quality of field observations. The demographic data acquired during this period give a poor understanding of population trends. From 2001-02, the coarse-scale measures of abundance generated by annual mark-resighting surveys were unreliable because they incorporated inaccurate sighting data. Colour-banding continued in both populations but largely within the survey compass. Banding effort fluctuated from season to season to meet the statistical criteria of mark-resighting analyses and the needs of the Pitt Island transfer project. Age, parentage and relatedness were unknown for the majority of individuals banded. As a result, the introduction of sample-monitoring terminated the black robin genealogical record, along with its potential to quantify accumulating rates of inbreeding in each population and the family lines and lineages which might be advantageous to new founder populations (Jamieson *et al.*, 2008).

Brief, infrequent visits to Rangatira Island resulted in incomplete or inconclusive productivity data from the sampled breeding pairs. These data have not yet been collated for analysis (Houston, 2008a). Short-term visits to both islands reduced alertness to shifts in black robin densities, range contractions and longer-term changes in habitat character. The effects of discontinuity in leadership and staffing were apparent in the field reports of this period. The marked lack of quantitative and qualitative commentary on population and habitat condition suggested that few observers had the familiarity necessary to detect changes. It seems evident that each newcomer regarded the situation encountered as ‘normal’. Short-term, episodic monitoring of the new Pitt Island population did not allow confident explanation of the transfer and breeding failures. As a result, the few demographic data gathered do not allow any form of analysis to assess whether inbreeding depression latent in population founders was expressed by the change in environment (Kennedy, 2006).

For black robins of known age and parentage in the established populations, index-monitoring and incidental sighting data have residual value in simple measures of longevity, pair-fidelity and territory occupation. Taken in their entirety, however, they do not describe the apparent declines in both populations, the period’s most significant events. It is not possible to discern predisposing and contributing factors, the timing, pattern and scale of declines, the changes in population structures, or the nature of any rebound in numbers. Black robin managers are therefore unable to determine whether the declines were expressions of compromised viability or simply a downward fluctuation in abundance. The best insights are emerging from the free-ranging pre-breeding ‘head-counts’ conducted in 2007-08 and 2008-09, monitoring methods most closely related to those used in the past.

## 4.6 Conclusions

The unambiguous strategy of increasing population sizes rapidly rescued the black robins from the immediate threat of extinction through stochastic demographic and environmental threats. Three factors contributed to success. First, managers treated the deterministic factors driving the species to extinction by removing the surviving black robins to better habitats. Second, managers reduced vulnerability to demographic misfortune by addressing the problem of the black robin’s low juvenile output through the obligatory renesting of females and the fostering of the additional offspring. Third, detailed knowledge of the populations was preserved in order to detect unforeseen problems and adverse trends. The strategy benefited from demographic serendipity, the odds of which were as low as the black robin numbers themselves. The most fortuitous were the chance mating of *Old Blue* and *Old Yellow* and the late onset of successful breeding by the ageing matriarch (Chapter Three).

Conversely, the odds against success steepened when managers adopted stand-off policies of wait-and-see based on optimistic assumptions about population viability and persistence. These reactive policies proved to be unsuitable responses to the stochastic demographic and environmental threats growing in inverse proportion to population sizes on Little Mangere and Mangere Islands (Chapter Three). Index-monitoring has proceeded on a similar basis, reassured by the unassisted population increases of the previous decade but without the insights necessary to assess viability and predict potentially harmful changes. On Mangere Island, experimental reductions in monitoring intensity between 1990-91 and 1992-93 also assumed that all would be well. This approach failed to detect cross-breeding events which threatened the black robin and tomtit genotypes locally (Chapter Eight). Critical knowledge gaps created at the same time seriously hindered remedies. Detection and treatment relied on more comprehensive forms of monitoring and longer-term familiarity with the populations at risk.

The decisive phase of the black robin recovery (1980-81 to 1989-90) conformed to the presumption of Caughley’s (1994) ‘declining population’ paradigm that diminishing numbers alone were the rightful object of remedy if extinction was to be avoided. Viability was measured in the currency of numbers: its loss in Little Mangere Island's ancestral population 'was proved in 1976 with the drop to only three potential pairs' (Butler and Merton, 1992: 60). This pre-occupation was entirely justified when the species hovered on the brink of extinction. The only option was to raise population sizes quickly, then deal with viability problems later. The pre-occupation with numbers-building remained in place after the crisis had passed, however, implying confidence that expansion in population sizes alone would insure the species against the more cryptic genetic threats to viability associated with the founding bottlenecks, inbreeding and population sizes capped by limits on available habitat.

There were few apparent reasons to question this confidence. The low rate of juvenile production in the relict population transferred to Mangere Island might have aroused suspicions had managers known the extent and causes of breeding failures, but later, when inbreeding had been most intense under management, black robin productivity responded satisfactorily to the demands of multiple-clutching. Key measures such as fertility, hatch-rates and juvenile survival were not indicative of a problem during the period of augmented breeding effort (Butler and Merton, 1992; Holmes, 1994; Arden and Lambert, 1997). Investigation of black robin genetics revealed anomalously low genetic variation but researchers concluded that this had had no serious implications for short-term viability (Mallinson, 1992; Holmes, 1994; Ardern and Lambert, 1997). Strong population growth under managed conditions reinforced these conclusions, and the more modest growth in the post-intervention phase was what managers had expected to see. These factors eased later decisions to rely on coarser-scale measures of population size as indicators of short- and longer-term viability.

During and after the period of intensive management, the recovery programme adopted few measures to minimise the potential for genetic malfunction. Close-order monitoring and the establishment of a sister-population preserved options for future responses but neither was explicitly intended to moderate inbreeding risks. Inter-island transfers ensured gene flow between the two populations but this and options to disrupt closely related pairings benefited from rather than prompted the transfers. The potential value of gene exchanges after management ceased was subordinated to the goal of monitoring undisturbed (natural) population trends.

The strong rebound of the black robin populations appears to support Craig's (1991) hypothesis that New Zealand's island endemic bird species are more immune than naturally outbred species to the effects of heightened inbreeding and depleted genetic variation. However, the anecdotal and published evidence for this rests largely on the relatively short-term measures of viability (productivity and juvenile survival) visible during the period of intensive management when inbreeding depression may have been masked by management activities. Field data for the post-management period were not interrogated for potential inbreeding effects on vital rates under natural conditions. Similarly, the potential role played by genetic impairment in recently indicated population declines has gone unexplored because managers responded ambivalently to the declines and tolerated compromised insights from the under-performing index-monitoring regime. Suspicions of inbreeding depression aroused by the hesitant breeding performance and mortality of adults and offspring on Pitt Island have not been investigated. The operative Recovery Plan makes no provision for follow-up testing of genetic variation or divergence in the two small, closed populations on Mangere and Rangatira Islands. And monitoring of current intensity and quality is unlikely to detect the more subtle, cryptic effects of extremely low genetic variability on adaptive potential which are expressed over many generations rather than cohorts (Jamieson *et al.*, 2008).

Chapter Six of this study addresses these shortfalls by investigating the accumulated field data for the demographic variables most likely to explain variations in population growth since intensive management began. The neglected post-management data are of particular interest. Chapter Seven quantifies levels of inbreeding in the populations and assesses whether a relationship exists between their predicted effects on individual fitness and the demographic variables identified as having most influence on population trends.

Finally, variations in the standard and coverage of data available for analysis reflect changes in the focus and intensity of management since 1980-81. Data are comprehensive and attention to biological detail greater when contact with the black robins was more frequent and intrusive during the better resourced intervention phase. Quality began to fluctuate during the resource-stressed monitoring phases of management. In general, managers were pre-occupied with the reduced condition of the species and measured productivity and survival primarily. They did not pay much more than passing attention to peripheral factors. They noted (at best) but did not systematically record important viability factors such as the incidence of disease, morphological abnormalities or aberrant behaviour, or the influence of environmental factors or habitat quality variables (micro-climates and vegetation types) on black robin behaviour, survival and productivity. Nor were key demographic variables measured routinely or precisely. For instance, data are inconsistent or lacking on the causes of egg, nestling or nest failure (infertility, loss to avian predators, nocturnal petrel-strikes or multiple other factors), the causes of juvenile and adult mortality, the fates of most recovered rimshots, the causes of pair-bond failure, or the gender of unmated offspring and adults.

Comparison of population dynamics in decline and recovery phases would have benefited from longer and more comprehensive records of the pre-1980-81 ancestral populations on Little Mangere and Mangere Islands and post-intervention populations. Reliable data for these periods are in short supply. Interactions with sympatric tomtits and other species were not measured routinely, nor was the effect of black robins on other species. In practice, attention to all such variables would have asked too much of frantic field-workers but some well within reach (for example, the fertility of failed eggs) were neglected, especially during the post-management periods when observer quality and experience was less consistent.

Lapses in quality are inevitable in a recovery programme of this duration but the severity of many described in this chapter is symptomatic of discontinuity in management, short-term perspectives and reliance on assumption to substitute for direct observation. Chronic under-resourcing was, and continues to be, responsible for many of these difficulties. In contrast, it has become clear during the course of this study that data quality was highest and most consistent when gathered under conditions of stability in project leadership and field teams, each of which cultivated degrees of sensitivity to the black robin populations which were unattainable by other means. These conditions appear to have been met most effectively when project leaders were closely involved in the field work year after year and rates of turn-over in experienced observers were minimal.

The fluctuations in data quality and the many gaps in black robin records have required me to rely on estimates or compensating generalisations which reduce empirical precision in the demographic record. These adjustments are explained in Chapter Five.

# CHAPTER FIVE
# COLLATION OF DEMOGRAPHIC DATA

## 5.0 Introduction

This chapter introduces the field records on which this study's analyses are based. It explains briefly how I have collated and verified raw demographic data from these diverse, often unstructured sources, and how I have compensated for gaps and omissions.

The field records were compiled annually during the four phases of black robin management outlined in Chapter Four. Records from the intensive management phase (1980-81 to 1989-90) and post-management phase (1990-91 to 2001-02) are the most detailed and therefore the most informative for my analyses. They span the period of recovery in the two sister-populations on Mangere and Rangatira Islands after each had passed through a single-pair founding threshold (Mangere Island, 1980-81; Rangatira Island, 1983-84). They provide a near-continuous daily account of population dynamics during successive breeding seasons (spring to early autumn). I have described continuity losses in the post-management period in Chapter Four: *Section 4.4*.

In contrast, the records of the initial investigatory phase on Little Mangere and Mangere Islands (1971-72 until 1979-80) and the current period of index-monitoring (2002-03 until present) are significantly less informative and offer incomplete insights to population trends. I have explained the reasons for this in Chapter Four.

Finding the field records was an unexpectedly difficult task. Some were held in the official filing systems of DOC and its wildlife-management predecessor, the New Zealand Wildlife Service. With puzzling exceptions, I found closed official files in the regional collections of Archives New Zealand, central government's official record-keeping agency. However, the black robin management project had no centralised collection point for the other data-rich paraphernalia of field work (field notebooks, black robin logs, hut logbooks, charts, lists, maps, field instructions or briefing notes, graphs, photographs). I and other project leaders had lodged some hut logbooks, field notebooks and black robin diaries with Archives New Zealand but the remainder were held by project participants, some of whom were indisposed to allow access. Other records languished forgotten in DOC office files, boxes or cupboards where the danger of disposal continues to grow as new staff inherit the unfamiliar collections. The degree of dispersal was so considerable that many former and current black robin workers I spoke to could only guess where to search for missing material.

Mining the field records for demographic data has been extraordinarily challenging. First, the records kept in the field were intended primarily for operational uses. Scientific uses were very much secondary considerations. Daily observation data were raw, unrefined and often of an informal, narrative nature. Recording methods lacked an orthodox unifying format, so that recording conventions changed within and between management phases. Second, record quality, consistency and content varied considerably within and between seasons, in part because the record-keepers themselves differed from the meticulous to the minimalist. The majority were sincere, earnest and adequate in their efforts. Institutional pressures to reduce monitoring intensity were also to blame (Chapter Four). Third, omissions, misconceptions and inaccuracies in daily records were generally not corrected or annotated in hindsight to reflect what was learned subsequently. I looked to end-of-season reports for clarification but found that they often perpetuated the errors, so that none could be accepted uncritically as an authoritative summary. End-of-season or multi-season data were tabulated, most carefully during the cross-fostering years, but these helpful summaries were rarely included with end-of-season reports. For these reasons, much of the information in records had to be checked for accuracy. I chose to rebuild the demographic record from the ‘ground up’ rather than import potentially inaccurate data.

## 5.1 Data collected in the field

The individual life-histories of black robins form the basis of the demographic data available to this study. The intrusive methods used to recover the species during the intensive management period enabled observers to follow the fate of each egg laid until death. As explained in Chapter Four, this also became the driving ambition of post-management monitoring. The observation effort yielded life-histories for 2177 eggs known to have been laid between 1980-81 and 2001-02 (Chapter Six: Table 6.14). Survival, breeding and territory data were gathered for all 1354 hatched black robins from 1980-81 until 1998-99 on

Rangatira Island (19 breeding seasons, 11 generations based on a generation-time of 1.7 years; Chapter Three) and until 2001-02 on Mangere Island (22 seasons, 18 generations).

Black robins were marked as nestlings at 10-19 days or at the next convenient opportunity with uniquely numbered metal bands and colour-band combinations (one to three colours). This was essential for tracking each individual within and between seasons. From the commencement of banding in March 1972 until the end of full-population monitoring in 2001-02, 1075 black robins were marked (Table 5.1). In contrast, 230 have been banded in both island populations during the 2002-03 to 2007-08 period of sample-monitoring. From February 1975, when all 11 black robins alive were marked for the first time, to March 2002, only four are known to have fledged and died without having been caught and banded.

Pre- and post-breeding censuses were conducted as near as possible to the onset of courtship feeding in late spring and as late as possible in the breeding season. These head-counts searched actively for black robins which may have been overlooked previously, including offspring from undetected nests or pairs. Between censuses, each mated black robin was visited at one- to five-day intervals on average to record location, activity and the fate of breeding attempts. Visit-frequency declined during the full-population monitoring period. Regardless of management regime, predicted hatching or fledging dates necessitated daily visits. Offspring were observed daily (at best) until made ‘friendly’ in the manner I have described in Chapter Four. Unmated birds were visited less frequently but were watched carefully nonetheless because they had the potential to attract hitherto undetected mates. When conservation budgets permitted in the early stages of the intervention period, observers assessed the survival of adults and young in late autumn and winter.

Observers gathered the same types of data during the intensive management and full-scale monitoring phases. While noting pairings, clutch sizes, egg fates, nestling and fledgling numbers and fledgling fates, observers also recorded the dates of egg-laying, hatching and fledging for each clutch along with coincidental information such as nest sites, territory occupancy and intraspecific interactions. Fledglings were followed after achieving independence and while roaming as juveniles. Censuses and daily observations alike provided survival and longevity data. The cause of mortality in black robins found dead was investigated by experienced observers, though seldom with absolutely conclusive results. Disappearances during breeding seasons were not treated as deaths until repeated searching had been unsuccessful or the individuals failed to appear in the next season. Dispersal of adults and juveniles within and between seasons was recorded by noting where and with whom individuals appeared or settled. Notes were made by experienced observers on the incidence of disease, morphological abnormalities and aberrant behaviour.

Table 5.1 Total by natal habitat of black robins fitted with uniquely numbered metal bands and colour-band combinations during the four management phases between 1971-72 and 2007-08. Totals exclude two individuals fitted with replacement metal bands and one fitted with colour-bands only.

| Population | | Initial | Intensive | Post | Total | Index |
|---|---|---|---|---|---|---|
| L MANGERE | Whole island | 27 | - | - | 27 | - |
| MANGERE | Robin Bush and Douglas Basin | 3 | 62 | 212 | 277 | 44 |
| RANGATIRA | West Woolshed and western outliers | - | 34 | 150 | 184 | 62 |
| | East Woolshed and eastern outliers | - | 32 | 276 | 308 | 63 |
| | Top Bush | - | 70 | 209 | 279 | 47 |
| | Unspecified | - | - | - | - | 14 |
| PITT | Caravan Bush | - | - | - | - | - |
| | Total | 30 | 198 | 847 | 1075 | 230 |

## 5.2 Recording of data in the field

Documenting of field information grew in sophistication as the volumes of data increased with the black robin abundance. Early observers used personal field notebooks. By 1980-81, daily observations and management commentaries were committed to the black robin section of a general bird log kept on Mangere Island. In 1981-82, data were centralised in dedicated black robin notebooks, a practice maintained until the end of intensive management in 1989-90. At the same time, field-workers began to keep hut log-books in which more generalised social and biological commentaries on island life were written alongside helpful narrative summaries of progress with the populations. These informal summaries have often substituted for primary records which I have not been able to locate.

In 1991-92, soon after comprehensive monitoring commenced, record-keeping for the larger Rangatira Island population made an important change from recording observations for all black robins by day to reporting daily observations by black robin. This simple adjustment made it easier for incoming observers (and my study) to relate new information sequentially to old. This helpful practice was adopted piecemeal for the smaller Mangere Island population. Qualitative observations on nest sites, behaviour and interactions were still included. Large wall charts were introduced to plot progress with the growing numbers of nesting attempts. The charts had two functions. First, they alerted managers to key dates in the breeding cycle (start to incubation, hatching, banding of nestlings, fledging). Second, they summarised schematically the data committed to log-books so that errors and other information needs could be detected at a glance. Finally, each observation of an adult or fledged black robin was logged in a daily roll-call register (a tick-chart or log-book) which functioned as both a running population census and a means of signalling the need to investigate the whereabouts of missing individuals. For my study, the roll-calls gave important clues to time-of-death.

Banding information was recorded in a master list detailing the colour-band combinations in use on black robins known or believed to be alive and available for use. To avoid duplications, combinations were reused only after two seasons had passed since the disappearance of the previous holder. The master list recorded the colour-combinations fitted, the number on the metal band, given name, parents, clutch number, date, and weight and age at banding (days since hatching). Banding details were often repeated in black robin log-books and occasionally in hut log-books. Official band-return schedules were completed in accordance with Banding Office requirements. As early as 1983-84, project leaders routinely included given names on the schedules, a small but invaluable expedient enabling managers to relate band-schedule data to other forms of record.

Simultaneous checking of data consistency in the various records was achieved using reconciliation tables of various descriptions (a blackboard on Rangatira Island; Table 5.2). If figures did not balance, observers were obliged to find and remedy the source of error, if necessary by returning to the field for confirmatory observations.

Observation aids preserved important seasonal information. Portable booklets listing given names and colour-bands allowed observers to check an individual's identity on the spot.

These lists have acted in retrospect as supplementary sources of information on numbers and presence each season. Track maps supplied to novice field-workers often plotted the relative location of mated and single black robins. These now assist understanding of territory numbers and distribution, features which were not otherwise plotted systematically.

Table 5.2 Example of a black robin reconciliation table used to ensure the consistency of field data in diverse records. These data are transcribed from the entry for 24 February 1996 in the Rangatira Island hut log-book, October 1991–May 1996 (Archives New Zealand, Accession CABK 808). Observers guilty of careless record-keeping soon came to loathe table updates.

| | | | |
|---|---|---|---|
| DATE | 24.02.96 | | |
| EGGS | Number known laid | | 162 |
| | Lost through rimshots | 6 | |
| | Evicted or deserted | 9 | |
| | Disappeared or predated | 20 | |
| | Incubated full-term | | 127 |
| | Failed to hatch | 45 | |
| | Still to hatch | 0 | |
| NESTLINGS | Known alive | | **0** |
| | Dead or disappeared | 17 | |
| FLEDGLINGS | Known alive | | **10** |
| | Known dead | 4 | |
| | Missing probably dead | 10 | |
| | Missing probably alive | | **0** |
| JUVENILES | Known alive | | **32** |
| | Missing probably alive | | **9** |
| | Missing probably dead | 0 | |
| ADULTS | Known alive | | **93** |
| | Missing probably alive | | **5** |
| | Missing probably dead | 3 | |
| TOTAL | Robins known or presumed alive | | **149** |

Interim and end-of-season reports summarised seasonal information but detail, scope and commentary varied significantly for the reasons explained in Chapter Four. Project leaders differed in the value they placed on these reports as definitive accounts of population status. Pre- and post-breeding census results were commonly reported along with summarised breeding data (pair numbers, eggs laid, numbers of nestlings, fledglings and juveniles). Individual pair summaries, banding details and lists of the black robins seen were rarely tabulated. Mid-season reports generally suffered from a shortened view of events (for example, population totals did not include birds reappearing later). I found that this was a problem in primary records too. Adjustments were usually necessary in post-management census totals after 'dead' black robins reappeared in the following season. Typically, the resulting contradictions and corrections went without comment by authors, creating confusion over which account was correct.

## 5.3 Data collation

To place this study's analyses on the strongest possible empirical basis, I have collated and verified field data meticulously. I have attempted to minimise data omissions and the inferences (statistical or otherwise) which omissions necessitate. The goal of empirical accuracy has obliged me to make decisions wherever appropriate on how to deal with incomplete or ambiguous information.

Primary and secondary data sources of all kinds from 1971-72 until 2008-09 (Table 5.3) were collected and sorted by season and population. Original records were copied if they could not be retained for the study. The 18 island-years of hut and black robin log-books (1980-81 until 1988-89) held by Archives New Zealand were hand-transcribed over a period of seven months.

I contacted project leaders, field-workers, researchers and associates of the black robin programme to find missing records. Most were willing and able to help. Even so, I have been unable to locate all primary records for some seasons. Official band-return schedules are the sole form of primary record available for the initial management period (1971-1972 to 1979-80). Observations on Mangere Island between 1990-91 and 1992-93 appear to have been recorded only as brief, sometimes cursory, comments in the hut-log. I can find no primary records for the 2002-03 to 2007-08 seasons on Pitt Island. In these instances, my data have been gleaned from secondary sources.

Table 5.3 Nature and diversity of black robin records consulted for this study.

| Primary sources | Secondary sources |
|---|---|
| Black robin log-books | Hut log-books |
| Black robin monitoring data forms | Official field reports |
| General bird observation log-books | Interim and end-of-season reports |
| Breeding progress wall-charts | Field identification lists |
| Daily roll-call registers | Seasonal data summaries |
| Personal field notebooks | Pre-season briefing material |
| Robin master lists | Personal diaries |
| Track-and-territory maps | Academic publications (papers, theses) |
| Official band-return schedules | Popular publications (magazine articles, newspaper reports, books) |
| Index monitoring survey forms | Official correspondence and news releases |
| Incidental sighting forms | Personal correspondence |
| Museum specimen registers | |

Demographic data were transferred to Microsoft Excel (2002) flat-file spreadsheets for inspection and verification. I sorted the data into four complementary demographic categories: individual life-history summaries and, for each population, annual roll-calls, annual breeding summaries and annual productivity tables. Other individual parameters (longevity, territories, dispersals, inbreeding coefficients, population-scale vital rates) were calculated from the data in these first-tier collations. All collations were cross-checked to ensure accuracy and consistency (see *Section 5.4* below).

### *5.3.1 Life-history summaries*

Life-history information for each black robin comprised:

- given name
- band number and colour-band combination
- sex (male, female or unverified)
- hatching and banding dates
- age and weight at banding
- mother and father
- parenting history (raised naturally or fostered)
- clutch number
- provenance (black robin, black robin x tomtit hybrid)
- natal population

- populations to which the individual dispersed or was transferred
- breeding population(s) and population in which the individual died
- age at first breeding and when first producing juveniles
- dates of death (if known) or last observation and date of first failing to appear
- age at death
- inbreeding coefficient.

Inbreeding coefficients were estimated relative to the founder population using pedigree software (Chapter Seven: Was Inbreeding A Problem?). Populations were defined as Mangere Island and either Woolshed Bush or Top Bush on Rangatira Island (Chapter Six). Sex was confirmed by mate choice. Courtship behaviour was usually reliable but occasional temporary same-sex pairings of black robins (both sexes) could mislead. If a black robin did not pair or breed, its sex was estimated on the basis of adult behaviour or weight at banding (weight relative to nest-siblings or nestling weights in general; see for instance, Charteris, 2004b). Although experienced observers were correct more often than not when estimating sex by this means, the method was fallible. Even so, I was more inclined to accept estimated assignments from experienced observers than from observers I did not know. Otherwise, I treated unconfirmed assignments of sex in records as indicative only, and if records gave no indication at all, I classed the individual conservatively as of unknown sex.

Parental data during the intensive management and monitoring phases were confirmed by direct observation in the field. The identity of mothers, fathers or both were unknown for 22 banded black robins (11 on Mangere Island; 11 on Rangatira Island). To fill the gaps, I made educated guesses in all but one case, deducing the likely identity of the unknown parent(s) from field information, my own familiarity with the populations and by eliminating local black robins which were accounted for at the appropriate times (paired or sedentary in other territories). The parents of black robins hatched in the initial phase of management (1971-72 to 1975-76) and the index-monitoring phase (2002-03 to present) are usually unknown.

If hatch-dates were not recorded, I used the estimated age at banding to calculate the probable date. Age at banding was noted routinely by most observers, but if not recorded, I deduced the probable date from other information given (apparent age at first sighting or capture, time of season, behaviour, interactions with other individuals).

Time-of-death was rarely determined precisely in the field for fledged black robins (only 11.3% were found dead or dying). The remainder disappeared. Nestlings were more likely to be recovered dead (46.6%). Those missing from nests were almost certainly dead unless disappearing within days of their due fledging date. The practice in the field was to search for missing birds in order to confirm death. None of the missing birds could migrate from the islands, so if searches were unsuccessful or the birds failed to reappear in the following season, they were classed as dead.

To cope with unknown dates-of-death, I listed the dates on which each black robin was last seen and first failed to appear. The mid-point in the interval was used to calculate a surrogate date-of-death in later analyses (Chapter Six). Because many last sightings were the last date of observations rather than true date of death, I was obliged to treat the first failure to appear as the dates on which observations were resumed in the new season. This unavoidable expedient increased the likelihood of error in surrogate date-of-death estimates.

Finally, in qualitative comments, I summarised what was known of the individual's likely status and condition at last sighting (alive or dead; moulting; fit, injured or ailing). I also recorded the identity of mates in each season of adult life, and defined rearing, fostering and transfer histories (including the identity of mothers at fledging), changes to given names or bands, and other incidental details clarifying life-history.

Many gaps remaining in these information classes may be closed if new field records come to light, but most reflect the achievable state of knowledge. Data are most deficient for sex, ages at first breeding and first productive breeding, and dates of death.

### *5.3.2 Annual roll-calls*

I collated presence-absence data for all fledged black robins into annual roll-call spreadsheets. These spreadsheets listed given name, sex and the population in which an individual resided at each pre-and post-breeding census (Mangere Island, Woolshed Bush and Top Bush). Individuals dying as nestlings were not included, even if banded and named.

Each season's roll-call identified pairings and unmated birds. I sorted successful pairs (those producing juveniles) from others attempting or failing to breed.

Pre-breeding roll-calls listed the black robins known to have been alive at the end of the previous season and seen in the following spring, but for obvious reasons I could not list those dying in spring before observers reached the islands. They were consigned to the category of individuals missing or confirmed dead since the previous season. To assist analysis of age-related mortality rates, I chose to list separately the juveniles surviving from the previous season.

Post-breeding roll-calls listed adults and juveniles alive at the end of the season. Those of any age disappearing or known to have died since the pre-breeding census were listed separately. In cases of doubt over whether a black robin was alive at season's end, I made judicious use of available field evidence along with my experience and local knowledge to make a judgement. This introduced potential errors to the roll-calls. In both pre- and post-breeding roll-calls, juveniles and yearlings were sexed in retrospect if they had paired or bred. I distinguished them from non-breeders whose sex was unknown or estimated only.

The roll-calls served two functions. First, they allowed me to determine population sizes definitively at each census. Reconciling running totals between years was an important means of checking accuracy. Second, the roll-calls assisted calculation of individual life-spans and population mortality rates. Individuals could be traced from birth year to death, a valuable resource not previously available to black robin managers or researchers.

### *5.3.3 Breeding charts*

I used breeding charts based on Excel flat-file spreadsheets to document the day-by-day breeding activities of every pairing from 1980-81 to 2001-02. My charts were adapted from those used in the field during the full-population monitoring phase. They consolidated observation data in black robin log-books with other information scattered unsystematically through primary and secondary records.

The charts plotted daily breeding data for all known intraspecific and black robin x tomtit pairings in the Mangere and Rangatira Island populations. The fates of every egg known to have been laid were tracked clutch-by-clutch from first to final dates of observation. For those laid in the cross-fostering seasons (1980-81 to 1989-90), tracking at the individual scale unravelled the bewildering complexity of transfer and fostering histories. Unlike the field originals, the charts benefited from hindsight by incorporating knowledge of offspring survival from the following season.

A validated resource of this kind has not previously been available. For my study, the charts have offered a point of easy reference for natal-season information on individual black robins (for example, hatching, fledging and last-sighting dates; length and timing of exposure to tomtit foster-parents; differences in natal and fledging sites), and on each breeding pair (number, timing and fate of any clutches laid). I have used the charts to resolve many uncertainties in life-history and roll-call data. For example, I could deduce the undocumented timing of breeding by a black robin pair by counting back from the dates of known events using incubation and nestling intervals. The charts helped me to interpret perplexing cross-breeding events on Mangere Island (Chapter Eight), and to judge the identity of unknown parents by illustrating which black robins were not occupied elsewhere at critical times.

### *5.3.4 Productivity tables*

I collated the clutch-fate data for each breeding pair into annual productivity tables from which breeding measures for each population and season were summarised (number of pairs breeding or attempting to breed; number of clutches and eggs laid; egg, nestling and fledgling mortalities, and the number of juveniles produced). As with the roll-calls, I distinguished effective pairs (those raising juveniles) from ineffective pairs (those failing to do so, or failing to lay eggs at all). The tables were an important means of standardising field data of highly variable quality.

I attempted to define clutch fates as accurately as I could but numerous uncertainties existed. Egg losses were problematic because field-workers rarely found evidence to suggest a cause of desertions or disappearances. It was rarely possible to tell reliably whether missing eggs had first been deserted by females. I followed the field records in assigning eggs to categories of ‘deserted’ or ‘disappeared’ (predated or lost through misadventure). However, I knew from experience that such field judgements were questionable, so for later productivity analyses (Chapter Six) I combined the two categories of loss. In the productivity tables, I excluded from both categories the small number of eggs failing to hatch but disappearing before they could be examined for signs of infertility or embryonic death. They were classed as ‘failing to hatch’ along with the failed full-term eggs which observers did inspect for cause of death.

To preserve precision in later productivity analyses, it was important to decide whether or not missing nestlings and fledglings had died before advancing to the next life-stage. For missing nestlings, I followed the practice adopted in the other collations of treating them as dead unless disappearing close to fledging age. If the latter, I used field records or my local knowledge to judge the likelihood of survival. I considered that the error rate introduced to analyses by these judgments would be lower than if I treated all missing late-stage nestlings as dead.

Fledglings disappearing well before independence were generally treated as dead but were searched for nonetheless (in practice, very few reappeared later). The failure of parents to carry food was almost always (but not universally) an indication that missing fledglings had died or had wandered out of territory. For fledglings missing when approaching independence, I took into account the timing of disappearances, parental experience, the moulting status of parents, the character of surrounding habitat (densely occupied by black robins, discrete or extensive, regularly or rarely visited by observers), fledgling behaviour (degree of responsiveness to hand-clapping; intrepid and gregarious, retiring and elusive), observed interactions with other black robins, and observer experience. If still in doubt, I deemed a late-stage fledgling dead if observers had had sufficient time to look it. If well advanced fledglings disappeared close to the conclusion of a season’s observations, I assessed their fates (dead or independent) on a case-by-case basis using the cues listed above.

## 5.4 Verification

The disordered state of the field data was a fertile source of error (see Mallinson, 1992, for a detailed explanation of the difficulties created for researchers). To preserve the potential in field data for detailed insights, I chose not to tolerate errors in my collations. As a result, collation and verification alike have submitted the black robin field records to the most thorough and comprehensive summary analysis they have received to date. I minimised errors by three means. First, my collations proceeded chronologically from the earliest to the latest seasons in order to preserve continuity in seasonal accounts. This was an important means of ensuring accuracy in life-span data.

Second, collating by spreadsheet allowed me to sum and reconcile totals by sex, population or other class of information. Like the universally loathed reconciliation tables of field work (Table 5.2), this proved to be the most effective means of detecting transcription errors or dealing with mistakes, omissions and ambiguities in the original data. When in a roll-call summary, for instance, a pre-breeding population total exceeded the post-breeding total of the previous season, I was prompted to check for the source of error and to make the necessary correction.

Third, confirmation of corrections was sought wherever possible from the original records. This was a compelling reason to locate missing records. If the records were deficient, I deduced what I could from other verified information the records offered, as I have explained when calculating unobserved hatch-dates or time of death. For instance, population censuses were bedevilled by inconclusive sighting of colour-band combinations. To deduce who the ‘mystery’ individual might have been, I compared the colours seen against the lists of colour-banded black robins confirmed alive before and after such sightings. Local knowledge (my own or others’) of black robin origins, habits or territory occupancy was an important means of validating such deductions. Observers did this routinely in the field to resolve uncertainties as they arose.

## 5.5 Summary

Systematic collation of raw black robin field data into life-history summaries, annual roll-calls, breeding charts and productivity tables involved a degree of sorting and verification not previously attempted in the course of black robin management.

The four forms of collation allowed me to define in detail a comprehensive set of individual and population parameters for this study’s analyses (Table 5.4).

Table 5.4 Demographic parameters and annual trends defined from field records and secondary accounts of the black robin recovery programme on Mangere and Rangatira Islands, 1980-81 to 2001-02.

| **Individual** | **Population** |
|---|---|
| • Parents | • Founders |
| • Natal clutch number | • Annual pre- and post-breeding sizes |
| • Siblings | • Distribution |
| • Sex | • Rates of growth |
| • Survival and longevity | • Sex ratios |
| • Mates | • Breeding pair numbers |
| • Territory | • Effective breeding pair numbers |
| • Annual reproductive output | • Collective annual productivity |
| • Offspring | • Rates of recruitment |
| • Inbreeding coefficient | • Rates of survival and mortality |
| • Breeding and demise populations | • Rates of immigration and emigration |
| • Provenance (black robin, hybrid) | • Pedigree (assuming paternity by social males) |
| • Fostering history | • Levels of Inbreeding |
|  | • Incidence of cross-breeding |

# CHAPTER SIX
# POPULATION TRENDS AFTER 1980

## 6.0 Introduction

In this chapter, I summarise key demographic trends in the recovering black robin populations between 1980-81 and 2001-02. I also outline trends discernible in the seven years of piecemeal demographic data available from the sample-monitoring period (2002-03 to 2008-09).

The trends reported commence at or soon after the founding of each population. As explained in Chapters Three (History of Decline) and Four (Management of Extinction Threat), the black robins on Mangere and Rangatira Islands trace their origins to the few survivors of the declining ancestral population on Little Mangere Island. The last seven individuals transferred to Mangere Island in 1976-77 formed the nucleus of the population from which the Woolshed Bush and Top Bush sub-populations on Rangatira Island were founded. Three years after intensive management commenced on Mangere Island in 1980-81, four adults were moved to the Woolshed Bush in preparation for the 1983-84 season. The Top Bush population was founded in the following season (1984-85) after two juveniles produced in the Woolshed Bush dispersed and settled there, joining another juvenile dispersing there after transfer from Mangere Island.

The aim of this chapter is to outline the nature of the black robin's recovery during both the management period (1980-81 to 1989-90) and the monitoring period (1990-91 to 2001-02). No undisturbed black robin populations have survived to indicate how much recovery may have been influenced (if at all) by the ancestral population's prolonged persistence at very low numbers, decline towards extinction and subsequent passage through the founding *Old Blue-Old Yellow* bottleneck. Comparisons between the two sister-populations, descended from the same founders and linked genetically thereafter by inter-island transfers (Chapter Four), offer the most immediate alternative means of inquiry. Accordingly, this chapter focuses on differences in population trends and attempts to determine the variations in vital rates which explain them. The ultimate aim of these comparisons is to identify variations in performance which may signify intrinsic vulnerability to decline and risks to short- and longer-term viability. The demographic variables identified are therefore those most likely to be of interest to conservation managers charged with monitoring the health of extant and future black robin populations.

This chapter consolidates, extends and in some cases amends Butler and Merton's (1992) comprehensive account of trends during the black robin's rescue (summarised in Higgins and Peter, 2002). Their account draws to a close soon after the inception of post-management monitoring (1991-92). The new information I present on population trends after management ended fills a conspicuous gap in the literature on black robin recovery.

The chapter also reports the results of my habitat micro-climate investigations on Rangatira and Mangere Islands. These investigations set out to assess whether differing environmental conditions in black robin habitats might be an explanatory variable for observed differences in population trends. Earlier research on the islands had attempted unsuccessfully to address this question by using the doubly labelled water technique to quantify daily energy expenditure in black robins as a measure of habitat quality (Williams, 2003). Findings were to be compared with other indirect measures of habitat quality: the record of black robin breeding success, survival and population density in each habitat, and the density and diversity of invertebrates. Sampling of the latter was too brief and limited in scope to be conclusive (David Bryant, pers comm.), and spoiled blood samples from Mangere Island precluded between-island comparisons of black robin energy budgets. No significant difference could be detected in the energy expenditure of black robins living in the Top Bush and Woolshed Bush forests on Rangatira Island (Williams, 2003). This result suggests intuitively that habitat quality did not differ markedly.

My decision to assess environmental differences over six consecutive calendar seasons (the expected life of the data-logger batteries), addressed the problem that energy budgets measured on a single summer's day could not reflect the quality of habitats within and between years, especially during winters when habitat character may be a crucial determinant of population trends. My decision was also prompted by the impressions of many black robin field-workers that climatic conditions in the Top Bush forest on Rangatira Island were generally colder and harsher than those in the lower-lying and more sheltered forests of the Woolshed Bush and Mangere Island.

## 6.1 Methods

As I have explained in Chapters Four and Five (Data Collation and Verification), all analyses of demographic trends are based—unless otherwise specified—on whole-population data acquired through direct observation in the field.

### *6.1.1 Analytical perspectives*

As outlined in Chapter Four, the black robin recovery programme comprised two management phases in which full-population monitoring occurred: intensive management centred on intervention in breeding to boost reproductive output and population sizes (1980-81 to 1989-90), and post-management monitoring to ensure that populations sustained satisfactory rates of growth without further assistance (1990-91 to 2001-02). Full-population monitoring ceased on Rangatira Island in the 1998-99 breeding season but continued on Mangere Island until 2001-02.

In this chapter, I retain the distinction between management phases for analytical purposes. Demographic trends during the intensive management phase were driven by highly invasive activities designed to maximise productivity and minimise mortality. During this period, for example, rates of population growth and reproductive output on Mangere Island were affected by the transfers of black robin eggs, nestlings, juveniles and adults to Rangatira Island (Chapter Four: *Section 4.3*). In contrast, trends on both islands from 1990-91 onwards were not disturbed by management and offer the only available detailed insights to population dynamics operating under natural conditions. This chapter emphasises post-management trends for this reason.

For analytical purposes, I have separated the Rangatira Island population into two sub-populations: the Woolshed Bush and Top Bush. In reality, these are geographical divisions in a single black robin population, linked through spontaneous dispersal of juveniles and adults, and through the transfers uniquely associated with intensive management (Chapter Four). Nevertheless, I anticipated that these sub-populations might differ in ways capable of yielding insights to viability and extinction vulnerability. Where appropriate, results are reported for the Rangatira Island population as a whole, which anticipates a need to compare population trends on each island rather than in each sub-population.

For easier reading, I refer to the birds on Mangere Island and Rangatira Island as ‘populations’. The term ‘sub-populations’ refers exclusively to Rangatira Island where the distinction is made between the Woolshed Bush and Top Bush.

### *6.1.2 ‘Demise-site’ and ‘natal-site’ data collations*

Demographic trends for black robins cannot always be explored on a closed-population basis. During the intensive management phase, 52.3% of black robins were transferred or dispersed naturally between populations. Thus, they were not raised in or did not reach independence, breed or die in their natal habitats. After management activity concluded, 17.4% of adults and juveniles on Rangatira Island dispersed and settled away from natal habitats.

I have accounted for the natural and managed movements of black robins at all life-stages when collating demographic data in the ‘open’ populations. These collations place each bird in the population caring for it as an egg, nestling, fledgling, juvenile or adult. Under management particularly, individuals might pass in and out of populations several times before settling in a territory as a juvenile or adult. For ease of reference, I have used the term ‘demise-site’ to describe these data. Unless otherwise specified, all my analyses are based on data collated in this way.

I have used a second ‘natal-site’ collation which assumes that no movement of individuals occurred at any life-stage (in other words, it assumes that black robins were raised throughout by their biological parents and did not move from natal populations). This form of collation had an essential verifying function. It made it simpler for me to trace each egg through successive life-stages until death so that its life-history was complete. Preserving the analytical connection between parent and offspring in this way is also appropriate when analysing genetic issues (relatedness and fitness; see Chapter Seven: Was Inbreeding A Problem?).

Neither form of collation explains all demographic trends on its own. For instance, trends derived from ‘natal-site’ data ignore the fact that the quality of foster-parental care, or differences in habitat type, food resources and population densities will have affected the productivity and longevity of a dispersing or transferred bird. ‘Demise-site’ trends make implicit allowance for those factors but minimise the importance of fitness characteristics inherited from parents. Fortunately, the two perspectives overlap closely after intensive management stopped. On Rangatira Island, all black robins remained with their biological parents until reaching independence, and on Mangere Island, the population was wholly closed during post-management seasons (there were no neighbouring populations to disperse to).

### *6.1.3 Tomtit foster-nest locations*

Before analysing demise-site data for Rangatira Island, it is necessary to place fostered black robins in the correct sub-population caring for them at successive life-stages. This is not a problem for black robin foster-nests but I have been unable to determine the location of many tomtit foster-nests—the records alluded to in Powlesland *et al*. (2001) have not been made available. Where I could not deduce nest locations from other information, I have assumed that Mangere Island eggs and nestlings destined for tomtit foster-care on Rangatira Island were placed exclusively in Woolshed Bush foster-nests. This assumption has some validity. Tomtit pairs were more numerous in the Woolshed Bush, more convenient to managers and in closer proximity to back-up pairs than those in Top Bush (pers obs; see also Chapter Four).

I have also assumed that the tomtit-fostered offspring of Rangatira Island black robins stayed in their natal sub-population. None was fostered to Mangere Island because tomtit breeding did not resume there until 1989-90 (Chapter Four, and Chapter Eight: Hybridisation).

My two assumptions will result in small but unavoidable errors in analyses of productivity and survival for the Rangatira Island sub-populations. For example, the number of eggs reported as hatching or failing to hatch in Top Bush foster nests is likely to be exaggerated since tomtit nests were generally fewer in that habitat.

The lack of locality data for tomtit foster-nests is inconsequential to post-management analyses and to ‘natal-site’ summaries for either management phase.

### *6.1.4 Pre- and post-breeding census data*

I have relied primarily on pre-breeding census counts to explain population growth trends, since post-breeding counts include black robins dying before being recruited to breeding populations. I have used post-breeding census data to calculate survival and mortality rates.

### *6.1.5 Dispersals and transfers*

I use the term ‘dispersal’ to refer to the spontaneous movement of juveniles and adults from one sub-population to another, followed by a definable period of settlement. By this definition, dispersals occurred only on Rangatira Island where the sub-populations were not closed. I have classed each individual’s movement from a sub-population as a separate dispersal event, so that the multiple movements made by some in the same season are several events. Black robins dispersing after transfer from Mangere Island required me to assume an original departure point in the Woolshed Bush. I could find few records specifying other liberation sites on Rangatira Island.

I have differentiated dispersals from management-related transfers of birds between sub-populations and between islands. Inter-population transfers had the potential to distort analyses of trends during the intensive management seasons because some relocated black robins were returned to natal populations, and in some cases, away again. To avoid overstating the contribution gross transfer totals made to trends, I have based analyses on net transfer movements. These ignore any intermediate transfers of an individual (as say, fostered eggs or nestlings) if ultimately managers returned it to its natal habitat.

### *6.1.6 Breeding pairs*

My productivity summaries for each season class breeding pairs as ‘effective’ if producing juveniles (regardless of juvenile survival) and ‘ineffective’ if laying eggs but failing to produce juveniles. This distinction applies to post-management seasons only; during intensive management seasons, pairs could not be deemed successful if their offspring were raised to independence by others. Effective pairs may suffer clutch failures but not the failure of all clutches in a season. My productivity summaries omit pairs which formed (however briefly) but did not lay eggs, along with known or suspected cross-pairings between black robins and tomtits (see Chapter Eight).

I accept that the use of juvenile output to define success distinguishes this from most other studies of New Zealand and Australian *Petroica* in which fledgling output is the criterion (Chapter Two: Black Robin Biology). However, juvenile output gives the truer measure of breeding success (Russell, 2000).

### *6.1.7 Productivity*

Productivity is defined by pair rather than by female. The female measure disguises the number of productive males since each female may breed productively with several mates. I have derived per-pair productivity measures at all life-stages in the breeding cycle (laying, hatching, fledging and independence). A population's productivity is the collective reproductive output of its constituent pairs at each such life-stage but especially in juveniles. Developing productivity indices is complicated by the demise- and natal-site issues I have already referred to. I address these complexities separately at the appropriate times in this chapter.

In analysing black robin productivity during the intensive management and post-management phases, I have distinguished between reproductive *output* and reproductive *performance*. Output is a quantitative measure of production. I have expressed it as the mean annual per-pair production of clutches and eggs laid, eggs incubated full-term and hatched, nestlings fledged and raised to independence, and juveniles surviving to breeding age (that is, into a second year of life). Reproductive output can be compared by management phase for all productivity parameters, but only during the post-management era was the output natural. The between-phase comparisons indicate how effective management was in raising output and how resilient the black robins were in responding reproductively to conservation measures.

Reproductive performance is a measure of success and failure. I have quantified this at the population scale as (1) gains at each life-stage in the breeding cycle (percentage overall of all eggs hatching, and all nestlings, fledglings and juveniles surviving) and (2) losses (percentage of all eggs lost as rimshots or through misadventure; of all eggs failing to hatch and of all nestlings, fledglings and juveniles dying). Between-phase comparisons of performance gains are possible only for clutch sizes and hatch-rates, the two intrinsic measures of reproductive success resistant to direct management effect. Success in other measures cannot be compared since the swapping of eggs, nestlings and juveniles between populations disguised true reproductive performance during the intensively managed era. A true indication of a population's fledging success cannot be obtained, for example, by relating the number of nestlings fledged to the number hatched if managers removed some of the nestlings from the population in the interval.

Between-phase comparisons of productivity failure are limited in the same way. Managers actively minimised threats to breeding during the intensive management seasons. The only measures of failure capable of valid comparison are the proportions of eggs laid as rimshots and the proportions of full-term eggs failing to hatch, since neither could be controlled directly. Even then, managers minimised the potential costs of rimshots by returning those detected early enough to incubation (Chapter Four).

### 6.1.8 Recruitment

Recruitment rates are the number of juveniles surviving and breeding in each population relative to the total number it produced in the previous season. The total produced includes any juvenile transferred or dispersing to the population between seasons. In order to define recruitment rates by sex, I have limited my calculations to juveniles surviving to pair and lay eggs in any post-natal season. This filter has two benefits. First, I did not have to make assumptions about the sex of juveniles dying before making confirmatory mate choices (27.2% of all juveniles produced). Second, it excludes unmated juveniles or those failing to lay eggs after pairing, none of whom contributed directly to population growth trends. Of necessity however—there being no alternative—I based the proportions of qualifying male and female recruits on the total number of juveniles produced.

### 6.1.9 Growth rates

Exponential rates of population growth annually ($r$) are calculated from pre-breeding census totals sorted by management phase by fitting a linear regression, using the equation $r = (\log_e N_t - \log_e N_0)/t$ in which $t$ is the increase in the population ($\log_e N$) over one interval of time (one year) (Sinclair, Fryxell and Caughley *et al.*, 2006: 80). Mean rates of growth in breeding-pair numbers and in the proportions of effective pairs are calculated by the same method.

### *6.1.10 Life-span estimations*

Individual life-spans could be determined for all black robins using annual pre- and post-breeding census data supplemented by exhaustive observations throughout each breeding season. I calculated life-spans from hatch-date to date of death. For many birds, one or both dates were not observed. If required to estimate hatch-dates, I counted back from the known or estimated age at banding or age at death in the nest. Observers recorded this brood information routinely. For a small minority of black robins banded as fledglings or adults, or not banded at all, I estimated probable hatch-dates from other cues (apparent age at first sighting or capture, time of season, behaviour, interactions with other black robins). These post-fledging estimations have a higher probability of error but with few exceptions this will be months, not years.

Given the high frequency of nest visits, dates of death were observed or estimated (within days) for dead or missing nestlings, and for fledglings just out of the nest. Most juveniles and adults died unobserved, typically between autumn and spring (that is, between annual observations; see Chapter Two: *Section 2.9.2*). For these I fixed a surrogate date-of-death mid-way between the dates on which each was last sighted and first failed to appear. The life-span dataset comprised 281 males, 267 females and 815 others of unverified sex (306 nestlings and 509 fledglings, juveniles and adults). Individual life-span data could be sorted by natal- and demise-site populations, management phase and sex.

### *6.1.11 Survival probability*

Trends in survival probability were analysed using R (version 2.8.1; R Development Core Team, 2008; www.r-project.org). My associate supervisor, Professor Richard Duncan, managed the scripting process and advised on the appropriate analytical model. To assist survival and later inbreeding analyses (Chapter Seven), I assigned each individual to one of six categories depending on its likely survival status at last sighting (Table 6.1). Black robins in category 0 were predominantly lost over winter, while most in categories 1 and 2 were nestlings which were found dead or had disappeared within one or more days of a nest inspection (that is, they were incapable of surviving independently). Five euthanased black robins were assigned to category 4 in order to distance them from analyses based on natural life-spans. Eight black robins hatched during the post-management phase and transferred to the doomed Pitt Island population between 2002-03 and 2005-06 (Chapter Four) were assigned to category 5 for the same reason (they had probably died prematurely as a result of the transfer).

We fitted the individual life-span data to the Kaplan-Meier survival estimator in R ('survival' library; R Development Core Team, 2008) to compare survival trends by sex, management regime and demise-site (the population in which a black robin died). The estimator was appropriate for the non-symmetrical survival data, the staggered entry and exit of individuals in the dataset, and the right-censoring of individuals alive at the end of the study period (category 3, n = 8, treated as last seen on 15 September 2008). We ran the model separately for the fitted covariates of demise-site, sex, management phase, and sex and management phase together.

Table 6.1 Survival categories to which black robins in the three Mangere and Rangatira Island populations were assigned according to information on fates available at last-sighting dates, 1980-81 to 2001-02.

| Category | Survival status at last sighting | *n* |
|---|---|---|
| 0 | Alive when last seen but died at some unknown time later | 682 |
| 1 | Found dead | 264 |
| 2 | Alive when last seen but almost certainly died soon after | 396 |
| 3 | Still alive at the end of the study | 8 |
| 4 | Euthanased for disease, cross-breeding or humanitarian reasons | 5 |
| 5 | Probable premature death on Pitt Island | 8 |

### *6.1.12 Environmental measurements*

To gauge environmental differences between black robin habitats, I measured air temperatures (°C) over the 2004-05 and 2005-06 breeding seasons and the intervening autumn-winter period. Measurements spanned six calendar seasons, from spring 2004 until summer 2005. Resource constraints did not permit me to measure wind-chill, arguably a more telling environmental variable.

Contemporaneous monthly-mean climate data for the Chatham Islands (NIWA, 2009) were available for the two black robin management phases but they were universal for all populations and lacked local precision. To ensure sensitivity to potentially small differences experienced by the populations, I recorded temperatures in the forest tracts occupied by each. The temperature data I gathered could not be related directly to the historical population trends I am analysing. Instead, I assumed that any differences I recorded between habitats would reflect the direction of historical differences, though the latter might not necessarily be of the same magnitude.

I deployed Hobo H8 Pro Series data-loggers in the centres of breeding for which I held historical data. Three data-loggers were deployed in each population (Woolshed Bush, Top Bush, Mangere Island; nine units in total). The deployment sites are listed in Appendix Four (Table 4A). Each data-logger was programmed to make high-resolution (fine-scale) measurements of ambient air temperature (ºC) on the hour night and day, every day. Loggers were fixed inside purpose-built radiation screens designed to protect them from airborne dust, salt spray and rain (*Figure 6.1*). The screens were placed in sites shaded from direct sunlight and mounted approximately one metre off the ground on PVC pipes designed to flex if the assemblies were struck by petrels or falling forest debris.

Prior to deployment, all nine loggers were run simultaneously at a sample site to test for consistency of measurement. All measurements commenced at 0100 hours on 1 October 2004. The three data-loggers on Mangere Island were uplifted on 10 February 2006. Rangatira Island's six data-loggers were retrieved on 17 February 2006. I standardised sampling periods for all sites by omitting all data collected after 0000 hours (midnight) on 10 February 2006.

Initially, I used exploratory analyses of the hourly data to assess (1) the temperature ranges experienced by black robins in each population during the six seasons sampled and (2) the differences in mean daily temperatures for each calendar season. I was interested in determining (3) which populations experienced the warmest and coolest temperatures in each season, and (4) the extent to which temperatures were warmer or cooler. To avoid introducing potentially erroneous values, missing data from failed data-loggers (see *Section 6.8*) were not substituted in any analyses.

Figure 6.1

Micro-climate data-logger station WSB 1, on the West Woolshed Bush track, Rangatira Island, 23 September 2004.
*Photo: K-J Wilson*

Temperature extremes were expressed as the highest and lowest hourly temperature recorded at each data-logger site in a calendar season. The mean of daily temperatures for each season was obtained by averaging hourly data (0100–0000 hours), first by day at each data-logger site and then for all three sites in each population's habitat. To determine which populations experienced the warmest and coolest conditions seasonally, I averaged the minimum and maximum daily temperatures from each trio of data-loggers. In addition to showing by how much (or little) ranges differed within calendar seasons, I was able to determine whether the differences were consistent season-by-season (that is, was the coldest habitat always the coldest?). Finally, to assess the extent to which one habitat was warmer or cooler than the other two in each season, I calculated the mean of differences in their daily temperatures and expressed the magnitude of variation from other habitats as the percentage difference.

After reviewing the results of these initial assessments, I submitted the data briefly to degree-day analyses in order to explore cumulative temperature differences between habitats.

Degree-day measures are commonly used to assess temperature effects on invertebrate communities (Worner, 2007) and are therefore a means of relating temperatures to black robin food supply, a potentially fundamental determinant of population trends. I measured the degree-day differences at the 5ºC threshold over the breeding seasons themselves (1 October – 28 February) and the intervening non-breeding months.

## 6.2 Results

### *6.2.1 Population sizes during the intensive management phase*

Black robin numbers in all three populations increased overall in response to the cross-fostering and associated conservation measures adopted from 1980-81 until 1989-90. In all populations combined, numbers rose from the five individuals remaining on Mangere Island in spring 1980 to 93 at the first spring census of post-management monitoring (October 1990; *Figure 6.2*; see also Appendix Four: Table 4B for census counts by age-class). Population distribution had become skewed towards Rangatira Island after cross-fostering commenced there in earnest in 1983-84, supported by transfers from Mangere Island at all life-stages (81.8% of net inter-island transfers between 1980-81 and 1989-90; Table 6.2). In spring 1990, the Woolshed Bush population comprised 41 adults and yearlings, the Top Bush 33 (74 in total for the island), and Mangere Island 19 (Appendix Four: Table 4B; and Table 6.3).

Under management, growth in pre- and post-breeding numbers in the Top Bush sub-population was consistently positive. Pre-breeding numbers on Mangere Island fluctuated markedly until 1986-87 then rose consistently. Annual growth in post-breeding numbers was more stable. Woolshed Bush numbers stalled between 1985-86 and 1987-88 (inclusive) but otherwise increased strongly overall. I attribute the hesitation to (1) random dispersals by juveniles and unmated adults under no apparent displacement pressure in the sparsely populated Woolshed Bush, and (2) to managers capitalising on the stability and experience of Top Bush pairings when fostering Woolshed Bush eggs and nestlings (Butler and Merton, 1992). Some of these fostered offspring were recruited locally. Dispersals and fostering alike contributed to the convergence in numbers in the two Rangatira Island sub-populations at the pre- and post-breeding censuses of 1987-88 (Table 6.3). At no other time did numbers in the Top Bush sub-population approach those in its island counterpart.

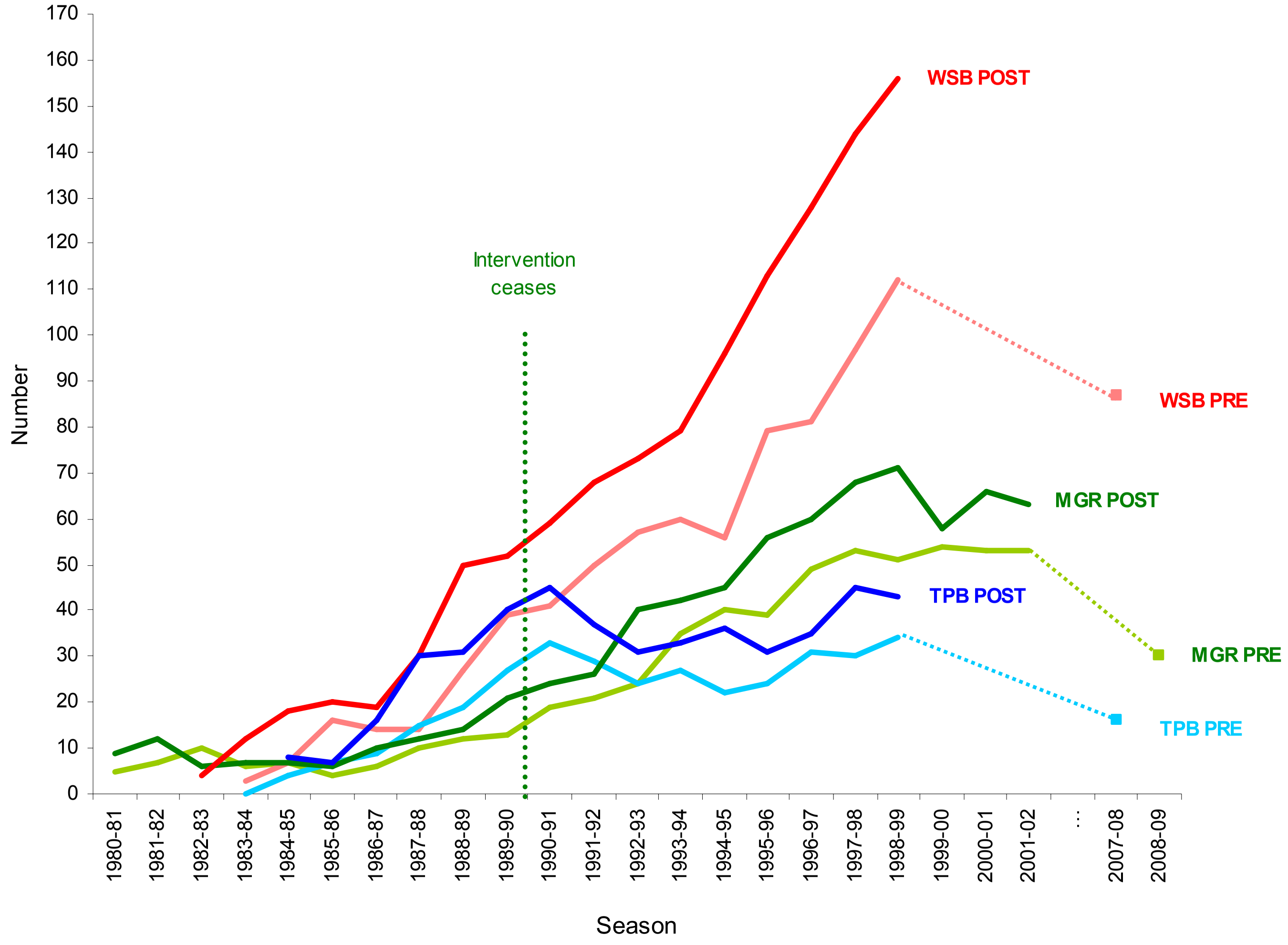

Figure 6.2 Growth trends in the three black robin populations, 1980-81 to 2001-02. Trends are based on annual pre- and post-breeding censuses on Mangere Island (MGR) and in the Woolshed Bush (WSB) and Top Bush (TPB) on Rangatira Island. Trends indicated after full-scale monitoring ceased in 2001-02 are based on the only reliable estimates available to date.

Table 6.2 Numbers by life-stage of black robins transferred between Mangere and Rangatira Islands during the ten intensive management seasons, 1980-81 to 1989-90. Net totals omit any transfers of individuals ultimately returned permanently to their natal sites. Survival is defined as living beyond the season of transfer.

**RANGATIRA TO MANGERE**

| | Eggs | | Nestlings | | Juveniles | | Adults | |
|---|---|---|---|---|---|---|---|---|
| Total | Moved | Survived | Moved | Survived | Moved | Survived | Moved | Survived |
| Gross | 2 | 0 | 8 | 6 | 5 | 2 | 7 | 4 |
| Net | 2 | 0 | 7 | 6 | 1 | 0 | 2 | 1 |

**MANGERE TO RANGATIRA**

| | Eggs | | Nestlings | | Juveniles | | Adults | |
|---|---|---|---|---|---|---|---|---|
| | Moved | Survived | Moved | Survived | Moved | Survived | Moved | Survived |
| Gross | 53 | 23 | 4 | 3 | 8 | 5 | 11 | 7 |
| Net | 44 | 14 | 3 | 2 | 8 | 5 | 11 | 7 |

### *6.2.2 Population sizes during the post-management phase*

After management ended in 1989-90, total black robin numbers continued to increase naturally (*Figure 6.2*). At the final pre-breeding census of full-population monitoring nine seasons later (spring 1998), 146 adults and yearlings were counted on Rangatira Island (Woolshed Bush, n = 112; Top Bush, n = 34; Table 6.3). Pre-breeding numbers on Mangere Island had reached 51. By the end of that final season, numbers had increased to 199 on Rangatira Island (Woolshed Bush, n = 156; Top Bush, n = 43) and 71 on Mangere Island—a combined total for both islands of 270 (the last confirmed total for the entire species). Three years later when full-scale monitoring concluded on Mangere Island (2001-02), pre- and post-breeding censuses counted 53 and 63 black robins respectively.

From 1990-91, positive population growth trajectories in the Woolshed Bush and on Mangere Island were punctuated by pre- or post-breeding censuses at which numbers stalled or declined. Growth was most consistent in the Woolshed Bush (17 of 18 censuses; Table 6.3). Annual increases on Mangere Island were less frequent (17 of 24 censuses). Reversals out-numbered pauses, were short-lived and—with the exception of the 1999-2000 post-breeding count (*Figure 6.2*)—were of modest scale.[42] In contrast to the Woolshed Bush where pre- and post-breeding numbers were rising steadily, pre-breeding numbers on Mangere Island levelled off (at between 51 and 54 individuals) in the final five seasons before full-scale monitoring ended. Growth in the Top Bush population fluctuated markedly, in contrast to strong increases under management. Numbers rose in only eight of 18 pre- and post-breeding censuses. As a result, the population took until the final season of full-population monitoring (1998-99) to recover from the abrupt contraction in numbers between 1990-91 and 1992-93 (*Figure 6.2*; Table 6.3).

The pronounced post-management fluctuations in Top Bush numbers coincided with transience in the population's distribution. At no time did black robins establish territories throughout the full extent of this large habitat. Two isolated breeding centres persisted during this phase but otherwise black robins formed ephemeral low-density clusters of breeding pairs which were usually well removed from others. These clusters appear to have formed in vacant habitat where dispersing individuals succeeded in attracting a mate, and usually persisted only for the life-span of the original settlers or their immediate offspring. This was not the pattern observed in the Woolshed Bush and on Mangere Island where breeding pairs and unmated black robins became dispersed throughout almost all available forest habitat.

### 6.2.3 Population sizes in the sample-monitoring phase

I have not been able to estimate population sizes during the sample-monitoring seasons. Distance-sampling and mark-resighting data contain numerous errors which have complicated NOREMARK estimates for the areas surveyed between 2002-03 and 2007-08 (Mangere Island and Woolshed Bush, Chapter Four). New estimates have yet to be generated from survey data corrected by this study (Moira Pryde, pers. comm.).

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[42] Thurley (2000) attributes the steep fall in 1999-2000 numbers to anomalously low reproductive effort and success in that season, without identifying any underlying factors.

Table 6.3 Pre- and post-breeding census counts in the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. The line drawn after 1989-90 represents the point of transition from intensive management to post-management monitoring. Figures given below the second line (the end of all full-scale monitoring) are the most reliable estimates available from sample-monitoring seasons.

| | Pre-breeding census | | | | | Post-breeding census | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Season | Mangere Island | Woolshed Bush | Top Bush | Rangatira Island | Total Pre-breed | Mangere Island | Woolshed Bush | Top Bush | Rangatira Island | Total Post-breed |
| 1980-81 | 5 | | | | 5 | 9 | | | | 9 |
| 1981-82 | 7 | | | | 7 | 12 | | | | 12 |
| 1982-83 | 10 | | | | 10 | 6 | 4 | | 4 | 10 |
| 1983-84 | 6 | 3 | 0 | 3 | 9 | 7 | 12 | | 12 | 19 |
| 1984-85 | 7 | 7 | 4 | 11 | 18 | 7 | 18 | 8 | 26 | 33 |
| 1985-86 | 4 | 16 | 7 | 23 | 27 | 6 | 20 | 7 | 27 | 33 |
| 1986-87 | 6 | 14 | 9 | 23 | 29 | 10 | 19 | 16 | 35 | 45 |
| 1987-88 | 10 | 14 | 15 | 29 | 39 | 12 | 30 | 30 | 60 | 72 |
| 1988-89 | 12 | 27 | 19 | 46 | 58 | 14 | 50 | 31 | 81 | 95 |
| 1989-90 | 13 | 39 | 27 | 66 | 79 | 21 | 52 | 40 | 92 | 113 |
| 1990-91 | 19 | 41 | 33 | 74 | 93 | 24 | 59 | 45 | 104 | 128 |
| 1991-92 | 21 | 50 | 29 | 79 | 100 | 26 | 68 | 37 | 105 | 131 |
| 1992-93 | 24 | 57 | 24 | 81 | 105 | 40 | 73 | 31 | 104 | 144 |
| 1993-94 | 35 | 60 | 27 | 87 | 122 | 42 | 79 | 33 | 112 | 154 |
| 1994-95 | 40 | 56 | 22 | 78 | 118 | 45 | 96 | 36 | 132 | 176 |
| 1995-96 | 39 | 79 | 24 | 103 | 142 | 56 | 113 | 31 | 144 | 200 |
| 1996-97 | 49 | 81 | 31 | 112 | 161 | 60 | 128 | 35 | 163 | 223 |
| 1997-98 | 53 | 97 | 30 | 127 | 180 | 68 | 144 | 45 | 189 | 257 |
| 1998-99 | 51 | 112 | 34 | 146 | 197 | 71 | 156 | 43 | 199 | 270 |
| 1999-00 | 54 | | | | | 58 | | | | |
| 2000-01 | 53 | | | | | 66 | | | | |
| 2001-02 | 53 | | | | | 63 | | | | |
| … | | | | | | | | | | |
| 2007-08 | | 87 | 16 | | | | | | | |
| 2008-09 | 30 | | | | | | | | | |

Head-count surveys have been more informative. After semi-structured monitoring of black robin encounters in September 2004, Kennedy and Wilson (2005) suspected population declines on both islands. Encounter rates in historical centres of distribution were unexpectedly low. On Rangatira Island, Kennedy and Wilson (2005) also noted reductions in density (western and upper central Woolshed Bush) and contractions in range (from Woolshed Bush outliers and the Top Bush) not signalled in the results of mark-resighting surveys. In tracts of the Top Bush populated historically, only six isolated black robins were encountered (five of unknown age). However, the probability of encounters was lower in the Top Bush because young black robins were not being made 'friendly' for transfer to Pitt Island, as they were in the Woolshed Bush at that time. Kennedy and Wilson's (2005) population assessments were also too brief and too early in the season for definitive pre-breeding counts on each island. In contrast to the mark-resighting surveys with which they coincided, however, the assessments involved purposeful searching on and off tracks in parts of the forests not frequented by sampling teams. Kennedy and Wilson were also free to linger in order to confirm the identity, sex and mates of black robins they encountered.

Between October and December 2007, incremental island-wide head-counts on Rangatira Island yielded more reliable indications of population size (Wickes, 2007; Merton, 2008b; Massaro and Briskie, 2008). These free-ranging searches revealed a 29.4% reduction from total pre-breeding numbers last confirmed with certainty in spring 1998. The Top Bush sub-population (n = 16) had fallen to 47% of 1998 numbers. The Woolshed Bush sub-population (n = 87) had declined less, to 87% of 1998 numbers. These figures did not include five to ten black robins thought likely to be present but not counted (reasons and sites unspecified; Massaro and Briskie, 2008). The survey was repeated in the following season, between October and December 2008, but Massaro and Briskie (2009) only gave an estimate of 120 black robins for Rangatira Island as a whole.

The Mangere Island population had declined also. Kennedy and Wilson (2005) encountered at least 24 individuals over two days of searching in late September 2004. Harvey (2009) reported a stable pre-breeding population of about 30 robins between 2006-07 and 2008-09. This is 56.6% of the total counted in spring 2001 (the final pre-breeding census of full-population monitoring era).

Too few data exist for any demographic parameter during the seasons after 2001-02 to assess whether the lower population sizes indicated by the head-counts were symptomatic of stability or instability, rebounds from steeper declines, or fluctuations around a post-colonising equilibrium.

The key points emerging from the three management phases are the growth in sub-population sizes on Rangatira Island under intensive management (at the expense of Mangere Island), the continued natural growth in the Woolshed Bush and on Mangere Island after management ceased, and the unforeseen instability of the Top Bush population under the same conditions. The three populations experienced declines of differing scale after full-population monitoring ended. Decline was most severe in the Top Bush and least severe in the Woolshed Bush. The timing of each decline is unknown but total numbers on each island fell independently. Given the character of black robin dispersals on Rangatira Island, it is less likely that sub-population declines there were independent.

## 6.3 Intra-island dispersal

Adult and juvenile dispersals between sub-populations were confined to Rangatira Island where they influenced breeding pair numbers under the two fully monitored management regimes.

Dispersing black robins moved primarily from the Woolshed Bush to the Top Bush (Table 6.4). The origins of this bias are unclear. An exploratory analysis of the movements suggests no positive relationship between population density and dispersal frequency during either management phase (Appendix Four: *Figures 4A* and *4B*). In fact, the total number of black robins dispersing decreased as population density increased in the Woolshed Bush during the post-management phase (see *Section 6.3.1* below). In the earliest of the intensive management seasons, dispersal frequency appeared to be inversely related to population size. For instance, the first two males and two females to settle in the Top Bush dispersed independently from the Woolshed Bush in which only one breeding pair held territory. This suggests a random dispersal habit in the black robin or dispersal in the search of potential mates. I have not assessed these possibilities systematically.

Features of island geography seem likely to have augmented dispersal rates. The routes taken by dispersing black robins were not documented during any management phase. Analysis of fledging-site data for dispersers indicates however that 89% of birds moving in both directions had fledged or resided as adults in bush tracts connected to two steep forest corridors linking the eastern parts of the Woolshed Bush and the Top Bush (*Figure 2.3*). The corridors had survived the farming era.

The majority of dispersing birds originated from the well populated East Woolshed Bush, an elongated chain of forest remnants and connected outliers which funnelled itinerants towards one of the two corridors. If dispersing by other routes between the Woolshed Bush and Top Bush, black robins were obliged to cross expanses of open grass- or shrubland patrolled by southern skuas and Australasian harriers.

### *6.3.1 Post-management dispersals*

After intra- and inter-island transfers stopped in 1989-90, natural dispersals accounted for all black robin movements between the two Rangatira Island sub-populations. Juveniles made 82.9% of these movements (Table 6.4). The proportion dispersing after achieving independence decreased markedly in post-management seasons. For instance, 72% of all female juveniles made dispersal movements during the intensive management phase but only 24.1% did so after the change in management regime. The decrease for males was more modest (Table 6.5). Overall, female juveniles were more likely than males to disperse. The bias in female movements was bi-directional during the intensively managed years but was evident only in movements to the Woolshed Bush in post-management seasons (11 of the 13 juvenile movements, Table 6.4).

As for juvenile females, adult females dispersed more often than adult males. The bias was pronounced and bi-directional in post-management seasons (nine of ten adult movements to the Top Bush; four of four movements to the Woolshed Bush; Table 6.4). Total adult dispersals decreased from 7.5% of black robins counted at post-breeding censuses during the intensive management period to 1.5% in post-management seasons (Table 6.6).

Table 6.4 Sum totals, sex and age-class of black robins dispersing by management phase between the Woolshed Bush and Top Bush sub-populations on Rangatira Island. Each movement from a sub-population is counted as a single dispersal event (for example, three females dispersed twice and another a third time, amounting to nine separate events). ‘Resident’ totals are the sum total of males or females counted annually in the destination habitat at pre-breeding censuses (including the newly arrived migrants). Ratios are the proportion of residents which are immigrants.

| | **WOOLSHED BUSH TO TOP BUSH** | | | | | | | | **TOP BUSH TO WOOLSHED BUSH** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Female | | | | Male | | | | Female | | | | Male | | | |
| Phase | Ad | Juv | Resident | Ratio | Ad | Juv | Resident | Ratio | Ad | Juv | Resident | Ratio | Ad | Juv | Resident | Ratio |
| Intensive management | 3 | 12 | 43 | 0.35 | - | 6 | 38 | 0.16 | 1 | 6 | 42 | 0.17 | - | - | - | - |
| Post-management | 9 | 27 | 126 | 0.29 | 1 | 28 | 127 | 0.23 | 4 | 11 | 278 | 0.05 | - | 2 | 346 | 0.006 |
| Combined | 12 | 39 | 169 | 0.30 | 1 | 34 | 165 | 0.21 | 5 | 17 | 320 | 0.07 | - | 2 | 404 | 0.005 |

Table 6.5 Proportions of black robin juveniles dispersing from the two Rangatira Island sub-populations in which they achieved independence. Each movement counts as a single dispersal event. Sex assignments are based on weights at banding and on post-fledging behaviour for juveniles failing to breed (intensive management, n = 2; post-management, n = 14).

| | Female | | | Male | | |
|---|---|---|---|---|---|---|
| Phase | Produced | Dispersed | % | Produced | Dispersed | % |
| Intensive management | 25 | 18 | 72.0 | 26 | 6 | 23.1 |
| Post-management | 158 | 38 | 24.1 | 196 | 30 | 15.3 |
| Combined | 183 | 56 | 30.6 | 222 | 36 | 16.2 |

Table 6.6 Proportions of black robin adults counted at post-breeding censuses dispersing between the two Rangatira Island sub-populations. Each movement counts as a single dispersal event. The sex of one non-breeding female (post-management) is estimated from her banding weight and post-fledging behaviour.

| | Female | | | Male | | |
|---|---|---|---|---|---|---|
| Phase | Alive | Dispersed | % | Alive | Dispersed | % |
| Intensive management | 25 | 4 | 16.0 | 28 | 0 | 0.0 |
| Post-management | 430 | 13 | 3.0 | 509 | 1 | 0.2 |
| Combined | 455 | 17 | 3.7 | 537 | 1 | 0.2 |

After management ceased, immigrants comprised 26% of all birds residing in the Top Bush—28.6% of females (range annually 13 - 54%), and 22.8% of males, (range 7 - 47%; Table 6.4). However, the proportions failing to breed after arrival were also high (25% of females, 34.5% of males). This rate of failure is explained perhaps by the lower probability of finding mates in the smaller Top Bush population, or in the less densely populated habitat. Settlement (especially by juveniles) in vacant tracts of habitat distant from the stable centres of black robin breeding cannot have helped. In contrast, immigrants from the Top

Bush augmented the Woolshed Bush population by a mere 3% overall—females by 5.4% (annual range 2% - 11%); males by 0.6% (range 0% – 3%). Unlike Top Bush immigrants, all 15 female arrivals and one of the two new males subsequently bred in the Woolshed Bush.

It is evident from these disproportionate rates of dispersal that the Top Bush population was dependent on annual immigration from the Woolshed Bush to support growth in numbers under natural conditions. Without this regular replenishment, the productivity of the resident population may not have been sufficient to sustain its numbers. As it was, the combined efforts of resident and immigrant black robins were barely adequate to sustain growth.

## 6.4 Rates of growth in pre-breeding populations

Mean rates of growth in pre-breeding numbers differed substantially between populations throughout the study period. For both management phases combined, growth was strongest in the Woolshed Bush population ($r = 0.201$). Transfers from Mangere Island during the intensive management seasons contributed to that population's lower overall growth rate ($r = 0.134$), and negligible post-management growth had a reducing effect on the overall rate in the Top Bush ($r = 0.114$; Table 6.7).

Intensive management accelerated growth rates in the Rangatira Island populations. Natural growth rates in the nine post-management seasons were much lower (*Figure 6.3*). The beneficial effects of management were revealed most sharply in the Top Bush where the mean rate of population increase declined by 97.3% after cross-fostering and transfers ceased (from $r = 0.373$ to 0.010; Table 6.7). In the Woolshed Bush, the natural rate of increase ($r = 0.116$) was 68.3% lower than the management rate. Rates combined for Rangatira Island ($r = 0.442$) far exceeded those on Mangere Island during the ten management seasons when productivity was harvested ($r = 0.072$). But when cropping ceased at the conclusion of management, the rate of growth in the Mangere Island population improved on the rebound, by 37.5% ($r = 0.099$). This rate of increase was higher than the collective rate for Rangatira Island over the post-management period.

Table 6.7 Mean annual rates of growth (*r*) in pre-breeding numbers by management phase in the black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02.

| **Intensive management** | *n* (years) | *r* | 95%CI |
|---|---|---|---|
| Mangere | 10 | 0.072 | ± 0.0737 |
| Rangatira | 7 | 0.442 | ± 0.1468 |
| Woolshed Bush | 7 | 0.366 | ± 0.1247 |
| Top Bush | 6 | 0.373 | ± 0.0427 |
| **Post-management monitoring** | | | |
| Mangere | 12 | 0.099 | ± 0.0266 |
| Rangatira | 9 | 0.083 | ± 0.0234 |
| Woolshed Bush | 9 | 0.116 | ± 0.0209 |
| Top Bush | 9 | 0.010 | ± 0.0408 |
| **All phases combined** | | | |
| Mangere | 22 | 0.134 | ± 0.0199 |
| Rangatira | 16 | 0.194 | ± 0.0516 |
| Woolshed Bush | 16 | 0.201 | ± 0.0382 |
| Top Bush | 15 | 0.114 | ± 0.0465 |

## 6.5 Productivity

The accelerated growth rates and resultant population increases on both black robin islands between 1980-81 and 1989-90 were engineered by the multiple-clutching of females and other protective measures explained in Chapter Four. The intervention disguised the natural variations in breeding effort and success which were expressed in the more modest population growth rates of the post-management seasons.

### *6.5.1 Trends in total breeding pair numbers during intensive management seasons*

Breeding-pair numbers on both islands were influenced by the managed increases in black robin abundance, and by inter-island transfers designed to minimise the numbers of unmated individuals (Butler and Merton, 1992). On Rangatira Island, the effects of natural dispersal contributed also.

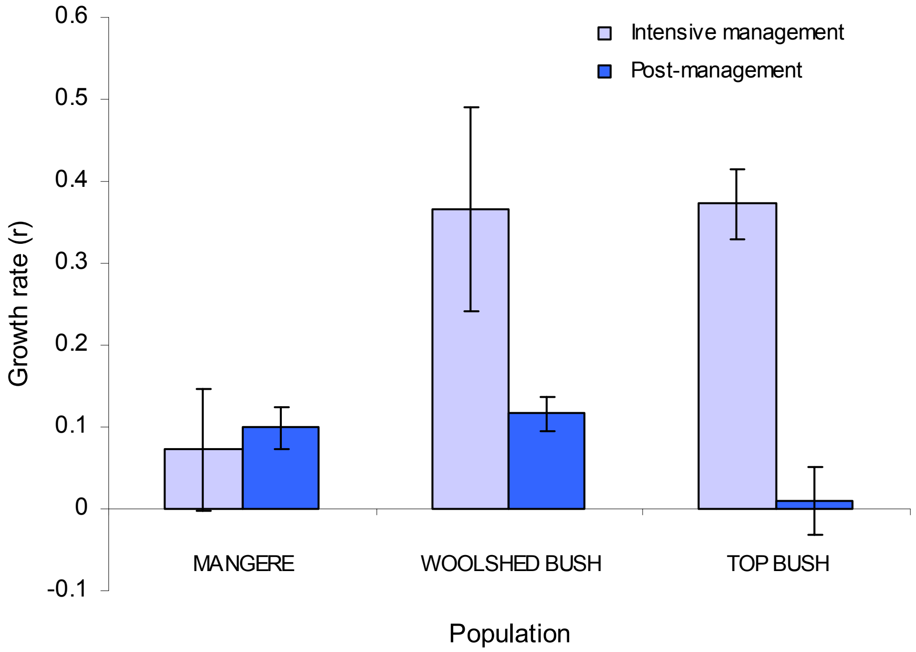


Figure 6.3 Differences in mean annual growth rates (*r*) in the three black robin populations on Mangere and Rangatira Islands during the intensive management and post-management monitoring phases. Exponential rates derived from pre-breeding census counts (95% confidence intervals).

After breeding commenced on Rangatira Island in 1983-84, pair numbers increased steadily from one to 20 in the Woolshed Bush and two to 12 in the Top Bush (Table 6.8), giving mean annual rates of increase of $r = 0.503$ and 0.382 respectively (Table 6.9). Increases were augmented by the net transfer of 44 eggs, three nestlings, eight juveniles and 11 adults from Mangere Island (Table 6.2). On Mangere Island, breeding pair numbers fluctuated annually between one and six pairs, so that mean annual growth in pair numbers ($r = 0.091$) was poorer than on Rangatira Island. Pair numbers benefited from more modest net transfers of two eggs, seven nestlings, one juvenile and two adults from Rangatira Island (Table 6.2). The juvenile and adult imports addressed the depleting effect of productivity cropping on pair numbers and ensured higher harvestable output from the Mangere Island breeding population.

Table 6.8 Breeding pair numbers in the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. Totals exclude non-laying pairs and known (*) or suspected (**) black robin x tomtit cross-pairings. Effective pairs (those raising juveniles) are identifiable only during post-management seasons (1990-91 onwards). Rangatira Island pair numbers for 2007-08 are estimates based on available field data (none available for Mangere Island).

| | Mangere | | Woolshed Bush | | Top Bush | | Rangatira | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | All | Effective | All | Effective | All | Effective | All | Effective | All |
| 1980-81 | 2 | | | | | | | | 2 |
| 1981-82 | 2 | | | | | | | | 2 |
| 1982-83 | 3 | | | | | | | | 3 |
| 1983-84 | 4 | | 1 | | | | 1 | | 5 |
| 1984-85 | 2 | | 1 * | | 2 | | 3 | | 5 |
| 1985-86 | 1 | | 2 * | | 3 | | 5 | | 6 |
| 1986-87 | 2 | | 5 | | 3 | | 8 | | 10 |
| 1987-88 | 4 | | 4 | | 5 | | 9 | | 13 |
| 1988-89 | 5 | | 9 | | 11 | | 20 | | 25 |
| 1989-90 | 6 | | 20 | | 12 * | | 32 | | 38 |
| 1990-91 | 6 ** | 4 | 19 | 14 | 15 | 8 | 34 | 22 | 40 |
| 1991-92 | 7 ** | 5 | 20 | 13 | 12 | 7 | 32 | 20 | 39 |
| 1992-93 | 9 ** | 8 | 23 | 12 | 9 | 7 | 32 | 19 | 41 |
| 1993-94 | 9 ** | 5 | 27 | 17 | 12 | 6 | 39 | 23 | 48 |
| 1994-95 | 14 ** | 8 | 27 | 23 | 9 | 7 | 36 | 30 | 50 |
| 1995-96 | 16 ** | 12 | 36 | 27 | 10 | 4 | 46 | 31 | 62 |
| 1996-97 | 17* | 10 | 36 | 29 | 11 | 6 | 47 | 35 | 64 |
| 1997-98 | 18 | 12 | 37 | 30 | 13 | 8 | 50 | 38 | 68 |
| 1998-99 | 20 | 15 | 41 | 31 | 15 | 6 | 56 | 37 | 76 |
| 1999-00 | 19 | 6 | - | - | - | - | - | - | - |
| 2000-01 | 18 | 12 | - | - | - | - | - | - | - |
| 2001-02 | 17 | 12 | - | - | - | - | - | - | - |
| … | | | | | | | | | |
| 2007-08 | - | - | ~ 30 | - | ~ 8 | - | ~ 38 | - | - |

Table 6.9 Exponential rates of growth (*r*) by management phase in the numbers of breeding pairs in the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02.

| **Intensive management** | *n* (seasons) | *r* | 95% CI |
|---|---|---|---|
| Mangere | 10 | 0.091 | ± 0.108 |
| Rangatira | 7 | 0.528 | ± 0.092 |
| Woolshed Bush | 7 | 0.503 | ± 0.111 |
| Top Bush | 6 | 0.382 | ± 0.101 |
| **Post-management monitoring** | | | |
| Mangere | 12 | 0.105 | ± 0.033 |
| Rangatira | 9 | 0.071 | ± 0.019 |
| Woolshed Bush | 9 | 0.102 | ± 0.017 |
| Top Bush | 9 | 0.008 | ± 0.052 |
| **All phases** | | | |
| Mangere | 22 | 0.132 | ± 0.024 |
| Rangatira | 16 | 0.221 | ± 0.059 |
| Woolshed Bush | 16 | 0.252 | ± 0.054 |
| Top Bush | 15 | 0.111 | ± 0.051 |

### *6.5.2 Trends in breeding pair numbers during post-management seasons*

Under natural conditions, mean annual growth in breeding pair numbers slowed in each Rangatira Island sub-population and improved on Mangere Island (following the release from cropping pressure). The rates converged on Mangere Island and in the Woolshed Bush ($r = 0.105$ and 0.102 respectively; Table 6.8).

Mangere Island pair numbers rose from six to 20 pairs between 1990-91 and 1998-99, increasing modestly by an average of two pairs over seven of nine seasons (range 1-5 pairs). Numbers then decreased by one pair annually to 17 pairs in 2001-02. Woolshed Bush numbers rose over six of nine seasons from 19 to 41 pairs. The annual increases were more variable, ranging from one to nine pairs ($\bar{x} = 3.66$), but growth was generally steady.

In marked contrast to earlier stable growth under management, Top Bush pair numbers declined overall from 15 to nine pairs by 1994-95, then commenced a slow recovery to 15 pairs in 1998-99. The slower rate of increase in the Top Bush (*r* = 0.008) depressed the collective growth rate on Rangatira Island (r = 0.071) below Mangere Island's rate (*r* = 0.105; Table 6.9).

### *6.5.3 Pair numbers after the conclusion of full-population monitoring*

Missed surveys and errors in survey data confuse the picture of breeding pair numbers during the sample-monitoring seasons on Rangatira Island after 1999-00 and on Mangere Island after 2002-03. Breeding pairs occupying a standardised sample area of Woolshed Bush were monitored from 1999-00 to 2003-04 (Department of Conservation, 2001a) but I have not been able to obtain the data for analysis (data misplaced; Dave Houston, pers. comm., July 2008). Nor is a definitive estimate of pair numbers in the Woolshed Bush and Top Bush possible from the island-wide head-count surveys conducted between October and December in 2007 and 2008.

I found that the head-count reports for 2007-08 contained incomplete or contradictory data. In the Woolshed Bush and its outliers, Merton (2008b) reported 31 territories occupied by pairs and another held by a single black robin (sex unspecified). Massaro and Briskie (2008) found 'nearly all nesting pairs' in the Woolshed Bush (active nests, n = 25) but did not specify total numbers of pairs or territories. My analysis of the 2007-08 count data collated separately by the Department of Conservation (2008) suggests a possible 30 pairs in the Woolshed Bush. This is considerably fewer than in 1998-99 when breeding and non-breeding pairs occupied 45 territories, and 27 unmated black robins (18 males, nine females) occupied others. For 2008-09, Massaro and Briskie (2009) reported 39 pairs in the Woolshed Bush without mentioning unmated birds. I have not been able to obtain the 2008-09 count data. Based on these reports, however, I would estimate a minimum of 30-35 breeding pairs today.

I am less certain of Top Bush pair numbers. For 2007-08, Merton (2008b) estimated at least 11 territories but did not distinguish between paired and unmated black robins. Massaro and Briskie (2008) reported for that only nine individuals were discovered in the Top Bush despite intensive searching, yet my analysis of their survey data (Department of Conservation, 2008) indicates a maximum of eight possible pairs in the Top Bush. In 2008-09, the Top Bush was not surveyed comprehensively (Massaro and Briskie, 2009). At the last definitive census in 1998-99, territories were held in the Top Bush by 17 breeding and non-breeding pairs and three unmated black robins (two males, one female; this study).

### *6.5.4 Proportions of effective pairs*

Effective pair numbers give a better indication of each population's breeding potential but are discernible only during the post-management seasons when broods were raised exclusively by biological parents. In contrast, 52.7% of juveniles produced during the intensive management seasons (1980-81 to 1989-90) were raised to independence by foster-parents (Appendix Four: Table 4C).

Under natural conditions, the annual proportions of effective pairs on Mangere Island declined gradually on average as total breeding pair numbers increased ($r$ = - 0.019). The mean rate of decline was similar in the Top Bush ($r$ = - 0.017) where overall pair numbers stagnated. Conversely, the proportions rose in the Woolshed Bush as breeding pair numbers increased ($r$ = 0.021; Table 6.10).

In none of the post-management populations did all breeding pairs in a season succeed in producing juveniles. In all post-management seasons combined, the Woolshed Bush possessed the highest proportion of successful pairs in its breeding population (74%) and the Top Bush population possessed the fewest (56%). On Mangere Island, 64% of all breeding pairs were effective (Table 6.10).

### *6.5.5 Reproductive output from egg-laying to fledging*

In analysing black robin productivity, I have distinguished between reproductive output and reproductive performance, as explained in *Section 6.1.7*. In this section, I confine my output and performance summaries to the intermediate life-stages of the breeding cycle (clutches and eggs laid, eggs incubated full-term and hatched, and nestlings fledged).

Intensive management of the three populations increased mean annual reproductive output pair$^{-1}$ at all intermediate life-stages. As with trends in population sizes and breeding pair numbers, the elevated output was an artefact of brood manipulation and other conservation measures which did not give a true indication of the black robin's natural reproductive potential.

Table 6.10 Mean annual rates of growth (*r*) in the proportions of breeding pairs which were effective (that is, they produced juveniles) in the three black robin populations on Mangere and Rangatira Islands during the post-management seasons, 1990-91 to 2001-02. Ranges express the lowest and highest annual proportions observed in any season. The overall proportion relates to the sum total of breeding pairs in all post-management seasons combined.

| | *n* (years) | *r* | 95% CI | Range (%) | Overall |
|---|---|---|---|---|---|
| Mangere | 12 | - 0.019 | ± 0.0266 | 32 – 89 | 0.64 |
| Rangatira | 9 | 0.014 | ± 0.0197 | 59 – 83 | 0.69 |
| Woolshed Bush | 9 | 0.021 | ± 0.0238 | 52 – 81 | 0.74 |
| Top Bush | 9 | - 0.017 | ± 0.0353 | 40 – 78 | 0.56 |

After intensive management concluded, natural output pair$^{-1}$ year$^{-1}$ was universally lower and output differences between the populations became less pronounced (Table 6.11). Reproductive performance declined in the two productivity measures not directly influenced by conservation activities. Average clutch-size declined on Mangere Island but remained more or less constant in the two Rangatira Island sub-populations (Table 6.12). The incidence of rimshots decreased sharply, particularly on Rangatira Island (Table 6.13). Hatch-rates declined in all three populations also, most obviously in the Top Bush. These trends are quantified below.

I have not attempted a systematic assessment of potential causes for the lower rimshot frequency (from a mean annual rate of 12.9% to 4.2% of eggs laid in all populations). Post-management observers were less likely to detect rimshots because nest observations were less intense and the salvage of the mislaid eggs was no longer imperative (pers. obs; Chapter Four). The reduction may also be related to lower egg-laying stresses after the obligatory renesting of females ceased. Clutch data are detailed enough to show whether first or only later clutches were affected, and perhaps why the phenomenon varied in severity by population and season (up to 20.4% of all eggs laid in 1989-90; Chapter Two), but analysis of those data is beyond the scope of my study.

#### *6.5.5.1 Woolshed Bush productivity from egg-laying to fledging*

Under natural conditions, the mean annual reproductive output of Woolshed Bush pairs (sum total = 266) decreased relative to managed output in all intermediate productivity measures (Table 6.12). On average, each pair laid 1.56 clutches (21.2% fewer than under management), 3.13 eggs (- 20.8%) and incubated 2.55 eggs to hatching age (- 44%). Production of nestlings ($\bar{x}$ = 1.88) and fledglings ($\bar{x}$ = 1.5) declined by 47.1% and 42.2% respectively (Table 6.11). Per-pair output lay within the ranges of the other populations for all these productivity measures (clutches laid, eggs laid, incubated full-term and hatched). The pair$^{-1}$ fledgling output was a third better than on Mangere Island and 4.1% higher than in the Top Bush.

Clutch sizes were unaffected by the change in management regime ($\bar{x}$ = 2.0 - 2.01 eggs, Table 6.12). The overall proportion of eggs hatching decreased to 73.7% of eggs incubated full-term (5.5% lower than under managed conditions). Despite laying five times more eggs during post-management seasons (Table 6.13), the proportion laid as rimshots (17.5%) was 76.6% lower than during management, the highest rate of decrease in the three populations.

On average, Woolshed Bush pairs incubated the highest proportion of eggs to hatching age under natural conditions (84.7%), though the difference with Mangere Island was slight. The majority of eggs lost to incubation were deserted or disappeared from clutches (often for unknown reasons in both cases). Natural proportions of full-term eggs hatching were similar to Top Bush rates, though black robins in each Rangatira Island sub-population were poorer than their Mangere Island equivalents at hatching eggs. The Woolshed Bush population fledged the greatest proportion of nestlings (80%), a rate which equated to 0.48 fledglings for each egg laid (n = 399, from 833 eggs; Table 6.14).

In summary, natural pair$^{-1}$ year$^{-1}$ output and breeding success in the Woolshed Bush compared favourably with output in the other populations but benefited from lower mean rates of egg and nestling mortality. Gross reproductive output also benefited from steady growth in the numbers of breeding pairs and the proportions of effective breeders (see *Sections 6.5.3* and *6.5.4* above). The net result was that Woolshed Bush pairs converted 17% more of their eggs into fledglings than Mangere Island pairs could manage and 20% more than Top Bush pairs.

#### *6.5.5.2 Mangere Island productivity from egg-laying to fledging*

As in the Woolshed Bush, per-pair productivity weakened on Mangere Island after management ended. Natural clutch numbers declined 36.7% to 1.41 pair$^{-1}$ year$^{-1}$. Pairs produced 2.75 eggs on average (- 40.9%) and incubated 2.24 to full-term (-17.3%). Natural nestling output was 1.73 pair$^{-1}$ year$^{-1}$ (- 19.9%). Fledgling production averaged 1.12 pair$^{-1}$ (- 26.3%). This was the smallest decrease in fledgling output in the three populations (Table 6.11). In all of these measures, natural pair$^{-1}$ output was lower than in the Rangatira Island sub-populations, particularly for fledgling production (25.5% and 22.6% lower than Woolshed Bush and Top Bush pairs respectively).

Natural clutch sizes (1.95 eggs) were 6.7% smaller in post-management seasons. The 77.2% of full-term eggs hatching also represented a small decrease. Relative to the Rangatira Island sub-populations, rimshot frequency had been anomalously low under management and remained inconsequential afterwards (2.8% of all eggs laid; Table 6.13). The population was as successful as Woolshed Bush black robins at incubating eggs to full-term (83.2%), benefiting from a similar rate of egg mortality (16.8% of all eggs under incubation). On the other hand, nestling mortality of 35.4% (the most severe of the three populations) took its toll on fledging success (64.6%). Each egg laid produced 0.41 fledglings (n = 190, from 467 eggs; Table 6.14), a marginally better rate than in the Top Bush but poorer than in the Woolshed Bush.

Overall, the natural reproductive output of Mangere Island robins was low in all intermediate productivity measures. Fledgling output was limited by smaller clutch sizes and lower egg production, and ultimately by a very high rate of nestling mortality. Incubation success and natural hatching rates were not limiting factors nor was overall growth in the numbers of breeding pairs. But the diminishing proportion of successful breeders was a potential constraint. Only 64% of pairs breeding throughout the post-management phase would eventually produce juveniles (Table 6.10). Despite these factors, the population converted its egg-laying investment into fledglings at a rate intermediate between the Top Bush and Woolshed Bush rates.

### *6.5.5.3 Top Bush productivity from egg-laying to fledging*

After management ceased in the Top Bush, mean annual per-pair output of eggs, nestlings and fledglings decreased as it had elsewhere. Pairs laid 28.5% fewer clutches ($\bar{x}$ = 1.69) and 28.1% fewer eggs ($\bar{x}$ = 3.63). This rate of output was greater than per-pair effort in the other populations. Pairs also exceeded output elsewhere in the mean number of eggs incubated to full-term annually ($\bar{x}$ = 2.77, 39.1% fewer than under management) and in nestlings produced ($\bar{x}$ = 2.06, - 41.7%). Fledgling production ($\bar{x}$ =1.44, - 45.3%) was a little less than Woolshed Bush output ($\bar{x}$ = 1.5) but better than Mangere Island effort ($\bar{x}$ = 1.12; Table 6.11).

Clutch sizes ($\bar{x}$ = 2.14 - 2.15) were unaffected by the change in management and were the largest of the three populations under both regimes (Table 6.12). Rimshot frequency fell by more than half to 5.7% of eggs laid overall but this was still the highest proportion under natural conditions. The population's hatch-rate had exceeded the others under management (85.2% of all eggs incubated full-term) but decreased to 74.1%, a natural rate much closer to that in the Woolshed Bush (73.7%) and on Mangere Island (77.2%; Table 6.13). This was the largest post-management correction in hatching success (and conversely, hatch-failure) in the three populations.

Despite Top Bush pairs incubating the greatest mean number of eggs to hatching age, incubation success was the lowest recorded (79.9% of all eggs remaining in nests), though not more than 5.5% less than the best rate in Woolshed Bush. The low rate is attributable to total egg losses from incubation of 20.1%, more than a fifth higher than on Mangere Island and almost 30% higher than in the Woolshed Bush. Nestling mortality (29.8%) was not substantially out-of-step with the other populations (Woolshed Bush, 20%; Mangere Island, 35.4%), and the population managed to fledge 70.2% of all brooded nestlings. The net result was that each egg laid produced 0.40 fledglings (n = 153, from 385 eggs; Table 6.13), almost matching Mangere Island's fledging success (0.41 egg$^{-1}$) but much less efficient than Woolshed Bush production (0.48 egg$^{-1}$).

Table 6.11 Mean annual per-pair output for effective and ineffective breeding pairs in the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. ‘Pairs’ gives the total number of pairs combined for the management phase. Ratios for 'Natal site production' refer to reproductive output which was unaffected by cross-fostering activities during the intensive management phase. Thereafter, ratios for the intensive management phase are based on totals which recognise the transfer of eggs, nestlings, fledglings and adults, and the dispersal of juveniles and adults during both phases.

| | | Natal site production | | | | Eggs | | | | Nestlings | | Fledglings | | Juveniles | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Yrs | Pairs | Clutches | Eggs | Rimshots | Incubated | Lost | IFT | FTH | Hatched | Dead | Fledged | Dead | *n* | Live ≥ 1 yr |
| Intensive management 1980-81 to 1989-90 | | | | | | | | | | | | | | | |
| MANGERE | 10 | 31 | 2.23 | 4.65 | 0.23 | 2.84 | 0.38 | 2.71 | 0.52 | 2.16 | 0.81 | 1.52 | 0.19 | 1.35 | 1.00 |
| WOOLSHED BUSH | 7 | 42 | 1.98 | 3.95 | 0.69 | 5.50 | 1.04 | 4.55 | 1.02 | 3.55 | 0.67 | 2.60 | 0.19 | 2.38 | 1.52 |
| TOP BUSH | 6 | 36 | 2.36 | 5.06 | 0.67 | 4.56 | 0.72 | 4.14 | 0.61 | 3.53 | 1.08 | 2.64 | 0.89 | 1.75 | 1.44 |
| All populations | | 109 | 2.17 | 4.51 | 0.55 | 4.43 | 0.75 | 3.89 | 0.74 | 3.15 | 0.84 | 2.30 | 0.42 | 1.88 | 1.35 |
| Post-management 1990-91 to 2001-02 | | | | | | | | | | | | | | | |
| MANGERE | 12 | 170 | 1.41 | 2.75 | 0.08 | 2.69 | 0.45 | 2.24 | 0.51 | 1.73 | 0.61 | 1.12 | 0.11 | 1.01 | 0.80 |
| WOOLSHED BUSH | 9 | 266 | 1.56 | 3.13 | 0.13 | 3.00 | 0.47 | 2.55 | 0.67 | 1.88 | 0.38 | 1.50 | 0.23 | 1.27 | 0.79 |
| TOP BUSH | 9 | 106 | 1.69 | 3.63 | 0.21 | 3.47 | 0.70 | 2.77 | 0.72 | 2.06 | 0.61 | 1.44 | 0.46 | 0.98 | 0.89 |
| All populations | | 542 | 1.54 | 3.11 | 0.13 | 3.00 | 0.51 | 2.49 | 0.63 | 1.86 | 0.49 | 1.37 | 0.23 | 1.13 | 0.81 |

| NOTES | | |
|---|---|---|
| | Rimshot | Egg laid on or over the nest rim and lost from production |
| | IFT | Incubated full-term |
| | FTH | Failed to hatch |

Table 6.12 Means per clutch of black robin eggs laid, nestlings hatched, fledged and reaching independence, and juveniles surviving to breeding age (≥ one year) on Mangere and Rangatira Islands, 1980-81 to 2001-02. Effective pairs cannot be distinguished in breeding populations during the intensive management phase ('INT', 1980-81 to 1989-90) because many broods were raised by foster-parents.

| | **Clutches *n*** | | Eggs | | Nestlings | | Fledglings | | Juveniles | | Juveniles living ≥ 1 yr | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | INT | POST | INT | POST | INT | POST | INT | POST | INT | POST | INT | POST |
| **Effective breeding pairs** | | | | | | | | | | | | |
| MANGERE | - | 157 | - | 1.97 | - | 1.53 | - | 1.17 | - | 1.10 | - | 0.87 |
| WOOLSHED BUSH | - | 308 | - | 2.07 | - | 1.41 | - | 1.23 | - | 1.10 | - | 0.68 |
| TOP BUSH | - | 112 | - | 2.21 | - | 1.34 | - | 1.10 | - | 0.93 | - | 0.84 |
| **Ineffective breeding pairs** | | | | | | | | | | | | |
| MANGERE | - | 83 | - | 1.89 | - | 0.65 | - | 0.08 | - | 0.00 | - | 0.00 |
| WOOLSHED BUSH | - | 106 | - | 1.85 | - | 0.62 | - | 0.20 | - | 0.00 | - | 0.00 |
| TOP BUSH | - | 67 | - | 2.06 | - | 1.01 | - | 0.45 | - | 0.00 | - | 0.00 |
| **All pairs combined** | | | | | | | | | | | | |
| MANGERE | **69** | **240** | 2.09 | 1.95 | 0.97 | 1.23 | 0.68 | 0.79 | 0.61 | 0.72 | 0.45 | 0.57 |
| WOOLSHED BUSH | **83** | **414** | 2.00 | 2.01 | 1.80 | 1.21 | 1.31 | 0.96 | 1.20 | 0.82 | 0.77 | 0.51 |
| TOP BUSH | **85** | **179** | 2.14 | 2.15 | 1.49 | 1.22 | 1.12 | 0.85 | 0.74 | 0.58 | 0.61 | 0.53 |

Table 6.13 Collective reproductive performance of all breeding pairs (effective and ineffective) in each of the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. Proportions are based on running totals from Table 6.14 (see notes below). Proportions for the intensive management phase use demise-site data which recognise the transfer of eggs, nestlings, fledglings and adults. Juvenile dispersal affects proportions surviving ≥ one year in both phases.

|  |  | % of Eggs Laid |  | % of Eggs Incubated |  | % of Eggs IFT |  | % of Nestlings |  | % of Fledglings |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Yrs | *n* | Rimshot | Lost | IFT | FTH | Hatched | Dead | Fledged | Dead | Indpdt | Live ≥ 1 yr |
| **Intensive management** |  |  | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* |
| MANGERE | 10 | 144 | 4.9 | 13.6 | 95.5 | 20.2 | 79.8 | 37.3 | 70.1 | 12.8 | 89.4 | 73.8 |
| WOOLSHED BUSH | 7 | 166 | 17.5 | 19.0 | 82.7 | 22.0 | 78.0 | 18.8 | 73.2 | 7.3 | 91.7 | 64.0 |
| TOP BUSH | 6 | 182 | 13.2 | 15.9 | 90.9 | 14.8 | 85.2 | 30.7 | 74.8 | 33.7 | 66.3 | 82.5 |
| All populations |  | 492 | 12.2 | 17.0 | 87.8 | 19.1 | 80.9 | 26.8 | 73.2 | 18.3 | 81.7 | 71.7 |
| **Post-management** |  |  | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* |
| MANGERE | 12 | 467 | 2.8 | 16.8 | 83.2 | 22.8 | 77.2 | 35.4 | 64.6 | 9.5 | 90.5 | 79.1 |
| WOOLSHED BUSH | 9 | 833 | 4.1 | 15.5 | 84.5 | 26.3 | 73.7 | 20.0 | 80.0 | 15.0 | 85.0 | 61.9 |
| TOP BUSH | 9 | 385 | 5.7 | 20.1 | 79.9 | 25.9 | 74.1 | 29.8 | 70.2 | 32.0 | 68.0 | 90.4 |
| All populations |  | 1685 | 4.1 | 16.9 | 83.2 | 25.2 | 74.8 | 26.6 | 73.4 | 17.1 | 82.9 | 71.5 |

Running totals …. % of
1 all eggs laid
2 eggs under incubation (incl. salvaged rimshots)
3 eggs under incubation (IFT = incubated full-term)
4 IFT eggs (FTH = failing to hatch )
5 IFT eggs
6 nestlings produced
7 nestlings produced
8 nestlings fledging
9 nestlings fledging
10 fledglings produced

Table 6.14 Productivity in the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. Population totals listed under 'Natal site production' were unaffected by cross-fostering activities during the intensive management phase. Thereafter, totals for that phase recognise the transfer of eggs, nestlings, fledglings and adults, and the dispersal of juveniles and adults during both phases. ‘Incubated’ totals in both phases include rimshots which were returned to incubation (thus disturbing the running totals).

| | | Natal site production | | | | Eggs | | | | Nestlings | | Fledglings | | Juveniles | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Yrs | Pairs | Clutches | Eggs | Rimshot | Incubated | Lost | IFT | FTH | Hatched | Dead | Fledged | Dead | *n* | Live ≥ 1 yr |
| **Intensive management** 1980-81 to 1989-90 | | | | | | | | | | | | | | | |
| MANGERE | 10 | 31 | 69 | 144 | 7 | 88 | 12 | 84 | 17 | 67 | 25 | 47 | 6 | 42 | 31 |
| WOOLSHED BUSH | 7 | 42 | 83 | 166 | 29 | 231 | 44 | 191 | 42 | 149 | 28 | 109 | 8 | 100 | 64 |
| TOP BUSH | 6 | 36 | 85 | 182 | 24 | 164 | 26 | 149 | 22 | 127 | 39 | 95 | 32 | 63 | 52 |
| All populations | | 109 | 237 | 492 | 60 | 483 | 82 | 424 | 81 | 343 | 92 | 251 | 46 | 205 | 147 |
| **Post-management** 1990-91 to 2001-02 | | | | | | | | | | | | | | | |
| MANGERE | 12 | 170 | 240 | 467 | 13 | 458 | 77 | 381 | 87 | 294 | 104 | 190 | 18 | 172 | 136 |
| WOOLSHED BUSH | 9 | 266 | 414 | 833 | 34 | 801 | 124 | 677 | 178 | 499 | 100 | 399 | 60 | 339 | 210 |
| TOP BUSH | 9 | 106 | 179 | 385 | 22 | 368 | 74 | 294 | 76 | 218 | 65 | 153 | 49 | 104 | 94 |
| All populations | | 542 | 833 | 1685 | 69 | 1627 | 275 | 1352 | 341 | 1011 | 269 | 742 | 127 | 615 | 440 |
| **Combined phases** 1980-81 to 2001-02 | | | | | | | | | | | | | | | |
| MANGERE | 22 | 201 | 309 | 611 | 20 | 546 | 89 | 465 | 104 | 361 | 129 | 237 | 24 | 214 | 167 |
| WOOLSHED BUSH | 16 | 308 | 497 | 999 | 63 | 1032 | 168 | 868 | 220 | 648 | 128 | 508 | 68 | 439 | 274 |
| TOP BUSH | 15 | 142 | 264 | 567 | 46 | 532 | 100 | 443 | 98 | 345 | 104 | 248 | 81 | 167 | 146 |
| All populations | | 651 | 1070 | 2177 | 129 | 2110 | 357 | 1776 | 422 | 1354 | 361 | 993 | 173 | 820 | 587 |

Overall, the Top Bush population made the greatest clutch and egg-laying investment under natural conditions but was ultimately the least successful at converting that investment into fledglings. Hatch-rate was not a limiting factor but the cumulative effects of egg and nestling mortality were. These are likely to have increased the incidence of renesting reflected in the elevated numbers of clutches and eggs per pair. Gross output was limited by volatility in breeding pair numbers after management stopped, coupled with an overall decline in the proportion of successful breeders (Table 6.10). The limited life-span of breeders may also have contributed (see *Section 6.7.1* below). However, despite these impediments, per-pair fledging production was not significantly poorer than on Mangere Island, suggesting that on balance Top Bush pairs were not intrinsically less able to perform at the intermediate stages of breeding.

Gross output of fledglings varied in the three populations but breeding performance up to the fledging stage in the breeding cycle did not appear to separate the populations markedly. The Woolshed Bush population performed better but the Top Bush and Mangere Island populations were similarly matched in fledgling production.

### 6.5.6 Juvenile production

Intensive management lifted the mean annual rate of juvenile production for all populations combined to 1.88 pair$^{-1}$. This rate of production was more than three times greater than that of the relict founder population on Mangere Island after 1976-77 (0.55 juveniles pair$^{-1}$ year$^{-1}$; Chapter Three: Table 3.3).

After management ceased, pairs in all populations produced fewer juveniles on average, following from their weaker reproductive output at intermediate life-stages. The combined rate declined from managed output by 39.9%, to 1.13 juveniles pair$^{-1}$ year$^{-1}$ (Table 6.11). Differences in juvenile production rates narrowed between populations under natural conditions (Table 6.11). Woolshed Bush pairs were the most successful at raising fledglings to independence ($\overline{x}$ = 1.27) and Top Bush pairs the least successful ($\overline{x}$ = 0.98). Mangere Island pairs were only marginally more productive than Top Bush breeders ($\overline{x}$ = 1.01).

Differences in fledgling mortality were considerable and penalised Top Bush production heavily. Mean annual pair$^{-1}$ fledgling output on Mangere Island had been low relative to the other populations ($\bar{x} = 1.12$) but overall, the population raised 90.5% of its fledglings to independence (Table 6.13), a mean loss rate of 0.11 fledglings pair$^{-1}$ year$^{-1}$ (Table 6.11). This equated to a mean of 0.37 juveniles produced from each egg laid in post-management seasons. Woolshed Bush pairs had been the best producers of fledglings ($\bar{x} = 1.5$) but lost twice as many ($\bar{x} = 0.23$ pair$^{-1}$ year$^{-1}$) in the interval to independence. The population reared 85% of its fledglings successfully (0.4 juveniles per egg laid). In marked contrast, the Top Bush population reared only 68% of its fledglings successfully. The anomalously high proportion dying (32%) equated to a mean loss of 0.46 fledglings pair$^{-1}$ year$^{-1}$, twice the number in the Woolshed Bush and quadruple the number on Mangere Island. Each egg laid in the Top Bush produced 0.27 juveniles under natural conditions (Table 6.14).

These relative rates of fledgling mortality persisted in both management phases, and the obvious disparity in Top Bush juvenile production persisted throughout (Tables 6.14 and 6.16). Mortality at this stage in the breeding cycle appears to have been a key factor responsible for the poor productivity outcomes for this population under natural conditions between 1990-91 and 1998-99.

### *6.5.7 Juvenile survival*

Under natural conditions on Rangatira Island, 19.2% of all juveniles produced dispersed between sub-populations after achieving independence in their natal territories (male and female totals combined, Table 6.5).

Demise-site collation of survival data (which recognise the dispersal movements) cannot relate the numbers of juveniles surviving to adulthood in each sub-population to the numbers originally produced because the survivors include juveniles produced elsewhere. For instance, the pronounced bias in juvenile movements into the Top Bush (Tables 6.4 and 6.5) results in inflated survival ratios for juveniles produced by Top Bush pairs (90.4%, Table 6.13). Conversely, the juvenile deficit in the Woolshed Bush appears to result in a suspiciously low 'survival' rate of 61.9% (Table 6.13).

Natal-site collation of survival data (that is, collation which assumed that juveniles did not disperse from natal populations) reveals that 72.9% of all juveniles produced by Woolshed Bush pairs survived to breeding age, regardless of where they settled. In contrast, only

54.8% of all juveniles produced in the Top Bush survived where they settled. These rates do not account for the effects on survival of dispersal or conditions in adopted habitats. In the closed Mangere Island population, the natal- and demise-site distinction was irrelevant—79.1% of all juveniles survived their first winters in non-management seasons.

Despite the complications caused by dispersals, demise-site survival data reveal accurately the numbers of juveniles achieving adulthood in each sub-population (Table 6.14). These numbers provide a rudimentary index of recruitment potential. Dividing the sum total of surviving juveniles by season number gives mean annual recruitment potential of 11.3 yearlings on Mangere Island and 10.4 yearlings in the Top Bush during post-management seasons. In contrast, the ranks of breeders in the Woolshed Bush could draw on an average of 23.3 yearlings annually.

## 6.6 Recruitment to breeding populations

The proportions of male and female juveniles actually recruited to breeding populations differed under each management regime. Recruitment during the management seasons was influenced by conservation activity which redistributed birds among the populations, before or after fledging. When pair numbers were precariously low, for instance, managers attempted to influence recruitment by moving potential mates for spare females between populations (Butler and Merton, 1992). During all intensive management seasons, proportionately more juvenile females than males attempted to breed in each population (Table 6.15). This imbalance disappeared in the Top Bush after conservation activities were suspended, and reversed to favour males in the other populations. Sexual asymmetry in recruitment ratios was most pronounced on Mangere Island (male $\bar{x} = 0.17$, female $\bar{x} = 0.31$) and least evident in the Top Bush (male $\bar{x} = 0.31$, female $\bar{x} = 0.35$). This relative asymmetry persisted in these populations during post-management seasons.

Under management, juveniles produced in the Top Bush (both sexes combined) were more likely to be recruited (66% of numbers produced) than those in the Woolshed Bush (54%) and on Mangere Island (49%). Under natural conditions, however, Mangere Island juveniles joined the ranks of breeders at the highest frequency (64%). The proportions recruited in the Woolshed Bush also increased (59%). Top Bush ratios declined from 66% to match recruitment in the Woolshed Bush. The suspension of conservation measures had least impact on recruitment in the Woolshed Bush and most in the Mangere Island sub-population.

Table 6.15 Mean annual recruitment ratios for juveniles produced in the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. Means for each sex are calculated by demise-site from the total number of juveniles produced.

| Phase | Seasons *n* | Males | Females | All |
|---|---|---|---|---|
| **Intensive management 1980-81 to 1989-90** | | | | |
| MANGERE | 10 | 0.17 | 0.31 | 0.49 |
| WOOLSHED BUSH | 7 | 0.25 | 0.30 | 0.54 |
| TOP BUSH | 6 | 0.31 | 0.35 | 0.66 |
| **Post-management 1990-91 to 2001-02** | | | | |
| MANGERE | 12 | 0.35 | 0.29 | 0.64 |
| WOOLSHED BUSH | 9 | 0.32 | 0.27 | 0.59 |
| TOP BUSH | 9 | 0.29 | 0.29 | 0.59 |

### *6.6.1 Female age of recruitment*

Regardless of management regime, significantly more females paired as yearlings than at two years or older (Table 6.16). This trend was most entrenched in Woolshed Bush females (management, 95.5 %; post-management, 93.8%). In contrast, pairing in year one was less common on Mangere Island (75% during management seasons, declining to 66.7% in the post-management period). Almost all of those deferring recruitment found mates for the first time at two years. In the Top Bush, the proportion of females recruited at year one rose from 80% to 92.7% after management stopped.

### *6.6.2 Male age of recruitment*

The majority of male recruits also paired first as yearlings but in both management phases this trend was generally weaker than for females. Yearling males entered the breeding population most commonly in the Top Bush (management, 95.2%; post-management, 86.8%; Table 6.16) and least frequently on Mangere Island (60% and 56.6% respectively). As with females, the incidence of first-year pairing decreased in all populations after management concluded, most obviously in the Woolshed Bush (from 81% to 67.7% of recruits). Mangere Island males delayed recruitment until ≥ two years in greater numbers than elsewhere (management, 40%; post-management 43.4%).

### *6.6.3 Female ages at first egg-laying*

The majority of mated yearling females in the Woolshed Bush laid clutches (81% during management seasons, increasing to 87.8% subsequently; Table 6.16). This upward trend, and the proportions laying, were very similar in the Top Bush. In contrast on Mangere Island, deferral of mating contributed to a pattern of egg-laying at older ages. Under managed conditions, 58.3% of female recruits laid at ≥ two years. This trend became more pronounced during post-management seasons (66.7%).

### *6.6.4 Age at first successful breeding*

I cannot define the ages at first successful breeding during the intensive management seasons because breeding pairs were not always permitted to raise their own offspring. Under natural conditions in post-management seasons, successful recruits were still more likely to be yearlings on Rangatira Island. This trend was greatest in the Woolshed Bush where 67.2% of females breeding productively for the first time were yearlings. Fewer yearling recruits were successful in the Top Bush (54.2%). On Mangere Island, the effects of delayed mating and laying were evident in the later ages at which female recruits were first successful. Only 27.8% were yearlings. More than a third of female recruits were not productive until three years or older (Table 6.16). Male recruits were even less likely to be successful as yearlings (50.7% in the Woolshed Bush and 53.1% in the Top Bush). As with females in these sub-populations, a marked shift towards first success at ≥ two years was apparent. On Mangere Island, 84.1% of male recruits were first productive at two years or older.

### *6.6.5 Success at first breeding attempt*

Yearling recruits of both sexes were capable of producing juveniles at their first breeding attempt. Top Bush pairs comprising yearling males or females proved to be highly successful producers of juveniles (females, 92.9%; males, 94%). This was also true of yearling females in the Woolshed Bush (97.7%) and of Woolshed Bush males to a lesser extent (72.9%). By comparison, first-year recruits were much less effective at their first attempt on Mangere Island. Pairs comprising yearling females produced the majority of juveniles at the first attempt (62.5%) but male productivity at this age was very low (36.8%). Male recruits on Mangere Island were most likely to be productive at their first attempt when two years old (57.9%; Table 6.16).

Ages at recruitment, first-breeding and first-success are likely to have been influenced by factors affecting the availability of mates such as sex ratio imbalances in populations and the chance spatial separation of potential mates. These factors may have contributed to the pattern of deferred recruitment on Mangere Island where, between seasons, male and female surpluses fluctuated markedly in both directions (Chapter Two: *Section 2.10*; Chapter Eight: *Figure 8.4*).

A density effect may also have been operating in the recovering populations. In the sparsely populated Top Bush, new breeders would not have had difficulty finding breeding space and resources. In contrast, this may have been a factor in the confinement of Robin Bush on Mangere Island as pair numbers increased towards carry-capacity (reached apparently when numbers levelled off in 1997-98). However, I have not systematically analysed the relationships between recruitment, breeding success, mate availability and population density.

The important feature of the recruitment trends I have reported is that under both managed and natural conditions black robins were capable of pairing and breeding successfully in their first adult seasons and often did so. On Rangatira Island, recruitment and first-breeding does not appear to have played a role in population fates. In the poorly performing Top Bush population, for instance, recruits of both sexes were mated in their first adult years at very high frequency and bred successfully at their first attempts. Deferred recruitment and breeding on Mangere Island denied the population the reproductive potential of the unmated birds, usually for one year, and may have contributed to the population's more modest productivity growth rates overall.

## 6.7 Survival

### *6.7.1 Life-spans*

Black robin life-spans ranged up to 14 years throughout the study period but ages ≥ 12 years were uncommon (nine males, four females of 1359 black robins studied). At the time of writing, only one individual (a Woolshed Bush male hatched in 1987-88) is known to have lived until 14 years of age. Equally old individuals may still be alive on Rangatira Island but I have not been able to obtain the 2008-09 resighting data held by the Department of Conservation.

A higher proportion of black robins hatched in the intensive management phase achieved ages of 12 years or more (1.46%, as opposed to 0.7% of post-management black robins). Black robins of both sexes in the Woolshed Bush and on Mangere Island proved capable of these long life-spans. In contrast, none residing in the Top Bush survived beyond seven years during management seasons or eight years in post-management seasons, regardless of their population of origin.

Mean life-spans differed between populations and declined overall in post-management seasons. Neither sex was consistently longer-lived than the other in populations or management phases. Black robins of known sex surviving ≥ one year on Mangere Island and in the Woolshed Bush died on average at four or five years during the intensive management seasons but on average at four years during post-management seasons (Table 6.17). Known-sex adults in the Top Bush usually died at two or three years under managed conditions and at two years in the following phase. Life-span means for males and females combined are lower if adults of unknown sex are included, since 74.3% of unsexed (unmated) black robins died as yearlings or two-year-olds.

### *6.7.2 Survival*

As signalled in their shorter mean life-spans, the proportions of all black robins surviving at each age-step in the Top Bush were conspicuously lower than in the other populations between 1980-81 and 2001-02. Survival probability for Woolshed Bush and Mangere Island black robins did not vary markedly (*Figure 6.4*).

Table 6.16 Proportions by sex and management phase of black robin recruits which succeeded at one, two and three + years in pairing, laying eggs, breeding productively and producing juveniles at their first breeding attempt in the three populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. Total *n* for each population is the number of juvenile recruits known or likely to have laid eggs. Age ratios in each productivity class relate to the total number of successful recruits in that class. These totals reduce as recruits die or if their breeding was not fully observed (in which case they have been omitted). Fostering during the intensive management phase disguised data on first productivity and productivity at first attempt.

| | | MALES | | | | | | | | | | | | FEMALES | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Paired (yr) | | | Eggs first laid | | | First productive | | | Productive first time | | | | Paired (yr) | | | Eggs first laid | | | First productive | | | Productive first time | | |
| Phase | *n* | 1 | 2 | 3+ | 1 | 2 | 3+ | 1 | 2 | 3+ | 1 | 2 | 3+ | *n* | 1 | 2 | 3+ | 1 | 2 | 3+ | 1 | 2 | 3+ | 1 | 2 | 3+ |
| **Intensive management 1980-81 to 1989-90** | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Mangere | **10** | 60.0 | 30.0 | 10.0 | 30.0 | 60.0 | 10.0 | | | | | | | **13** | 75.0 | 25.0 | 0.0 | 41.7 | 50.0 | 8.3 | | | | | | |
| Woolshed Bush | **21** | 81.0 | 14.3 | 4.8 | 57.1 | 28.6 | 14.3 | | | | | | | **22** | 95.5 | 4.5 | 0.0 | 81.0 | 14.3 | 4.8 | | | | | | |
| Top Bush | **21** | 95.2 | 4.8 | 0.0 | 95.2 | 4.8 | 0.0 | | | | | | | **20** | 80.0 | 15.0 | 5.0 | 80.0 | 15.0 | 5.0 | | | | | | |
| **Post-management 1990-91 to 2001-02** | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Mangere | **59** | 56.6 | 41.5 | 1.9 | 24.0 | 68.0 | 8.0 | 15.9 | 59.1 | 25.0 | 36.8 | 57.9 | 5.3 | **54** | 66.7 | 29.2 | 4.2 | 33.3 | 55.6 | 11.1 | 27.8 | 36.1 | 36.1 | 62.5 | 31.3 | 6.3 |
| Woolshed Bush | **90** | 67.7 | 32.3 | 0.0 | 64.7 | 34.1 | 1.2 | 50.7 | 39.1 | 10.1 | 72.9 | 27.1 | 0.0 | **84** | 93.8 | 6.3 | 0.0 | 87.8 | 10.8 | 1.4 | 67.2 | 29.7 | 3.1 | 97.7 | 2.3 | 0.0 |
| Top Bush | **43** | 86.8 | 10.5 | 2.6 | 89.2 | 8.1 | 2.7 | 53.1 | 31.3 | 15.6 | 94 | 5.6 | 0.0 | **43** | 92.7 | 7.3 | 0.0 | 87.2 | 12.8 | 0.0 | 54.2 | 29.2 | 16.7 | 92.9 | 7.1 | 0.0 |
| **All management 1980-81 to 2001-02** | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Mangere | **69** | 57.1 | 39.7 | 3.2 | 25.0 | 66.7 | 8.3 | | | | | | | **67** | 68.3 | 28.3 | 3.3 | 35.1 | 54.4 | 10.5 | | | | | | |
| Woolshed Bush | **111** | 70.1 | 29.1 | 0.9 | 63.2 | 33.0 | 3.8 | | | | | | | **106** | 94.1 | 5.9 | 0.0 | 86.3 | 11.6 | 2.1 | | | | | | |
| Top Bush | **64** | 89.8 | 8.5 | 1.7 | 91.4 | 6.9 | 1.7 | | | | | | | **63** | 88.5 | 9.8 | 1.6 | 84.7 | 13.6 | 1.7 | | | | | | |

Table 6.17 Mean age at which adult black robins died in the three populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. Means relate to black robins hatched during each management phase and are based on known-sex males and females only. Means for 'All' include adults of unknown sex.

|  | Seasons | Adults living ≥ one year |  |  |
|---|---|---|---|---|
| **Intensive Management** | *n* | Male | Female | All |
| MANGERE | 10 | 4.60 | 5.21 | 5.03 |
| WOOLSHED BUSH | 7 | 5.22 | 4.52 | 4.76 |
| TOP BUSH | 6 | 2.72 | 3.15 | 2.90 |
| All populations |  | 4.22 | 4.14 | 4.01 |
| **Post-management** |  |  |  |  |
| MANGERE | 12 | 4.65 | 4.26 | 3.98 |
| WOOLSHED BUSH | 9 | 4.42 | 4.00 | 4.05 |
| TOP BUSH | 9 | 2.89 | 2.49 | 2.34 |
| All populations |  | 4.20 | 3.74 | 3.68 |

Regardless of management regime, higher proportions of males survived than females (*Figure 6.5*). In contrast, unsexed black robins experienced very significantly higher mortality than known males and females.

This result was expected since black robins of unknown sex comprised individuals dying, usually as nestlings and fledglings, before achieving breeding age when mate choices would confirm their sex. The long tail to the survival curve for unsexed black robins represents unmated adults or adults whose sex observers did not note (a particular failing during the sample-monitoring years).

Survival was generally, though not markedly, better during the intensively managed seasons between 1980-81 and 1989-90 (*Figure 6.6*). When distinguished by sex and management regime, however, unsexed black robins survived at lower rates during intensively management seasons (*Figure 6.7*). Female survival rates under both management regimes tended to be lower than male rates.

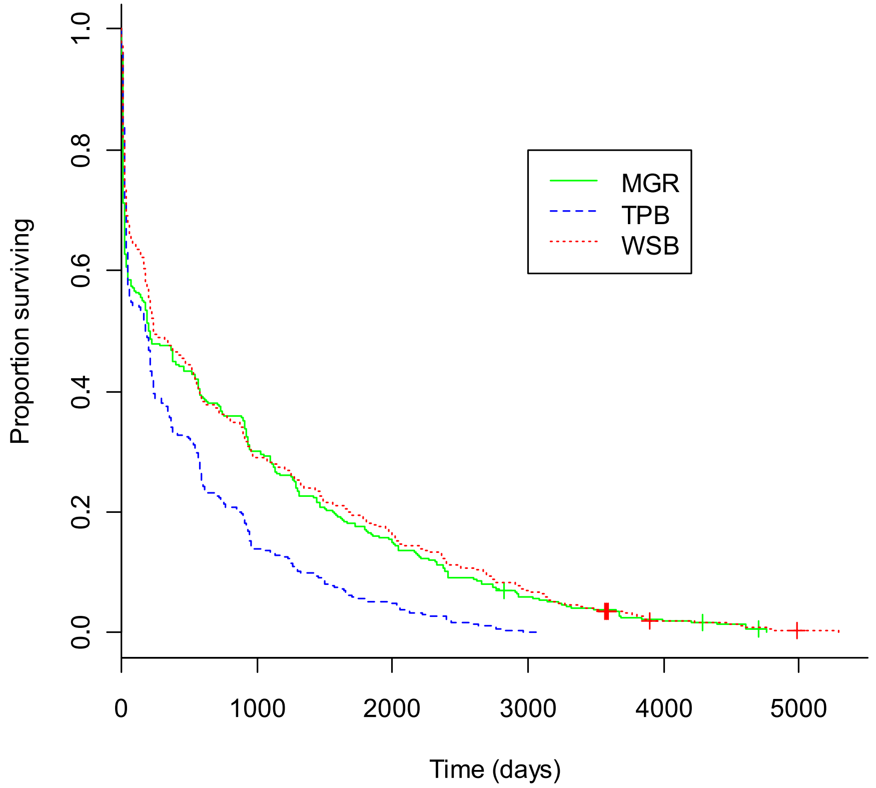


Figure 6.4 Proportions of black robins surviving over time since hatching in the Mangere Island (MGR), Woolshed Bush (WSB) and Top Bush (TPB) populations, 1980-81 to 2001-02. Survival curves calculated by Kaplan-Meier estimator. (+) indicates censored individuals (those still alive at the end of the study)

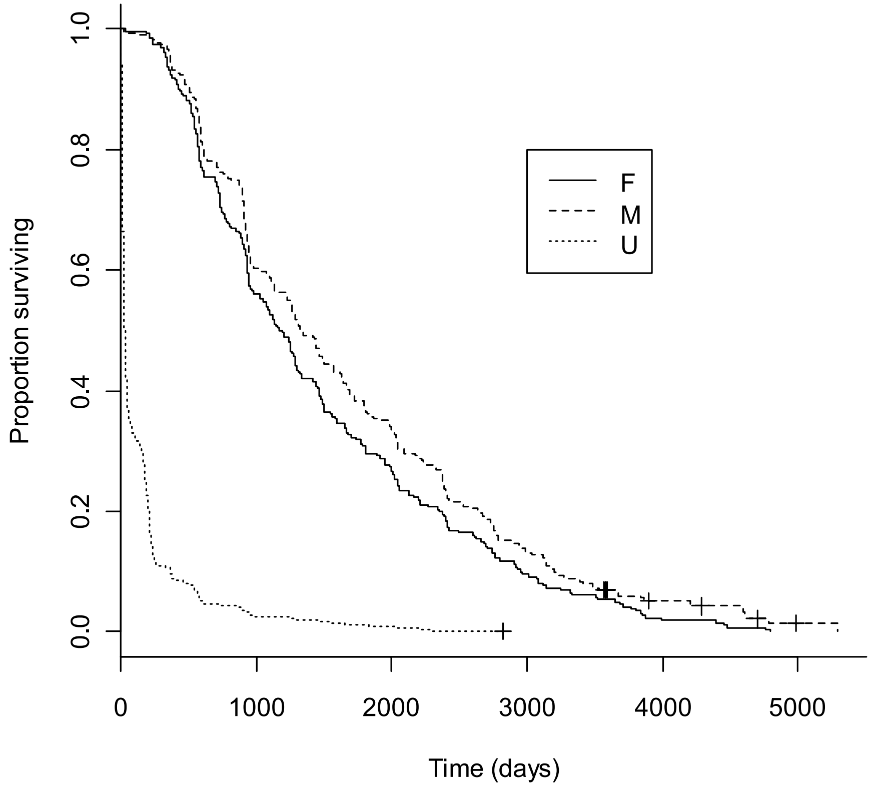
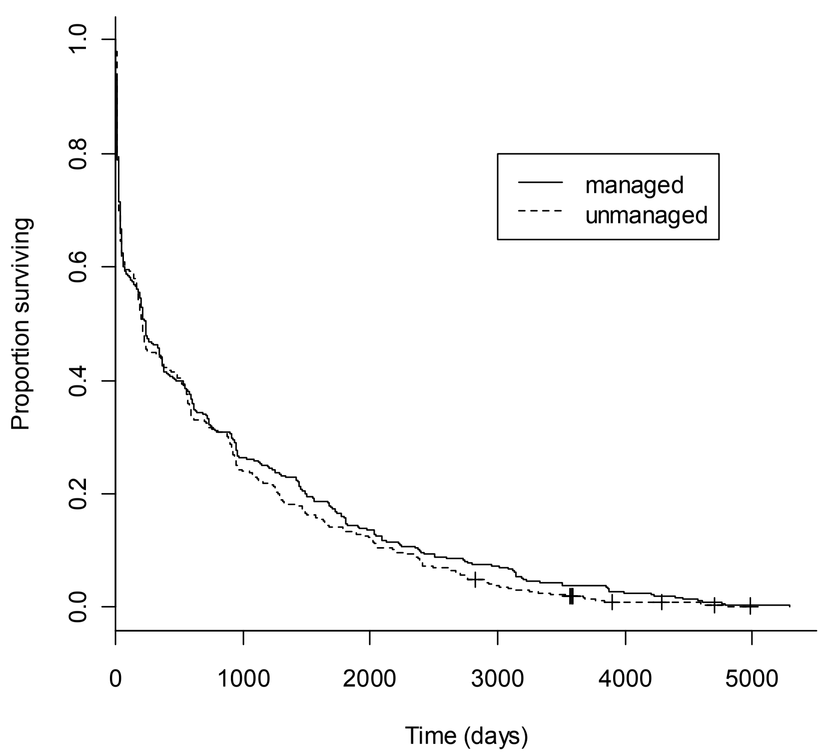


Figure 6.5 Proportions of black robins of verified and unknown sex surviving over time on Mangere and Rangatira Islands, 1980-81 to 2001-02. Survival curves calculated by Kaplan-Meier estimator.



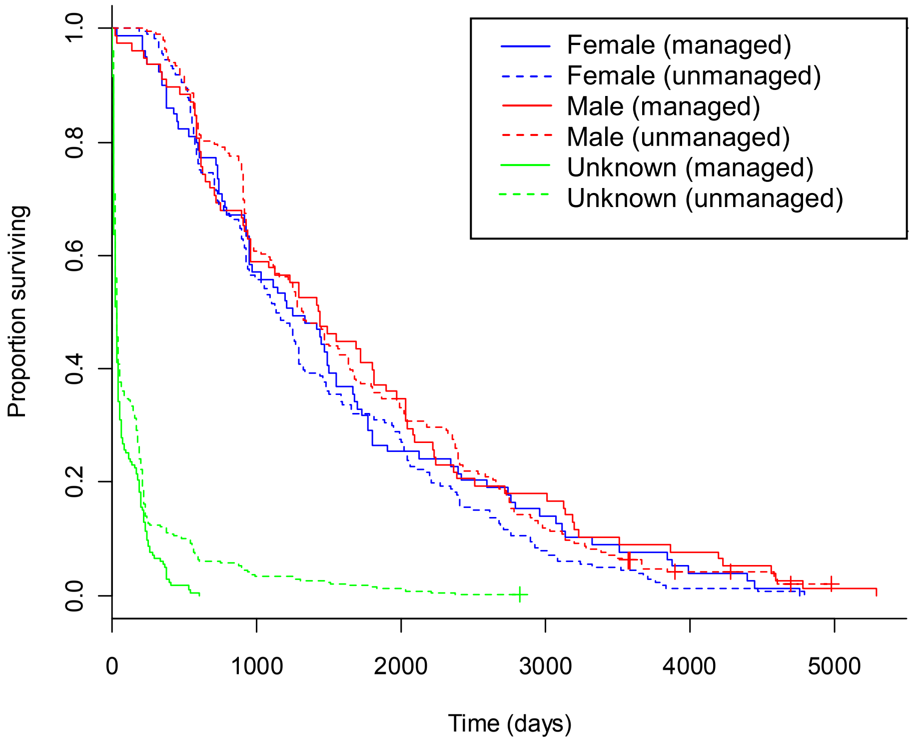


Figure 6.6 Proportions of black robins (both sexes combined) surviving over time during the intensive management ('managed') and post-management ('unmanaged') phases of recovery on Mangere and Rangatira Islands, 1980-81 to 2001-02. Survival curves calculated by Kaplan-Meier estimator.

Figure 6.7 Survival by management phase of black robin males, females and individuals of unverified sex on Mangere and Rangatira Islands, 1980-81 to 2001-02 Survival curves calculated by Kaplan-Meier estimator.

## 6.8 Environmental variation in black robin habitats

Faulty data-logger batteries terminated ambient air temperature measurements prematurely at three of the nine data-logger sites (WSB 2, TPB 5 and TPB 6, see Appendix Four: Table 4A). As a result, measurement periods varied from 16.3 months for the six functional data-loggers (WSB 1 and 3; TPB 4; MGR 7, 8 and 9) to 11 months at TPB 5 and eight months at WSB 2 and TPB 6**.**

### *6.8.1 Temperature extremes*

Over the six calendar seasons in which measurements were taken hourly day and night (spring 2004 to summer 2005 inclusive), ambient air temperatures in the forests inhabited by black robins ranged between 2.6 ºC (0800 hrs, 31 July 2005) and 23.05 ºC (1400 hrs, 31 January 2006; Table 6.18). Both extremes were recorded at data-logger station WSB 3, the eastern-most in the Woolshed Bush, on Rangatira Island's lower terraces. In fact, five of the six seasonal maxima and three of the six minima were recorded at this site (Table 6.18). Temperature extremes on Mangere Island lay within the ranges on Rangatira Island.

### *6.8.2 Seasonal differences in mean daily temperatures*

The mean daily temperatures for each of the six calendar seasons varied less than 1°C in all black robin habitats. Daily temperatures were warmest on average in the two summers, becoming progressively cooler in autumn, the spring of each year, and in winter (Table 6.19). By this relatively broad measure of air temperatures, the Woolshed Bush population enjoyed the warmest conditions most frequently, while the Top Bush population experienced the coolest most consistently. The differences were minimal.

### *6.8.3 Warmest and coldest habitats*

Over all seasons, the Woolshed Bush experienced the highest mean daily temperatures most frequently (53.9% of days). Mangere Island was warmest on 34.3% of days, and the Top Bush on 11.8% of days. Conversely, mean daily temperatures were lowest in the Top Bush on 65.2% of days. Mangere Island and the Woolshed Bush experienced the coolest daily means on 24.4% and 10.4% of days respectively.

Table 6.18 Ambient temperature extremes (ºC) recorded in each calendar season at micro-climate data-logger sites in the three black robin habitats on Mangere and Rangatira Islands, 1 October 2004 to 10 February 2006. Temperatures in **red** and **blue** denote the highest and lowest temperatures for each season. Empty fields indicate that data-loggers had failed by that time.

| | | **Woolshed Bush** | | | **Top Bush** | | | **Mangere** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Data-logger | | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | Date<br>Time (hr) |
| **Spring** | Min | 3.89 | 4.0 | 3.89 | **3.13** | 3.52 | 3.21 | 4.23 | 3.97 | 3.84 | 9 Nov 04<br>(1300) |
| 2004 | Max | 16.38 | 16.4 | **17.54** | 16.4 | 15.76 | 15.52 | 15.93 | 16.81 | 16.12 | 3 Oct 04<br>(0100) |
| **Summer** | Min | 6.01 | 5.99 | 5.75 | **5.29** | 5.42 | 5.35 | 5.93 | 5.7 | 5.6 | 31 Dec 05<br>(0500) |
| 2004-05 | Max | 19.95 | 20.18 | **21.07** | 20.54 | 20.97 | 19.97 | 19.73 | 20.04 | 19.78 | 15 Feb 05<br>(1400) |
| **Autumn** | Min | 6.06 | 6.11 | **4.78** | 5.45 | 5.96 | 5.5 | 6.16 | 6.19 | 6.16 | 30.May.05<br>(1800) |
| 2005 | Max | 18.85 | 18.83 | **19.42** | 18.97 | 19.38 | 18.47 | 18.73 | 19.23 | 18.95 | 07 Mar 05<br>(1200) |
| **Winter** | Min | 3.18 | | **2.6** | 3.13 | 3.15 | | 3.52 | 3.79 | 4.13 | 31 Jul 05<br>(0800) |
| 2005 | Max | 12.66 | | 13.89 | **14.16** | 12.95 | | 12.83 | 12.76 | 13.41 | 25 Jul 05<br>(1300) |
| **Spring** | Min | **2.84** | | 3.29 | 3.13 | | | 3.76 | 4.02 | 4.67 | 21 Sep 05<br>(0700) |
| 2005 | Max | 17.21 | | **19.28** | 18.78 | | | 17.28 | 17.07 | 18.14 | 21 Nov 05<br>(1600) |
| **Summer** | Min | 7.13 | | **6.82** | 7.18 | | | 7.81 | 8.01 | 8.16 | 11 Jan .06<br>(0500) |
| 2005-06 | Max | 21.04 | | **23.05** | 22.91 | | | 20.66 | 21.16 | 21.33 | 31 Jan 06<br>(1400) |

The seasonal means for minimum and maximum temperatures in each habitat reflect the same trends. Maximum temperature means were highest in the Woolshed Bush for all but the last summer season (Table 6.20). Mean minimum temperatures were lowest in the Top Bush in four of the six seasons. However, Top Bush means for the final two seasons may not fairly represent temperatures in this vast habitat since only one data-logger was still operating, at the habitat's eastern periphery.

Variations in the seasonal ranges for mean maximum and minimum temperatures in each habitat did not exceed 1.0 °C.

Table 6.19 Calendar-season means for daily temperatures (°C) in the forest habitats of the three black robin populations on Rangatira and Mangere Islands, 1 October 2004 and 10 February 2006. Means are calculated from temperatures recorded hourly between 0100-0000 hrs at three stations in each habitat and averaged across all days in a season. Means in **red** denote the warmest mean temperature in each of the six seasons; **blue** values denote the coolest.

| | **Woolshed Bush** | **Top Bush** | **Mangere** | **Variation (ºC)** |
|---|---|---|---|---|
| Spring 2004 | 10.40 | 9.91 | 10.42 | 0.51 |
| Summer 2004-05 | 13.66 | 13.21 | 13.49 | 0.45 |
| Autumn 2005 | 12.46 | 12.03 | 12.37 | 0.43 |
| Winter 2005 | 8.78 | 8.50 | 8.59 | 0.28 |
| Spring 2005 | 9.80 | 9.75 * | 9.80 | 0.05 |
| Summer 2005-06 | 13.72 | 13.81 * | 13.71 | 0.1 |

NOTE * Mean derived from temperatures at one data-logger station only (upper Long Drop track)

Table 6.20 Seasonal mean minimum and maximum temperatures (°C) in the three black populations on Mangere and Rangatira Islands, 1 October 2004 to 10 February 2006. **Red** and **blue** values denote the warmest and coolest means.

| | **Spring 2004** | **Summer 2004-05** | **Autumn 2005** | **Winter 2005** | **Spring 2005** | **Summer 2005-06** |
|---|---|---|---|---|---|---|
| **Mean minimum** | | | | | | |
| Woolshed Bush | 6.63 | 7.6 | 7.22 | 5.38 | **4.54** | 9.06 |
| Top Bush | **5.99** | **6.87** | **6.73** | **4.9** | 4.6 | 8.95 |
| Mangere | 6.74 | 7.21 | 6.98 | 5.28 | 5.08 | **8.68** |
| Variation in range | 0.64 | 0.73 | 0.49 | 0.48 | 0.54 | 0.38 |
| **Mean maximum** | | | | | | |
| Woolshed Bush | **14.52** | **17.92** | **17.01** | **11.8** | **15.23** | 19.05 |
| Top Bush | 14.08 | 17.75 | 16.68 | 11.5 | **15.23** * | **19.32** * |
| Mangere | 14.04 | **17.92** | 16.91 | 11.55 | 14.93 | 18.52 |
| Variation in range | 0.48 | 0.17 | 0.33 | 0.3 | 0.3 | 0.8 |

NOTE * Mean derived from temperatures at one data-logger station only (upper Long Drop track)

### *6.8.4 How much warmer or cooler were the habitats?*

Overall, Woolshed Bush tended to be the warmest of the three habitats and the Top Bush the coolest but the differences in relative warmth in all three habitats were small throughout the sampling period (Table 6.21).

Conditions differed most between the Woolshed Bush and the Top Bush. In the five seasons when the Woolshed Bush was the warmer of the two on average, the difference in seasonal mean daily temperatures ranged from 0.7% to 5.26% ($\bar{x}$ = 3.47%). In temperature terms, this equated to an average seasonal variation of 0.34 ºC (range 0.02 – 0.49 ºC).

Woolshed Bush and Mangere Island differed less. Woolshed Bush was 0.06% to 2.47% warmer in all seasons except spring 2004 ($\bar{x}$ = 1.04%). This equated to a negligible 0.09 ºC seasonal variation in warmth (range 0.02 - 0.18 ºC).

These results suggest that the Top Bush tended to be cooler than the more sheltered, north-oriented habitats of the Woolshed Bush and Mangere Island. However, the exploratory analyses I have used to assess temperature differences relied on sequential averaging of the hourly data to arrive at seasonal means. Smoothing the data in this way will have disguised the true extent of variation. In fact, the effect of temperature on plants and insects is cumulative and most often measured in terms of accumulated degree-days or physiological time (Worner, 2007).

Preliminary analyses of degree-day accumulation (5 ºC threshold) during daylight hours over the period of this study (standardised as 0700 to 1900 hours) show clearly that the Top Bush habitat was generally cooler. Fewer degree-days decrease the heat units available for invertebrate development. Fewer degree-days are likely to reduce the number of generations of some species and may as a consequence reduce the insect biomass available for black robin food. Over the first breeding season, for instance (1 October 2004 to 28 February 2005), the cumulative difference between the Top Bush and Woolshed Bush was 72 degree-days. The cumulative difference by the end of winter 2005 (to 30 September 2005) was 123 degree-days. For the same periods, the deficit between Mangere Island and Woolshed Bush was more modest (23 and 19 degree-days respectively).

Table 6.21 Extent to which the habitats of the three black robin populations on Mangere and Rangatira Islands were warmer or cooler than one another, 1 October 2004 and 10 February 2006. Relative warmth expressed as the percentage difference in mean daily temperature for each calendar season. Warmer habitats are denoted in **red** and cooler in **blue**. The variation expressed as temperature (ºC) is the mean of all daily differences between each pair of habitats.

| | **Spring 2004** | | | **Summer 2004-05** | | | **Autumn 2005** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **WSB** | **TPB** | **MGR** | **WSB** | **TPB** | **MGR** | **WSB** | **TPB** | **MGR** |
| **Woolshed Bush** (%) | | **5.26** | **-0.18** | | **3.77** | **1.46** | | **3.92** | **0.89** |
| Mean variation (ºC) | | 0.49 | 0.02 | | 0.45 | 0.17 | | 0.43 | 0.09 |
| **Top Bush** (%) | **-4.95** | | **-5.13** | **-3.59** | | **-2.2** | **-3.72** | | **-2.91** |
| Mean variation (ºC) | 0.49 | | 0.51 | 0.45 | | 0.28 | 0.43 | | 0.34 |
| **Mangere** (%) | **0.23** | **5.49** | | **-1.39** | **2.3** | | **-0.79** | **3.05** | |
| Mean variation (ºC) | 0.02 | 0.51 | | 0.17 | 0.28 | | 0.09 | 0.34 | |

| | **Winter 2005** | | | **Spring 2005** | | | **Summer 2005-06** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **WSB** | **TPB** | **MGR** | **WSB** | **TPB *** | **MGR** | **WSB** | **TPB *** | **MGR** |
| **Woolshed Bush** (%) | | **3.68** | **2.47** | | **0.7** | **0.06** | | **-0.53** | **0.14** |
| Mean variation (ºC) | | 0.28 | 0.18 | | 0.05 | < 0.00 | | 0.08 | 0.01 |
| **Top Bush** (%) | **-3.42** | | **-1.17** | **-0.62** | | **-0.73** | **0.56** | | **0.69** |
| Mean variation (ºC) | 0.28 | | 0.09 | 0.05 | | 0.05 | 0.08 | | 0.1 |
| **Mangere** (%) | **-2.18** | **1.28** | | **-0.06** | **0.83** | | **-0.07** | **-0.61** | |
| Mean variation (ºC) | 0.18 | 0.09 | | < 0.00 | 0.05 | | 0.01 | 0.1 | |

NOTE * Based on temperatures recorded at one data-logger station only (upper Long Drop track)

Much depends on data-logger placement and season, requiring additional work to clarify the magnitude of degree-day differences between sites and seasons, but that was beyond the scope of my study. At this stage, it is reasonable to assume that diurnal and nocturnal sub-canopy temperatures in the Top Bush might have been lower on average than in the other black robin habitats during the two management phases I have examined. Even if the differences varied in scale and direction from year to year, this environmental variable cannot be dismissed as a factor explaining the divergence in demographic trends in each black robin population.

## 6.9 Summary and discussion

The ‘New Zealand’ strategy adopted to conserve black robins from extinction achieved its short- and mid-term objectives. In 1980-81, the last population of five individuals was threatened most immediately by adverse demographic and environmental events. New Zealand wildlife managers succeeded in minimising vulnerability to these unpredictable threats by increasing black robin abundance and establishing a second larger population on Rangatira Island. Their conservation strategy addressed the intrinsic risk factor—the relict population’s inadequate rate of juvenile production—by multiple-clutching of females, fostering of the extra offspring and protective measures designed to increase survival at all life-stages. Nesting data in the pre-1980 population are too scarce to judge the magnitude of increase in clutch numbers, but intensive management boosted juvenile production four-fold over the rate achieved naturally by the Little Mangere Island survivors after transfer in 1976-77. The increased production resulted in the first positive growth in black robin numbers since at least 1971-72 and rapid expansion into available habitat on both island sanctuaries. The revival was greater and faster in Rangatira Island’s larger tracts of forest where the newly founded Woolshed Bush and Top Bush populations were the principal beneficiaries of active recovery measures.

The post-management trends reported in this chapter show the degree to which that recovery under management did not give a true indication of black robin viability. The two island populations remained capable of sustaining population increases after active conservation ceased but their rates of recovery were slower. The cumulative effects of brood manipulation, transfers, supplementary feeding and other activities disguised from managers the naturally lower and varying rates of reproductive output and survival which would dictate the fate of future black robin populations. The reversal of trends in the Top Bush subpopulation, a strong performer under management, was a striking illustration of how effective management had been, and how its effects could mask normal trends. Had managers merely left the black robins to get on with recovery unobserved, on the assumption of growth rates witnessed under active conservation, they would have over-estimated the intrinsic ability of the two island populations to rebound from set-backs or sustain themselves in the long-term.

After intensive management ceased, per-pair output in all populations combined was lower at all life-stages because each pair produced 29% fewer clutches and 31% fewer eggs on average (Table 6.11). Each pair's juvenile output decreased by almost 40% (to a rate still two-and-half times higher than that of the two to three pairs among the Little Mangere Island survivors prior to intervention; Table 3.3). Mean annual rates of population growth converged on both islands to become roughly comparable for the first time since intervention started. On Rangatira Island as a whole, lower production resulted in mean annual growth of 8.3% (Table 6.7), a fifth of the managed rate (a reduction of 81.2%). Once the Mangere Island population was released from the draw-down effects of transfers to grow naturally, the mean rate of increase rose from 7.2% to 9.9% p.a., an improvement of 37.5%.

While reproductive output varied under both management regimes, breeding success remained remarkably similar. The overall proportions of nestlings fledging, achieving independence and surviving to sexual maturity (one year) did not differ markedly (Table 6.13). The principal differences lay in the threefold reduction in the proportions of eggs laid as rimshots and the lower proportions hatching under natural conditions (74.8% of all eggs incubated full-term, a decrease of 7.5% from the intensive-management rate). The change in rimshot frequency may have been related to the lower probability of detection or the resumption of natural breeding patterns, as I have suggested in *Section 6.5.5* (above).

The decline in hatching success may be an artefact of reduced monitoring intensity during the post-management years (miscounted eggs or nestlings, failure to check for unhatched eggs after fledging). The scaling-back of supplementary food hand-outs (Chapter Four) may have contributed also, by causing incubating females to make more foraging trips with potentially harmful cooling effects on egg development, by increasing rates of incubation neglect, or by reducing egg mass and thermal retention. However, Mackintosh and Briskie (2005) found no evidence of such causal relationships in experimentally fed South Island robins on Motuara Island. An alternative explanation, supported by Mackintosh and

Briskie (2005), may be that the lower black robin hatch-rate is mildly expressed inbreeding depression emerging as inbreeding levels accumulated in the two island populations. I address this question in Chapter Seven (Was Inbreeding A Problem?). Mackintosh and Briskie (2005) observed that the hatch-failure rate in the insular population of South Island robins (24.1%; Byrne, 1999) was markedly higher than in their mainland ancestral population at Kowhai Bush (9%, derived from Powlesland, 1983). They attributed the higher hatch-failure rate to the loss of genetic diversity following the founding bottleneck of five individuals (Flack, 1974a; Ardern *et al*., 1997b).

The comparisons of individual population trends made in this chapter offer closer insights to black robin viability. The balance of recovery momentum shifted in the three study populations after management stopped. The Top Bush and Woolshed Bush subpopulations on Rangatira Island had grown strongly under management, supported by production on Mangere Island (Table 6.7). Under natural conditions, the Woolshed Bush population was the most productive and fastest growing, followed by Mangere Island. In contrast, seasonal fluctuations in numbers translated into inconsequential growth in the Top Bush population.

The variations in recovery rates were not attributable to the same factors. The Woolshed Bush and Mangere Island breeding populations increased at comparable rates (Table 6.9) but in the Woolshed Bush the proportion of effective pairs grew 2% annually on average while it declined on Mangere Island by the same rate (Table 6.10). Breeding pairs in the Woolshed Bush made greater clutch- and egg-laying investments, but both populations converted their investments into juveniles at a comparable rate (0.4 and 0.37 juveniles per egg respectively). Success in both populations was limited by similar rates of egg loss from incubation, but whereas Mangere Island suffered an unusually high rate of nestling loss, Woolshed Bush nestling losses were low. The overall hatch-rate of full-term eggs was greater on Mangere Island than in the Woolshed Bush (Tables 6.11 and 6.13). In each population, high proportions of juveniles survived to breeding age—80% and 93% respectively (natal-site data for juvenile survival). Survival probability was similar in both (*Figure 6.4*).

In the Top Bush, breeding effort matched or exceeded that in sister populations. Clutch and egg production was greater, perhaps because nest failures increased renesting frequency. The proportion of full-term eggs hatching exceeded the Woolshed Bush rate slightly (Table 6.13). Despite these healthy breeding investments, natural recovery momentum was minimal and unstable. Productivity was undermined by a high proportion of rimshots, high rates of egg and nestling loss from nests, and the highest mortality of fledglings and juveniles recorded under natural conditions (32% and 46% respectively; natal-site data for juveniles). These compounding failures weakened growth potential. Reduced rates of immigration from the Woolshed Bush undermined it further (Table 6.4) and the anomalously short life-spans of locally raised and immigrant adults also deprived the population of reproductive potential. Adult survival had been poor under management too. The proportion of effective pairs declined only gradually in the Top Bush (at a rate similar to Mangere Island's) but this slim advantage was offset by stagnating growth in the size of breeding population as a whole (Table 6.9).

External factors operating variably in each habitat and on different life-history stages in each population no doubt influenced trends but their relative effects and local importance cannot be determined from available field records. Systematic investigation and reporting of these factors was not the primary objective of the recovery project. The least that can be said is that productivity and survival trends were subjected to the broad range of external and intrinsic pressures reported by observers (Chapter Two: Black Robin Biology)—infirmity at birth, occasional morphological abnormalities, predation by starlings, poor nest-site selection, inadequate parenting, parental deaths, nest-mite infestations, avian pox, nocturnal petrel-strikes, tree- or branch-falls, egg-binding, cobweb entanglement, nest collapse, straying from parental care and sundry other forms of misadventure. Climatic events of varying severity and duration (storms, prolonged droughts, unusually humid summers, harsh winters) were also remarked upon by observers but their influences on productivity and survival were not quantified systematically. For example, observers learned to expect nestling mortalities from increased nest-mite densities during long humid periods (Butler and Merton, 1992) but in reporting the heavy infestations as the cause of death, they did not attempt to distinguish other underlying factors such as poor parenting skills.

My preliminary assessment of differences in ambient air temperatures indicate the strong probability of environmental influences on population trends, especially in the cooler Top Bush habitat where natural recovery was weak. The results point more confidently to an environmental effect than Williams (2003) was able to report from briefly comparing black robin energy expenditure in the Top Bush and Woolshed Bush. That study's finding of a negligible between-habitat difference in energy expenditure over two days does not rule out the possibility of cumulative energy costs of chronically cooler conditions for the Top Bush black robins. As I have suggested, retarded breeding cycles in invertebrate prey may result in cumulative shortfalls in available food biomass. Briefer periods of warmth daily and narrower upper temperature ranges may limit the timing and intensity of invertebrate activity, forcing black robins to make more energy-expensive foraging trips over longer distances or intervals. Thermoregulatory costs may increase metabolic rates, and poorer body condition may increase susceptibility to pathogens. None of these potentially disabling effects has been measured directly for any black robin population. Evaluation of relative wind-chill levels might make environmental effects more explicit, especially if assessed simultaneously with ground and arboreal invertebrate activity. Simple comparisons of foraging times for pairs raising offspring may be equally helpful in quantifying relative environmental effects on vital rates. Until these corroborating assessments are conducted, however, it is appropriate to assume that historically the Top Bush was the cooler of the three black robin habitats, and that lower ambient temperatures may have contributed to the poorer rate of recovery witnessed after management ceased.

The possibility of a depressive climatic effect in the Top Bush lends support to my conclusions in Chapter Three that browsing and clearing of the original forests on the black robin islands could precipitate fatal population declines, especially when windward edges were breached and chilling winds penetrated forest interiors. Some or all of the possible harmful consequences of climatic exposure may have been operating to extinction-inducing effect in the disintegrating forest remnant on Little Mangere Island (Chapter Three). There is support too for my suggestion that farming effects need only have reduced the quality of conditions in the Woolshed Bush to impose fatal pressures on the original Rangatira Island population.

Although the weaker post-management trends raise questions about black robin viability, there were positive indications of resilience in all three populations. From 1980-81 until the end of full-scale monitoring, the species as a whole sustained positive growth in numbers. Crucially, breeding pairs (including the nine-year-old ancestral female *Old Blue*) proved capable from the outset of the augmented productivity demanded by the intensification of breeding. The strong response to management was not suggestive of an intrinsically moribund species. Subsequent recovery benefited from viability measures in which all three populations remained generally comparable throughout. Although black robin hatch-rates were low relative to those recorded in mainland congeners (Powlesland, 1983; Mackintosh and Briskie, 2005) and declined after management stopped, they were sufficient to support overall population growth under protected conditions. Average clutch sizes remained largely constant between management regimes. Yearling black robins remained capable of breeding successfully from the outset (Table 6.16). Major disparities did not emerge over time in the proportions of effective pairs in each breeding population. In broad terms, breeding effort was not the problem faced by the three bottlenecked populations, even in the Top Bush where recovery was ultimately inadequate.

The Top Bush population raises the strongest questions about black robin viability. In reality, this population acted throughout the study period as a sink for Woolshed Bush production. As a closed population, the Top Bush may never have been viable and self-sustaining. By treating it analytically as though it were discrete, however, singular vulnerabilities have emerged which were not so apparent in the other two populations prior to the end of full-scale monitoring. Adult life-spans were shorter under the management and monitoring regimes, and mortality rates in fledglings and juveniles were anomalously high. These failures appear to have imposed the greatest constraints on natural recovery in that population. There are insufficient data to support a clear relationship between these critical failures and external factors alone. None of the field records I have consulted for this study alluded to specific threats operating uniquely or more severely in the Top Bush environment (other than field-workers' perceptions of a harsher climate). Therefore I am compelled to look for other explanations. In the next chapter, I investigate the possibility that the Top Bush failures were related to inbreeding effects which have not so far been considered in this thesis.

Inbreeding depression is an explanatory variable which can be tested in hindsight from the demographic record and may be common to all three populations. All were closely related genetically. That is not to say that the Woolshed Bush and Mangere Island populations were exposed to problems at the life-stages impeding Top Bush recovery but testing for relationships with inbreeding may indicate that these viability failure-points were latent under the prevailing conditions.

Inbreeding effects may also explain the independent declines in black robin numbers on Mangere and Rangatira Islands soon after monitoring intensity was reduced (*Section 6.2.3*). Other explanations are problematic and became difficult to test when crucial insights to population trends were lost after full-population monitoring ended. The decreases may have had their origins in the return of each island to its natural carrying-capacity once the black robins were deprived of regular breeding-season food hand-outs (Department of Conservation, 2009). Kennedy (2010) argues, however, that the 2.0 – 2.5 *Tenebrio* larvae each black robin would have received as a daily average was an inconsequential addition to normal food intake. Alternatively, the transfers of 38 adult and juvenile black robins to Pitt Island between 2002 and 2005 (Chapter Four) may have been destabilising. This does not seem a plausible explanation for Mangere Island which gave up only four individuals but declined by 43.3%, while Rangatira Island yielded 34 individuals and declined by approximately 25%.

Regenerative changes in the character of the forests on each island may have contributed, especially on Rangatira Island where Roberts *et al.* (2007) predicted an emerging forest structure less favourable to black robins, and Kennedy and Wilson (2005) noted informally (but did not quantify) a more open and colder sub-canopy (Chapter Two: *Section 2.4.1*).

Whatever the factors triggering the declines, the reduction in numbers can be expected to increase the frequency of close inbreeding and the rate at which average levels of relatedness accumulate in the populations. The potential for harmful effects on viability are investigated in the next chapter, by assessing whether inbreeding has been a factor influencing historical population trends.

# CHAPTER SEVEN
# WAS INBREEDING A PROBLEM?

‘New Zealand’s wildlife is [possibly] less susceptible to inbreeding depression.’

Craig *et al.*, 2000: 68

‘It’s better to have screwed-up black robins than none at all.’

Don Merton

*NZ Wildlife Service Biennial Conference, 1981*

## 7.0 Introduction

In previous chapters, I have reviewed the factors driving the black robin towards total extinction after humans arrived in the Chatham Islands archipelago at least 450-500 years ago (McFadgen, 1994; King, 1989). The new extinction drivers comprised a lethal mix of deterministic changes in their environments (principally habitat disintegration and mammalian predation) and worsening exposure to stochastic demographic and environmental pressures as population sizes decreased (Chapter Three: History of Decline). The species’s retreat from its pre-human range was almost certainly hastened by ecological and behavioural adaptations to island life, the vulnerabilities inherent in its slow-breeding strategy and population closure, all of which increased sensitivity to the unfamiliar forms of disturbance (Chapter Two: Black Robin Biology). Renewal of these pressures is a constant risk confronting the recovered populations of today.

This history of population losses, decline and last-minute recovery also exposed the species to practically every possible genetic risk-criterion. This history gives black robin managers at least four reasons for concern about the potential for genetic threats to viability.

As I have outlined in Chapter Three, all major island populations in the black robin’s natural range were eliminated outright after the hostile processes of habitat change and mammalian predation were set in train following human contact. The inferences I have drawn from historical records indicate that the ancient, isolated populations on Chatham, Pitt, Rangatira and Mangere Islands were eliminated in as little as two to four decades, if not sooner. This suggests that deterministic extinction pressures overran the genetic costs of reduction and fragmentation before they could become significant or lethal in their own right. If these geographically isolated populations had acquired differing levels of sensitivity to change through ecological and genetic divergence on their respective islands, it made no difference to the final outcome. The lost populations have disabling implications for management of genetic risks today. First, they deprive existing and future populations of vital sources of genetic enrichment. Second, they deny managers undisturbed reference populations against which to judge the severity and implications of genetic impairment today, and the effectiveness of remedial management.

The sole surviving reservoir of genetic diversity in the species contracted severely following the elimination of Mangere Island's black robins in late 1892 or early 1893. This last small, locally adapted gene pool had probably extended across the ocean narrows to Little Mangere Island, an open-air flight of about 260 metres for occasional dispersers. Genetic variation evolving formerly in a combined population of several hundreds of black robins was suddenly restricted to about 35 individuals or fewer (Chapter Three: *Section 3.6.4*). Over almost nine decades (1892-93 to 1980-81), extreme genetic impoverishment resulted from chronic, obligatory inbreeding and genetic drift among such low numbers (Ardern and Lambert, 1997; Ma and Lambert, 1997a; Miller and Lambert, 2004). By the mid-1990s, black robins in both the Mangere and Rangatira Island populations were distinguishable by sex alone at the minisatellite DNA markers analysed at that time. Band-sharing coefficients (0.84 ± 0.04 SD) were exceeded only by those of the comparably reduced Campbell Island teal *Anas nesiotis* (0.87 ± 0.04 SD) as the highest reported for free-living avian species (Robertson, 2006; Jamieson, 2009). Unfortunately, the intriguing question of just how much diversity was lost cannot be answered conclusively because DNA in black robins collected in 1871, 1897 and 1990 (Miller and Lambert, 2006), prior to and just after the gene-pool contraction, has so far proven to be too degraded to analyse (Hilary Miller, pers. comm.).

Extant populations have been exposed to two further perils—a succession of bottleneck events and confinement to small population sizes for more than 26 years (and the foreseeable future) in the reduced forest habitats of Mangere and Rangatira Islands.

At least two evolutionary bottlenecks occurred when the species colonised New Zealand from Australia and then the Chatham Islands through trans-ocean dispersal (Fleming, 1950a, b; Miller and Lambert, 2006). Dispersal in the Chatham Islands may have had significant founder effects. Population extinctions after human contact subjected the species to progressive restriction of the gene pool. Severe bottlenecking occurred when the last seven black robins were transferred to Mangere Island in 1976-77, followed by the further decline to one effective breeding pair between 1979-80 and 1982-83 (Chapter Three). The Rangatira Island population was established from the few descendants of this pair. At this point, the potential for loss of genetic variation from source and new populations (that is, loss of what little heterozygosity may have remained by then) was countered by numerous transfers of individuals between the two islands and the simultaneous augmenting of reproductive output to increase population sizes (Chapter Four). However, as has been typical of crisis-translocations in New Zealand (Armstrong and McLean, 1995), managers did not have the opportunity to select for genetically appropriate founders. Ardern and Lambert (1997) concluded that these modern sequential bottlenecks were less penalising for genetic diversity and fitness than the ancestral population's nine-decade-long reduction to low numbers on Little Mangere Island. It is conceivable nonetheless that what little genetic variation the ancestral survivors carried with them did not include crucial rare alleles.

Finally, the black robin populations are typical of many recovering New Zealand bird species surviving as closed populations on protected islands. Though safe for the meantime from the deterministic threats causing their declines, they remain at risk of gradual fitness loss and genetic depletion through inbreeding and genetic drift. This is especially an issue if the size of their island sanctuaries or the habitat available keeps populations unnaturally small (Jamieson *et al.*, 2006, 2008; Jamieson, 2009). On Mangere Island, the small closed population of black robins in Robin Bush is severely habitat-limited and will remain so for decades at current rates of reforestation (*Figure 2.4*). On Rangatira Island, the population is larger but confined predominantly to the Woolshed Bush, ostensibly by environmental factors operating in the Top Bush which cannot be managed readily (climatic conditions, forest structure; Chapter Six). The Woolshed Bush is the smaller and more fragmented of the two forested areas available (*Figure 2.3*) and regenerating in ways which may lower carrying-capacity for black robins (Kennedy and Wilson, 2005).

Despite these factors predisposing the black robins to genetic malfunction, the species responded strongly to conservation management, as I have outlined in Chapter Six, and appears to have weathered the genetic storm so far. The aim of this chapter is to assess the possibility that the predicted genetic perils of such a history of decline and recovery may have been realised but remain cryptic and persist as an on-going stochastic threat to the viability of current and new populations. Deficient demographic data have not allowed me to determine whether harmful genetic changes aggravated the processes of collapse in the small ancestral population on Little Mangere Island. But their descendants may have inherited a legacy of genetic impairment expressed in the variable rates of population recovery I have identified in Chapter Six.

Specifically, this chapter examines whether heightened levels of inbreeding in the small ancestral and descendent populations may have resulted in inbreeding depression manifested as lowered fitness at key life-history stages. I am aware that inbreeding and random genetic drift are separate though compounding processes capable of eroding viability (as I have explained in Chapter One), but the fitness implications of each cannot be separated in the demographic record of black robin recovery. Given the advanced levels of genetic homogeneity in extant black robin populations, there is a strong probability of mutually reinforcing effects. Because my analyses depend wholly on the demographic record, I am only able to investigate potential genetic problems through reference to inbreeding.

The analyses reported in this chapter quantify the levels of inbreeding in the black robin study populations. From this, I assess whether correlations exist between individual and kinship breeding coefficients and the life-history variables which appear to explain observed variations in recovery trends (Chapter Six). The hypothesis tested is that there is no correlation between inbreeding and the following variables of interest: (1) survival, (2) hatch-rates, which declined overall in the three black robin populations after management ceased, and (3) production of fledglings, juveniles and yearlings. Population trends differed through failures at all of these life-history variables during the study period. Performance was demonstrably low in the Top Bush, the most distressed and apparently least viable of the populations recovering under natural conditions.

I have confined my investigation of inbreeding effects to the post-management period of black robin recovery when true differences in recovery rates became explicit and there was little management activity to mask evidence of fitness costs.

## 7.1 Methods

### *7.1.1 Master pedigree construction*

The valuable demographic record and pedigree of recovery during the periods of highly intrusive management and post-management monitoring is indispensable to my analyses. From this record, I constructed a master pedigree whose base was formed by survivors of the ancestral population on Little Mangere Island and their immediate descendants on Mangere Island prior to 1980-81. I omitted ancestral black robins which were unrelated to others in the pedigree. Therefore the base comprised the male and female from which all other black robins were descended (*Old Yellow* and *Old Blue*; Chapter Three: *Section 3.7*) and seven other individuals with which these two founders had bred or were related prior to 1980-81. The descendent population comprised all black robins hatched from 1980-81 until 1998-99 (inclusive) on Rangatira Island and 2001-02 (inclusive) on Mangere Island. The master pedigree contained 1363 individuals—1052 banded as nestlings, juveniles or adults, and 311 nestlings, fledglings and juveniles dying before being banded. Four known F1 hybrid offspring from black robin x Chatham Island tomtit cross-breeding events were omitted (Chapter Eight: Hybridisation). Individual inbreeding coefficients (*F*) and kinship (parental) coefficients were calculated from this master pedigree. For later analyses, I confined the master pedigree to birds alive at or after 1980-81 (n = 1358, including five ancestral black robins). A non-breeding individual suspected of being a hybrid on Mangere Island was omitted also.

Parental data for the pedigree were confirmed by direct observation of breeding or the banding of offspring while still associated with parents. From 1980-81 onwards, 651 pairs and 1070 clutches were observed (Chapter Six: Table 6.13). For each clutch, the social and biological (genetic) fathers were assumed to be the same (Chapter Two). Foster-parent data were ignored for individuals not raised by biological parents during the cross-fostering seasons (1980-81 to 1989-90).

I retained individuals in the pedigree if the mother, father or both were in doubt or unknown (11 on Mangere Island; 11 on Rangatira Island). The close genetic similarity of all black robins did not make it possible to identify parentage by molecular means (Ardern and Lambert, 1997; Ma and Lambert, 1997b). However, field records, personal familiarity with the populations and breeder histories, and knowledge of which potential breeders were nearby at the appropriate time (Chapter Five: Data Collation and Verification) allowed me to guess who the missing parent(s) might have been for 16 of the 22 individuals. The other six (five ancestral birds and one descendant) were left without parental information when calculating inbreeding coefficients. Because 13 of the 22 affected individuals bred successfully (seven on Mangere Island; two in the Woolshed Bush; four in the Top Bush), I judged that errors made (if any) in missing-parent assignments would interfere with estimates of inbreeding coefficients less than if I omitted these individuals from the pedigree or assumed that all were unrelated ($F = 0.0$).

The pedigree could be subdivided by management phase according to hatch-dates, and by population using either natal or demise-site (see below).

### *7.1.2 Inbreeding and kinship coefficient estimates*

I estimated the coefficient of inbreeding $F$ for each individual and the kinship coefficient for each breeding pair with the PEDSYS 2.0 pedigree database system (South-West Foundation for Biomedical Research, www.sfbr.org), using the Stevens-Boyce algorithm option (Boyce, 1983). The unique band numbers fitted to fledged individuals were used as identifiers, and I assigned a fictitious band number (in the B-93000 series) to each unmarked nestling, fledgling and juvenile. For the five ancestral black robins of no known parentage, I followed the conventional practice (Jamieson *et al.*, 2007) of assuming that their parents were unrelated. As a result, PEDSYS estimated that all nine individuals in the master pedigree's base population were unrelated ($F = 0.0$).

Individual inbreeding and kinship coefficients were estimated relative to the base population. Given the inevitability of close inbreeding in the small ancestral population on Little Mangere Island, the assumption of a wholly unrelated base population was expected to underestimate values for the individual $F$ and kinship coefficients of descendants.

To calculate levels of inbreeding coefficients accumulating over time in the pedigree, I used natal-site data for each population, which was consistent with the nature of productivity data analysed (*Section 7.1.4* below).

### *7.1.3 Life-span estimations*

I based my analyses of potential inbreeding effects on survival on the black robin life-spans calculated by the methods specified in Chapter Six (*Section 6.1.10*). This was the life-span data used for the Kaplan-Meier estimations of survival probability (*Section 6.1.11*).

### *7.1.4 Productivity*

To assess the implications of inbreeding for fecundity, I prepared a master dataset of reproductive output for breeding-age females. The methods used to collect and collate the productivity data from field records are outlined in Chapters Four and Five. For each female (n = 246), the dataset listed by breeding season her age, mate or mates of the year (if any), the age of mate(s), breeding habitat (Woolshed Bush, Top Bush, Mangere Island) and reproductive output at each life-history stage (number of clutches and eggs laid per clutch; eggs incubated full-term; nestlings, fledglings and juveniles produced, and the number of juveniles surviving ≥ one year). These were natal-site data which assumed that biological parents had raised their own offspring entirely (Chapter Six: *Section 6.1.2*). The kinship coefficient of each pairing was included. The dataset included 26 females which survived to breeding age but did not lay any eggs before full-scale monitoring ceased. It omitted others fledging but not reaching breeding age within the study period. Thirteen non-breeding black robins merely suspected of being females were omitted also, as were two females known to have bred solely with tomtits (Chapter Eight).

To allow sorting for later analyses, I distinguished females and breeding effort in the master dataset by several criteria. A female was designated ‘single’ when unmated in a season but if paired and not laying, her productivity values for that season were set to zero. I included one female breeding with both black robins and tomtits but treated her as ‘single’ when cross-breeding. Clutch-cycles ending prematurely on the death of the female (n = 66) or male (n = 22) were identified. I ignored eight desertions after clutch-failure and six other mid-cycle desertions of unknown cause because deaths and desertions did not always result in breeding failure (Chapter Two). This was usually true if a parent was lost late in the breeding cycle. The dataset identified by clutch all juveniles produced by each female and the number surviving ≥ one year. All juveniles and adults were identified by their unique band numbers for assignment of hatch-dates and inbreeding coefficients from a subsidiary dataset. Females and males in the dataset could be sorted by population (using breeding site) and management phase (using the year of breeding). Male productivity could be interrogated also.

### *7.1.5 Environmental factors*

I chose not to include environmental variables as an explanatory factor in inbreeding analyses because the air temperature data showing cooler conditions in the Top Bush (Chapter Six: *Section 6.8*) were not gathered at the time of the population trends examined by my study. I acknowledge the strong possibility that any environmental effect operating at that time may have influenced the magnitude of inbreeding effects measured by my analyses.

## 7.2 Analyses

All analyses were conducted using R (version 2.8.1; R Development Core Team, 2008; www.r-project.org), with significance set at $\alpha = 0.05$. My associate supervisor, Professor Richard Duncan, managed the scripting process and advised on the appropriate analytical models.

### *7.2.1 Analysis of inbreeding effects on survival*

I wanted to assess whether an individual's degree of inbreeding ($F$) was positively or negatively correlated with survival probability. I was interested in assessing correlations by sex, the population in which the individual settled and died (demise-site), and management regime (intensively managed or unmanaged). As explained above, the Kaplan-Meier survival dataset was used, from which black robins dying prematurely had been omitted to avoid skewing results.

To eliminate variations in the depth of parental data in the dataset and to ensure that coefficients of $F = 0.0$ were genuine, I followed the practice of restricting the black robin pedigree to individuals with both sets of grandparents known (Jamieson *et al.*, 2007). The pedigree then comprised 1322 black robins, of inbreeding coefficients $\geq F = 0.03125$. Exploratory analyses using first, all black robins alive in and after spring 1980 (n = 1358) regardless of parental information and second, individuals with both parents known (n = 1343), merely accentuated the result obtained with the pedigree of uniform depth.

To test the hypothesis that an individual's level of inbreeding affected survival probability, we ran the life-span data in a Cox Proportional Hazard model to which individual coefficient of inbreeding *F* was fitted as a covariate with sex, demise-site, and management phase. Sex, demise-site and management phase were categorical covariates. These were coded so that one category (female, intensive management, and Mangere Island, respectively) was set to zero, with parameter estimates for the remaining categories showing the effect relative to the zero category.

### *7.2.2 Productivity analyses*

We used a Generalised Linear Mixed Model (GLMM) with normal and Poisson error distributions to assess whether the effects of accumulating inbreeding and kinship levels, along with other covariates, explained observed variations in female fecundity in the three black robin populations (Chapter Six). The GLMM was run in the R statistical package (R Development Core Team, 2008) using the library 'lme4'.

Following from my findings in Chapter Six, we selected hatch-rate (the proportion of fully incubated eggs hatching) and production of fledglings, juveniles and yearlings (juveniles surviving ≥ one year) as response variables for separate iterations of the model. Hatching success in all three populations decreased during the post-management period (Chapter Six: Table 6.13). Although the overall proportion hatching under natural conditions was only 7.5% lower, we considered that the decrease may signal an emerging inbreeding effect capable of weakening population resilience in the future. As response variables, production of fledglings, juveniles and yearlings reflected rates of mortality in (respectively) nestlings, fledgling and juveniles. These rates varied in each population, and were particularly penalising for the Top Bush population where growth under natural conditions was severely limited by poor fledgling and juvenile survival. We chose to analyse fledgling production despite concerns that the proportion of nestlings surviving to fledge was probably determined by unique external factors not operating for fledgling and juvenile survival (starling predation, nocturnal petrel strikes on nests).

Data for the response variables were drawn from the female productivity dataset in which values for hatch-rate and production of fledglings, juveniles and yearlings were given by female and clutch (*Section 7.1.4*). To reduce noise in the data, the set was modified to eliminate females in seasons when they were single and pairs in which one of the parents died before completion of the last clutch-cycle.

Because many fledglings and juveniles shared parents, we fitted male and female identity (using their unique band numbers) as random effects to control for the non-independence of data involving the same parent. Breeding season was added as a random effect to allow for unmeasured influences of climate, habitat changes, predation and other seasonally varying factors on productivity. As explanatory variables, we fitted fixed effects for male and female age (log-transformed), and breeding population (relative to Mangere Island). Kinship coefficients were fitted to test the effect of parental inbreeding on productivity. To ensure uniformity in kinship depth and genuine $F = 0.0$ values, we restricted the female productivity dataset to pairs for which all four parents were known (thus, all grandparents were known for offspring). Paternal and maternal inbreeding coefficients $F$ were fitted also (using the grandparent-restricted dataset described in *Section 7.2.1*), anticipating that the degree to which each parent was inbred might also explain productivity variations.

We ran the GLMM for post-management productivity alone (1990-91 to 2001-02) for two reasons. First, exclusion of the intensive management seasons eliminated possible fitness-masking effects of obligatory multiple-brooding, intra- and inter-island transfers, nest protection and supplementary-feeding. Second, the potentially confounding effects of fostering during the intensive management era were eliminated (that is, the influence of foster-parents and foster-sites on survival). The post-management productivity dataset comprised 449 breeding attempts (162 females, 163 males).

## 7.3 Results

### *7.3.1 Incidence of inbreeding*

Individual inbreeding coefficients $F$ were estimated on the basis of known mothers and fathers for all descendants of the founder pair, *Old Blue* and *Old Yellow*. *Old Blue* and one pre-1980-81 male were the exceptions. The four grandparents of all but 36 birds were known. Pedigree depth measured in black robin generation time (1.7 years; Chapter Two) varied according to management phase and the periods over which data were collected for the populations themselves (Table 7.1).

All but 24 (1.8%) of the 1358 individuals included in the master pedigree were estimated to be inbred (Table 7.2). In reality, the proportion of inbred birds was almost certainly greater than this, since the founder pair and one other breeding at the outset—four of the 24 black robins with $F = 0.0$ in the pedigree—were survivors of the tiny obligatorily inbred ancestral populations prior to 1980-81 and likely to be very closely related.

Table 7.1 Generation depth in the pedigree of each black robin population on Mangere and Rangatira Islands between 1980-81 and 2001-02 (generation time = 1.7 years; Chapter Two). The number of observation seasons is given as *n*.

| | | Management phase | | | | |
|---|---|---|---|---|---|---|
| Population | *n* | Intensive | *n* | Post | *n* | Combined |
| Mangere Island | 10 | 5.9 | 12 | 7.0 | 22 | 12.9 |
| Woolshed Bush | 7 | 4.1 | 9 | 4.7 | 16 | 9.4 |
| Top Bush | 6 | 3.5 | 9 | 4.7 | 15 | 8.8 |

Overall, accumulating inbreeding $F$ ranged from 0.0 to > 0.4 over the first ten years of intensive management, and from 0.25 to > 0.6 in the non-management seasons. In all populations, the accumulation was faster in known (breeding) males than females during the intensive management seasons but this pattern reversed when management ceased (Table 7.2).

Mean levels of inbreeding $F$ in the pedigree accumulated over time at different rates in each population (*Figure 7.1*). Post-1990 fluctuations in the Top Bush are likely to have been induced by the higher rates of adult turn-over (through earlier demise and immigration from the Woolshed Bush) and the significant variations developing in population size after management activity ceased (Chapter Six).

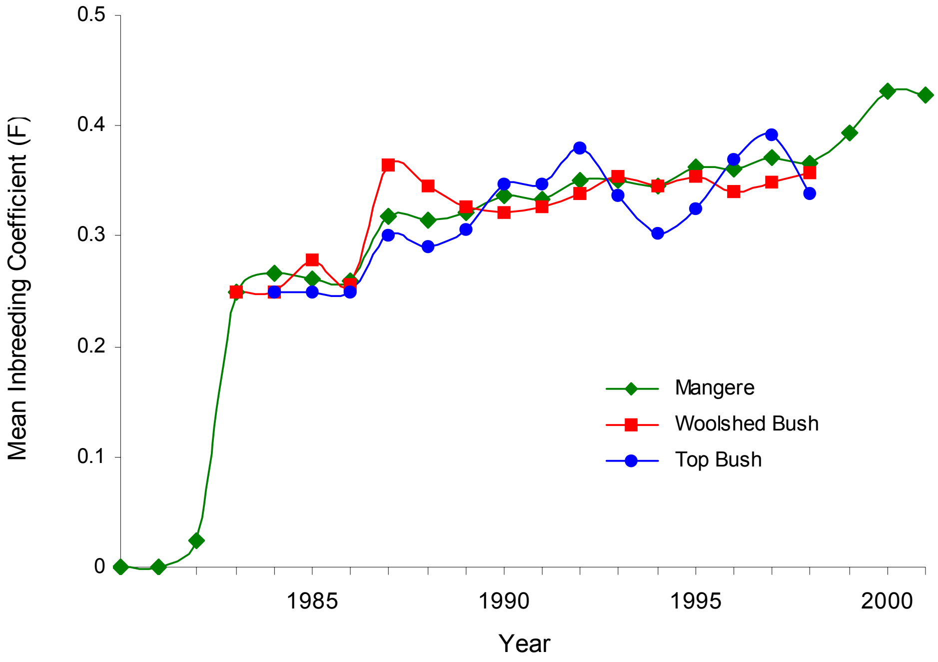


Figure 7.1 Mean levels of individual inbreeding coefficient *F* accumulating annually in the three black robin populations on Mangere and Rangatira Islands between 1980-81 and 2001-02.

During the management phase, inbreeding means were influenced by gene flow associated with natural dispersals on Rangatira Island and by management-related transfers between the three populations. Relative to the Rangatira Island sub-populations, Mangere Island's lower mean level of $F = 0.236$ is likely to reflect the removal of individuals from the population for management reasons. After management ceased, the Mangere Island population became fully closed and mean inbreeding levels accumulated more quickly than elsewhere, even for Rangatira Island combined (Table 7.2).

### *7.3.2 Inbreeding and survival probability*

The hypothesis that individual inbreeding *F* had no effect on survival probability was supported by the Cox Proportional Hazards model. A non-significant positive relationship with life-span was indicated for both sexes combined over the two management phases (1.57; $p = 0.377$; *Figure 7.2*).

Sex and demise-site were the most influential explanatory variables for poor survival. Relative to females, mortality rates were much higher for unsexed black robins, which were principally birds dying as nestlings and dependent fledglings (7.495; $p > 0.05$). There was also a very significant negative relationship between survival at each age-step in the Top Bush as a habitat relative to Mangere Island (0.7838, $p = 0.0023$). These results for unsexed black robins and the Top Bush were consistent with the unusually high rates of mortality reported in Chapter Six (*Sections 6.7.1* and *6.7.2*; *Figures 6.5* and *6.6*).Conversely, slightly higher survival probability was indicated for males relative to females (1.153; $p = 0.111$), for birds hatched during the unmanaged seasons (1.165; $p = 0.039$) and for those living in the Woolshed Bush (1.0784, $p = 0.292$).

### *7.3.3 Inbreeding and fecundity*

The GLMM did not support the hypothesis of a nil inbreeding effect on reproductive output. A consistent negative relationship with reproductive performance at all four life-history stages measured was found for male inbreeding $F$ (*Figures 7.3 – 7.6*). Female $F$ had no deleterious effect on any of the fecundity parameters. Kinship showed no effect on reproductive success except for yearling output where a possible negative correlation was indicated (*Figure 7.6*).

Male inbreeding $F$ grew in explanatory power at successive life-stages in the breeding cycle. The degree to which fathers were inbred was negatively, but not significantly, related with lower hatching success (-1.38, $p = 0.239$; *Figure 7.3*). Black robin male inbreeding tended towards significance as an effect for fledgling output (-1.27, $p = 0.065$; *Figure 7.4*). Noise in the nestling survival data may have disguised the true extent of inbreeding cost at this life-stage. Male inbreeding $F$ was strongly related to juvenile output (-1.922, $p = 0.015$; *Figure 7.5*) and with the number of juveniles reaching sexual maturity (-2.22, $p = 0.018$; *Figure 7.6*).

Reproductive performance was enhanced by paternal age which was a slightly stronger predictor of breeding success than maternal age. Natal-site effects varied but as the breeding cycle advanced beyond hatching, the Top Bush became progressively more prominent as an explanation for breeding failure. This trend is symptomatic of the cumulative effects of breeding failure at successive life-stages in that habitat (Chapter Six: Tables 6.14 and 6.16).

Table 7.2 Mean levels of individual inbreeding coefficient (*F*) accumulating by sex and management phase in the pedigree of the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. The pedigree comprises ancestral black robins still alive in spring 1980 and their descendants (n = 1358). Coefficients *F* are estimated relative to the founder population (two pairs, only one effective) at the commencement of intensive management in 1980-81.

| | **Mangere** | | | **Woolshed Bush** | | | **Top Bush** | | | **Rangatira** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***F*** | Female | Male | Unkn | Female | Male | Unkn | Female | Male | Unkn | Female | Male | Unkn |
| **Intensive management phase** | | | | | | | | | | | | |
| 0.00 | 4 | 2 | 9 | 2 | 2 | | 2 | 0 | 0 | 4 | 2 | 2 |
| >0.0 | | | 1 | | | 2 | | | | | | |
| 0.125 | | | | | | | | | | | | |
| 0.25 | 6 | 5 | 6 | 11 | 8 | 19 | 14 | 12 | 35 | 25 | 20 | 54 |
| > 0.25 | 3 | 3 | 6 | 5 | 7 | 10 | 5 | 8 | 29 | 10 | 15 | 39 |
| > 0.30 | 3 | 6 | 12 | 14 | 15 | 20 | 7 | 7 | 26 | 21 | 22 | 46 |
| > 0.40 | | 1 | 3 | 2 | 4 | 9 | 2 | 1 | 1 | 4 | 5 | 10 |
| Sex mean | 0.210 | 0.267 | 0.234 | 0.282 | 0.293 | 0.301 | 0.268 | 0.289 | 0.291 | 0.276 | 0.291 | 0.295 |
| Popn mean | 0.236 | | | 0.294 | | | 0.286 | | | 0.290 | | |
| **Post-management phase** | | | | | | | | | | | | |
| 0.00 | | | | | | | | | | | | |
| >0.0 | | | | | | | | | | | | |
| 0.125 | | | | | | | | | | | | |
| 0.25 | | | | | 2 | | | 1 | 1 | | 3 | 1 |
| > 0.25 | | | | 15 | 14 | 33 | 10 | 8 | 31 | 25 | 22 | 64 |
| > 0.30 | 36 | 41 | 112 | 64 | 81 | 189 | 25 | 27 | 115 | 89 | 108 | 304 |
| > 0.40 | 10 | 11 | 60 | 6 | 5 | 36 | 8 | 3 | 28 | 14 | 8 | 64 |
| > 0.50 | 10 | 3 | 8 | | 1 | 4 | 1 | 1 | 7 | 1 | 2 | 11 |
| > 0.60 | | | 2 | | | | | | | | | |
| Sex mean | 0.404 | 0.385 | 0.396 | 0.337 | 0.337 | 0.352 | 0.354 | 0.339 | 0.351 | 0.343 | 0.337 | 0.351 |
| Popn mean | 0.396 | | | 0.346 | | | 0.35 | | | 0.347 | | |

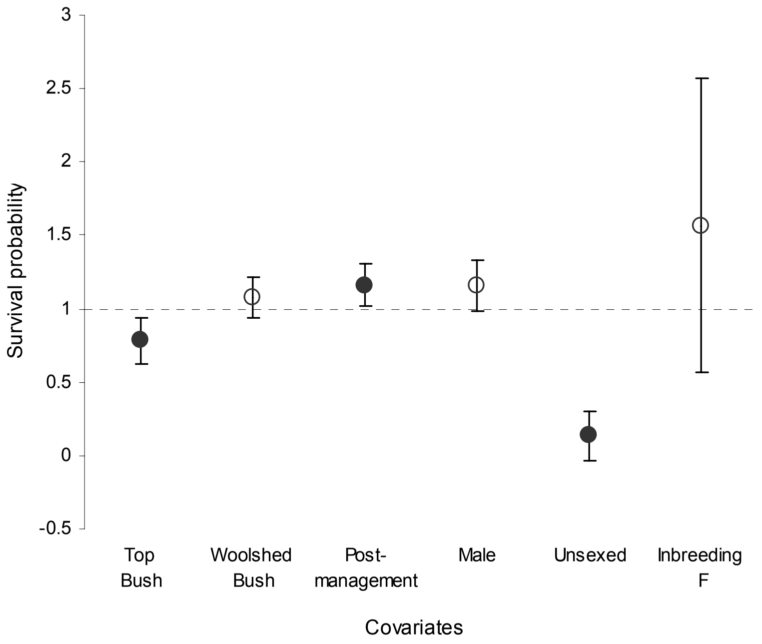


Figure 7.2 Probability of black robin survival (1980-81 to 2001-02). Individual life-span for both sexes combined fitted to Cox Proportional Hazard model with covariates of sex (relative to females), demise-site (relative to Mangere Island), management regime (relative to intensive management) and individual inbreeding coefficient $F$ (relative to non-inbred individuals). Filled circles indicate $P < 0.05$.

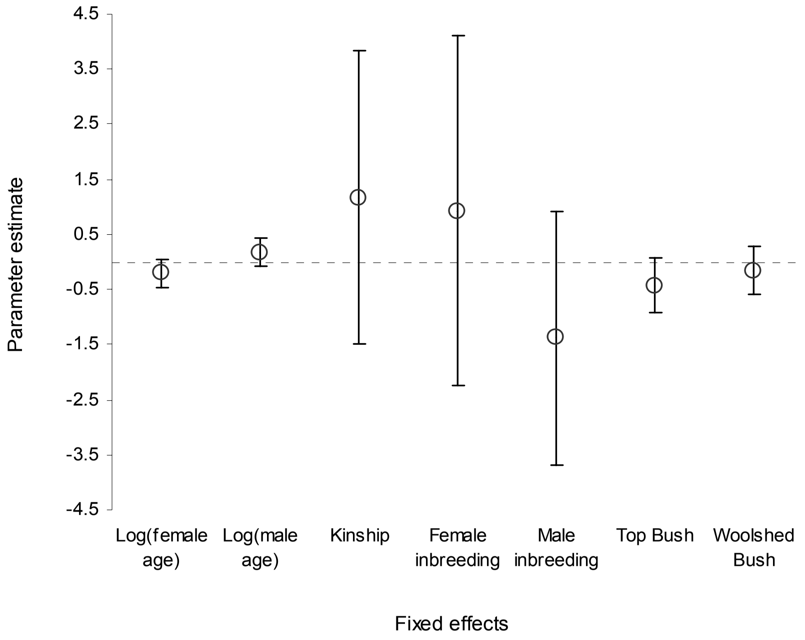


Figure 7.3 GLMM correlation of black robin hatch-rates with the ages and inbreeding coefficient $F$ of mothers and fathers, the kinship coefficients of parents, and natal habitats during post-management seasons. Hatch-rate defined as the proportion of all fully incubated eggs hatching on Mangere and Rangatira Islands between 1990-91 and 2001-02.

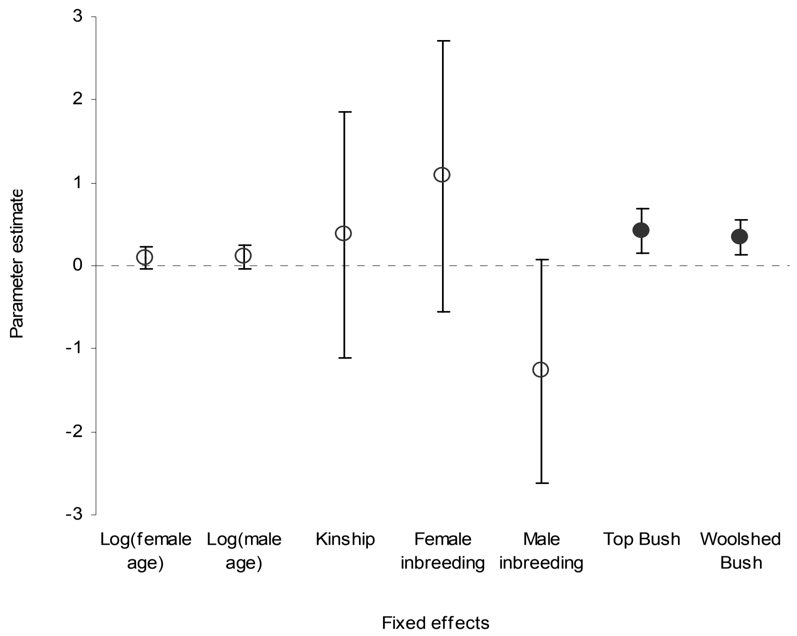


Figure 7.4 GLMM correlation of black robin fledgling production with the ages and inbreeding coefficient *F* of mothers and fathers, the kinship coefficients of parents, and natal habitats during post-management seasons, 1990-91 to 2001-02. Filled circles indicate $P < 0.05$.

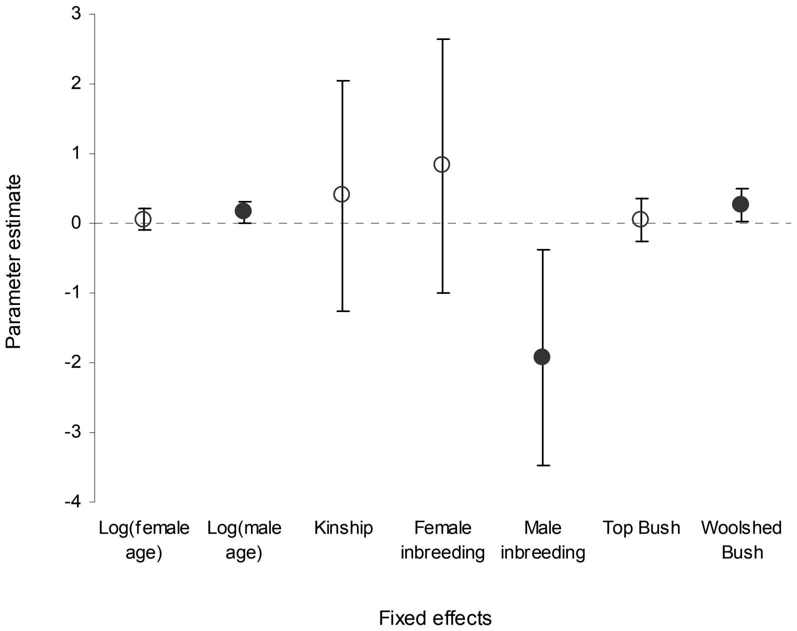


Figure 7.5 GLMM correlation of black robin juvenile production with the ages and inbreeding coefficient *F* of mothers and fathers, the kinship coefficients of parents, and natal habitats during post-management seasons, 1990-91 to 2001-02. Filled circles indicate $P < 0.05$.

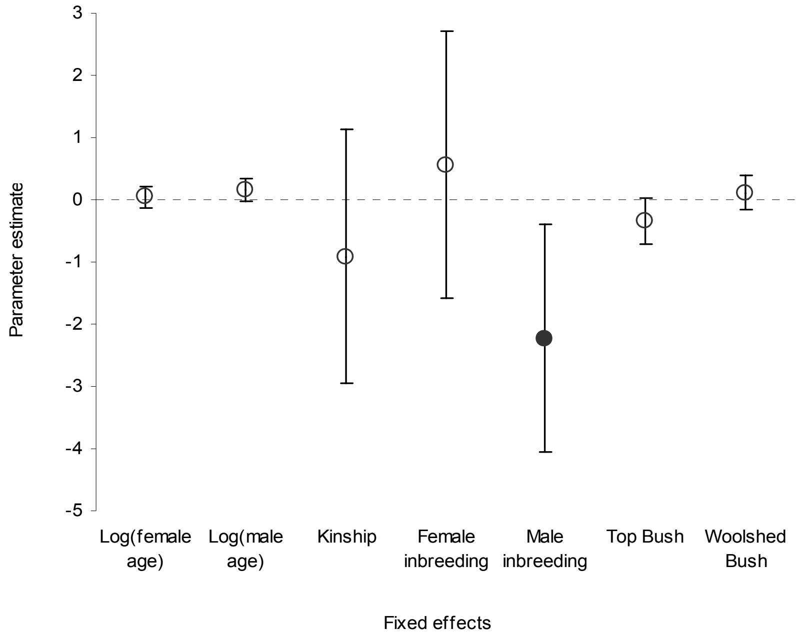


Figure 7.6 GLMM correlation of black robin yearling production with the ages and inbreeding coefficient *F* of mothers and fathers, the kinship coefficients of parents, and natal habitats during post-management seasons, 1990-91 to 2001-02. Filled circles indicate $P < 0.05$.

To assess specific inbreeding and habitat effects using yearling production (the ultimate expression of breeding success) as the response variable, we tested for two-way interactions between habitat and male and female inbreeding F, and habitat and kinship. There were no significant effects for these terms.

## 7.4 Conclusions

The two small black robin populations on Mangere and Rangatira Islands, descended from a single breeding pair but genetically isolated since 1990-91, are highly inbred. Only a tiny proportion of individuals at the base of the modern pedigree (< 2 %) are considered to be unrelated. This is a minimum indication of inbreeding—the true extent is probably significantly greater, since the ancestral founding pair was inevitably related, perhaps very closely. Average levels of individual inbreeding *F* accumulating in each population were nearly three times higher than the nearest reported for insular populations of wild birds (ancestrally inbred takahe, a non-passerine, distributed on four small islands in northern

New Zealand, $F = 0.123$ based on all pairs; Jamieson *et al*., 2003). Black robin relatedness far exceeds the range reported for naturally outbred bird populations of the northern hemisphere ($F = 0.009 – 0.051$; Kruuk *et al*., 2002: Table 2). The differing genetic histories and varying depths of the pedigrees reported complicate direct comparisons, but evidence of inbreeding depression in other less inbred bird populations suggests that the black robins have been overdue for detrimental inbreeding effects. For example, survival probability was significantly lower in inbred juveniles of a translocated population of North Island robins (a *Petroica* congener) whose average level of inbreeding was about 8% of black robin levels ($F = 0.027$, Tiritiri Matangi Island; Jamieson *et al*., 2007).

The results reported in this chapter confirm the prognosis of a harmful inbreeding effect for black robins. There is now evidence that the two populations on Mangere and Rangatira Islands have experienced inbreeding depression expressed, at least since 1990-91, as reproductive fitness costs which have had cumulative depressive effects at successive life-history stages late in the breeding cycle. There is no compelling evidence that survival probability for either sex had been compromised under the conditions prevailing since intensive management ceased.

A significant finding of our analyses is that inbreeding costs were acting selectively through breeding males alone. Sex-differentiated inbreeding depression has been reported previously, but not for males. In inbred insular takahe populations, fledging success was negatively correlated with female inbreeding $F$ (Jamieson *et al*., 2003). And in a small, closed, insular population of naturally outbred song sparrows *Melospizia melodia*, significantly lower hatch-rates ultimately limited the number of juveniles inbred females produced during their lifetimes (Keller, 1998).

The degree to which black robin mothers were inbred or pairs were related did not appear to affect breeding success. In other studies of wild birds, kinship $F$ has been negatively related with breeding success (hatch-rates in great reed warblers *Acrocephalus arundinaceus*, Bensch *et al*., 1994; hatch-rates in blue tits *Parus caruleus*, Kempenaers *et al*., 1996). Although parental relatedness does not appear to have caused problems for black robins so far, the suspicion of a deleterious kinship effect on yearling production (*Figure 7.6*) is suggestive of a latent threat which may be expressed as inbreeding levels accumulate further in the pedigree or conditions change for the populations.

We have not attempted to investigate why inbreeding depression should be expressed in males but not females, or the course of male inbreeding effect on offspring. We expect that genetic inheritance from inbred fathers may impose fitness costs on offspring, perhaps as early as the nestling stage (affecting fledgling production) or later, in fledglings and juveniles, as our results suggest. We do not have data to show what morphological or behavioural penalties inbred males experienced themselves. It is conceivable that lower resilience or weaker behavioural disposition could influence claims to optimal territories, defence of territory from disruptive intruders, foraging ability or attentiveness to parental duties. These issues cannot be addressed from the demographic record and would require further research in a marked and pedigreed black robin population. It is evident from our results, however, that if male inbreeding affects breeding success early in the clutch-cycle, the costs will be cumulative as the cycle advances. Further modelling may quantify the specific nature of costs at each stage.

We have no evidence that inbreeding depression in breeding males was synonymous with population decline. During the post-management seasons, black robin populations on both islands continued to grow naturally, albeit at rates significantly lower than during the ten seasons of obligatory renesting and cross-fostering. Our results indicate, however, that inbreeding depression is likely to have slowed the rate of natural recovery by limiting the number of juveniles produced and surviving to be recruited. Under the conditions of that time, the number doing so was evidently sufficient to maintain overall growth. The fact that inbreeding did not appear to affect survival was advantageous for growth. It preserved reproductive potential in the generally long-lived adult populations, a critical factor compensating for lower juvenile output.

For males, there was the added advantage of age-related breeding success, which was a stronger effect than for females, and arguably a factor mitigating paternal inbreeding costs. There are two possible explanations for the stronger influence of male age. It may be an artefact of parental performance improving from a poor start. Yearling males often neglected parental duties, a trend indicated by the lower proportions of males breeding successfully as yearlings (Chapter Six: Table 6.16). This trend did not persist as males acquired breeding experience. In contrast, females generally bred successfully from earlier ages. Experience may also have counted when males were required to feed first-clutch fledglings, second-clutch nestlings and the brooding female. This was a crucial time for dependent fledglings, when many could be neglected or abandoned by fathers.

Our results support the findings of Chapter Six that breeding success in Woolshed Bush, measured in the GLMM as gross production of offspring at each life-history stage, was higher than on Mangere Island and in the Top Bush. This, and higher relative survival probability, is the compelling explanation for the Woolshed Bush's superior growth rate after management activity ended. Conversely, our results indicated that negligible growth in the size of the Top Bush population was explained by the low survival probability of black robins settling there and inferior rates of offspring production at each life-history threshold in the breeding cycle. The strong positive correlation with fledgling production in the Top Bush (a measure of nestling mortality) may be deceptive. Clutch-failures early in the cycle (merely suggested by the negative but non-significant relationship with hatch-rate; *Figure 7.3*) was likely to increase the probability of renesting, so that gross output of offspring (for example, fledglings, *Figure 7.4*) would appear to be higher relative to the other populations. Nonetheless, the trend shown in the model indicated progressive deterioration in Top Bush breeding success, culminating in lower yearling output than elsewhere (*Figure 7.6*).

We did not find conclusive evidence that inbreeding was a factor explaining population trends in the Top Bush, though there is expected to be a more severe inbreeding effect if environmental conditions are harsher (Keller *et al.*, 2002; Frankham *et al.*, 2002). The finding in Chapter Six that the Top Bush black robins (the least inbred on average of the three populations; Table 7.2) generally experienced the coldest conditions suggests the heightened probability of an inbreeding effect. This was demonstrated in small populations of Darwin's finches on Isla Daphne Major (Galapagos Islands) where episodic inbreeding depression of significant effect flared among inbreeding birds during periods of low food availability (Keller *et al.*, 2002). If, as Worner (2007) suggests, colder average conditions lower insect biomass available over time to foraging birds, inbreeding depression may have contributed to the faltering performance of Top Bush black robins after management assistance was withdrawn (Chapter Six). Our preliminary exploration of interactions between inbreeding and habitat was inconclusive. It would be prudent to investigate this relationship more closely, especially as inbreeding depression may be triggered by exposure to environmental conditions varying from those in which ancestral inbreeding occurred. If a relationship exists between inbreeding and environment, there are significant implications for site selection when establishing new black robin populations from tomorrow's more highly inbred source populations. The change may be more important than the quality of the new conditions (Jamieson and Ryan, 2000), suggesting that establishment in better habitats may still trigger debilitating inbreeding effects.

A key question raised by our findings is why such anomalously inbred black robin populations experienced inbreeding effects in males only and inbreeding costs which did not stall population growth altogether. A persuasive explanation is that the species has indeed been purged of genetic load by its century-long history of tight bottlenecks and associated inbreeding, as proposed by Ardern and Lambert (1997). There is support for this explanation from recent New Zealand studies. Jamieson *et al.* (2003) considered that the purging effects of background inbreeding might explain the sex-specific bias in reproductive success in four small closely related takahe populations on offshore islands. Laws and Jamieson (unpublished data) concluded that weak evidence of inbreeding depression (measured as juvenile survival) in a small, severely bottlenecked, genetically depleted population of Stewart Island robins on Ulva Island was partly attributable to historical purging of genetic load in the bottlenecked source population. In contrast, inbreeding depression was strongly expressed (as juvenile mortality) in Tiritiri Matangi Island's North Island robins sourced from large genetically diverse mainland populations from which genetic load was much less likely to have been purged (Jamieson *et al.* 2007).

Our findings suggest that the two black robin populations possess residual genetic load despite their history of reduction, chronic inbreeding and advanced genetic impoverishment. Measurement of lethal equivalents (Morton *et al.*, 1965) would help to confirm this. Residual load has implications for the future of the populations and their management. Deleterious effects have been expressed so far through male reproductive performance alone but this may not remain the case as average levels of relatedness rise in existing populations or if they are subjected to significant or sudden environment change. Contractions in population sizes, such as those occurring recently on Mangere and Rangatira Islands, increase the incidence of close inbreeding and amplify the risk of both depression and the loss of alleles. Stalled or minimal population growth exposes the two small populations and any daughter-populations to the same risk (Jamieson, 2007a).

The results of our analyses lend tentative support to Craig's (1991, 1994) speculative hypothesis of reduced susceptibility to inbreeding depression in New Zealand's insular endemic birds but do not support the assumption made commonly by New Zealand wildlife managers (Chapter One) that the genetic costs of population declines, persistence at low numbers, and consequent inbreeding are inconsequential for future viability. Genetic malfunction was not shown to equate to declines in the two extant black robin populations under the conditions prevailing during the study period. But we cannot be certain that this was true of the following years in which declines did occur (Chapter Six) or that it was not implicated in the failure of the Pitt Island translocations (Kennedy, 2006). Inbreeding may have significant consequences for the years ahead, especially if populations are challenged by adverse environmental conditions, new pathogens or other unforeseen pressures. The evidence of individual inbreeding effects and the suggestion of emergent kinship effects indicate that the assumption of negligible genetic risk underpinning the so-called 'New Zealand cure' (Groombridge, 2007) may be unsafe.

# CHAPTER EIGHT
# HYBRIDISATION

## 8.0 Introduction

Under natural conditions, the inter-breeding of reproductively isolated bird species can be evolutionarily constructive and a mechanism of avian speciation (Grant and Grant, 1997). The black robin may have acquired its tomtit characters through an ancient inter-breeding event before or after arrival in the Chatham Islands (Miller and Lambert, 2006). Conversely, anthropogenic hybridisation can expose distinct avian genotypes to the risk of extinction at population and species scales through genetic introgression or through demographic costs such as reproductive wastage (sterile offspring, reductions in offspring fitness), poor cross-mating success, skewed reproductive advantages or displacement by better adapted hybrids (Rhymer and Simberloff, 1996).

Species introductions and the loss or fragmentation of habitat are common triggers of anthropogenic hybridisation (Rhymer and Simberloff, 1996; Lande, 1999) and often work in combination. The changes break down the evolutionary mechanisms (ecological barriers, behavioural adaptations) isolating related species reproductively (Taylor, 1975). In populations reduced by habitat stress, demographic instability (sex imbalances, isolation from conspecific mates) may predispose individuals to breeding with available congeners. In New Zealand, for example, a history of habitat loss and mammalian predation has reduced endemic black stilts *Himantopus novaeseelandiae* to a small but highly dispersed population obliged by the shortage of preferred conspecific mates to inter-breed at times with the ubiquitous pied stilt *H. h. leucocephalus* (Pierce, 1984; Green, 1994; Wallis, 1999; Department of Conservation, 2001c).

Species isolated on islands are particularly exposed to hybridisation threats because habitats changes can be more extensive, there may be fewer populations, habitat partitioning may be narrower and the juxtaposition of species closer than for mainland populations. On Mangere Island, mammalian predation and major contractions in available forest habitat have resulted in the severely reduced population of forest-specialist Forbes' parakeets hybridising with similarly reduced sympatric Chatham Island red-crowned parakeets (Taylor, 1975, 1985; Department of Conservation, 2001b). Protection of both parental genotypes from an enveloping hybrid swarm (the multiple back-crossing of fertile hybrids with the parental and hybrid populations) depended on the culling of hybrids which have proven equally able to exploit the recent recovery of forest habitat. Early culling also selected (deliberately and accidentally) against the red-crowned parakeet population on Mangere Island to protect the smaller and more localised Forbes' parakeet population (Department of Conservation, 2001a)

Conservation biologists and wildlife managers dealing with critically endangered species must decide whether inter-breeding with former reproductively isolated congeners is natural or anthropogenic in origin. If natural, the threatened genotype may vanish; if anthropogenic, direct intervention to preserve it will be necessary. Similarly, decisions over localised hybridisation (between insular congeners, for example) may determine whether valuable genetic variation in a population of a rare or declining species is lost or preserved. Intervention preserves options for the future and may minimise the risk of inter-breeding threats migrating to unaffected populations through hybrid dispersal.

Inattention to the risk of hybridisation, hesitation in managing it or failure to detect it may result in fatally compromised viability or the development of a hybrid swarm, in the midst of which the detection, much less the recovery, of the parental genotypes could soon become exceedingly difficult. No action was taken, for example, to protect New Zealand's indigenous grey duck *Anas superciliosa* (a species disadvantaged by changes to wetland quality and extent) from introgressive hybridisation with introduced and more adaptable Mallard ducks *Anas platyrhynchos*. The swarm which developed through neglect is predicted to culminate in the outright loss of the grey duck as a distinct New Zealand species (Rhymer *et al*., 1994).

In all three examples cited, wildlife managers have not been able to rely on inferior hybrid fitness or sterility to moderate the threats from introgression or demographic cost. It is not axiomatic that hybrids will suffer outbreeding depression in all cases (Rhymer and Simberloff, 1996). Nor can managers rely on the traditional morphological approaches to detecting and managing hybridisation after the event. More recent molecular tools do better and can determine the extent and history of hybridisation (Ma and Lambert, 1997a) but they too are not infallible (Allendorf *et al.*, 2001).

This chapter examines the history, causes and risk of recurrent hybridisation between black robins and Chatham Island tomtits, the congener with which black robins coexisted naturally in the Chathams archipelago (Fleming, 1939b; Powlesland *et al*., 2001). Present-day black robin managers regard both the probability and consequences of further hybridisation as negligible. The operative black robin management strategy specifies no precautionary monitoring for cross-breeding (Department of Conservation, 2001a). The policy is based on the misapprehension that observed black robin x tomtit cross-breeding arose entirely as an unintended consequence of conservation management which ceased in 1989-90. As this chapter reveals, unrelated cross-breeding events occurred long after that time.

My brief account of historical black robin x tomtit cross-breeding is primarily descriptive and synthesises a more detailed work in progress to document the full history and causes of inter-breeding. Butler and Merton's (1992) description of cross-breeding early in the intensive management phase (1980-81 to 1989-90) is helpful. Ma and Lambert (1997a, b) summarise the historical context of later cross-breeding events and Hardersen (1996) and Hutching (2004) refer to them, but otherwise the factors predisposing black robins and tomtits to cross-breeding under conditions apparently unrelated to management have been little documented or analysed. This summary also meets the need to quantify hybridisation as an extinction threat. This threat tends to be underestimated by conservation biologists and wildlife managers pre-occupied with the causes of deterministic extinction (Rhymer and Simberloff, 1996).

## 8.1 History of black robin x Chatham Island tomtit hybridisation

During the two central phases of black robin management (intervention, 1980-81 to 1989-90; post-management monitoring, 1990-91 to 2001-02), at least one black robin female on Mangere Island and two on Rangatira Island mated with male tomtits. On Rangatira Island, managers also intervened to prevent a hybridising pair-bond establishing between a black robin yearling believed to be a female and tomtits with which she was interacting. The three black robin females breeding with tomtits (1.2% of 246 black robin females reaching breeding-age in these periods) produced at least nine clutches (≥ 11 eggs) from which two F1 hybrid nestlings are known to have fledged (*Figure 8.1*; Table 8.1).

Figure 8.1 *Tobin*, the female F1 hybrid offspring of a tomtit male x black robin female pairing on Rangatira Island in the 1989-90 season (see Table 8.1).
*Photo: Don Merton*

The two Rangatira Island cross-breeding black robins had selected the tomtit males as their first mates. One died naturally without ever mating with black robins. The other was transferred to Mangere Island (then tomtit-free; see below) where she could breed only with her own kind. After doing so successfully, she was returned to Rangatira Island where she mated with black robin males exclusively (Butler and Merton, 1992). This switching of mate-choices does not appear to hold true in reverse—no black robin females from this period or later were observed to breed with tomtits after having paired with black robins. However, the mate-selections of the Mangere Island female are unknown for the seven seasons in which she was overlooked by monitoring teams. She was mated with a tomtit when discovered in her final year.

Table 8.1 Breeding outcomes of black robin x Chatham Island tomtit cross-pairings known from observation of breeding attempts or indicated by the appearance of F1 hybrid offspring, 1980-81 to 2001-02. Outcomes for the backcross-breeding of an F1 hybrid male x tomtit female are included at the foot of the table.

| Habitat | Female | Age | Reared by | Season | Clutch # | Eggs | Nestlings | Fledglings | F1 Name | Fate |
|---|---|---|---|---|---|---|---|---|---|---|
| **Black robin female x tomtit male** | | | | | | | | | | |
| Rangatira | *Marion* | 1 | Tomtit | 1984-85 | 1 | 1 | | | | Egg infertile |
| | *Marion* | 2 | Tomtit | 1985-86 | 1 | 2 | | | | One egg infertile, one egg broken (starlings?) |
| | | | | | 2 | 1 | | | | Egg infertile |
| | *Maggie* | 5 | Tomtit | 1989-90 | 1 | 1 | | | | Egg missing (starlings?) |
| | | | | | 2 | 3 | 1 | 1 | *Tobin* ♀ | *Tobin* destroyed as adolescent; one rim-shot (broken); failed egg not examined; tomtit male destroyed also |
| | *Ali I* | 1 | Tomtit | 1985-86 | | | | | | Not permitted to breed with courting tomtits; transferred to Mangere Island |
| Mangere | *Peg III* ? | 4 | Robin | 1992-93 ? | 1 | ≥ 1 | ≥ 1 | ≥ 1 | *Robin A* ♂ | *Robin A* destroyed after breeding in two seasons |
| | *Peg III* | 8 | Robin | 1996-97 | 1 | 2 | 2 | | | Nestlings destroyed before fledging, along with parents |
| **Chatham Island tomtit female x *Robin A* (F1 hybrid) male** | | | | | | | | | **F2 Name** | |
| Mangere | Tomtit | - | - | 1993-94 | 1 | 3 | 2 | 2 | *Tom V* ♀<br>*Pitt* | *Pitt* disappeared over winter 1994; *Tom V* destroyed 1994-95; failed egg not examined |
| | Tomtit | - | - | 1994-95 | 1 | 3 | 2 | | | Nestlings destroyed before fledging, along with parents; failed egg not examined |

On both islands, other cross-breeding events were possible after unmarked birds resembling black robins but of unknown parentage (Mangere Island, n = ≤ 10, 1991-92 to 1993-94; Rangatira Island, n = 11, 1990-91 to 1995-96) appeared in populations where all individuals were believed to have been fully accounted for. Suspicions were not aroused unduly on Mangere Island until irrefutable evidence of cross-breeding emerged five years after the first of the unmarked individuals appeared. Until then, all unmarked birds were considered to be genetically pure progeny of black robin pairings or breeding attempts which monitoring teams had missed.

On Mangere Island, the unexpected appearance of unmarked individuals coincided with a three-year period (1990-91 to 1992-93) during which a dramatically scaled-down monitoring regime was trialled by resource-stressed black robin managers (Chapter Four: Management of Extinction Threat). This experimental regime proved to be inadequate (Merton, 1993, 1994) and full-population monitoring resumed in 1993-94. Four of the unmarked individuals were eventually colour-banded, suggesting that some of the ten originally observed had been double-counted. The mate-choices, breeding behaviour and offspring histories of these newly banded individuals indicate now that three of the four were probably genetically pure black robins. The fourth seems likely to have been the sibling of a known hybrid. It died naturally at age ≤ 4 (hatch-date uncertain), apparently without mating. A fifth unmarked bird (known subsequently as *Robin A*; Table 8.1) avoided banding but was followed closely.

On Rangatira Island, eight unmarked individuals were eventually banded and followed closely. None aroused suspicion of being hybrids. On both islands, however, observers could not be sure that they had banded and followed all of the unmarked individuals originally counted.

Back-crossing commenced on Mangere Island in 1993-94 but black robin managers did not recognise this for what it was. The fifth unmarked individual (*Robin A*) had mated with a tomtit female in regenerating forest and scrub on the periphery of the Robin Bush. To casual observation, *Robin A* was morphologically indistinguishable from a black robin and was considered to be one. His cross-breeding confounded black robin managers. Until that time, only black robin females with cross-fostering histories had inter-bred with tomtits. Merton (1993, 1997) considered that *Robin A*'s mate-choice originated from imprinting on tomtit parents after a black robin female had laid in a tomtit nest or black robin eggs had been placed there, mischievously or otherwise. *Robin A*'s edge-dwelling habit, choice of territory, open-country perching behaviour (*Figure 8.2*), fragmentary fluting calls and trilling at the nest (Kennedy, 1993b, 1996b) were explained in the same way. The egg-dumping explanation had no precedent and unsanctioned fostering was an unconvincing suggestion. Adoption as a fledgling by tomtits was also postulated, but the only precedent for this involved tomtit foster-parents reclaiming a black robin fledgling they had raised after it had been returned to neighbouring black robins for rearing (Butler and Merton, 1992).

In 1995-96, three years after his discovery, minisatellite DNA analyses revealed that *Robin A* was an F1 hybrid from a tomtit male x black robin female breeding event (Lambert, 1996, Ma and Lambert, 1997b). At that time, black robin managers knew of no such cross-pairing but a year later the discovery of a cross-breeding female with a hybrid brood (*Peg III*, Table 8.1) suggested that she may have been his mother. The possibility of other undetected cross-breeding females could not be ruled out. *Robin A* and his tomtit mate fledged two F2 hybrids in 1993-94 (*Figure 8.3*; see also Hardersen, 1996) and had hatched three F2 hybrid nestlings in 1994-95 (Table 8.1) when managers intervened to prevent further cross-breeding by the pair and their progeny.

No further hybridising events were reported on either island after the discovery of *Peg III* in 1996-97. After 2001-02, monitoring intensity was scaled down significantly on Mangere Island and therefore was less likely to detect hybridisation (see Chapter Four for further details).

## 8.2 Management of hybridisation events

All hybridising events were treated as artefacts of human disturbance to the natural environments of both species (Minister of Conservation, 1994; Aviss, 1995). Though small in relation to the number of conspecific pairings, the incidence of black robin x tomtit cross-pairing and back-crossing (0.01% of total clutches laid, n = 1081, 1980-81 to 2001-02) was considered a threat to the small black robin population in the first instance, and to both parental genotypes secondarily. Management responses followed the policy adopted throughout New Zealand that, unless constructive hybridisation would benefit the species of concern, protection of threatened parental taxa took priority even if the ecological implications of cross-breeding were in doubt (Aviss, 1995).

Black robin x tomtit cross-pairings on Rangatira Island were broken up either by culling the offending tomtit or by transferring the black robin to Mangere Island (tomtit-free between 1975-76 and 1988-89). When the transfer option was not available after tomtits were returned to Mangere Island, one or both cross-breeders were culled (Butler and Merton, 1992; Kennedy, 1993b, 1996b).

Hybrid offspring were invariably culled in case they had inherited the superior mobility of tomtits and dispersed to breed undetected in the parent populations or in populations on other islands (Merton, 1993).

Figure 8.2 *Robin A* (a male) was morphologically indistinct from genetically pure black robins on Mangere Island and was considered to be one until molecular analyses revealed that he was the F1 hybrid progeny of a tomtit male x black robin female mating. *Photo: Sönke Hardersen*

Figure 8.3

*Tom V* (top right), the female F2 hybrid progeny of F1 *Robin A* (father) in the company of her tomtit mother, Mangere Island, 1993-94.

*Photo: Sönke Hardersen*

Specimens were retained for diagnostic DNA profiling of hybrids and to confirm their parentage (especially the identity of *Robin A*'s unknown mother) but the universally low genetic diversity of black robins frustrated these objectives (Ardern and Lambert, 1997; Ma and Lambert, 1997a). Profiling was foreseen as a means of testing for hybridisation in the future (Kennedy, 1996b).

What little *post mortem* and molecular data exist from the specimens suggests sexual dimorphism in hybrids. First- and second-generation hybrid females (*Figures 8.1* and *8.3*) may be phenotypically intermediate between black robins and tomtits, resembling dark 'smudgy' tomtit females. F1 hybrid males may resemble black robins (*Figure 8.1*; Te Papa Collection List for *Petroica traversi*, OR 025468; Ma and Lambert, 1997b) but this assumption is based on a single sample (*Robin A*). I was unable to access the sample to confirm its sex.

The policy of swift elimination was resisted by some black robin managers arguing that hybrid fertility and vigour should be tested by allowing F1 hybrids to breed under conditions of close observation. If hybrids were infertile, then unmonitored black robin populations of the future would be jeopardised only by the wasted reproductive effort and not by introgression (Kennedy, 1993b). The breeding success of the F1 hybrid male *Robin A* answered these questions and confirmed that recurrent introgressive hybridising could lead to a potentially unmanageable hybrid swarm in unmonitored populations. Confirmation that cross-breeding might recur unseen did not influence later decisions to reduce monitoring intensity (Department of Conservation, 2001a).

The realisation that F1 hybrids (*Robin A*) could resemble black robins triggered an intensive effort to obtain DNA samples from black robins of unknown parentage on Mangere Island. Samples were taken from 20 tomtits also, to help with molecular detection of cross-breeding. None of the suspected hybrids was found and were all assumed dead (Amey and Studholme, 1996). Rangatira Island populations were not investigated in this way but earlier DNA-related research had revealed no signs of genetic mixing in the 61 black robins sampled (58.6% of the population; Holmes, 1993, 1994; Ardern and Lambert, 1997). The Mangere Island survey revealed incidentally that introgression was a serious threat to the tomtit genotype. Genetic diversity in the small tomtit population (n = 51) was discovered to be depleted (Ma and Lambert, 1997b), suggesting that it and the Rangatira Island population from which it was derived by transfer were, like the black robins, descendants of reduced, ancestrally inbred populations.

The immediate risk of further cross-breeding was managed in both black robin populations by continuing with comprehensive monitoring during the breeding seasons. Locating the cross-paired black robins and tomtits was considered to be the most reliable means of detecting cross-breeding in time to intervene. On Mangere Island, more time was devoted to searching the scattered bush areas outside the Robin Bush. Vigilance was rewarded in 1996-97 when the female *Peg III* was discovered with a tomtit mate and hybrid brood [43] in the largest aggregation of scrub in the Douglas Basin (*Figure 2.4*). It was this discovery which strengthened concerns about the provenance of the ten or so unmarked individuals encountered since *Peg III* had disappeared (thought dead) eight years before, in 1988-89.

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[43] The DNA sampling team had captured *Peg III* two months earlier in the same locality but had construed her interest in a local tomtit male to be aggression, not cross-breeding behaviour (Amey and Studholme, 1996).

Full-population monitoring ceased on Rangatira Island in 1998-99 and was replaced with pre- and post-breeding index-monitoring (distance-sampling in 1999-2000, and mark-resighting from 2000-01 onwards). The mark-resighting method was adopted exclusively on Mangere Island after 2001-02. These labour-saving alternatives to full-scale monitoring are significantly less sensitive to the signs of hybridisation or the subtle behavioural anomalies of hybrids. Current monitoring practice is therefore unlikely to detect introgression before it is well advanced.

## 8.3 Causal factors

Mal-imprinting, habitat fragmentation and unnaturally small population sizes appear to have been the proximate causes of black robin x tomtit cross-breeding. Mal-imprinting was an unintended consequence of conservation management, but the timing of another conservation initiative—the reintroduction of tomtits to Mangere Island—contributed also. This last factor has been overlooked in previous accounts of hybridising events on Mangere Island.

### *8.3.1 Mal-imprinting*

Sexual mal-imprinting on tomtit foster-parents was the unifying explanation for all hybridisation events on Rangatira Island (Table 8.1; Butler and Merton, 1992). Black robin offspring were never fostered to tomtits on Mangere Island, but a small number of males and females fostered to tomtits on Rangatira Island were transferred to Mangere Island to breed. None of these showed signs of sexual mal-imprinting.

Receptiveness to tomtit courtship behaviour emerged as a side-effect of cross-fostering in the first fully fostered black robin female surviving to breed (that is, she was hatched and raised to independence entirely by tomtits). This mal-imprinting effect was not evident until 1984-85, four seasons after cross-fostering commenced. A small number of black robin females had been raised by their biological parents in the interim, thus avoiding—by chance—a very small breeding population dominated by mal-imprinted females. Fully fostered black robin males (n = 12) showed no reciprocal preference for tomtit females, nor was mal-imprinting in fostered females shared by female siblings in the same nest. Female receptiveness to tomtits was remedied in 1985-86 and thereafter by the policy of returning all fostered black robin nestlings to black robin pairs whenever possible for fledging and rearing to independence (Butler and Merton, 1992). Following the change to temporary fostering, 36 of the 53 females fostered to tomtits survived to breeding age. None showed a preference for tomtit mates (this study).

Sixteen black robin females were fully raised by tomtits on Rangatira Island during the cross-fostering programme (1980-81 to 1989-90). Eight survived to breeding age, among them the three Rangatira Island females breeding with tomtits or responding to courtship overtures (Table 8.1). Of the other five, three formed pair-bonds with black robin males and two did not live long enough as adults to do so. Two of the three mal-imprinted females on Rangatira Island remained constantly aloof from the company of their own kind. Their detachment may have been a habit acquired through tomtit-upbringing or it may have been coincidental—some naturally raised black robins of both sexes remained aloof in later seasons too. Whatever the explanation, the preference for territories on the periphery of the resident black robin population increased the likelihood of contact with potential tomtit mates operating in relative freedom from territorially defensive black robin males.

The risk of cross-breeding by any fully fostered black robin female ceased when the last of them passed out of the populations through transfer (Mangere Island, 1987-88) and natural attrition (Rangatira Island, 1997-98; this study).

### *8.3.2 Cultural transmission of sexual mal-imprinting*

The cross-breeding black robin female on Mangere Island (*Peg III*; Table 8.1) was raised entirely by her biological parents. Her father was fully tomtit-raised and her mother partially so (Table 8.2). Merton (1997) argued that enough of their ‘cross-culturally acquired characteristics’ had been transmitted during parenting to influence her mate-choice. This argument was extended to the unknown parents of the unmarked ‘black robins’ (including *Robin A*) discovered outside the Robin Bush between 1991-92 and 1996-97.

The evidence for cultural transmission is weak. The majority of black robin offspring reared to breeding age by partially or fully tomtit-raised parents did not cross-breed (Table 8.2). Two of the three which did cross-breed had no contact with black robin parents at any time (that is, they were fully raised by tomtits from earliest incubation). Only the third

(*Peg III*) was raised by black robin parents which were themselves fostered.[44] Any tomtit affinities acquired from her parents failed to affect her 11 surviving siblings. The fourth female treated as a potential cross-breeder (*Ali I*; Table 8.1) was raised entirely by black robin parents with no cross-breeding history at all.

Table 8.2 Numbers of breeding-age offspring produced by tomtit-fostered black robin parents and numbers among them later cross-breeding with Chatham Island tomtits on Rangatira and Mangere Islands. Names in **red** denote cross-breeding offspring which were themselves fostered to tomtits (fully fostered in all cases).

| | Offspring | | Offspring later cross-breeding | | |
|---|---|---|---|---|---|
| Tomtit-raised parents | Male | Female | Male | Female | Name |
| Mother fully fostered | 11 | 12 | - | - | - |
| Mother part-fostered | 71 | 65 | - | 2 | ***Maggie***<br>*Peg III* |
| Father fully fostered | 23 | 14 | - | 3 | ***Marion***<br>***Maggie***<br>*Peg III* |
| Father part-fostered | 58 | 52 | - | - | - |

### *8.3.3 Habitat fragmentation*

Sexual mal-imprinting on tomtit foster-parents is the leading explanation for cross-fostering-phase inter-breeding on Rangatira Island, but it does not adequately explain post-fostering hybridisation on Mangere Island. Instead, the interacting effects of habitat change and small population size appear to have created the predisposing conditions for inter-breeding on Mangere Island.

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[44] The relationship between *Peg III*'s cross-breeding and her parents' fostering histories may simply have been coincidental. Because tomtit-raised breeders of either sex out-numbered black robin-raised breeders 4 to 1 in her natal season, her probability of being raised by fostered parents was unusually high.

Anthropogenic changes to Mangere Island's forest cover were more profound than on Rangatira Island. The island was almost completely deforested during more than a century of livestock browsing and pastoral farming (c.1860 to 1968; Chapter Three: History of Decline). Despite natural regeneration assisted by revegetation programmes (Atkinson, 2003), the largest area of forest habitat is the small Robin Bush isolate (7.9 ha). This is surrounded by outlying fragments of bush and scrub cover, mostly in the Douglas Basin. This fragmented habitat is sub-optimal for the forest-specialist black robins, and may be so for the tomtits too. In contrast, on Rangatira Island both species have large areas of contiguous forest cover available to them, within and between which they can disperse.

The extent and quality of breeding habitat reduces Mangere Island's black robin and tomtit populations to unnaturally small sizes, accentuating the probability of inter-breeding and introgression (Rhymer and Simberloff, 1996; Ma and Lambert, 1997b). In addition, differing histories of extirpation (Chapter Three) and asynchronous re-introduction of the two species to the island (see below, and Chapter Four) have disturbed the natural sympatry between black robins and tomtits.

A telling feature of cross-breeding on Mangere Island is that it did not occur within Robin Bush where Amey and Studholme (1996) found tomtit densities to be highest. All cross-breeding on the island was detected outside the Robin Bush where at least five of the ten unmarked 'black robins' (including the F1 hybrid *Robin A*) were also encountered.

In the confinement of Robin Bush, young black robins and unmated adults commonly cluster near the bush edge (pers. obs.; field records consulted by this study), predisposing a few to movement beyond. Beyond the perimeter, new territory opportunities and refuge from territorial conflict within the bush exist only in fragmented habitat depauperate in black robin mate-choices. Occasionally, young non-site-fixed black robins stray beyond the Robin Bush perimeters but no black robin pairs are known to have established territories outside the Bush or in the Douglas Basin (data collated by this study). In contrast, tomtits utilise open habitat (Flack, 1976a) and pairs breed in and outside the Robin Bush today (pers. obs.).

The critical contribution of habitat fragmentation to cross-breeding on Mangere Island is likely to be the isolation it imposed on dispersing black robins. What role habitat character and reduced numbers played in tomtit population dynamics on Mangere and Rangatira Islands is difficult to determine in hindsight. Pre-occupation with black robin recovery neglected study of the tomtits, so that little is known of the habitat-disturbance effects which may have predisposed tomtit males to breed with black robin females on either island.

### *8.3.4 Small population size*

The unnaturally small black robin population on Mangere Island was exposed to two conditions likely to have accentuated the probability cross-breeding in poor or limiting habitat: annual imbalances in sex ratios and diminished opportunities to acquire conspecific mates. Evidence suggests that the small tomtit population may have been exposed to at least the former condition for some time after reintroduction to the island.

#### *8.3.4.1 Sex-ratio imbalances*

Merton (reported in Kennedy, 1993b) suggested that *Robin A*'s cross-breeding (while he was still regarded as a black robin) was attributable to shortages of black robin mates arising from skewed sex ratios on Mangere Island. There is no evidence that shortage of mates in the familiar, relatively undisturbed habitat of the Robin Bush resulted in cross-breeding. There is a strong inferential link between mate-shortage and cross-breeding events outside Robin Bush.

Sex-ratio imbalances in the small black robin population could not have contributed to female cross-breeding until tomtits were reintroduced to the island after 1986-87 (see *Section 8.3.4.3* below). Thereafter a female surplus arose only in 1989-90 (*Figure 8.4*), the season in which *Peg III* appears to have settled outside the Robin Bush. Naturally fluctuating sex ratios in post-management seasons (1990-91 to 2001-02) resulted in higher numbers of unmated black robin males and females. Surpluses were skewed in both directions (*Figure 8.4*) but none of the unmated black robins or others occupying Robin Bush was observed to mate with the reintroduced tomtits (this study).

A pronounced male-skew in the tomtit population of 1996-97 (33 males - 18 females; Amey and Studholme, 1996) did not have observed hybridising consequences inside the Robin Bush either but may have contributed to events in the fragmented habitat beyond. It is not known when this skew developed or for how long it persisted after 1996-97.

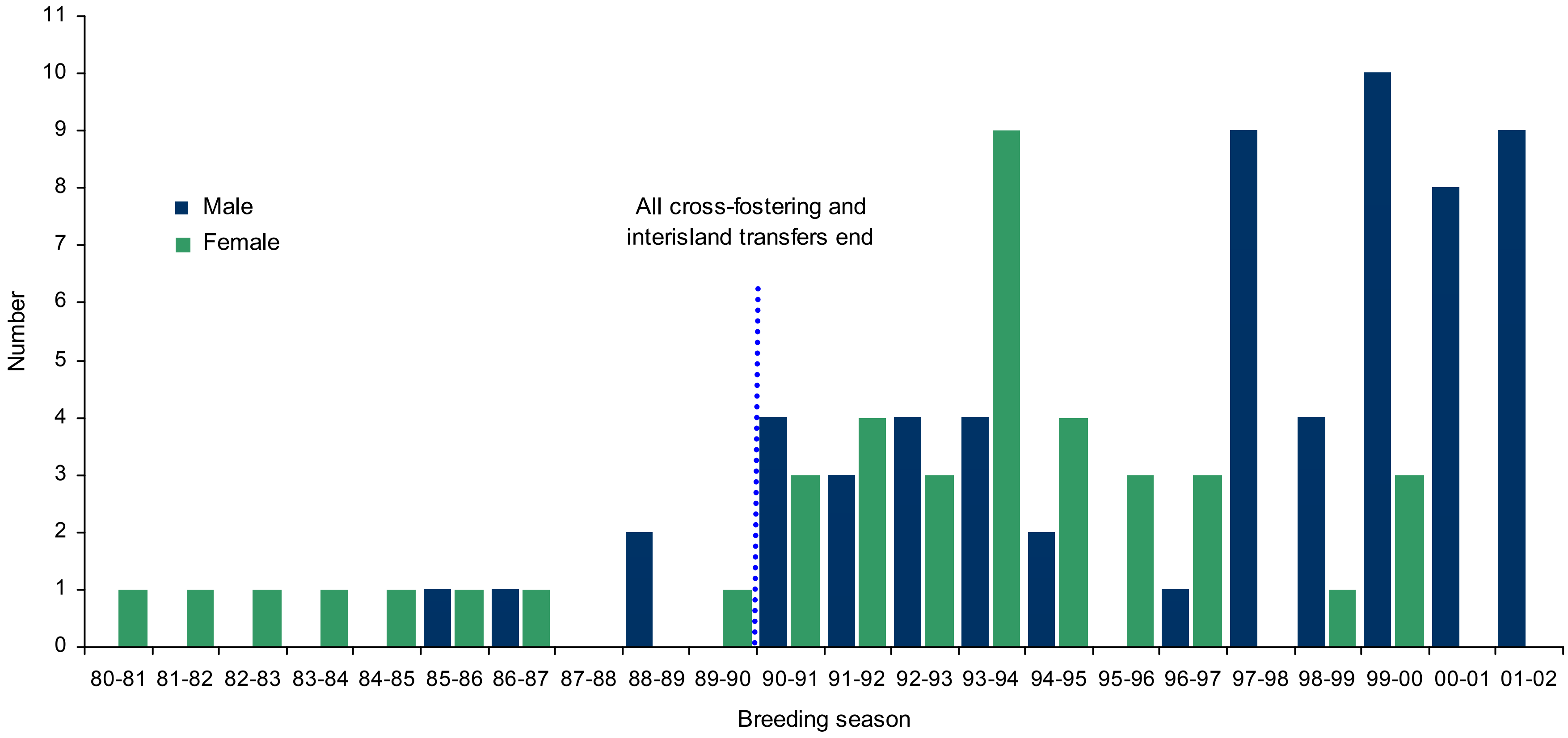

Figure 8.4 Numbers of unmated breeding-age males and females annually in the black robin population on Mangere Island between 1980-81 and 2001-02

#### *8.3.4.2 Inability to find mates*

On Mangere Island, extensive inter-breeding did not follow from bi-directional imbalances in black robin mate availability after 1986-87. However, isolation from potential conspecific mates in fragmented habitat comes closest to explaining the tomtit mate-choice of the dispersing female *Peg III* and the reciprocal choice of her tomtit mate. Separation from potential black robin mates may also have contributed to the cross-breeding by mal-imprinted females on Rangatira Island. As noted earlier (*Section 8.3.1*), two of the cross-pairings (one consummated, the other apparently forming) were located in the isolated tracts of forest from which unmated black robin males were absent at the time.

*Peg III* could not be found in January 1989 and it is supposed now that she had dispersed from the Robin Bush as a free-ranging juvenile. She had not been made ‘friendly’ before she disappeared. The Bush was lightly populated at that time (black robin n = 14), so her movement beyond the bush perimeter may have been random and consistent with the nature of juvenile movements observed in comparable population densities on Rangatira Island (Chapter Six: Population Trends After 1980). The experimentally reduced monitoring regime pursued in subsequent seasons failed to detect her. If settled in the Douglas Basin by spring 1989, she was well removed from the 12 black robins then in the Robin Bush, and unable to compete for any of the six males in the population. There were no spare black robin males to seek her out in that season (*Figure 8.4*). In the next season, all four spare black robin males remained in Robin Bush. In 1989-90, her mate-choices were limited to the tomtits newly released into her habitat in the preceding April or their progeny of following seasons.

#### *8.3.4.3 Introduction of Chatham Island tomtits*

To reduce competition for scarce space and resources, Mangere Island’s population of 19 tomtits was eliminated prior to the transfer of the last seven robins from Little Mangere Island in 1976-77 (Flack, 1976c, f). The species was reintroduced from Rangatira Island on four occasions between 1986-87 and 1987-88 (transfers of one to nine birds, Merton, 1989) but none of the transfers resulted in re-establishment. In April 1989, 21 non-site-attached tomtits (13 males, 8 females) were liberated into the Mangere Island habitat (Merton, 1989; Grant, 1989). Some were taken as far as the Robin Bush (Ron Nilsson, pers. comm.) but most were released in the Douglas Basin. This larger liberation succeeded in its purpose despite the tomtits having to compete with the 14 established black robins. Up to six tomtit adults were seen in the next season, some breeding successfully in and around the Robin Bush periphery (Mangere Island hut logbook entries, 1989-90). Despite several searches, none was found alive in the Douglas Basin nor was the isolated, elusive *Peg III* seen there. There is no evidence to suggest that in that season she bred with a tomtit or that she bred at all, but the reintroduction and immediate breeding success of the tomtits ensured that this was a possibility. The first hint that she might have mated and bred productively was the appearance of an unmarked 'black robin' of unknown provenance in the Douglas Basin after breeding had concluded in the 1991-92. *Robin A*'s appearance in 1992-93 is strongly suggestive of a tomtit mate by at least that season.

## 8.4 Discussion

Hybridisation between black robins and Chatham Island tomtits is unique among the modern New Zealand *Petroica*. Despite the degree to which populations of sympatric mainland congeners are confined and reduced in many parts of their ranges (Heather and Robertson, 1996; Higgins and Peter, 2002), the literature reports no instance of cross-breeding.

Events on Mangere and Rangatira Islands between 1984-85 and 1996-97 confirm that hybridisation should not be underestimated as a threat to populations reduced to unnaturally small sizes by deterministic extinction pressures (Rhymer and Simberloff, 1996). There is no evidence of historical hybridisation during the period of black robin decline, suggesting that extirpation of each island population was too swift. Instead, the cross-breeding threatened population recovery. Cross-pairing individuals deprived the black robin and tomtit populations of breeding potential at times when the numbers in each were critically low. The processes of introgression had also commenced but were arrested before advanced genetic mixing could imperil either parental genotype. Had cross-breeding not been detected at the first instance, large-scale culling would have been penalising. However, culling and other forms of intervention now deprive today's conservation managers of information critical to gauging the potential for hybrid swarms in the future. Though first-generation hybrids proved to be fertile and were not behaviourally bound to mating exclusively with other hybrids, the fertility, fitness and mate-preferences of second- and third-generation hybrids remain unknown (no F1 females or F2 hybrids of either sex were permitted to breed). Cross-breeding between parent populations appears to have been sexually unidirectional (only black robin females and tomtit males hybridised) but this may not be true of hybrids if they solicit reciprocally.

The events described on Mangere and Rangatira Islands illustrate the potential of hybridisation to arise from well-intentioned and otherwise successful conservation management. The reintroduction of tomtits to habitat on Mangere Island in which black robins were already established brought the populations of both species into sudden juxtaposition when each was exposed to the perils of demographic instability associated with small size—in this case, isolation from potential mates. Cross-fostering overrode the behavioural and reproductive barriers to inter-breeding, elevating the risks associated with highly manipulative management of critically small populations (Ma and Lambert, 1997b). Had fully fostered black robins simply been left to their own devices after fledging, unobserved cross-fostering may inadvertently have increased rather than lessened extinction risk.

The later cross-breeding on Mangere Island supports predictions that habitat decline and small population size predispose reproductively isolated congeners to inter-breeding (Taylor, 1975; Rhymer and Simberloff, 1996). Sexual mal-imprinting on tomtit foster-parents appears to have played much less a role in events than believed (if any at all). On the evidence available, inter-breeding was confined to the areas of degraded habitat in which one of the parent populations (the black robin) was disadvantaged and the other (the tomtit) was more suited. The ecological and behavioural mechanisms separating the black robins and tomtits reproductively did not break down in the Robin Bush which was habitat familiar to both, despite its small size and confinement. Evolved preferences for conspecific mates prevailed under less modified conditions, even in seasons of significant and unpredictable sex-ratio imbalances. This was true also in the larger intact habitats on Rangatira Island where mate surpluses existed but tended to be less erratic (Chapter Two: *Section 2.10*). On Mangere Island, the shortage of suitable conspecific mates only became a liability to the small black robin population in severely fragmented habitat.

The Mangere Island events have the more ominous implications for the future of the black robin and tomtit populations while habitat constraints reduce population sizes. Chance had a significant role to play in the isolation of *Peg III*, suggesting an unpredictable dimension to cross-breeding which did not operate in the Rangatira Island context. Chance may have been given a hand by the random dispersal behaviour of non-site-fixed black robin juveniles, particularly (but not exclusively) females (Chapter Six).

### *8.4.1 Will cross-breeding happen again?*

Two of the three factors predisposing black robins and tomtits to cross-pairing historically—habitat fragmentation and small population size—continue to operate on Mangere and Rangatira Islands. Sexual mal-imprinting on tomtit foster-parents can be discounted now and there is no evidence to suggest that cultural transmission of tomtit mate-preferences is a threat.

Habitat fragmentation is the most potent factor predisposing black robins and tomtits to cross-pairing activity in the future. The risk is greater for the black robins whose biological vulnerabilities (forest-interior habit and low productivity) make the species more sensitive to changes in habitat quality (Chapters Two, Three and Six). A black robin dispersing by chance or displacement outside forest perimeters has a higher probability of encountering tomtits which are better adapted to living and breeding there.

The implications of fragmented habitat for cross-breeding on Rangatira and Mangere differ only in scale. On Mangere Island today, habitat is as limited and confining as it has been for the last two decades. The recent planting of a forest corridor between the Robin Bush and the Douglas Basin plantings could encourage more black robins to move into the latter, perhaps increasing the probability of finding a black robin mate. However, this probability is offset by the apparent reluctance of black robins to establish pair-bonds in this sub-optimal habitat. The cross-breeding risk posed by serendipitous isolation in the Douglas Basin vegetation will not diminish until an extensive, mature forest cover develops. At current rates of canopy closure, this will take decades.

In contrast to Mangere Island, Rangatira Island possesses broad expanses of contiguous forest habitat and closely positioned forest outliers. These suggest a lower probability of hybridisation. However, black robin densities in the Woolshed Bush interior had already reached the point at which, by the mid-1990s, individuals were dispersing to and settling in isolated bush outliers and the tracts of tall scrub in *Muehlenbeckia* fields beyond (data collated for this study). In the Top Bush, black robin densities have always been low and breeding centres sparsely distributed (Chapter Six). Dispersing juveniles often settle remotely in isolation from other black robins. Recent disintegration of Top Bush breeding centres (Kennedy and Wilson, 2005; pers. obs.) has exaggerated this condition. The possibility of hybridisation cannot be ruled out.

### *8.4.2 Conservation management implications of cross-breeding*

The black robin and tomtit populations of the Chatham Islands are too seriously reduced in range and number to allow future cross-breeding to take an evolutionarily creative course. The ecological value of a novel *Petroica* genotype of uncertain viability is outweighed by the conservation risks of reducing the parent genotypes to single populations.

The future of extant black robin and tomtit populations cannot be taken as assured if cross-breeding recurs and is not treated swiftly. Cross-breeding and introgression may not remain confined to population peripheries. Given the depleted genetic diversity of each species (Ardern and Lambert, 1997; Ma and Lambert, 1997a, b), neither can afford to lose genetic variation accumulating in extant populations. Nor can natural selection be left to purge the effects of introgression because the populations may not be responding naturally to selection pressures.

Very early detection of cross-breeding was the key to effective management in the past. Conversely, poor monitoring courted the disaster of a hybrid swarm on Mangere Island. Detection of cross-pairings as they form or breed avoids the very considerable difficulties of managing advanced introgression. The legacy of uncertainty over sexual dimorphism and the nature of phenotypic variation in black robin x tomtit hybrids makes hybrid recognition in the field problematic. The longer the delay in responding to cross-breeding, the more complex, costly and uncertain are the prospects of rebuilding from a core of verifiable parental genotypes (Rhymer and Simberloff, 1996; Allendorf *et al*., 2001).

Detailed knowledge of the black robin populations was unquestionably the most advantageous asset for effective management of the cross-breeding risks. The crucial insights obtained from full-population monitoring were indispensable to detecting past cross-breeding events, interpreting their causes and minimising the effects of preventative management on the parent populations. The consequences of substituting inferior forms of monitoring on

Mangere and Rangatira Islands are fully illustrated in the penalising lapses in monitoring between 1990-91 and 1992-1993 (Merton, 1993, 1997; Chapter Four). Current index-monitoring methods offer even fewer insights than were available to observers on Mangere Island at that time. Precautionary management and follow-up of cross-breeding suspicions are very significantly disadvantaged as a result.

The lessons learned from past hybridising events make clear what measures represent ideal pro-active management of cross-breeding risks. The less rigorously these measures are applied, the higher the probability that observation will fail to detect inter-breeding:

- comprehensive black robin monitoring of consistently high quality, incorporating concerted surveys of distribution throughout habitats
- simultaneous monitoring of tomtit populations wherever they coincide with black robins
- closer familiarity with black robin and tomtit populations and their habitats, derived from longer and more frequent contact within seasons and from year to year
- continuity in monitoring and management teams sustained through retention of skilled staff, knowledge transfer of higher quality and the reinstatement of a collegially owned and grounded black robin management culture
- selection of experienced observers who know what to look for, how to interpret what they see and how to record it appropriately
- accelerated replanting of forest habitat on Mangere Island.

# CHAPTER NINE
# CONCLUSIONS

## 9.0 Introduction

This study set out to examine extinction vulnerability in the two small, chronically inbred sister-populations of Chatham Island black robins recovering on Mangere and Rangatira Islands from historical decline to a single-pair bottleneck between 1979-80 and 1982-83. Each island is a habitat-limited refuge from deterministic extinction threats. To assess vulnerability to decline historically and in the future, my evaluation of extrinsic and intrinsic extinction risks has drawn extensively on diverse historical sources and an often detailed demographic record of population collapse and recovery spanning 30 years.

Clarification of black robin risk factors has addressed two closely related theoretical and management questions. First, do threatened insular endemic birds have naturally lowered susceptibility to the predicted genetic consequences of small population sizes? This was the hypothesis advanced by Craig (1991, 1994) to explain the persistence of New Zealand bird populations reduced by anthropogenic change to unnaturally low numbers. These populations persist in relict habitats or have been successfully established on small protected islands from founder numbers as low as five randomly selected individuals. Craig's hypothesis of elevated immunity to inbreeding effects argued that insular endemic birds in New Zealand and elsewhere differ from outbred species of continental contexts. They are assumed to be naturally more inbred through evolutionary confinement to small population sizes and through traits as sedentary habits, stable territorially based breeding systems and limited dispersal ability. These typical adaptations to insular life are expected to have exposed genetic load to the purging processes of natural selection.

The second question investigated by my study concerns the conservation implications of the first. Is the mid- and long-term viability of threatened insular endemic bird populations guaranteed solely by treating deterministic extinction pressures and reversing population declines? This has been the strategy adopted widely in New Zealand to preserve critically threatened birds from extinction. Translocation to protected islands or to 'islands' of protected habitat, many of them very small, has rarely been followed by measures to minimise potential genetic threats to persistence. This so-called ‘New Zealand cure’ for threats to the viability of insular endemic birds (Groombridge, 2007), and the theoretical support it receives from Craig (1991, 1994), are at odds with central tenets of genetics theory. These predict inevitable genetic compromise in reduced, isolated, obligatorily inbred wildlife populations which will threaten mid- and long-term viability even after the deterministic causes of decline have been treated.

I have analysed the black robin decline and subsequent recovery to test these questions empirically. Their underlying assumptions have been addressed by assessing which intrinsic and extrinsic factors responsible for population losses and decline in the tiny vestigial population on Little Mangere Island increase extinction vulnerability in present-day and future populations. I have analysed trends in the two extant populations to assess which demographic variables limited rates of recovery and signal problems for future viability. The fitness implications of these variables have been examined through correlations with levels of inbreeding in the populations to gauge potential threats from continued inbreeding. These insights have been complemented by critical review of past management strategies, their consequences for the management of extinction threat in the past and their appropriateness for the remedy of future threats.

## 9.1 Extinction-risk factors

This study’s detailed analysis of black robin life-history traits shows that the species is inherently extinction-prone and suggests for the first time that it is the most intrinsically vulnerable of the 13 south temperate *Petroica* species in New Zealand and Australia. The Snares and Auckland Island tomtits may be the exceptions but little is known of their biology (Chapter Two: Tables 2.4 and 2.5). As a classically *K*-selected species with associated island-dweller traits and the ‘slow’ breeding strategy common among southern passerines (Russell *et al*., 2004), the black robin possesses the ecological and behavioural attributes which account for the disproportionate representation of insular endemic birds in global avifauna extinction rates (Myers, 1979; King, 1985a, b; Atkinson, 1989, Reid and Miller, 1989; Johnson and Stattersfield, 1990; Smith *et al*., 1993). *K*-selection is characteristic of many threatened terrestrial birds in New Zealand and other oceanic islands (Bell, 1991; Wilson, 2004), but relative to the other south temperate *Petroica*, the black robin possesses specialist evolutionary adaptations to stable, predator-free island environments which increase its vulnerability to novel threats. Sensitivity is heightened particularly by preference for forest-interior habitat, which restricts foraging and breeding ranges and exaggerates stresses imposed by fragmenting forest cover. Reluctance to traverse open spaces limits the black robin's ability to exploit distant habitat and broader foraging opportunities. Poor powers of flight have extinguished inter-island gene flows and recolonising potential. The black robins nest in hollows or cavities in the lower forest strata, well within the hunting ranges of introduced mammalian predators or avian competitors such as starlings. Crucially, my study shows that reproductive output is the lowest known of the south temperate *Petroica* species (Tables 2.4 to 2.7), a consequence of low average clutch sizes, a long breeding cycle and short breeding seasons. The species trades low output potential for long investments in parental care, with the result that pairs generally raise one brood only in the short nesting season. The black robin does not have recourse to the mainland robin's food-caching habit as a means of extending breeding seasons into periods of food scarcity.

The black robin possesses a degree of resilience to change but some biological advantages can become liabilities when change is radical. As a small passerine, it is capable of breeding sooner and faster than larger-bodied *K*-selected non-passerines such as kakapo and takahe, both also reduced to critically small population sizes (Neill, 2008; Wickes and Crouchley, 2008). Males and females can breed successfully at year one and often do in current populations. Females can renest successfully (up to twice) or can make up to four breeding attempts if previous efforts fail. Territories and pair bonds are durable, resistant to the effects of breeding failure and frequently long-lasting. This is advantageous when pairs produce well but has the potential to prolong unproductive pair-bonds. As I have shown in Chapter Three, this problem nearly proved fatal to the species when only two pairs remained after transfer to Mangere Island in 1976-77. Fidelity in closely related pairings may also aggravate inbreeding problems for very small populations. The risks in a wholly insectivorous diet are moderated by the diet's broad diversity but black robins forage extensively on or near the forest floor where rodents and the predatory flightless weka present on larger islands in the group will compete aggressively if introduced. These foraging traits limit the potential for reintroduction to the major predator-affected islands in the black robin's former range (Pitt and Chatham Islands). On Little Mangere Island, ground-prey shortages induced by petrel activity (compounded no doubt by the cooling and desiccating effects of wind penetration) were debilitating (Flack, 1976a). Both sexes are generally long-lived in suitable habitats (up to 13 or 14 years in rare cases), a factor favouring population persistence. But, as indicated by the high rates of adult and juvenile mortality in Little Mangere Island's deteriorating forest (Chapter Three) and anomalously short lifespans in the colder Top Bush (Chapter Six), longevity may be significantly compromised in sub-optimal habitats. The black robin may be more sensitive to forest type and quality than has been expected. My study suggests that the extent of habitat suitable for black robins may be much less than appears to the observer.

The black robin's life-history attributes and slow breeding strategy were appropriate in its benign pre-human environments but they became fatally disadvantageous when mammalian pests arrived, forest habitats deteriorated and mortality rates increased. Tellingly, the black robin has not persisted in some hostile Chatham Islands habitats still populated (for now) by its nearest relation, the Chatham Island tomtit. The tomtit's social, breeding and foraging strategies are similar but the species possesses a critical reproductive advantage in a shorter breeding cycle and larger average clutch sizes, both of which result in brood potential twice that of the black robin's (Tables 2.4 and 2.5). This and other biological advantages (tolerance of open spaces which extends breeding and foraging ranges, and perhaps inter-island dispersal powers) have allowed the tomtits to survive long-lasting and varied threats in the black robin's traditional habitats. The persistence of South Island robins in the presence of predatory rodents, cats, and mustelids at Kowhai Bush is similarly indicative of that species's superior reproductive output (Powlesland, 1983; Flack, 1976d, 1979; Flack and Lloyd, 1978). The South Island robin's high reproductive potential has allowed the population on predator-free Motuara Island (58 ha) to grow unassisted from five individuals introduced in 1973 (Flack, 1974a) to 600 birds two-and-a-half decades later (Byrne, 1999; Boessenkool *et al.*, 2007). In contrast, the seven black robins introduced to Mangere Island in 1976-77 declined to five until very actively assisted over ten years to reach 93 individuals in spring 1990 (Chapter Six).

The extent to which the black robin's sensitivity to threats is natural or compromised by its genetic history can no longer be ascertained through comparisons with undisturbed reference-populations. Whichever the case, evolutionary adaptation to local conditions did not equip black robin ancestors to withstand the changes associated with human contact. My scrutiny of sketchy historical records has identified habitat destruction and mammalian predation as the main extinction drivers (Chapter Three). The records are generally uninformative about the timing of direct exposure to these unfamiliar pressures but inferences drawn from the few clues given, coupled with analysis of the population collapse on Little Mangere Island and findings on the black robin's narrow biological tolerances, suggest swift elimination from Pitt, Rangatira and Mangere Islands, perhaps within two to three decades of first exposure to predators and habitat change. Not enough is known of the Chatham Island extinction to be sure of its timing.

My historical research allows important conclusions to be drawn about external threats and their implications for small, isolated populations of black robins and birds similarly lacking the ability to cope:

- For black robins, change in the character and quality of forests alone appears to have been fatal historically. This is the only plausible explanation for extinction of the original Rangatira Island population, and was the observed driver of population collapse on Little Mangere Island. Given the black robin's forest-interior habit, contracting and fragmenting forest cover will act directly on population sizes by restricting living and foraging space. Preliminary evidence of a climatic effect restricting populations in the Top Bush on Rangatira Island today (Chapter Six) points to further reductions in carrying-capacity when forest interiors are opened to weather.

- Predation by partially arboreal kiore, the earliest, smallest and perhaps least adept passerine-predator of the three rat species introduced to New Zealand (Atkinson, 1978), was possibly the sole cause of extinction on Chatham Island. This assumes a fatally large or sustained irruption of rats after first arrival (Chapter Three). Other studies show that black robin adults, eggs and nestlings fit within the kiore's prey size range, reach and foraging habits (Atkinson, 1978; Lovegrove, 1996; Brown, 1997; Holdaway, 1999). If my assumption of kiore extinction is correct, the black robin can be added to the global list of insular bird extinctions attributable to this commensal rodent (Atkinson, 1978, 1985; Holdaway, 1999; Towns *et al.*, 2006).

- On Mangere Island, extensive loss and fragmentation of forest cover appears to have been a principal factor eroding the ecological and behavioural barriers to inter-breeding between black robins and sympatric tomtits (Chapter Eight). The same factors explain the hybridising of their ecological associates, the rare Forbes' and ubiquitous Chatham

Island red-crowned parakeets (Taylor, 1975, 1985; Department of Conservation, 2001b). The consequences of introgression for both *Petroica* congeners are profound while their populations remain small and genetically depleted (Ardern and Lambert, 1997; Ma and Lambert, 1997a, b). This underestimated implication of habitat change is a crucial threat to both *Petroica* genotypes while only two small populations of each survive in protected habitats.

- Two potentially advantageous features of black robin distribution proved to be completely ineffective defences against habitat and predator threats on some islands. Ironically, all black robin recovery strategies have striven to capitalise on these very features (Flack, 1971; Butler and Merton, 1992; Kennedy, 1993a; Department of Conservation, 2001a). Large population size and distribution over 90,000 ha conferred no immunity to outright loss on the Chatham Island. Nor did isolation on a remote island prevent threats migrating through an ecological associate (the sooty shearwater) to Little Mangere Island. Whether or not the destructive densities of shearwaters on the island resulted from displacement of the species from larger breeding sites elsewhere in the archipelago (no firm evidence of this exists), their catastrophic effects on forest stability and regeneration signalled that remoteness is no barrier to threats arriving through avian vectors. Strongly flighted organisms can introduce a variety of extinction pressures—(1) competition or predation from starlings, dunnocks, blackbirds (or wasps *Vespula* spp. and Indian mynas if the last two reach the Chathams); (2) pathogens (Miller and Lambert, 2006); (3) the destabilising effects of petrel burrowing on forest structure (Flack, 1976a; Roberts *et al*., 2006, 2007), or (4) the dispersal of black robin x tomtit hybrids (Merton, 1993; Chapter Eight).

- Failure of the seven ancestral black robins to rebound naturally after transfer to Mangere Island in 1976-77 signalled that the species seemed inherently unable to recover after deterministic extinction threats reduced it to critically low numbers. The failure offered a sobering insight to lethal stochastic demographic pressures (Chapter Three). Chance played a disproportionate role in mortalities and pairings on Mangere Island but natural reproductive output barely kept pace with losses and ultimately failed to do so. This also appears to explain the fate of the translocated population on Pitt Island where, in the presence of an unquantified mouse threat, larger founder numbers gave no assurance of establishment in a fragmented but recovering habitat (Chapter Four). A prudent conclusion from my assessment of founder fates on both islands is that the black robin will require active assistance again to recover from severe knock-downs or to establish in further parts of its range.

The deterministic threats eliminating the original black robin populations acquired their potency from the species's inherent sensitivity to their effects. Alone or in combination, habitat change and predation appear to have overwhelmed the populations rapidly and probably well before the stochastic processes of genetic erosion could acquire any lethal force of their own. These remain lethal threats, no matter what success black robin management has in offsetting inherent vulnerability or restoring genetic resilience through population increases. For these reasons, protection from external threats is rightly the first priority to safeguard the viability of black robin populations and those of other species similarly at risk.

## 9.2 Population recovery

Despite a grievous history of decline, severe bottlenecks in ancestral and descendent populations and unavoidable inbreeding, the black robin recovered after translocation to islands free of the habitat and predation threats driving the species towards extinction. While unmanaged, the seven survivors of the last tiny, chronically inbred population were incapable of producing enough juveniles for recovery, but when reproductive effort was intensified by management, the species's response was strong from the outset. Response and recovery through the following ten years of very demanding breeding intervention were not indicative of a moribund species.

Under management, populations grew rapidly and expanded into most parts of available habitat. After management ended, natural rates of recovery were significantly slower. Management had little effect on breeding success in the species as whole but it achieved its objective of raising population sizes quickly by increasing gross reproductive output. When finally left to recover naturally, Mangere Island's pre-breeding populations grew at a rate comparable overall to their larger sister-populations on Rangatira Island, but growth levelled off towards the end the study period, suggesting that carrying-capacity had been reached in the small, isolated forest habitat. Growth was still positive in the Rangatira Island population when full-scale monitoring had ended three years earlier.

Under unmanaged conditions, the Woolshed Bush and Mangere Island emerged as the two centres of black robin productivity and growth. The Woolshed Bush was the stronger of the two. Contrary to all indications of viability given by strong growth and productivity under managed conditions, natural reproductive output in the Top Bush habitat was poor and recovery ultimately negligible. This population was supported under both management regimes by dispersal from the Woolshed Bush, especially by juvenile females. After management stopped, immigrants comprised 26% of the Top Bush population, whereas black robins dispersing from the Top Bush amounted to only 3% of Woolshed Bush numbers. The Top Bush population was clearly a sink for Woolshed Bush production and may never have been viable if wholly reliant on its own resources.

In all three populations combined, each pair produced almost 40% fewer juveniles on average after management ceased, a reflection of lower breeding investments in clutches (29% fewer) and eggs (31% fewer). Though reduced as expected after multiple-clutching ended and lower relative to New Zealand and Australian congeners (Tables 2.4 to 2.7), these investments were sufficient to preserve recovery momentum on both islands under the prevailing, largely threat-free conditions.

Natural recovery varied in each of the three study populations. Breeding effort was generally comparable. No consistent measure of fertility was applied in the field (Chapter Four) but, as a surrogate, hatch-rates (the proportions of all fully incubated eggs hatching, and the mean annual rates pair$^{-1}$) were also comparable. Breeding success was the problem. Rates of recovery—similar in the Woolshed Bush and Mangere Island and inferior in the Top Bush—were influenced by differing levels of mortality at various life-history stages. No single life-history variable was a crucial determinant of variations. Top Bush recovery was unique in its unusually high rates of fledgling and juvenile mortality. Recovery was further compromised by diminished immigration after management ceased and the low survival probability of locally raised and immigrant black robins. Life-spans no longer than eight years deprived the population of important breeding potential in both sexes. Survival probability and life-spans were higher in the Woolshed Bush and on Mangere Island.

The field records used by my study reveal (or speculate about) the nature of external factors operating on the black robin populations but not their relative effects on underlying vital rates. It would require systematic field study to clarify these non-genetic threats, their trends and their implications for viability. Black robin observers attributed mortality informally to diverse factors ranging from adverse weather events, predation by starlings, avian pox and nest-mite irruptions, death of a parent and poor nest-site selection, to unusual events such as nocturnal petrel strikes on nests, entanglement in cobwebs, egg-binding, tree-falls and numerous other forms of misadventure. Poor parenting, dependent young straying out-of-territory, pair-bond failure, disruptions from neighbouring bachelors and inherent infirmity (rarely said to be congenital) were also proffered as explanations. Little can be done in hindsight to quantify the effects of these factors on recovery rates. The uncertainties surrounding them frustrate explanations of demographic trends. If viability is in doubt in the future, this is an important issue for monitoring and management.

My study has thrown important light on the potential of environmental variables to limit population recovery. Micro-climate measurements taken over two breeding seasons and the intervening winter (2004-2005; Chapter Six) provide compelling evidence that climatic conditions in the poorly performing Top Bush were generally colder than in the Woolshed Bush and on Mangere Island. Unlike the Top Bush (and Pitt Island's Caravan Bush in which black robins failed to establish), the Woolshed Bush and Mangere Island forests are oriented to the sun and relatively sheltered from prevailing winds. My investigation of sub-canopy temperatures probably understates the environmental differences because wind-chill could not be measured. However, the evidence procured argues for further study to define the relationships between consistently cooler conditions and black robin productivity and survival. Aside from helping to explain the poor Top Bush recovery, better knowledge of the role of climate is likely to help black robin managers assess the suitability of habitats for new black robin populations. In the meantime, I suggest that higher energy costs, retarded replenishment rates in insect communities, briefer periods of prey activity and lower available prey biomass are possible environmental effects explaining the poor reproductive output and high rates of adult and offspring mortality in the Top Bush. Any such costs may have been particularly punishing during winter when adult and juvenile mortality was greatest in all three populations (Chapter Two).

Genetic factors may have influenced population recoveries but did not halt them or cause declines during the study period. Total numbers on each island increased overall. Considered in isolation, however, the Top Bush population raises questions about a possible interaction between inbreeding and the cooler environmental conditions. Average levels of relatedness in the small Top Bush population were comparable to those in its larger neighbour during the period of unmanaged recovery (Table 7.2)—a consequence perhaps of immigration or high turn-over of breeding adults—but harsher conditions are generally expected to elicit or increase the severity of inbreeding depression (Keller *et al*., 2002; Frankham *et al*., 2002). Conceivably, the food-stress trigger for inbreeding depression in Darwin's finches (Keller *et al*., 2002) may have its parallel in environmentally induced prey deprivation for the Top Bush black robins. Modelling of interactions between habitat and inbreeding did not confirm such a relationship (Chapter Seven) but if the new evidence of inbreeding depression in black robins is to be tested for detrimental effects, the faltering Top Bush population is the most plausible place to begin.

The recovery trends I have analysed offer no convincing explanation for the population declines on Mangere and Rangatira Islands during the sample-monitoring seasons. These relatively sudden and curiously coincident decreases in population sizes raise legitimate questions about black robin viability. The declines indicated by early-season head-counts in 2007-08 (Massaro and Briskie, 2008; Harvey, 2009) were significant—decreases of more than 43% on Mangere Island and about 25% on Rangatira Island since full-scale monitoring was suspended (Chapter Six).

The Top Bush population appears to have declined most severely (by about 53% at the last comprehensive head-count in 2007-08; Massaro and Briskie, 2008). The pronounced fluctuations in Top Bush numbers, the ephemeral nature of breeding concentrations and negligible overall growth up until 1998-99 suggest a population hovering at or near its viability threshold. Its past function as a sink population implies sensitivity to reductions in the numbers of immigrants from the Woolshed Bush. The causes of its decline may originate there, in what was the most productive and fastest growing breeding centre. Kennedy and Wilson (2005) surmised that the decrease in black robin numbers first suspected in September 2004 might reflect cooler and more exposed conditions in the central Woolshed Bush where forest regeneration had resulted in a taller, more open forest structure. The temperature analyses conducted by this study do not support a climatic explanation. The micro-climate data-logger closest to the forest centre (WSB 2, Appendix Four: Table 4A) did not register unduly cooler temperatures (Table 6.18), and my analyses of mean temperatures and degree-day differences showed the Woolshed Bush to be warmest of the three habitats measured. However, the replacement of senescent multi-stemmed akeake trees in the centre of the bush by the increasing dominant ribbonwoods (Roberts *et al.*, 2007) may have reduced carrying-capacity. The tall straight-stemmed ribbonwood offers black robins little understorey cover and inferior opportunities for nesting and foraging. Mapping of black robin territories in the Woolshed Bush, a relatively simple exercise, would allow comparisons of distribution and density to be made with historical territory distribution data available but not analysed by my study.

The Mangere Island population had ceased to grow in the final five seasons of the study period, fluctuating annually between 51 and 54 birds at pre-breeding counts (Table 6.3). My study has found no indication of instability predisposing the population to decline. Informal comparisons of historical and current forest character indicated no significant regenerative changes in the Robin Bush (Kennedy and Wilson, 2005). As a first step, territory mapping would help to test a possible redistribution effect of any forest changes.

The declines on both islands occurred independently and may have been caused by different factors. However, the coincidence of timing and decreases over similar intervals imply the working of one or more common factors. The absence of explanations in the trends I have analysed points to factors unique to the sample-monitoring period. Both islands may have returned to a naturally lower carrying-capacity when the frequency and quantity of food hand-outs was reduced during the sample-monitoring seasons. Preliminary estimates of average intake of cultivated *Tenebrio* larvae during breeding seasons (≤ 2.5 per day) suggest an inconsequential addition to individual diets (Kennedy, 2010). Black robins received no hand-outs at other times, including winter when food was most limiting. Transfers of birds to Pitt Island between 2002 and 2005 would have caused ‘mortality’ spikes in the source populations but potentially destabilising effects are not indicated by the relative extent of declines in each. The Woolshed Bush lost 34 individuals (14 in spring 2002 and 20 in late summer 2004; Chapter Four: Table 4.1) but declined significantly less than Mangere Island which gave up only four individuals over two seasons.

No useful trend data were gathered during the periods of decline, and sample-productivity data from Rangatira Island had been mislaid at the time of writing. Although my study has found no convincing evidence of predisposing factors, the highly detailed demographic data I have assembled have the potential to yield important explanatory insights if subjected to more powerful statistical modelling. Variations in individual life-history trends over time during the study period may be informative and will indicate specific information requirements from current populations. Manipulation of known variables to predict times-to-extinction should also help to focus remedial management, if in fact any is needed. The declines may simply be indicative of fluctuations around a new natural equilibrium in each population.

Finally, the value in treating the Top Bush and Woolshed Bush as analytically discrete sub-sets of the Rangatira Island population has been demonstrated by my study. The unexpected reversal of trends in the Top Bush after intensive management ended gives striking insights to first, the beneficial effects of management and second, their capacity to disguise natural levels of viability in small populations. The Top Bush population contributed little to the welfare of its larger and more resilient neighbour in the Woolshed Bush during the post-management period but showed the potential draw-down effects of sub-optimal habitat and population sinks on its margins. The post-management trends discernible in the Top Bush gave valuable insights to the dynamics of a barely viable population, insights which were less obvious in the other apparently more resilient populations. Investigation of explanatory factors has pointed more clearly to the probability of harmful climatic effects on recovery trends in inbred populations. The discrete Top Bush pedigree also provides a better basis than a Rangatira Island pedigree for testing the potentially limiting or disabling effects of inbreeding depression on fitness parameters in a poorly performing population.

## 9.3 Inbreeding and viability

The black robins are highly inbred as a result of population extinctions, persistence of the relict ancestral population at very low numbers on Little Mangere and Mangere Islands over nine decades (1892-93 to 1980-81) and passage to recovery through the *Old Blue-Old Yellow* bottleneck (Chapters Three and Seven). Current populations possess average levels of relatedness three times greater than the highest reported in another species in genetic literature (insular populations of inbred takahe, $F = 0.123$; Jamieson *et al*., 2003). On average, the small Mangere Island population, closed genetically since 1990-91, is the most highly inbred ($F = 0.396$, both sexes combined; Table 7.2) and the large Woolshed Bush population is the least inbred ($F = 0.346$). The difference may reflect the longer period over which Mangere Island inbreeding was measured. Even so, these are likely to be significant underestimates of relatedness, since ancestral black robins at the base of the pedigree were almost certainly very closely related.

Contrary to perceptions in genetic literature (see for instance, Frankham *et al*., 2002; Frankham, 2005) and the optimistic predictions of earlier researchers (Butler and Merton, 1992; Ardern and Lambert, 1997), the descendants of the last tiny ancestral population have not escaped genetic harm. This study found evidence of disabling inbreeding effects on black robin fecundity during the post-management seasons. Intensive management seasons were not analysed. Inbreeding-related fitness costs were indicated by strong negative correlations between levels of inbreeding in fathers and reproductive failures at life-history stages late in the breeding cycle. This appears to be the first avian evidence of inbreeding costs acting selectively through breeding males. Maternal inbreeding *F* and kinship (parental) inbreeding had no harmful implications for productivity, although an emerging kinship effect on yearling production (juvenile survival) is possible. Inbreeding did not appear to influence survival probability for either sex during the study period.

Male inbreeding *F* showed a strengthening negative effect on breeding success at successive stages in the breeding cycle after hatching (fledgling, juvenile and yearling output). Hatching success was negatively but not significantly related with the degree to which fathers were inbred but a stronger probability of nestling failure (fledgling production) was indicated. Fledgling and juvenile mortality were strongly correlated with paternal inbreeding, reflecting perhaps the cumulative effects of inbreeding-related failures at earlier stages in the breeding cycle. Paternal age, equated with breeding experience, showed a mitigating beneficial effect at all breeding thresholds. The Top Bush also demonstrated a strengthening negative correlation with reproductive failure but exploratory modelling of two-way interactions between habitats and inbreeding (individual and kinship) showed no significant effect.

Genetic depletion, chronic inbreeding and sex-differentiated inbreeding depression did not equate to declines in either island population after they were left to recover naturally. However, the reproductive costs imposed by inbred fathers are highly likely to have slowed the recovery by reducing the numbers of juveniles produced and surviving to be recruited into breeding populations. Under the protected conditions prevailing at that time, production by inbred fathers was still sufficient to preserve recovery momentum. Recovery benefited from the fact that inbreeding did not disadvantage reproductive output by inbred females or pairs, and did not affect adult survival, thus maximising their reproductive potential. This was the case prior to the end of full-population monitoring on each island and for the average levels of relatedness accumulating in the populations' pedigrees at that time.

The grievous genetic histories of the black robin populations and their anomalously high levels of inbreeding imply that fitness costs should have been expressed in both sexes and more severely than my study has shown. Inbred *Petroica* congeners (North Island robins on Tiritiri Matangi Island) experienced juvenile mortality at levels of inbreeding substantially lower than the black robin's (Jamieson *et al*, 2007). A compelling explanation is that the prolonged history of reduction to low numbers and chronic inbreeding has purged the black robin of genetic load, as was suggested by Ardern and Lambert (1997). In contrast, the North Island robins on Tiritiri Matangi Island were sourced from large, more genetically diverse mainland populations in which genetic load was likely to have been retained. If correct, this assumption supports the explanation of purging offered for the weakly expressed fitness costs observed in a tightly bottlenecked and genetically impoverished population of South Island robins on Ulva Island (Stewart Island; Laws and Jamieson, unpublished data).

Comfort taken from the potentially advantageous effects of purging (if any) must be tempered by the evidence that black robins have retained some genetic load, fixed perhaps in the small populations on Mangere and Rangatira Islands. This does not appear to have had fatal implications for population viability during the study period, but it would be unwise to assume that fitness costs will not deepen or diversify as individual inbreeding coefficients accumulate further or if the populations are subjected to changed conditions. The probability of more extensive and severe fitness effects is elevated by decreases in population sizes, such as those occurring recently, those associated with cropping to establish new populations, or those resulting from periodic fluctuations to low numbers. All such events act effectively as additional bottlenecks, increasing rates of inbreeding and augmenting the threat to advantageous rare alleles in the genome.

The immediate threat posed to breeding success by inbred males implies a need to manage and monitor extant populations for genetic health. This has not been a consideration for black robin managers (Department of Conservation, 2001a). Among other things, founder selection for new populations will benefit from excluding highly inbred males whose compromised reproductive potential could jeopardise establishment, expansion and viability in the new site. The augmented management and monitoring requirements necessary to measure genetic health are addressed in recommendations made in Chapter Ten (Management Recommendations).

My study has identified an inbreeding threat to viability but further work is required to clarify its implications for black robin persistence. Genetic load should be quantified, along with the extent to which viability is already compromised. How much latitude do current fitness effects leave the populations to withstand new extinction pressures? What are the implications of rising levels of relatedness? Closer evaluation of inbreeding effects is needed on earlier life-history stages (clutch numbers, clutch sizes). Relationships between environmental variables and inbreeding effects should be examined more closely.

Most importantly for future management, it is highly desirable to assess carefully the implications of increased levels of inbreeding for population growth, focusing particularly on life-history and other variables which are amenable to management. Research of this sort should ensure that remedies are appropriately directed and effective. The demographic record and pedigree available to this study provides an exceptionally solid platform for the necessary predictive modelling.

## 9.4 Lessons from past management

The effort involved in saving the black robin from extinction has been extraordinary, yet stock has rarely been taken of the management lessons to be learned from the investment. My study has made a start.

### *9.4.1 Did the New Zealand cure work?*

The approach taken by wildlife managers to save the black robins defined the 'New Zealand cure' in action in almost every respect and has been widely celebrated as an endorsement of New Zealand wildlife management practice. True to Caughley's (1994) 'declining population' paradigm, researchers and managers of the time identified the external factor driving the species to extinction (forest collapse) and attempted to remove the threat by reversing the forest's decline on Little Mangere Island. When rapidly declining numbers showed that strategy to be impractical, they removed the black robin from the threat. The prior research and final translocation to safer habitat on Mangere Island were crisis-driven. Managers had no choice in the composition of the founders for the new population: the only black robins available were the seven remaining. Management has proceeded from that point until now on the assumption that stochastic genetic threats were unimportant.

Although the overall strategy of treating deterministic and stochastic demographic threats worked (the species is not extinct), the approach common to many such emergency translocations in New Zealand failed the black robins. Managers made the optimistic assumption that release into better habitat would be enough to ensure a natural rebound in numbers. A cautious management strategy committed to minimising disturbance was understandable when numbers were critically low and the black robin's tolerance of intrusions at the nest was untested. Better habitat was not enough—the species did not recover and finally declined. The strategy was nearly fatal. Better knowledge of the factors causing the breeding failures might have quickened awareness of the black robin's inherently low reproductive output (a threat from within) and prompted earlier intervention when there were more black robins to work with.

Twenty-six years later, the same strategy failed the species on Pitt Island. Managers monitored the founders of the new Caravan Bush population but not closely enough and without anticipating the need to intervene to assist establishment. Misplaced confidence in black robin viability and the species's natural capacity to exploit the new habitat opportunities proved fatal on that occasion. The translocations failed with no clear indication of why. Little has been learned from the Pitt Island experiment to inform future translocation projects.

The near-miss on Mangere Island and the failure on Pitt Island are valuable indications that standard New Zealand translocation practice—release and hope (Armstrong and McLean, 1995)—is not universally applicable for all threatened species.

### *9.4.2 The hazards of numbers-watching*

Numbers-watching has been the dominant feature of black robin management from the outset. The underlying assumption throughout was that black robin abundance equated to black robin viability. Once intervention was unavoidable in 1980-81, managers were pragmatically committed to raising black robin numbers quickly. When numbers were critically low, this was the appropriate and only means of navigating the species out of danger from stochastic demographic and environmental threats. It worked. However, preoccupation with numbers-building persisted long after the immediate extinction crisis had passed. Numbers-building was a crucial driver of conservation effort but it was inherently focused on external threats without due consideration of the more cryptic, longer-acting threats from within. Numbers-watching had numerous unhelpful effects on management.

- As the two small populations grew strongly in response to intensive management, confidence also grew that precautionary genetic management was unnecessary. Aside from the incidental genetic pay-offs of inter-island transfers, little was done to anticipate the potentially harmful implications of historical and contemporary inbreeding. Management for longer-term viability was treated justifiably as a secondary issue while numbers were very low (for instance, very closely related pairings were tolerated) but this remained the case throughout the period of active recovery.

- The intensive monitoring which followed was unduly concerned with quantifying trends in abundance as signals of instability in the unmanaged populations. The programme subordinated proactive genetic management to the reactive goal of disturbing natural recovery trends as little as possible.

- The monitoring programme treated its valuable store of productivity data as ‘money in the bank’, for use in interpreting population declines if needed. The positive growth trajectories of both island populations convinced managers that there was no need to analyse the data between seasons for subtle signs of genetic and non-genetic threats.

- In the early 1990s, the unfortunate experiment with ‘flying-squad’ monitoring on Mangere Island was based on the conviction that pre- and post-breeding numbers were the only necessary measures of population status. This was called ‘efficiency’. Black robin x tomtit hybridisation went undetected and could not be remedied without resumption of full-population monitoring. Irremedial gaps were opened in the Mangere Island pedigree.

- Resource-stressed managers were comforted by black robin numbers when deciding to surrender the invaluable advantages of full-population monitoring. The decision has deprived managers of any understanding of subsequent population declines.

- The index-monitoring alternative is solely numbers-focused and has failed black robin management as a means of detecting and interpreting declines. Like earlier problematical reductions in monitoring intensity, it assumes all will be well. It is inherently reactive without the providing enough information on how to react.

As a result of the numbers mind-set, black robin managers did not undertake any form of precautionary genetic management once the more immediate extinction pressures were treated.

### *9.4.3 Monitoring intensity*

The black robin recovery project has demonstrated the value in both the most and the least effective forms of monitoring practice. Each placed radically different value on contact and familiarity with the small black robin populations, the species's vulnerabilities and population trends.

Intensive monitoring made few assumptions about the unforeseen. At crucial times, it gave managers early warning of problems. The nearly fatal mal-imprinting issues on Rangatira Island were detected immediately and remedied with the knowledge immediately at hand (Chapters Four and Eight). Little during the establishment of new population on Rangatira Island was left to chance. Comprehensive knowledge of vital rates in each population increased the potential to manage all classes of threat. It laid the foundation for management of genetic compromise, the principal threat to viability still operating after the populations were protected from deterministic pressures. The resulting longitudinal record of black robin demography and recovery is a rare asset for conservation biology in general.

Monitoring of reduced intensity traded off the benefits of short-term gain (largely savings in resources and time) against conservation effectiveness and potentially greater costs later. It resulted in a monocular focus on the black robins alone, especially their numbers, so that awareness of influences and changes in the populations' broader ecological contexts contracted markedly. Stand-off monitoring proved to be disadvantageous when managers were confronted with the stochastic demographic and environmental threats growing in inverse proportion to population decreases on Little Mangere and Mangere Islands. Stand-off monitoring failed to detect the cross-breeding events on Mangere Island which nearly developed into an unmanageable hybrid swarm. Managers were caught completely unawares and left flat-footed for explanations and remedies. This has also been the consequence of today's index-monitoring regime whose rudimentary indices of abundance have yielded no useful insights to the declines occurring since 2001-02. The failure of the Pitt Island translocations is unexplained as a result of deficient monitoring. Managers are therefore inadequately informed to manage the next translocations.

It is an unpalatable truth in times of resource-stress that viability management is best served by detailed demographic insights to threatened population dynamics. They serve management at the time and in the future. Monitoring of reduced intensity serves neither appropriately and is generally false economy.

### *9.4.4 Management and monitoring quality*

Many of the pressures exerted on management and monitoring quality during the black robin recovery programme are familiar to conservation biologists (chronic resource shortages, logistical difficulties, inhospitable habitats). Some were avoidable. The heavy demands of the black robin programme made the quality lapses arising from them more telling and explicit. Recovery was not helped by the following factors.

- Planning and management perspectives were usually short-term and strongly influenced by single-year funding cycles. This problem has become more acute under existing institutional arrangements. The longer-term ecological demands of the black robin programme were difficult to prepare for and meet.

- Discontinuity in project leadership and field-teams had visibly detrimental consequences for management and monitoring quality. Costly mistakes of the past were repeated and few consistent standards were applied from year to year in field practice, the nature of the data gathered and the way it was reported. The perils of short-term or fragmented perspectives extended into seasonal and strategic planning.

- A crucial consequence of discontinuity was the loss of the collegially mediated culture of black robin management inherited from the intensive monitoring period. The current institutional arrangements of DOC have exacerbated the continuity problem and are philosophically hostile, though not deliberately so, to restoration of a management culture (Kennedy and Perkins, 2000; Kennedy, 2003). Its absence from black robin management has resulted in the loss of powerful collegial peer-review mechanisms (in and out of the field) and of vital self-correcting, adaptive management functions. There is now little passage of knowledge and experience between successive generations of black robin workers, and no apprenticeship into the skills and complexities of conserving this and similarly threatened species in the region. There is a critical lack of collegially agreed and applied standards for black robin work and its reporting. The culture's place has been taken by goal-directed outlooks, embedded in secularising management prescriptions and contractual obligations on black robin workers, all of which insist more on the quantity than the quality of work done (Kennedy, 2003).

- The store of knowledge and experience accumulated since 1971-72 is indispensable to black robin management but field practice has often failed to borrow from it. In the past, unwillingness to apply valuable lessons has been costly, as was demonstrated in the fate of the Pitt Island translocations. Failure in Caravan Bush was symptomatic of insensitivity to the value of translocation experiences and the methods proven to ensure successful establishment of new black robin populations.

## 9.5 Theoretical and management implications

The findings of this study lend qualified support to Craig's (1991, 1994) hypothesis that small populations of threatened insular endemic birds may be inherently less susceptible to inbreeding depression through evolutionary adaptation to conditions of reduction and isolation. The black robin's long history of persistence at very low numbers and rapid passage to recovery from the single-pair bottleneck may be critical explanatory factors. The expression of reproductive fitness costs in inbred black robin males only in such highly inbred and genetically depleted populations appears weak relative to costs imposed on significantly less inbred congeners. Genetic load in the species, fixed or otherwise, has still to be quantified but the indications from this study are that natural selection operating on very low numbers of inbred ancestors and population founders may have had beneficial purging effects for the species. Confidence in this conclusion must be tempered, however, by the possibility that the rapid increases in population sizes engineered by intensive conservation management may have moderated the severity of fitness effects, as genetic theory predicts they will (Jamieson *et al.*, 2008). Estimation of lethal equivalents will help to clarify uncertainties and provide a benchmark for later assessments of inbreeding risks.

The evidence of inbreeding depression in black robins confirms the predictions of conservation geneticists that arbitrary reduction and confinement to small, closed populations set in train extinction-inducing processes of genetic erosion which undermine viability and threaten population persistence (Brook *et al.*, 2002; Frankham, 2005). My findings add empirical weight to the argument that stochastic genetic threats continue to increase extinction vulnerability in small inbred populations even after more immediate deterministic pressures have been relieved. In the black robin populations, inbreeding depression acted cryptically and cumulatively on reproductive output to reduce the numbers of juveniles available for recruitment. Similarly, there is support for the prediction that genetic threats exaggerate the inherent risks imposed on small populations by life-history traits limiting population growth (Taylor *et al.*, 2005, 2007; Boessenkool *et al.*, 2007; Taylor and Jamieson, 2008). Without healthy populations to refer to, it is not possible to determine whether the black robin's reproductive potential is naturally low or a reflection of historical inbreeding effects, but relative to other south temperate *Petroica* species (Chapter Two), black robin viability appears to be particularly at risk if inbreeding amplifies this vulnerability. Recovery in the two populations has almost certainly been slowed during the post-management period when inbreeding effects were assessed, and it is prudent to assume that future responses to downward fluctuations in abundance or unforeseen set-backs will be weaker as inbreeding levels rise in the capped populations.

My study supports the assumption made by conservation biologists that deterministic threats are the principal object of remedy to save threatened bird populations from extinction (Shaffer, 1981; Caughley, 1994; Soulé and Mills, 1998; Lande, 1999). The extinction pressures characteristically associated with human activities rapidly eliminated the original large black robin populations. Natural or human-induced habitat change threatened the last population on Little Mangere Island. My analysis of trends in the small population of ancestral survivors transferred to Mangere Island also supports the prediction that stochastic demographic and environmental pressures can operate lethally on low numbers even if the original causes of decline are removed (Gilpin and Soulé, 1986; Hedrick *et al.*, 1996).

My findings do not support the assumption made traditionally by New Zealand wildlife managers that the predicted genetic costs of unnaturally low numbers are inconsequential threats to the viability of threatened endemic bird populations. The so-called 'New Zealand cure' was the best strategy to avert immediate extinction but not the one most suited to assuring the black robin's long-term persistence. Minimal or incidental management of potential genetic risks (despite the species's obvious exposure to major risk criteria) neglected the principal remaining threat to viability once the populations had been secured against deterministic pressures. Later management focuses have been more ambivalent.

Inbreeding in the black robin populations did not result in population declines under the conditions operating during the study period. As inbreeding levels continue to accumulate (faster if the populations remain at current sizes or decrease further), the reproductive penalty identified by my study may become more severe and diversified. Without the option of gene replenishment from healthy sister-populations to increase genetic diversity and to moderate inbreeding effects, the black robins must survive for the foreseeable future on the attributes they have inherited from their evolutionary and genetic histories. The implications of the latter must be a matter for concern, especially as the species is already inherently at risk through its specialist ecological and behavioural traits. The black robin's long-term persistence depends on how well it responds to unforeseen pressures. Protection from well understood external threats is in place but the need for remedial genetic management is strongly indicated, along with careful sustained monitoring of its effectiveness.

Finally, a number of implications can be drawn from this study which may benefit the conservation of critically threatened birds world-wide (not necessarily the insular species alone).

The first is self-evident but bears constant restatement. The viability of free-living bird populations is best preserved by avoiding declines to unnaturally small size in the first place. For conservation managers and species alike, prevention is more ecologically advantageous and cost-efficient than cure. The financial cost of the black robin's recovery has never been fully quantified but probably runs to several millions of dollars. The investment—which has yet to assure the long-term persistence in today's modest population of about 150 birds—has consumed a significant proportion of New Zealand's chronically stressed conservation budgets. Inevitably, work on other threatened species in New Zealand has been affected as a result.

Second, critically endangered populations can be recovered despite declines to very low numbers. Thus, giving up should never be an option. The black robin's recovery demonstrated that species with even the most grievous genetic histories can be preserved from extinction, in the first instance by raising numbers rapidly, as has been stressed throughout this study. Equally, the crises themselves serve extinction biology by quickening the impetus to invent and experiment. Among other advances, the techniques of cross-fostering in the wild (Butler and Merton, 1992) were pioneered through last-minute desperation to retrieve the black robins from the threshold of total extinction.

Third, effective recovery programmes require basic knowledge of species biology and demography yet the necessary studies are often lacking or are too brief to acquire important information on life-histories and longitudinal trends. Responses to annual declines in the black robin's ancestral population on Little Mangere Island were nearly fatally delayed by limited understanding of black robin biology and demography (Chapters Three and Four). Russell (2000) pleads rightly for data on the survival of fledglings and juveniles, life-history stages which are commonly neglected by ornithological studies. As this study has shown, post-fledging survival data were crucial to detecting key threats to black robin viability. The benefits of biological ground-work are far-reaching. For instance, managers raising bird numbers quickly by boosting juvenile output will be well served by knowing what rates of breeding success to expect—and what rates are adequate to preserve viability—in populations skewed disproportionately towards first-time breeders. Equally, understanding natural fluctuations in annual productivity, survival and dispersal may avoid costly misreading of trends and their causes. Basic biological inquiry is therefore worthy and crucial for managing extinction risks.

Fourth, management of genetic health in small compromised populations is highly sensitive to the quality and duration of pedigree and demographic data. As shown by this study, pedigrees constructed from fully colour-marked populations are indispensable to determining the rates and severity of inbreeding. Pedigrees also enable managers to choose genetically valuable founders for new populations. Annual productivity data give direct measures of inbreeding-related fitness costs, especially if gathered for each pair and clutch through to completion of the breeding cycle. Rates of longevity and survivorship over generations fulfil the same function, by determining how fitness costs are expressed, which life-history variables to manage, and how effectively intervention may be addressing threats to viability. Without the advantages of pedigree and demographic data, management of cryptic genetic risks becomes something of a lottery.

Fifth, the ‘slow’ breeding typical of temperate southern hemisphere birds is evolutionarily attuned to prolonged, relatively intensive parental investments in low numbers of offspring (Chapter Two: *Section 2.11*). Thus, population persistence is dependent on the output and recruitment of relatively few juveniles. In such species then, juvenile output and recruitment are crucial demographic variables to monitor. Monitoring regimes focused solely on indices of abundance may fail to detect the threat arising from shortfalls in juvenile production, especially if the appearance of viability is preserved by the characteristically long life-spans of adults and territory stability. This was precisely the error made by black robin managers after rescuing the last seven birds from Little Mangere Island (Chapter Four).

Sixth, ‘slow’ breeding strategies are appropriate in stable threat-free environments but potentially hazardous to viability if conditions change. The small, largely invariable clutch sizes and long breeding cycles of slow-breeding strategists do not allow them to increase reproductive output spontaneously in response to unnatural rates of mortality. This was a point first made in Chapter Two and exemplified through black robin analyses in subsequent chapters. Moreover, the long nesting intervals of multi-brooded southern birds expose females to greater dangers on the nest. As a result of these intrinsic disadvantages, managers should anticipate heightened susceptibility to change, expressed perhaps through relatively swift declines in species possessing more specialised life-history traits, as is the case with the insular black robins. Recoveries too may be slower than in faster-breeding birds capable of more prolific or variable seasonal output. Correspondingly, managers should anticipate the need to augment natural rates of productivity through intervention when slow-breeders are confronted with unfamiliar conditions (for example, new threats *in situ*, or translocation to new habitats). As experience of the black robin recovery has made clear (Chapters Three, Four and Eight), optimistic policies of minimal disturbance and transfer-and-forget may not be adequate.

And last, the value of observing threatened populations and their habitats systematically to define the causes and character of declines cannot be stressed enough to field workers and conservation administrators alike. Among its many benefits, competent monitoring at close quarters will help frugal managers to direct their efforts to best effect. This benefit will be realised, of course, only if observation data are analysed routinely (Chapter Four). The black robin experience reveals the risk of investing conservation effort unwittingly in sink populations whose viability may always be questionable. Similarly, this study has shown that habitats which appear suitable for species of interest may actually be sub-optimal and therefore a poor guide to the suitability of potential translocation sites. These are avoidable mistakes.

# CHAPTER TEN
# MANAGEMENT RECOMMENDATIONS

## 10.0 Introduction

It has been a primary motivation of this study to identify key threats to the viability of black robin populations and to make informed recommendations for their management. Similarly threatened insular endemic bird species are expected to benefit by implication. The following suggestions aim to strengthen current practice so that black robin managers are better prepared to deal with potential threats.

I am acutely aware that resourcing levels have the final say on what is eventually done. However, my primary duty is to the black robins and other threatened species. For this reason, I have chosen to translate my research findings into management recommendations in two ways. First, I outline the best technical advice for management of long-term viability. I have not leavened this by second-guessing the options forced upon black robin managers by resource constraints. Given current resource stresses, this advice will be regarded as unrealistic, but the most prudent management options need to be stated. If nothing else, they are reason to argue for better support and funding.

Second, I have recognised current realities by presenting what I consider to be minimum acceptable options for management. These relate primarily to population monitoring, which is often regarded as consuming scarce resources for little apparent reward. Inadequate monitoring is false economy, as Chapter Four of my study has emphasised. My suggestion for a minimal monitoring regime is intended to improve on current practice until better alternatives are developed or are affordable.

In what follows, I deal first with what is optimal for black robins and managers alike. Then I outline a baseline monitoring regime which is both more sensitive than current index-monitoring to changes in population condition and more advantageous to investigating viability threats.

In making these recommendations, I am aware (and have indicated as much in Chapter Four) that the chief impediments to proper management of the black robins and like species in New Zealand are institutional. The solutions to DOC's resourcing difficulties and inadequate wildlife management arrangements are political. They lie beyond the scope of my study but have been explored in previous research (Kennedy and Perkins, 2000; Kennedy, 2003).

## 10.1 Managing immediate threats

There is no question that the principal threats to black robin persistence are deterministic factors capable of driving them to extinction quickly. Most such external threats are well known to wildlife managers familiar with New Zealand's history of bird extinctions and endangerment (Wilson, 2004). New threats to the black robins may emerge as longer-term environmental changes such as global warming take effect. However, only some external pressures have *in situ* remedies available. For instance, techniques now exist to prevent and eradicate mammalian predators (mice, rats and cats) arriving from elsewhere in the archipelago (Atkinson, 2001). Eradication of predatory weka (present nearby on Pitt Island) has also been achieved elsewhere (Middleton, 2007). But dealing with these threats may not be straightforward. It is not certain in the prey-rich environments of Mangere and Rangatira Islands, for instance, that eradication would succeed before black robin losses (direct and collateral) were catastrophic.

The arrival of new pathogens and increased competition with predatory starlings are recognised as serious threats (Department of Conservation, 2001a) but few remedies are available at present. Similarly, accidental fire could be devastating given the remoteness of the black robin islands from any fire-fighting infrastructure. Should global warming extend the ecological ranges of predators such as introduced Indian mynas, wasps or other insect pests, black robin managers would lack effective responses. Roberts *et al.* (2006, 2007) warn that the single-age-structure forests of the black robin islands are unusually vulnerable to broad-scale wind-throw from severe storm events. Little could be done *in situ* to reverse the sudden, severe contractions in black robin numbers which would ensue from the loss of large tracts of forest. These could be grave reversals in the Woolshed Bush (currently the optimal centre of black robin breeding) or in the Robin Bush (the only breeding habitat on Mangere Island).

The Black Robin Recovery Plan (Department of Conservation, 2001a) has established the first line of defence against some such serious contingencies with measures which are well-established in island-management practice throughout New Zealand—strict quarantine and surveillance for pests and disease, and rigorous control of human access to the black robin islands. The unchecked illegal harvests of *titi* continue to breach this line of defence annually (Department of Conservation, 2001a). The Recovery Plan's principal safety-nets against the failure of threat quarantine, however, are the expansion of population sizes and founding of new populations within the black robin's natural range. These prudent strategies are essential to moderate the threat of further genetic malfunction and also offer some protection from intractable longer-term pressures such as harmful regenerative changes in the character of black robin habitats which may cause extant populations to decline.

The findings of this study allow important observations to be made on the means chosen by black robin managers to achieve the Recovery Plan's twin ten-year objectives of population and range expansions. It is timely to discuss these. Not only have these objectives not been realised since they were set in 2001, but the entire recovery strategy is due for review in 2011. Moreover, the holding strategy of monitoring and protecting existing populations has kept the islands free of pests and other immediate threats (so far) but has neither prevented or explained a decline in black robin abundance.

## 10.2 Short-term objective—Increasing population sizes

In 2001, the Black Robin Recovery Plan directed management to a ten-year target of 250 adults distributed among at least three stable, self-sustaining populations (Department of Conservation, 2001a). Two hundred and fifty was the number required to move the species to a lower conservation ranking. This threshold is administrative rather than ecological and understates the need for management adjusted to the particular conservation requirements of each population. It is imperative to achieve the largest possible sizes in each in the shortest possible time as the first step to protecting viability against threat-induced fluctuations in numbers and stochastic changes in genetic structures.

Substantial increases in numbers cannot be achieved on Mangere and Rangatira Islands until the two populations are released from the constraints imposed by historical reductions in forest cover, a persistent legacy of farming on each island (Chapter Three). The finding of this study that effective habitat size is less than the area of forest available (Chapter Six) has significant implications for managing population growth. Rangatira Island possesses in the Top Bush the largest expanses of closed-canopy forest available to the species, yet the habitat appears to be sub-optimal under existing conditions. Orientation to the prevailing winds and cooler sub-canopy temperatures are probably contributing factors. This may also be true of the fragmented Caravan Bush habitat in which black robins failed to establish between 2002 and 2005 (Kennedy, 2006; Chapter Four). Until the particular physical and biological impediments to black robin success in the Top Bush can be identified, managers should not regard it as under-exploited habitat or make investments in increasing black robin numbers there.

The priority should be to maximise numbers in the Woolshed Bush, since unmanaged productivity and population growth in this more disaggregated habitat have been stronger and more stable than elsewhere. This goal is especially pressing if the recent 22% decline in Woolshed Bush numbers (Chapter Six: *Section 6.2.3*) is indicative of lower carrying-capacity following adverse changes in forest structure.

The pragmatic response is to expand the area of available forest. Localised revegetation of open spaces between forest fragments would achieve this, particularly among the scattered eastern outliers of the Woolshed Bush, as recommended by Roberts *et al.* (2006). The few post-1998-99 data on relative densities in the Woolshed Bush (Kennedy and Wilson, 2005) suggest that its sheltered eastern areas are favoured by black robins. If so, staged reforestation of the sheltered, gently sloping eastern terraces behind Thinornis Bay should be a priority. Natural extension of the eastern forest perimeters has stalled through smothering by *Muehlenbeckia* (Roberts *et al.*, 2006) but my observations indicate that seed from akeake trees will germinate if small spaces created in the blanketing *Muehlenbeckia* ground-cover are kept open while seedlings establish.

Increases in black robin numbers on Mangere Island cannot be achieved without extensive reforestation of the open grasslands inherited from the farming era. Reforestation will benefit other threatened species such as Forbes' parakeets, tomtits and Chatham petrels (the latter if reintroduced or colonising from Pitt and Rangatira Islands). My research has indicated two necessary adjustments to the existing revegetation plan due for review shortly (Atkinson, 2003).

Black robin numbers on Mangere Island are tightly constrained by the limited area of Robin Bush (about 5 ha of forest cover), with obvious implications for the levels of inbreeding which are higher in this population than elsewhere (Chapter Seven: Table 7.2). Expansion of contiguous forest cover must be a priority. This is best achieved by integrating the Robin Bush isolate with the extensive Douglas Basin plantings (about 11 ha) on a broad front. Integration would treble the extent of closed-canopy habitat available. Eliminating fragmentation within and between the two forested areas would also address a major factor predisposing dispersing black robins to cross-breeding with tomtits, as I have argued in Chapter Eight (Hybridisation).

The second reforestation requirement is unavoidable if the Recovery Group intends to proceed with the reintroduction of black robins to Little Mangere Island (Department of Conservation, 2001a, 2008; Merton, 2008a). If the two island populations were naturally united, as I have suggested in Chapters Three and Seven, re-establishment in the tiny ancestral habitat should also attempt to restore the original ecological and genetic linkages. Black robins should be able to disperse between the islands, a natural and cost-effective means of managing genetic integrity on both. This can only occur through reforestation of the western (or hut) peninsula and all ridges and slopes beyond to the Douglas Basin. This is a substantial long-term undertaking. Until accomplished, however, any new population marooned on Little Mangere Island will require constant, costly monitoring of numbers and genetic integrity to preserve it as a viable 'life-boat' population in case of losses elsewhere. Forest enhancement would certainly improve this situation and benefit other forest species such as Forbes' parakeet, but the logistical difficulties are formidable.

Selection for forest type on both islands is important. The black robins and other species will benefit most from early establishment of the robust pioneering akeake which provides nest-cavities and foraging opportunities on trunks and branches, generates abundant seed and leaf-litter, and does not shed its foliage in winter. Matipo is also desirable. The fast-growing deciduous ribbonwood should be kept to a minimum, since this offers few of the same advantages, appears to compete aggressively with akeake for space, and produces open, colder forest interiors little favoured by black robins, other cavity-nesters and petrels requiring take-off trees.

## 10.3 Short-term objective—Establishing new populations

The founding of new black robin populations has been a long-standing objective of management (Flack, 1971). It aims to return the species to further parts of its natural range and to secure it on as many islands as possible as insurance against catastrophes (Department of Conservation, 2001a). The strategy may have the additional longer-term benefit of diversifying the black robin gene pool (Butler and Merton, 1992), though this will be realised only if rates of inbreeding and deleterious genetic drift are minimised by maintaining populations consistently at the maximum sizes permitted by island area (Frankham *et al.*, 2002; Jamieson *et al.*, 2008).

As my study has illustrated, future translocations have the benefit of past experience to draw on. This will be critical because there are currently no other large, threat-free islands available in the Chathams archipelago. The remaining options are restricted to problematic 'islands' of protected habitat in the hostile Pitt and Chatham Island environments. The failure of black robins to establish in Caravan Bush indicates that translocations to such sites are neither straightforward nor assured of success, even with large numbers and multiple liberations of founders (38 adults and juveniles in this case; Chapter Four).

Where the circumstances of each translocation project allow, the following considerations should be taken into account when choosing new sites, founder sizes and follow-up programmes for management and monitoring.

### *10.3.1 Reintroduction to real rather than virtual islands*

The history of black robin management has shown that reintroduction to threat-free geographically isolated islands has a greater chance of success than liberation into protected reserves in predator-populated environments (Chapters Three and Four). Given the black robin's poor powers of flight and reluctance to traverse extensive open space, founders and offspring cannot disperse from real islands. They will be easier to trace. Threat quarantine protects the whole habitat and the population is not constantly vulnerable to the failure of artificial barriers to pest invasions. Because new threats are localised, the probability of complete eradication is higher.

Pitt Island (6,325 ha) is unquestionably the best option for black robins and the numerous other critically threatened terrestrial and marine birds in the region. Conservation managers must persevere with their efforts in the Pitt Island community to obtain consent for the island-wide eradication of weka, mice and feral cats and the containment of farmed and feral livestock (cattle, pigs and sheep).

In the meantime, the only remaining island option is Little Mangere Island. It has the advantages of geographical isolation but population size will be severely curtailed in the small area of regenerating forest (about 4-5 ha). If, as Merton (2008a) suggests, only eight territories are available (of perhaps 18-20 originally), numbers may be held at no more than 20 individuals until reforestation restores linkages with the Mangere Island population. At current rates of replanting, that prospect is many decades away. It will be necessary to manage and monitor genetic integrity carefully (see below) to avoid exposing the fitness of any new population to the high levels of inbreeding and drift which depleted genetic diversity historically.

### *10.3.2 Reintroduction to discrete habitats in hostile environments*

Large, geographically discrete areas of fully protected habitat are preferable to protected partitions if black robins are being reintroduced to Pitt or Chatham Islands. Given the black robin's intolerance of open spaces, discrete habitats reduce the probability of dispersal by valuable founders, and concentrate the founder population within manageable areas. The risks of genetic harm from closure of populations in such sites can be managed later by inter-site transfers (*Section 10.4* below).

The wisdom of this policy is well demonstrated by past experience. The decision to transfer the last seven black robins to Mangere Island's small forest remnant, rather than to the larger, better habitat on Rangatira Island proved critical to recovery of the species (Chapters Three and Four). Even moderate dispersal from release points in the Woolshed Bush would have compromised opportunities for pairs to form, especially as later match-making relocations of itinerant black robins were ineffective (Chapter Two: *Section 2.5*). The failure of the Pitt Island transfers between 2002 and 2005 was no doubt hastened by the fact that non-site-attached black robins ranged freely into predator-infested habitat beyond the protected boundary of Caravan Bush.

### *10.3.3 Site preparation*

Potential threats in reintroduction sites should be identified and remedied before black robins are introduced. These threats (hazardous plants such as piri piri *Acaena* spp., predators, competitors, inadequate food supplies or habitat fragmentation) may waste important founders and reduce the probability of successful establishment.

Success in Caravan Bush was jeopardised by at least two threats. Natural vegetation recovery had commenced only a decade beforehand, hardly enough to repair the significant degree of fragmentation in the forest cover after a century of browsing by domestic livestock. And mice, the only rodent species on Pitt Island, were still present. Any threat they might pose to black robins was not addressed. Depletion of invertebrate prey communities would appear likely as mice compete directly for the ground-dwelling prey exploited by black robins. Mice are also known predators of eggs and nestlings of other New Zealand *Petroica* species (Moors and Flack, 1979). The mouse threat may have been aggravated by the removal of cats and weka, increasing the possibility of episodic predation of black robin nests. Furthermore, black robin presence severely limited options for mouse eradication, since the birds were vulnerable to ground-set traps and toxins accumulating in the food chain.

### *10.3.4 Post-transfer management to ensure establishment*

Planners of future black robin liberations must anticipate the need to manage founders actively from the outset and assist them to breed successfully. Sustained, intrusive intervention may be needed, making extensive use of the methods proven during the intensive management period from 1980-81 to 1989-90 (Chapter Four).

Since black robin management commenced in 1971-72, translocations have succeeded only if assisted and where population increases were managed. Conversely, the failures followed from simply liberating black robins into new habitat and leaving them to establish naturally. This was the flawed approach taken in 1976-77 when the last seven black robins were transferred to Mangere Island, and was essentially the approach adopted for the Caravan Bush transfers (Chapters Three and Four). Both founder-populations faltered but only the Mangere Island population received the active assistance it needed to grow quickly. Had managers not intervened, extinction was inevitable. Unlike their more productive and versatile congeners, the mainland robins, which have established without assistance from small founder sizes (Taylor *et al*., 2005), black robins are constrained in their ability to establish by their shorter breeding seasons, lower reproductive output, specialist forest requirements and sensitivity to habitat quality (Chapters Two and Three).

The survival and establishment of founders is the primary objective of intervention, especially if they possess scarce genetic qualities needed to counteract the bottleneck effects of translocation. Rapid increases to large numbers are desirable to overcome stochastic demographic and environmental threats, as illustrated on Mangere Island (eventually) and Rangatira Island. Rapid population increases also minimise the potential genetic costs of the founder event(s) and subsequent inbreeding.

If resource constraints threaten to compromise the quality and duration of post-liberation management, initial liberations should be confined to small numbers of founders, supplemented as quickly as possible once a nucleus of breeders has been consolidated. The alternative of relying on large founder numbers to compensate for inadequate follow-up did not succeed in Caravan Bush, especially when the quality of the habitat itself was questionable.

### *10.3.5 Selection of founders to minimise genetic threats to viability*

Ideally, founders should be selected for genetic qualities likely to maintain population fitness and heterozygosity as prerequisites for short- and long-term viability. Predictive modelling of founder selection suggests that candidates should represent the genetic diversity in the source population's original founding base (Haig *et al*., 1990). This is best determined from pedigrees in which all individuals are identifiable. Furthermore, the founder population should possess the common and rare alleles present in source populations. The alternatives of selecting the most reproductively successful individuals, or selecting individuals at random, are likely to result in loss of genetic variation (Haig *et al*., 1990). The advantages of highly fecund founders (the potential to maximise offspring production) may be outweighed if their genes dominate the genetic structure of the new population at the expense of valuable rare alleles.

The results of my study (Chapter Seven) indicate that highly inbred males should be excluded from black robin founder-populations. The negative correlations found between male inbreeding *F* and the survival of nestlings, fledglings and juveniles do not augur well for a new population's establishment prospects. If environmental conditions at the new establishment site vary significantly from those of the source population, the inbreeding depression in males may be expressed more strongly. The phenomenon of environmentally dependent inbreeding depression—latent depression triggered by shifting inbred birds to new environments (including better ones)—has been suggested in small insular populations of translocated South Island saddlebacks (Hooson and Jamieson, 2004) and takahe (Jamieson and Ryan, 2000). As a precaution against the expression of any latent inbreeding depression in females under altered conditions, it would be advisable to select for low female inbreeding *F*.

Black robin managers are now at a serious disadvantage in applying these principles after terminating the long-running pedigree and productivity monitoring. Individual inbreeding coefficients and founder representation cannot be defined. Nor does monitoring at current intensity permit the fecundity of potential founders or their breeding heritage to be ascertained. Negligible genetic differentiation between individuals complicates molecular determination of pedigrees but more comprehensive analyses may reveal levels of heterozygosity worth managing (see *Section 10.4* below). This last option should be explored. Until genetically important individuals can be identified by other means, black robin founders will have to be randomly selected. The attendant risks of genetic depletion can now be managed only by the conventional means of increasing numbers rapidly to minimise levels of inbreeding.

### *10.3.6 Post-transfer monitoring of new populations*

For genetic and other reasons, new populations should be monitored annually by competent observers so that harmful trends can be detected, explained and remedied swiftly to ensure successful establishment. This is best achieved by detailed recording of population pedigrees, individual life-histories and breeding performance. The demographic record of recovery will enable managers to assess genetic threats more reliably than by other means (see below). Close monitoring will be critical during the establishment phase when it is highly desirable to know, for instance, whether most or only one or two pairs are breeding successfully. Routine molecular assessments of genetic diversity are advisable (see below).

Documenting of management activities and vital rates is necessary for non-genetic reasons. It will help to define the pressures on the new populations and ensure that lessons learned at considerable expense are applied elsewhere. Annual population counts alone will not suffice, since they do not reveal anything of underlying demographic problems, as has been demonstrated by the failure of sample-monitoring to explain recent declines on Mangere and Rangatira Islands.

Once establishment seems assured by commonly agreed criteria (consistently strong growth rate or reproductive output, low rates of adult mortality, full habitat occupancy), and the population is stable or growing after supplementary management has been withdrawn, I suggest that monitoring revert to the minimum model I propose below (*Section 10.5*). If doubts remain about the stability of the new population, monitoring of productivity should resume at regular intervals (no more perhaps than every three to four years, and spanning at least three consecutive seasons to allow for annual variations). More regular monitoring should resume if the need is indicated by signs of problems.

Adequate monitoring will be difficult to achieve under present resource constraints and in logistically taxing habitats such as Little Mangere Island. Even so, it is unacceptable to have translocations fail without any objective understanding of why. Translocation theory and practice requires careful documenting of establishment projects, especially those which are unsuccessful (Armstrong and McLean, 1995).

Design of monitoring and management regimes would benefit from a critical review of the failed Pitt Island transfers. This is an urgent prerequisite for consideration of new translocation proposals. The review should attempt to define without prejudice the ecological, management and institutional impediments to the establishment of black robins in Caravan Bush.

### *10.3.7 Monitoring of source populations*

Finally, it is essential to understand the impacts of founder removal on source populations. It may not be coincidental, for instance, that black robin numbers on Rangatira Island had declined 29.4% by 2007-08 after removal of 34 individuals from Woolshed Bush in 2002 and 2004 (Chapter Six: *Section 6.2.3*). Although the Black Robin Recovery Group requires the viability of the Mangere and Rangatira Island populations to be clarified before new translocations will be considered (Department of Conservation, 2008), post-transfer viability must be assessed also. This presupposes more insightful monitoring than is currently conducted.

## 10.4 Management of genetic threats to viability

Black robin managers should anticipate more severe and diversified inbreeding effects in the two black robin populations. Precautionary genetic management is advisable to maintain population fitness and longer-term responsiveness to unforeseen selection pressures.

The aim of genetic management is to maximise genetic variation in small inbred populations, with associated benefits for fitness. However, the efficacy of genetic management is not well understood in New Zealand bird species (Jamieson *et al*., 2006). Measures adopted for black robins will be largely experimental and should be monitored closely to detect adverse effects specifically and to inform future genetic management practice generally.

Management of genetic health in small populations is served best by knowledge of productivity (which provide fitness measures), population demography and pedigrees in which genetic relationships among individuals can be determined (Haig *et al*., 1990; Jamieson, 2009). Estimation of lethal equivalents likely in extant populations (using historical data) is highly desirable. Measurement of genetic diversity in populations is also highly advantageous though molecular analyses are still inferior substitutes for detailed records of population demography from longitudinal studies (Pemberton, 2004). The value of detailed demographic observations is stressed in the recommendations which follow.

### *10.4.1 Maximise population sizes*

Reducing the probability of inbreeding is accepted currently as being the most effective means of maximising population fitness and genetic diversity (Hedrick and Kalinowski, 2000). Large populations and fast rebounds from declines reduce the frequency and intensity of inbreeding.

### *10.4.2 Monitor genetic variation within and between populations*

DNA samples of sufficient type and quantity should be gathered from all populations at regular intervals for molecular assessment of genetic diversity. Heterozygosity invisible to past analyses may be revealed by the more powerful techniques of today and the future. New fitness-related DNA markers should be assessed also. Selection of sampling regimes, frequency, sample types and DNA markers is beyond the scope of this study but can be determined through consultation with conservation geneticists.

Conventional genetic thinking suggests that variation in and between populations is likely to diverge through mutation over hundreds of generations. However, evidence from longitudinal studies of an inbred population of Scandinavian wolves *Canis lupus* descended from three individuals (Bensch *et al*., 2006) and a closed insular population of mouflon *Ovis aries* founded from two individuals in 1957 (Kaeuffler *et al*., 2007) indicates that natural selection may play a role in maintaining and increasing heterozygosity over shorter time-scales, even if (in the case of the wolves) mean inbreeding coefficients are rising. Whether or not natural selection operates advantageously in this way for black robins, any differentiated heterozygosity emerging in particular populations or environments increases options for the selection of founder populations and remedial gene-exchanges between populations.

### *10.4.3 Inter-population exchanges*

The efficacy of routine gene-exchanges is not well understood. Predictions of reversed inbreeding effects through inter-population transfers of at least one individual and up to ten per generation (Mills and Allendorf, 1996) are supported by computer-modelling for naturally outbred species (Frankham *et al*., 2002; Wang, 2004). There is some empirical support for beneficial effects, as was demonstrated by the recovery of a chronically inbred population of greater prairie chickens *Tympanuchus cupido pinnatus* after birds were introduced from a larger, more genetically diverse sister-population (Westemeier *et al*., 1998). As is typically the case for threatened New Zealand birds (Jamieson *et al*., 2006), no such healthy sister-populations exist for black robins, but future genetic divergence between populations may suffice as an alternative, especially if loci are found to be fixed for different alleles (Frankham *et al*., 2002).

Each black robin population should receive at least one individual per generation from another population. This means inter-island exchanges at no more than two-yearly intervals. Ideally, the individuals selected for transfer should be genetically differentiated from the recipient population and should have a proven breeding heritage. They must reproduce after transfer. Clutch transfers may substitute (if the fostered offspring survive to breed) and could avoid the many forms of social disruption associated with juvenile or adult exchanges. Transfers of birds carry an associated risk of disease transmission which should be minimised by routine screening of source populations.

Because efficacy is not well quantified, any inter-population exchanges of black robins should be treated as experimental. Systematic adjustments in the number and provenance of individuals may be required, along with changes in the frequency of transfers (Mills and Allendorf, 1996). Monitoring for beneficial and adverse effects is essential. The most practical means of discerning any such effects is by observing fitness parameters in each population (see below). Monitoring of genetic diversity (above) could also be instructive.

## 10.5 Population monitoring

The aim of population monitoring is to prevent black robin extinction. For this, black robin monitoring regimes must equip managers with the knowledge necessary to understand population viability, explain changes in status and predict future trends. In operational terms, this means monitoring of:

- annual trends in established and new populations
- the impacts of unusual events, catastrophes or founder selection on source populations
- the effects of any remedial management

The quality and intensity of monitoring had a direct bearing on the ability of black robin managers to anticipate and remedy problems in the ancestral and descendent populations. Much now depends on the type and quality of future monitoring. The more comprehensive it is, the better a manager's ability to identify or predict changes in trends or viability, thus enhancing the black robin's prospects of long-term persistence (the overarching goal of current management; Department of Conservation 2001a). Conversely, as my study has illustrated (Chapter Four), monitoring of lesser intensity will rapidly erode management effectiveness and responsiveness.

### *10.5.1 Desirable elements of monitoring*

The inability of latter-day managers to detect and explain recent population declines (Chapter Six) signals that monitoring intensity has been reduced too far. Before making recommendations on alternative monitoring regimes, however, my critique of past monitoring practices (Chapter Four) justifies the observation that ecologically sound monitoring combines two elements—quantitative measurement of chosen demographic parameters (adequate on its own), and qualitative understanding of populations and their environments. The two in combination achieve otherwise unobtainable synergies and enhance management, as illustrated during the critical period of intensive conservation activity (Chapter Four). As a monitoring attribute, sensitivity growing from familiarity, knowledge and experience of the black robin populations has been radically undervalued in recent years, so much so that transient observers discouraged from 'looking around' by the snapshot demands of index-monitoring failed to both sense and detect potentially catastrophic population changes. In what follows then, it should be implied that experience, knowledge and continuity in black robin observation are crucial qualities for effective monitoring.

These qualities are customarily brought willingly to monitoring by skilled, motivated observers. If black robin management is to benefit from them, present-day managers will need to critically review:

- the 'flying-squad' approach of index-monitoring (is it really value for money?)
- the operational emphasis on completing the task rather than completing it well
- the policy of regular turn-over in black robin project leaders and field staff
- the practice of using unskilled, one-trip observers or a succession of contractors

- the currently minimal standards for quantitative and qualitative reporting of field work and monitoring results
- the absence of an apprenticeship, mentoring and peer-review system founded on cultural transmission in the field of skills, knowledge, experience and standards.

A review of these issues will be a challenge in the current institutional environment, which relies predominantly on contractual obligations, standard operating procedures and operational guidelines to legislate for quality.

### *10.5.2 Population modelling*

As I have suggested in my conclusions (Chapter Nine), black robin management would be significantly advantaged by more powerful predictive modelling of historical demographic data (or suitable data acquired in the future). This option should receive immediate consideration. Modelling has the potential to identify the life-history stages likely to be compromising the stability and viability of black robin populations. It can be used to identify further information needs and assess the likely genetic consequences of changes in population sizes. In the meantime, my finding in Chapter Six—that no single life-history factor explained historical differences in population trends—means that monitoring must attempt to cover all bases. Focusing randomly on key vital rates or life-history stages may not be safe if they are uninformative in isolation or change in their importance over time.

### *10.5.3 Optimal monitoring*

Ideally, black robin monitoring should aim to give managers an unequivocal understanding of annual population trends and the demographic variables shaping them. Trends in abundance and underlying vital rates express the interacting effects of extrinsic and intrinsic forces acting on the populations. Accurate, timely interpretation and prediction of trends relies especially on measuring vital rates.

To ensure accurate measurement in each black robin population, a number of minimum monitoring requirements would have to be met:
- fully colour-marked populations
- close observation (to completion) of annual breeding attempts

- annual pre-breeding census
- population pedigrees based on full knowledge of parentage
- analysis of field data between seasons

A proposal for monitoring at this intensity will be seen as an uncritical return to the practices of the past. There is no denying, however, that black robin management was well served by such monitoring between 1980-81 and 2001-02, particularly at critical times such as the cross-fostering seasons and establishment of black robins on Rangatira Island (Chapter Four). The mal-imprinting and cross-breeding crises were dealt with swiftly because managers were very familiar with the populations (Chapter Eight). Monitoring of this intensity would serve managers well in future decisions and unforeseen crises. Importantly, it would provide managers with an adequate platform for managing genetic threats to black robin populations.

Any such monitoring regime, or variations of it, would be strengthened by including indicators of external variables which influence trends. These were not monitored historically but might include:

- tomtit densities (if declining in parallel with black robins, a common environmental factor may be operating)
- changes in forest structure (measurable through regular photo-point or other simple quantitative indices of vegetation change)
- starling densities (a measure of predation and disease threats)
- sub-canopy temperature and humidity (measures of environmental stress obtained cheaply at permanent data-logger stations and highly desirable base-line information for selection of new population sites).

Past experience has shown that efficiencies can be achieved in intensive monitoring of this kind by using skilled observers familiar with black robin behaviour and the geography of their habitats. Observation frequency can be reduced but potentially at the cost of knowing less about breeding attempts or black robin fates. The focus of monitoring should be sharpened by analysing annual field data systematically between seasons so that observers are aware of which demographic variables require more attention than others.

Clearly, monitoring of all demographic and chosen external variables implies a significant investment of time and observers throughout the black robin breeding season. Current resourcing arrangements will not support that. However, it goes without saying that if fewer variables are measured, understanding of population trends will diminish significantly, with predictable consequences for ability to interpret and respond appropriately to emerging extinction pressures. I need to stress that measurement of potential genetic threats to viability is particularly sensitive to reductions in demographic monitoring, as I have explained earlier. This is true also for measuring the effectiveness of genetic management and selection of genetically appropriate founders for new populations. Without the demographic insights to support the necessary decisions, genetic management of black robins will remain largely a lottery.

### *10.5.4 The integrated approach to monitoring*

Full demographic monitoring requires the near-continuous presence of observers throughout breeding season. This could not be justified for black robins alone but might be sustainable if black robin monitoring were integrated closely with work on other threatened plant and animal species on the islands. Integration was the norm historically but is not a feature of current operational practice in the Chatham Islands.

Four practised field staff stationed semi-permanently on Rangatira and Mangere Islands (two on each), from spring to autumn (as needed), could manage a range of threatened species tasks on each island. This 'game-keeper' approach to species management creates opportunities for multiple synergies of effort. It has numerous advantages over existing flying-squad tactics, which are inherently inflexible, insensitive to contingencies and unresponsive to the needs of black robins or any other species. On-the-ground familiarity with the populations will augment the quality and consistency of management. Among other things, observers on the spot are appropriately placed and informed to act as circuit-breakers for problems before they become serious or insurmountable.

The 'game-keeper' approach has precedents in the past employment of long-term contractors and, further back, in the rotational deployment of field teams between 1980-81 and 2001-02. These precedents suggest the minimum criteria for successful integrated management:

- competent, versatile, multi-skilled operators well-attuned to island life
- agreement on seasonal tasks and work standards
- an expectation that game-keepers will return for successive seasons and train their replacements in the field
- creative employment arrangements reflecting (1) the contingent nature of multi-species work and (2) the special social demands of isolation
- a shift in species recovery planning perspectives to maximise the benefits of integrated management on the ground.

### *10.5.5 Minimum monitoring regime*

The current index-monitoring regime (mark-resighting) is not meeting the minimum requirements for black robin monitoring. Abundance estimates made for the proportions of the populations sampled have proven to be too variable to show trends reliably (Chapters Four and Six). The method is sensitive to errors in the sighting data supplied for NOREMARK estimators, and these appear to have been extensive in the past (Chapter Four), with no immediate prospect of improvement. Moreover, sample-monitoring, and monitoring of abundance itself, give only a partial indication of population status and may not reflect detrimental changes adequately or quickly. The focus on abundance is not intended to reveal anything of the vital rates in which harmful changes will be both expressed and more easily explained. The current regime makes no provision for precautionary monitoring of productivity, the vital complement to abundance monitoring.

An immediate priority for determination of the method's future is to re-run the NOREMARK estimators with the historical data cleaned to remove errors. This study has contributed significantly to that process by identifying the errors and suggesting appropriate corrections (Kennedy, 2007b, c). Re-runs may reveal the timing and extent of recent population declines. If not, the appropriateness of the mark-resighting method is questionable. Until it is demonstrated to be reliable and robust, or an alternative index-monitoring method is developed, it is prudent to adopt an interim approach more sensitive to the management needs I have identified at the beginning of this section.

The following recommendation makes provision for monitoring abundance and vital rates, and—depending on degree of standardisation—is much less labour-intensive than the optimal monitoring approach. However, it provides insufficient data for population modelling. It does not make any allowance for precautionary management of genetic integrity in extant and new populations, except to ensure that population contractions are detected quickly. Routine monitoring of genetic diversity (above) and disease screening should continue as independent activities.

I propose a two-stage regime. The first stage aims to detect potentially harmful declines in black robin numbers by annual baseline monitoring of population sizes. Because gross numbers are fallible indicators of viability (Chapters Three and Four), their primary function in this regime is to indicate declines. Declines indicated consistently over three seasons (see below) will then trigger intensive monitoring designed to define (1) their causes; (2) the life-history stages at which threats are affecting population dynamics, and (3) the appropriate application of remedies.

This proposal has crucial benefits for managers. It provides a known, banded population against which to validate index-monitoring alternatives, and it will have defined the distribution of breeding populations managers may have to monitor if persistent declines are indicated.

### *10.5.6 Baseline monitoring of population sizes*

Population sizes on Mangere and Rangatira Islands have always been assessed more accurately by head-counts than by index-monitoring (Chapters Four and Six). I recommend that head-count monitoring resume.

I acknowledge that historical head-counts were achieved over long periods of observation in which the probability of encountering all black robins was high. Therefore, this proposal is ideally suited to the integrated game-keeper approach to multi-species management. Time-limited head-counts standardised for yearly replication are problematic and will increase the probability of error. If standardised, the head-count methodology will have to be configured to ensure statistical power, especially as the second phase of productivity monitoring will be triggered by declines of set magnitude.

### Phase One Annual head-count censuses in the Woolshed Bush, Top Bush and on Mangere Island no later than mid-October

If not standardised, head-count surveys should be conducted annually in the Woolshed Bush, Top Bush and on Mangere Island, commencing no later than the first week of October. Two surveyors on each island should search all areas of potential habitat, lingering to (1) verify the number and identity of black robins encountered, and (2) determine the identity of unseen mates. The principal emphasis is on counting the banded adults and unbanded juveniles surviving the winter (see below). Incidental sightings of other individuals later in the season should be recorded carefully and added to the census counts. No post-breeding count is required, although given that the black robin's slow-breeding strategy carries inherent risks to viability if juvenile production is inadequate, it is highly desirable to establish the number of juveniles produced each year.

Current index-monitoring effort on each island amounts to about 20 person-days a year (two observers for two five-day pre- and post-breeding mark-resighting surveys). This effort should be reinvested in the early season head-counts.

Head-count accuracy depends on

- unique colour-banding of most or all black robins
- skilled, motivated observers who are very familiar with the habitats
- mandatory noting of sex, mate and territory (relative to formed tracks)
- a centrally managed banding database, available to surveyors in the field

Initially, a greater investment of time will be necessary to bring adult populations up to fully or near-fully colour-banded status. The effort of finding and banding black robins will be useful in establishing abundance bench-marks. From that point on, banding effort can be expected to decline considerably. The majority of birds banded in spring will be yearlings. If not complemented by post-breeding head-counts, assessment of annual juvenile production will have to be based on the numbers of unbanded birds presenting at pre-breeding head-counts.

Standardising of head-counts will require careful design to ensure multi-year replication and minimal error in counts. Ideally, the counts should be restricted to two observers for the chosen survey interval (defined for statistical power) and should commence before females retire from view to incubate (that is, very late September to early October). To minimise the effects of annually varying rates of dispersal, surveys should be conducted in all forested areas in the Woolshed Bush and Robin Bush. Standardising of head-counts will have to segregate incidental sightings from survey-period data but this information should be recorded carefully anyway.

### Phase Two Contingency monitoring of productivity and survival

Head-count surveys should continue annually if population sizes remain stable or increase. If declines of 10% or more are indicated in each of three consecutive seasons, monitoring of pair numbers, productivity and survival should commence immediately. The first two years of decline will forewarn managers of this necessity. The 10% trigger-threshold is based on the mean annual rate of decline apparent in the Mangere Island population between 2001-02 and Harvey's (2009) estimate of pre-breeding numbers in 2006-07 (a 43.4% decline overall; an annual average of 8.7% over five seasons).

Productivity and survival monitoring should confine itself to the Woolshed Bush and Mangere Island breeding populations, the two strongest and most similar in productivity historically (Chapter Six). The aim is to quantify breeding outcomes for all or large standardised samples of pairs throughout the season so that managers can explain trends at each life-history stage for offspring. Survival monitoring should aim to define and explain adult and juvenile mortality rates. This study provides a guide to historical breeding and survival data under natural conditions between 1990-91 and 2001-02, though the analyses to which new demographic data are submitted may benefit from more powerful statistical modelling.

Productivity and survival monitoring should continue annually until managers are confident that the declines are not indicative of a serious threat to populations, or that the causes have been identified and treated effectively. Positive corrections in the affected demographic parameters and subsequent population increases should be used as indications of the latter.

The operative Black Robin Recovery Plan (Department of Conservation, 2001a) is entirely silent on the nature of management responses to population declines but I would expect intensive monitoring of this kind to have commenced had index-counts indicated the recent declines accurately.

## 10.6 Assisting research

Access to historical and new demographic data on black robin populations is crucial to good research outcomes. Managers can assist this by centralising and cataloguing field records annually. As I have learned from my study, even the most insignificant of field records is worth retaining, more so because future research needs cannot be predicted. Rationalising of existing placements with archival institutions may be required, since historical records have become widely dispersed and are exceedingly difficult to trace.

Research will also benefit from greater consistency in observation standards. All observers should understand the minimum expectations required. A collegial culture of black robin mentoring and management would help to ensure this. The recent introduction of a banding database available to field-workers (Dave Houston, pers. comm., October 2009) should minimise the errors in recording of band combinations which have crippled index-monitoring and frustrated my study.

Significant improvements in reporting practices and subject-matter are essential. Very little quantitative and qualitative information is available in formal reports or informal logbooks from the seasons after full-population monitoring ceased. This was also a problem with reporting in the two previous management phases. Reports should include:

- dates for the report and the field visit(s)
- the names of authors and observers
- areas traversed
- tabulated lists of the black robins seen and banded, along with sighting dates and all relevant biological information (sex, mates, activity)
- tabulated summaries of productivity data
- comment on factors limiting the accuracy of data reported

- qualitative comment on population trends, the behaviour of black robins and ecological associates, habitat changes, apparent threats and any other issues deemed relevant
- other sources of information

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## PERSONAL COMMUNICATIONS

Hilary Aikman (Technical Support Officer, Biodiversity; Department of Conservation, Northland). Phone communication over monitoring decisions of the Black Robin Recovery Group 1999-2004 (1 August 2008).

Amanda Baird (Programme Manager, Threatened Plants; Department of Conservation, Chatham Islands). E-mail, dated 06 May 2008, outlining numbers of indigenous and exotic taxa by category, and subsequent discussions about the original flora of the islands.

— (Programme Manager, Threatened Plants; Department of Conservation, Chatham Islands). E-mail communication in response to request for information on the original Mangere Island reforestation programme (19 September 2008).

Brian Bell (Retired Director of Protected Fauna, New Zealand Wildlife Service, and architect of most early wildlife conservation initiatives in the Chatham Islands, 1960s to 1987). Conversations concerning livestock removal from Mangere and Rangatira Islands, reforestation of Mangere Island, the condition of both islands prior to 1980 and pre-1980 black robin monitoring, 2008 and 2009.

Professor David Bryant (Institute of Biological Sciences, University of Stirling, Scotland). Conversation concerning mutual benefits from the black robin energetics research project and my proposal to measure black robin micro-climates; Christchurch, 2004.

Bill Carter (Chatham Island historian, Pitt Island descendant, author of forth-coming farming histories of Mangere, Rangatira and Pitt Islands). Numerous conversations and e-mail communications between 2006 and 2009.

John Dugdale (Entomologist, *Manaaki Whenua* Landcare Research). E-mail dated 16 May 2008 in response to inquiry from ESK about the clammy, seasonally ubiquitous and evidently distasteful caterpillars on mahoe *Melicytus chathamica* in black robin habitats.

Dr Rowan Emberson (Senior lecturer, Entomology, Lincoln University). Conversation about the deleterious effects of mice on Pitt Island's invertebrate communities, prior to ESK's visit to Caravan Bush, February 2006.

Dr Brian Gill (Curator of Land Vertebrates, Auckland Museum). E-mail response to inquiry from ESK for further information on bird fossil surveys on the Pitt Island in 2002. Dated 25 June 2008.

Robert Gregory-Hunt, 77, Pitt Islander now residing in Christchurch. Conversation (30 June 2009) about evidence of black robin persistence on Pitt Island in the 1930s and 1940s, and the arrival dates of mice and wekas.

Dr Rod Hay (Scientist. Research and Development Group, Department of Conservation, Christchurch). Communications over black robin sightings on Little Mangere Island during post-graduate field research on black robin vocalisations, 1973-1974.

Ian Hogarth (Wildlife Officer, New Zealand Wildlife Service). Visited Rangatira Island (with Brian Bell) in early summer 1961 to shoot the last sheep. Hogarth and Bell also visited Mangere and Little Mangere Islands. Conversation in June 2009.

David Houston (Technical Support Officer, Biodiversity, Department of Conservation, Wellington). E-mail to ESK, dated 4 July 2008, in response to an inquiry about DOC's analyses of sample productivity data from Rangatira Island.

— (Technical Support Officer, Biodiversity, Department of Conservation, Wellington). Phone communication (1 August 2008) over progress with renewed analyses of monitoring data, and other problems with the NOREMARK method.

— (Technical Support Officer, Biodiversity, Department of Conservation, Wellington). E-mail to ESK, dated 14 October 2009, indicated that a black robin banding database was now available to improve the quality of observation data from mark-resighting surveys.

John Kendrick (Former New Zealand Wildlife Service photographer and film-maker). Conversation in July 2009 concerning the state of the Little Mangere Island forest when he visited in 1968 and the existence of film or images.

Ken Lanauze Snr (Pitt Island resident). Conversation on Rangatira Island during an Open Day for Pitt and Chatham Islanders in the mid-1990s. Ken introduced weka to Pitt Island in the early 1960s.

Kenneth Lanauze (Pitt Island resident, son of Ken Lanauze Snr and nephew of Sam Gregory-Hunt). Conversation (by phone, 9 June 2009) concerning the likelihood that Pitt Islanders refer to tomtits as 'robins'. Wide-ranging discussion about Pitt Island wildlife and Mangere Island history.

Dr Melanie Massaro (Canterbury University, black robin researcher, Rangatira Island, 2007-08 to 2009-10). Presentation to the Black Robin Recovery Group, 5 May 2010, in which first evidence of Chatham Island red-crowned parakeets evicting black robins from nest-cavities was revealed. Nests were evicted only from trees occupied by both species.

Dr Don Merton (Black recovery programme leader, 1980-81 to 1990-91). E-mail communication to confirm the origins of genetic research on the 2 post-management black robin populations, 18 August 2009.

Dr Hilary Miller (Allan Wilson Centre for Molecular Ecology and Evolution, School of Biological Sciences, Victoria University, Wellington, NZ). E-mail (dated 21 April 2008), in response to my inquiry, explaining that the comparison of mitochondrial and minisatellite DNA in modern black robins and specimens collected from Mangere and Little Mangere Islands between 1871 and 1900 had been inconclusive as a result of DNA degradation in the older specimens.

Rod Morris (Participant in the early biological studies of black robins on Little Mangere Island and member of the transfer team, 1976-77). Conversations (June 2009) about the condition of the island's bush after 1972-73.

Geordie Murman (Formerly Protected Fauna Officer, New Zealand Wildlife Service, and Department of Conservation). Key participant in black robin management. E-mail exchanges with ESK (June 2009) on the provenance of kopi berries distributed on Mangere and Rangatira Islands.

Ron Nilsson (Formerly Protected Fauna Officer, New Zealand Wildlife Service and Department of Conservation). Ron was one of the team which liberated the tomtits on Mangere Island on 13 April 1989. Conversation to confirm release-site details, July 2009.

Dr Fiona Petchey (Director, New Zealand Radiocarbon-Dating Laboratory, University of Waikato, Hamilton). Phone and e-mail communications (June 2009) over recalibrated dates for midden-site charcoal excavated at the seven Waihora Mound Moriori occupation sites, Point Durham, Chatham Island.

Moira Pryde (Scientific Officer, Research and Development Group, Southern Regional Office, Department of Conservation, Christchurch). E-mail communication dated 07 April 2009, regarding progress with revised NOREMARK analyses.

Graeme Taylor (Petrel ecologist, Department of Conservation, Wellington). Series of e-mail exchanges on matters relating to the rediscovery of kiore on Chatham Island and the post-farming condition of Rangatira Island (June 2009).

Rowley Taylor (Vertebrate ecologist visiting Little Mangere Island in November 1973 and November 1976 to study Forbes' parakeet ecology). Conversation (July 2009) to clarify bush condition on the island at those times.

Alan Tennyson (Palaeontologist, National Museum of New Zealand *Te Papa Tongarewa*). E-mail dated 19 May 2008. Discussion about the apparent absence of black robins from Rangatira Island.

Dr Graham Turbott (1937-38 Chatham Islands expedition member, retired Director of the Auckland Museum). Conversation (29 June 2009) over the condition of the bush on Little Mangere Island in January 1938 and the possibility that black robins had survived on Pitt Island until that time.

Dr Geoff Walls (Consultant ecologist). Informal discussions about the differing vegetation of islands in the Chatham Islands archipelago, March 2008 and June 2009.

Kerry-Jayne Wilson (Long-standing member of the Black Robin Recovery Group). Comments on draft of Chapter Four, August 2008.

# APPENDIX ONE

## Chatham Islands topography, climate and flora

The Chathams archipelago is a loosely dispersed group of oceanic islands formed from a combination of prolonged volcanism and episodic submergence and uplift. The principal islands in the group are generally low-lying—none exceeds an elevation greater than 294 metres a.s.l. The high points indicate centres of ancient volcanic action, most evident today in the precipitous cliffs on weather (southern and western) shorelines and in the steep topography of many of the outer islands. The group's two major landmasses—Chatham Island *Rekohu/Wharekauri* (90040 ha) and Pitt Island *Rangiauria* (6325 ha)—are permanently inhabited. Numerous outliers of varying sizes are distributed around these two large islands, most at the southern extremity of the group, but only four possess woody vegetation cover of significant stature (Little Mangere Island, 8-9 ha; Mangere Island, 113 ha; Rangatira (South-East) Island, 218 ha; and Star Keys, c.10 ha).

The archipelago straddles latitude 44°S where it is exposed to persistent salt-laden winds from the south and west known as the 'Roaring Forties'. The group's landmasses are of insufficient area to generate their own weather, which is strongly determined by the marine winds and the shifting convergence nearby of warm sub-tropical and colder subantarctic waters (the Subtropical Convergence). The climate is temperate and noted for its rare inconsequential frosts, mid-summer droughts and frequent gales throughout the year. Rain falls often, is localised, occasionally heavy and prolonged, and varies annually from 715-1050 mm (Cockayne, 1901; Roberts *et al.*, 2007). Temperatures average 11°C year-round (extremes range from 0°C to more than 20°C; see also Chapter Six: Table 6.8), and high summer humidity often exceeds 80% (Thompson, 1983; Atkinson, 1996).

The indigenous flora of the Chathams possesses an unusually high degree of diversity and endemism (11%, 47 of 435 native taxa, all plant categories; Amanda Baird, pers. comm., May 2008), as is typical of islands isolated geographically and in geological time from mainland or continental landmasses. It also exhibits an unusual mix of plants related to species in the warmer northern and colder southern or subantarctic regions of New Zealand. Wind- and salt-tolerant forest appears to have been a dominant vegetation type prior to human contact (Cockayne, 1901) but tree species are relatively few in comparison with the marked diversity of shrubs, herbs and ferns in the flora (Given, 1996).

### How typical are present-day habitats?

The present-day forests of Mangere and Rangatira Islands do not resemble the more structurally and floristically diverse habitats elsewhere in the island group. Chatham and Pitt Islands, which would have supported the largest populations of black robins, were mantled historically in a locally variable mosaic of forest, shrub- and wetlands (Dieffenbach, 1841; Cockayne, 1901; King, 1989). The original character of these communities was strongly influenced by drainage and soil-type (Amanda Baird, pers. comm., May 2008).

The pre-human character of the vegetation in which black robins evolved is difficult to discern precisely because—with the few uninformative exceptions on the smallest, inhospitable outliers—the types and distribution of plant communities throughout the archipelago have been modified significantly since human arrival at least five to six centuries ago (McFadgen, 1994; Holdaway, 1999). Moriori, the original East Polynesian colonisers, were responsible for the peat fires noted by Europeans in 1807 (Richards, 1982) but the degree to which Moriori were living in regrowth forests at the time of European contact is uncertain. The Maori who arrived in 1835 (King, 1989) lit extensive fires and permitted their cattle, horses and abundant pigs to roam at will (Travers, 1868). These reducing effects augmented the intensive and more systematic land-use changes associated with the pastoral farming of a growing European population.

The historical processes of change have been compounded by the introduction of 366 exotic plant taxa (Amanda Baird, pers comm., May 2008) and feral browsers such as Australian brush-tailed possums. Introduced predators—cats, mice, rats (in order of arrival) *Rattus exulans, R. norvegicus, R. rattus,* pigs and weka—are also likely to have modified habitat character by eliminating key ecological associates such avian and reptile seed-dispersers, insect pollinators and the densely populated oceanic petrel communities which acted as abundant sources of marine nutrients.

Henry Travers (1868) reported that Pitt Island was all but fully covered in bush at the time of his visit (1863-64) but says very little about its character, aside from comments on the prevalence of introduced weeds. A comment on the richer collecting opportunities on Pitt Island (Travers, 1868: 176) suggests that the bush there might have fared better than on Chatham Island. On Chatham Island, Travers encountered evidence of a once extensive bush cover in the many impenetrable remnants and in the massive trunks of an old-age forest buried deep within the peat at some sites. Cockayne (1901) describes a range of vegetation communities on Chatham Island differing in type and composition from north to south according to elevation, topography, drainage and climate. Akeake, the tree daisy *Olearia traversii*, was common in almost all forested localities, often alongside other canopy species such as ribbonwood *Plagianthus chathamicus,* matipo *Myrsine chathamica,* karamu *Coprosma chathamica*, hoho *Pseudopanax chathamica*, mahoe *Melicytus chathamicus,* kopi *Corynocarpus laevigatus,* and tarahinau *Drachophyllum arboretum*. These species also feature in the canopy structure of Pitt Island forest remnants.

In contrast, the pre-human composition of vegetation cover on Mangere and Rangatira Islands is not well known since no naturalists visited before browsing animals were first introduced—on Rangatira Island: pigs before 1831, sheep in 1841, goats c.1842 (Richards, 1982); on Mangere Island: goats and rabbits perhaps as early as the late 1850s (see Chapter Three: *Section 3.5*). The character of vegetation communities of both islands was obscured thereafter by 120 years of dissembling change induced by the periods of intensive pastoral farming (goats, sheep, cattle), the deleterious impacts of which were exacerbated by burning, systematic clearing for cropping and later periods of over-grazing (Chapter Three). The cumulative effects of farming caused forest desiccation, local fragmentation, canopy collapse and soil erosion (Bill Carter, pers. comm; Bell, 1953; Ritchie, 1970; Richards, 1982; Roberts, 2004).

There are compelling indications that vegetation on both islands was originally more diverse than it is today. Drummond (1910a) attributes to Henry Travers a single generalising statement about Mangere Island: ‘At the time of Mr Travers’s visit [September 1871], [Mangere Island] was covered densely with forest, of the same kinds as are found on other members of the Chathams group’.[45] The original woolshed on Rangatira Island was built from the trunks of mature tree-ferns, the great number of which suggests that they were harvested on the island (*Figure 1A*). Tree-ferns *Dicksonia squarrosa* are still present but

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[45] This reported statement is at odds with an earlier reference to the island’s bush, though that description is more a matter of inference. In Travers and Travers (1872: 214), Henry Travers says that Pitt Island possesses bush ‘of the same class as that on the main [Chatham] island’ but does not say the same of Rangatira and Mangere Islands in the sentences which follow immediately.

very rare on Rangatira Island (Bell, 1953; Taylor, 1991) [46] and are not recorded on Mangere Island (pers. obs.). Likewise, kopi are rare on Rangatira Island and were absent entirely from Mangere Island in the mid-1970s (Brian Bell, pers. comm.).[47] Curiously, neither island yields evidence of nikau palms *Rhopalostylis* "Chatham" which were once abundant on adjacent Pitt Island (Walls *et al*., 2000). Both islands are well within the flying range of parea, the indigenous fruit pigeon. Strongly flighted parea, the largest of avian seed-dispersers locally, were present on Pitt Island historically (Travers, 1868; Fleming, 1939b).

Drier soil conditions, reflected in the scarcities of ponding water, streams, peat, tarahinau (and perhaps the nikau palms), may have diminished historical similarities with the major islands. Travers refers, for instance, to the stony nature of Mangere Island (Travers and Travers, 1872). Differences in community scale certainly seem likely, and both islands were probably more drought-prone than the larger landmasses. Removal of forest cover and understorey during the farming era (Chapter Three) may have induced even drier conditions which are inhibiting the recovery of the moisture-demanding tree-ferns and kopi. Oceanic petrels are strong determinants of vegetation type and structure, as Flack (1976a) remarked of Little Mangere Island's declining forest cover. Nocturnal burrowing constantly ploughs the soil and the nightly ground-activities of petrels can sweep the forest floor clear of seedlings and leaf litter.

On Mangere Island which is now predominantly covered in a deep sward of introduced grasses, burrowing is concentrated in the small area of forest inhabited by the black robins

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[46] Isolated examples of tree-ferns (about one metre high) may now be found on sheltered forest margins near the woolshed and around the perimeter of Kokopu Swamp, indicating that recovery is underway. Solitary dead stems of mature tree-ferns have been encountered during Chatham Island petrel field-work in the Top Bush (Graeme Taylor, pers. comm.). *Cyathea cunninghamii,* another more drought-intolerant tree-fern species present in the Chatham Islands, is not recorded at all on the island (Taylor, 1991).

[47] Logan. C. Bell photographed dying kopi trees on the west coast of the island (apparently on the coastal slope above Skua Gully) in January 1953 but did not mention how widespread kopi were elsewhere in the bush (Bell, 1953). By 1983-84, kopi trees were extremely rare on the island. Berries collected from two large trees just inside the entrance of the Woolshed Bush were widely scattered in the Woolshed Bush and Top Bush by Geordie Murman, a New Zealand Wildlife Service (NZWS) officer working on the black robin cross-fostering programme (Murman, pers. comm.). There were no kopi trees on Mangere Island when the NZWS reforestation programme began in the mid-1970s. In the late 1970s, Brian Bell and Peter Fisher (NZWS) distributed half a sack of kopi berries among replanted akeake trees in the Douglas Basin and at the southern end of Robin Bush. The berries were harvested from the Weisner property at Kaingaroa, northern Chatham Island (Brian Bell, pers. comm.).

(Robin Bush). On Rangatira Island, however, the ‘ploughing’ of soil is a dominant feature of the forest environment (Roberts, 2004; Roberts *et al.*, 2007). Millions of oceanic petrels breed on the island (West and Nilsson, 1994) in densities which may be unnaturally high as a consequence of habitat loss elsewhere in the archipelago. The cumulative effects of burrowing and seedling mortality may restrict the range of tree species on both Mangere and Rangatira Islands to those capable of persisting on dry, unstable, nutrient-saturated soils.

The degree to which the recovering vegetation communities on Mangere and Rangatira Islands were naturally simpler in structure and diversity than those on neighbouring islands awaits clarification (Geoff Walls, pers. comm.). If they are atypical of pre-human habitats today, it does not follow necessarily that they are sub-optimal. Aside from their superior invertebrate communities (a product of the marine nutrients conveyed ashore by petrels and the absence of introduced predators), areas of closed canopy are more extensive than in the diverse and mixed-height bush remnants on Pitt Island today. Browsing and competing land-uses no longer inhibit regeneration. As Chapter Two has outlined, these qualities are important for black robin persistence. Ultimately, what constitutes typical black robin habitat will not be understood until population densities in the transitional forests of Mangere and Rangatira Islands can be compared alongside those in restored, protected and predator-free habitats on the larger islands.

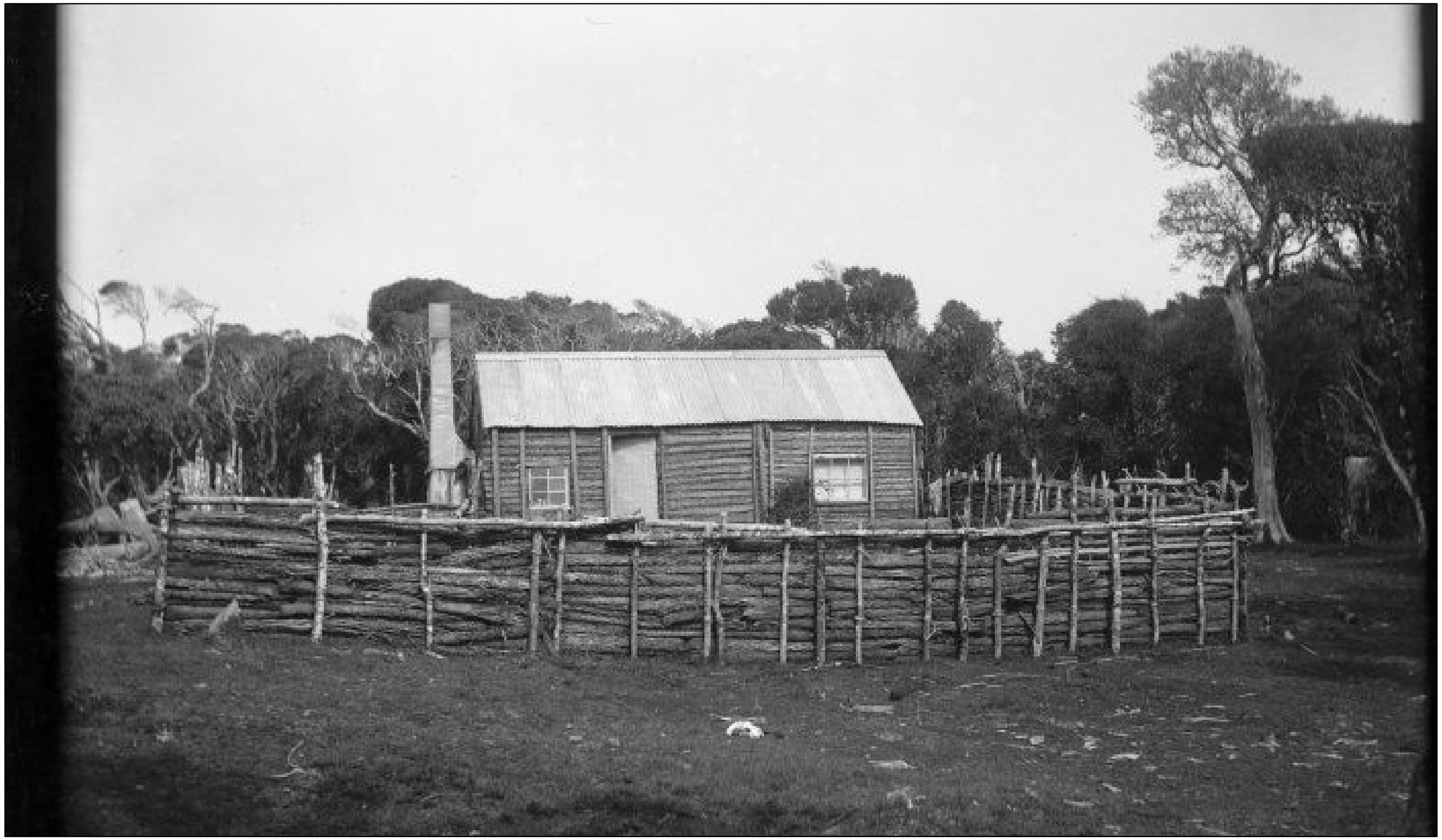
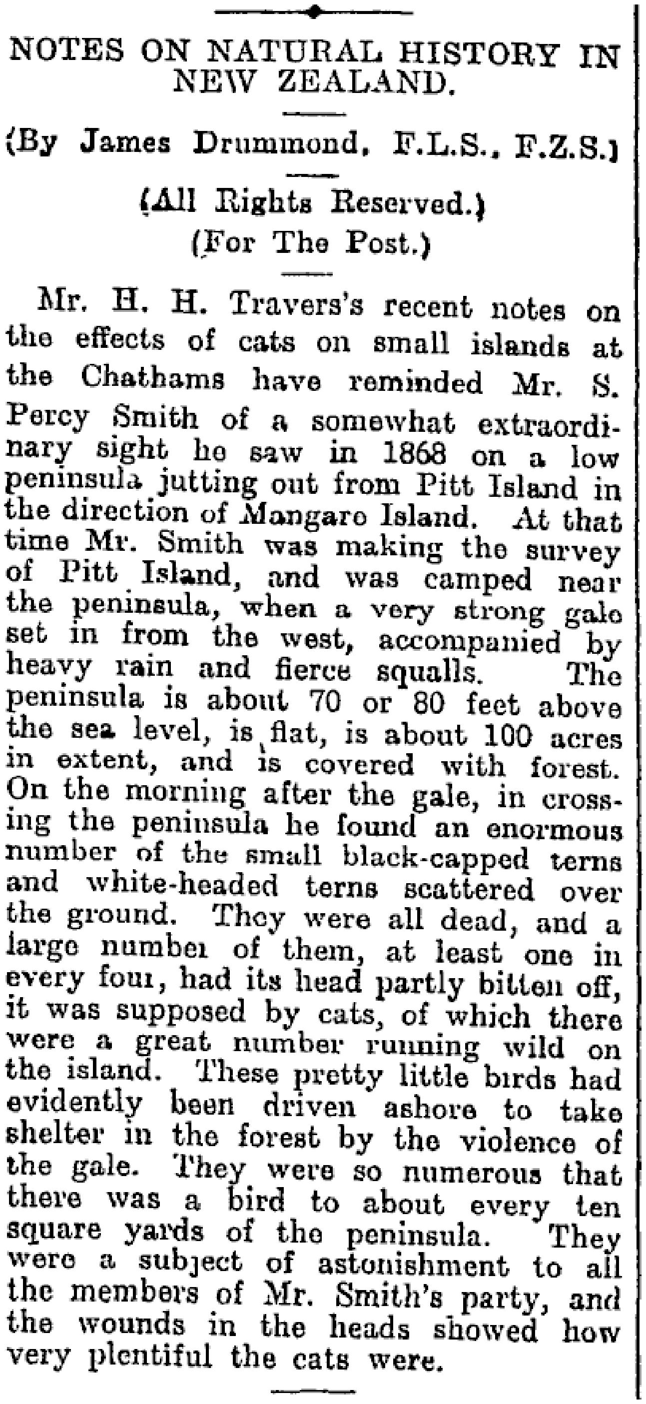


Figure 1A Tom McClurg’s woolshed on Rangatira Island in about 1915. According to farming historian Bill Carter, the use of pungas (tree-fern trunks) was a traditional form of construction in the Chatham Islands. Pitt Islanders believe that tree-ferns were plentiful enough on the woolshed flats of the island to supply the quantities used for the shed and surrounding fence. McClurg was also a fisherman but there is no evidence that he shipped the pungas across from Pitt Island (Carter, pers. comm.). *Photo: National Digital Heritage Archive (No. 1/2-037648), Alexander Turnbull Library*

# APPENDIX TWO

## Mr S. Percy Smith’s account of feral cat abundance on Pitt Island in 1868

From the newspaper column *In Touch with Nature: Notes on Natural History in New Zealand* (Drummond, 1910b).



### NOTES ON NATURAL HISTORY IN NEW ZEALAND.

(By James Drummond, F.L.S., F.Z.S.)

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(For The Post.)

Mr. H. H. Travers's recent notes on the effects of cats on small islands at the Chathams have reminded Mr. S. Percy Smith of a somewhat extraordinary sight he saw in 1868 on a low peninsula jutting out from Pitt Island in the direction of Mangaro Island. At that time Mr. Smith was making the survey of Pitt Island, and was camped near the peninsula, when a very strong gale set in from the west, accompanied by heavy rain and fierce squalls. The peninsula is about 70 or 80 feet above the sea level, is flat, is about 100 acres in extent, and is covered with forest. On the morning after the gale, in crossing the peninsula he found an enormous number of the small black-capped terns and white-headed terns scattered over the ground. They were all dead, and a large number of them, at least one in every four, had its head partly bitten off, it was supposed by cats, of which there were a great number running wild on the island. These pretty little birds had evidently been driven ashore to take shelter in the forest by the violence of the gale. They were so numerous that there was a bird to about every ten square yards of the peninsula. They were a subject of astonishment to all the members of Mr. Smith's party, and the wounds in the heads showed how very plentiful the cats were.

# APPENDIX THREE

## Alternative date for black robin extirpation on Pitt Island

### Conversations with Pitt Islanders Kenneth Lanauze (10 June 2009) and Robert Gregory-Hunt (30 June 2009)

Kenneth (Dorse) Lanauze is a Pitt Islander and nephew of Sam Gregory-Hunt whose account of seeing black robins on Pitt Island in summer 1938-39 is recorded in Aikman (2002). Kenneth knows the small piece of bush in which his uncle said he saw the black robins. The bush, of which only inconsequential fragments exist now, was situated at the neck of the small peninsula on the north-western corner of Pitt Island (Tarawhenua Point; *Figure 3A*). It lay directly across the narrowest part of the peninsula from Paremata Cove (the Boat Harbour) and faced Mangere Island which is approximately 2.8 km distant. In Kenneth's recollection, the bush comprised mostly low matipo and *Muehlenbeckia* vine but this may not be indicative of its form and composition in 1938-39.

Kenneth understands that two other Pitt Islanders, Laurie Smylie and Bert Hunt, had also encountered black robins on Pitt Island at about the same time. Bert Hunt was a generation older than Gregory-Hunt. He was mustering sheep to the old Waipaua sheep-yards south of the Waipaua Stream, on the island's south-east coast. Hunt is said to have seen black robins in bush near the keketehere *Olearia chathamica* 'clears' in the south-east corner of the Waipaua Block. Smylie farmed at Waihere on the island's west coast, overlooking Mangere Island. He was Gregory-Hunt's age and a descendant of the island's Paynter family. Smylie knew of black robins in bush closer to Paremata Cove, between Kaingaroa Head and Waihere Head hill. Bill Carter believes that this might be the bush present near the grave-site of Steve Gregory-Hunt, in the vicinity of the Rauceby homestead. Kenneth Lanauze has no recollection of when black robins were last seen at any of these sites, or of how many were seen.

Robert Gregory-Hunt, a Pitt Islander who left the island in 1957, is also certain of seeing black robins in the matipo bush on Tarawhenua Point up until at least 1942. I asked him to describe black robins and tomtits, which he did with a reasonable degree of accuracy. The black robins were 'black all over… not a patch of lighter colour anywhere'. He says he saw them many times while working with his father in that part of the farm.

I asked Kenneth and Robert why they thought it was that Charles Fleming did not learn of the black robins on Pitt Island when actively searching for them in 1937-38. Robert felt that Fleming may have spoken with locals who took no interest the island's birdlife. Kenneth's response was that Pitt Islanders have always been very cautious about sharing local knowledge with outsiders. Both are plausible explanations, but Fleming's travelling companion and climbing guide, Alan Wotherspoon, was an adventurous ornithologist and local teacher who had interacted with Pitt Islanders on numerous occasions. Presumably he would have known the best local sources of bird information. Wotherspoon also made bird observations on Pitt Island a year later, in the summer of 1938-39 when Sam Gregory-Hunt said he had encountered black robins (Fleming, 1939c). Equally, the range of other local contacts Fleming had at that time suggests that local knowledge of black robins would have to have been extremely well guarded.

As soon as Fleming arrived in the Chatham Islands, he asked Chatham Islanders as to whether and where the black robins were still in existence (McEwen, 2005). Fleming also communicated with Pitt Islanders or people who knew Pitt Island well. He was advised locally and extensively on bird matters by Robert Paynter who had been raised on Pitt Island but was by then domiciled at Kaingaroa on Chatham Island (Fleming, 1939a, b, c). He was also advised by Dick Clough who had strong family connections with Pitt Island. Clough took him by boat to his island destinations. And Terry Prenderville who went ashore with Fleming on Little Mangere Island was connected by birth with Pitt Island families. Moreover, Fleming spent a morning making bird observations on Pitt Island with Wotherspoon and Graham Turbott, a young ornithologist from New Zealand, just a few days before the momentous ascent of Little Mangere Island (McEwen, 2005). It is difficult to comprehend how the existence of black robins on Pitt Island up to that time—even in small numbers—could have been unknown to or kept secret by so many locals.

### Buller (1890) reference to black robins on Pitt Island

Buller (1890: 37) says in reference to the disjunct distribution of 'black robins' in the Chatham Islands and more distant Snares Islands that '[the black robin] occurs on the Chatham Islands, and on Pitt's Island, adjacent thereto'. This single allusion to Pitt Island has the ring of a generalising statement. It contradicts specialist first-hand knowledge of that time that black robins were found only on Mangere Island (Travers and Travers, 1872) and Buller's own statements that the robin was absent from both Chatham and Pitt Islands (Buller, 1888). A possible explanation is that Buller treated Mangere Island as an adjunct to 'Pitt's Island', a misconception encouraged perhaps by references to it (and Rangatira Island) as merely one 'of several small rocky islets' in the vicinity (Travers and Travers, 1872: 213). Any confusion of island names, especially by people who had not visited the southern part of the Chathams archipelago, could explain the later mis-labelling of the black robin specimens Travers obtained from Mangere Island in 1871 (see above; Alan Tennyson, pers. comm.). In my view, no weight can be placed on Buller's 1890 statement.

### 1909 description of 'robins' on Pitt Island

The strongest support for Sam Gregory-Hunt's contention comes from R (Robert) E. Paynter, a Pitt Island resident, who is reported in a newspaper column of 1909 as saying that 'robins' were still common on the island despite the ease with which cats killed them (Drummond, 1909). The article is reprinted below.[48] Like his father Richard, Robert Paynter was a part-time collector and amateur naturalist (Broun, 1910). At face value, his description of the 'robins' is compelling, though his reliability as a bird observer is called into question by his mention of broken-wing displays by parents protecting nests. Paynter may have used the wrong terminology.

Distraction displays of this sort have not been recorded during the many latter-day nest-inspections of black robins (collated data; pers. obs.). But Buller (1888 (2): 41) records his own observation of a North Island tomtit female 'fluttering away with wings outstretched and quivering, as if unable to fly, and apparently to divert attention from the nest.' And on Little Mangere Island, Flack (1976a: 28) noted that black robin adults sometimes showed distress at his proximity to nests through 'calls or mildly agitated flights, once with momentary partial opening of the wings'. Paynter may have witnessed similar agitation.

Because Paynter's description of 'robin' nesting and parental behaviour could readily apply to tomtits, I asked Kenneth Lanauze and his wife Judy whether Pitt Islanders used the generic term 'robins' to refer to tomtits. Both assured me that no such generalising term

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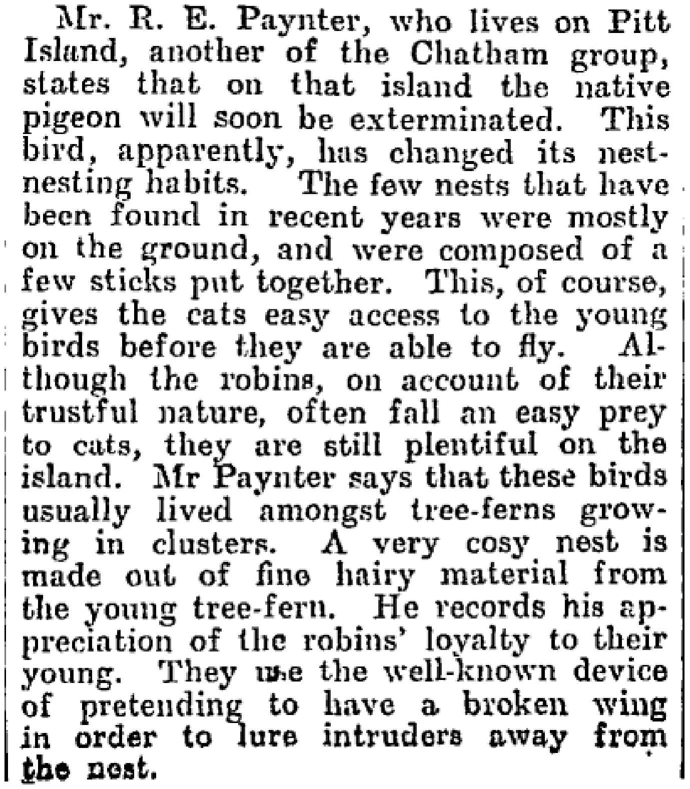
[48] The article is a second-hand account, leaving open the possibility of misreporting, but the column itself was moderated by noted New Zealand naturalist, James Drummond, who might be expected to have known the difference between black robins and tomtits.

was part of local vernacular and that Pitt Islanders then and now would know the difference between the two birds.



Mr. R. E. Paynter, who lives on Pitt Island, another of the Chatham group, states that on that island the native pigeon will soon be exterminated. This bird, apparently, has changed its nestnesting habits. The few nests that have been found in recent years were mostly on the ground, and were composed of a few sticks put together. This, of course, gives the cats easy access to the young birds before they are able to fly. Although the robins, on account of their trustful nature, often fall an easy prey to cats, they are still plentiful on the island. Mr Paynter says that these birds usually lived amongst tree-ferns growing in clusters. A very cosy nest is made out of fine hairy material from the young tree-fern. He records his appreciation of the robins' loyalty to their young. They use the well-known device of pretending to have a broken wing in order to lure intruders away from the nest.

This is not to say that Paynter did, and we should be careful not to impute today's greater familiarity with the species to Paynter's time. If indeed black robins were confined to Little Mangere Island by that time, local consciousness of them may have been no more than mere understanding that they existed there. On Pitt Island, Paynter's need to differentiate between black robins and tomtits may therefore have been less obvious to him.

Fleming (1939b) offers evidence that Paynter might have known black robins through personal experience of them. He reports (1939b: 509) that 'Mr R. Paynter' had seen several pairs of Chatham Island bellbirds on Little Mangere Island in 1906.[49] Paynter could not have missed the black robins there unless he did not climb to the top of the island or they were in very low numbers at that time. Curiously, Fleming says earlier (1939b: 507) that

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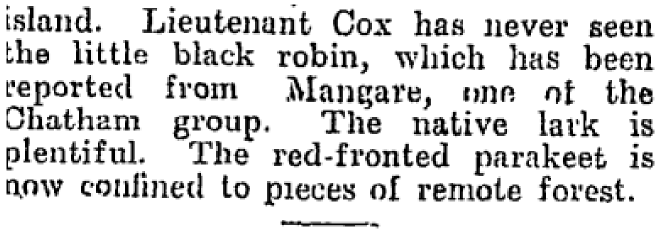
[49] Fleming is taken to be referring to Robert Paynter here and not to his father Richard, who died in 1933. Doubt about which of the two was on Little Mangere Island arises solely from Fleming's qualifying statement (1939b: 509) that Paynter knew the bellbirds 'well in the 'eighties from Pitt Island.' Robert Paynter was born in 1879 (Bill Carter, pers. comm.) and would only have been 10 years old by the end of the 1880s.

the black robins had ‘not been authentically recorded for about thirty years’. In fact, allowing for first published reports of extirpation on Mangere Island as early as 1894 (Buller, 1894a), the time elapsed is actually closer to 45 years. Fleming’s ‘thirty years’ hints at the possibility that Paynter may have mentioned seeing black robins on Pitt Island in or prior to 1909. Whatever Paynter may have communicated, Fleming makes nothing of it, perhaps through scepticism, because he goes on to say that he has been told by islanders that the black robin was still present on Little Mangere Island at the time of his visit in 1937-38. Fleming’s expedition companion, Turbott, does not recall Fleming mentioning alterative survival sites and is sure that he would have said so had he been told of any (Graham Turbott, pers. comm.).

Paynter’s allusion to robins on Pitt Island in 1909 is itself contradicted in the same newspaper column (Drummond, 1909). Reporting the conspicuous decline of birds on Chatham Island, Whangamarino resident and noted plant naturalist F. A. D. Cox implies that the black robin is confined solely to ‘Mangare’ (by which presumably he meant Little Mangere Island).



island. Lieutenant Cox has never seen the little black robin, which has been reported from Mangare, one of the Chatham group. The native lark is plentiful. The red-fronted parakeet is now confined to pieces of remote forest.

## Discussion

Other than the anecdotal accounts of Paynter and latter-day Pitt Islanders, I have not been able to find evidence which contradicts the views of eminent naturalists and ornithologists that black robins had disappeared from Pitt Island by 1863. To be fair, extirpation of black robins can only be inferred from the latters’ reports—none states explicitly that black robins no longer existed on Pitt Island. However, these individuals visited the Chatham Islands in the spirit of scientific inquiry to collect black robins and other vanishing species before it was too late, or were corresponding with Chathams bird collectors such as Charles Traill, W. Hawkins and Henry C. Palmer, some of whom were actively searching for black robins on their behalf (Travers, 1868; Travers and Travers, 1872, Forbes, 1893, Rothschild, 1907, Fleming, 1939a, b).

Other evidence weighs against the probability of black robins surviving on Pitt Island into the 20th century. Similarly vulnerable sympatric species such as the Chatham Island fernbird and Chatham Island rail (Tennyson, 2004) were extinct on all islands in the group by 1894 (Buller, 1894a). Feral cats were so numerous on Pitt Island that 19th- and early 20th-century observers felt obliged to comment. The black robins were extirpated from Mangere Island very soon after cats were introduced. And the low reproductive output of the species suggests greater vulnerability to decline and extinction than in other New Zealand (or Australian) *Petroica* (Chapter Two). The processes of forest decline on Pitt Island were well in train before the turn of the 19th century. Photographs of Paremata Cove in the late 1880s also show disintegrating forest cover in which the margins are in retreat, the understorey has become exposed by wind and livestock, and soil is eroding (*Figures 3B* and *3C*).

There are possible explanations for the black robin reports of Paynter, Gregory-Hunt, Hunt and Smylie.

- The most parsimonious explanation is that the black robins seen by all Pitt Islanders were tomtit males. Present-day black robin workers glimpsing the black dorsal plumage of male tomtits are often convinced that they have seen black robins (pers. obs.). However, this explanation assumes that the Pitt Islanders could not distinguish tomtits from black robins under any circumstances. If some (the older Bert Hunt perhaps) had harvested *titi* (sooty shearwaters) from Little Mangere Island instead of the more readily accessed Mangere and Rangatira Islands, then this assumption is certainly unfounded. Sam Gregory-Hunt's estimate of '15-16' black robins also suggests a lower probability of making this mistake, unless of course he was counting the same birds several times—a difficulty confounding all black robin observation until every bird was individually marked (first achieved in 1974-75).

- Black robins did survive on Pitt Island. This explanation is difficult to support if it is taken to imply that the black robins seen just before World War II were remnants of the original population. The combined effects of mammalian predators and hostile change in habitat quality on Pitt Island were more profound than those likely to have extirpated the black robins on Chatham Island and Rangatira Island. In addition to the loss of eggs and nestlings to cats, predation of adults would have deprived the black robins of breeder longevity, their last biological advantage (Chapter Two). Apart from Robert Paynter's reference in 1909, no other observations of black robins on the island are reported (anecdotally or otherwise) since Travers's visit in 1863-64 (Travers, 1868). This was a period in which interest in collecting rare species remained high. Fleming was still collecting rare species in 1937-38 (Fleming 1939a, b; McEwen, 2005), and Paynter himself could hardly have overlooked the considerable commercial value of black robins if, as his other collecting activities suggest (Broun, 1910), he was obliged to supplement his income (Bill Carter, pers. comm.).

- The black robins seen were vagrants. If so, the birds reported by all Pitt Islanders could only have come from Little Mangere Island, perhaps via the largely tree-less, cat-populated Mangere Island (2.4 km from Pitt Island at its closest point), or from a vestigial population on Rabbit Island (300 metres distant from Tarawhenua Point; *Figure 3A*). The latter is unlikely since any black robin population on the tiny Rabbit Island (*terra nullis*) would soon be apparent to locals harvesting *titi* annually, just as they do today. The possibility of dispersal (natural or storm-induced) from Little Mangere Island would be stronger if the birds had been seen in a single location on Pitt Island. To disperse to several locations and be noticed, vagrant black robins or populations would require multiple migration events or a long lag-time until the descendants of a recolonising pair became sufficiently numerous. Despite very close contact with the black robins since 1980-81, there is no verified instance of individuals dispersing across water or being blown from forests during storms.

- The black robins were translocated to Pitt Island from Little Mangere Island. There is no evidence to support this and no-one has claimed the achievement itself or knowledge of it.

It would be poor science to dismiss the 20th-century extirpation date unequivocally. Until further information is available, however, it is difficult to reconcile the biological evidence with any of the possible explanations offered here. That evidence is a combination of expert historical knowledge and the significantly more advanced understanding we have of black robin biology today. But like the lay-person, experts are fallible and there is much to learn about black robins yet. For the meantime, the weight of evidence favours an extirpation date on Pitt Island prior to 1863 more strongly than a later termination date.

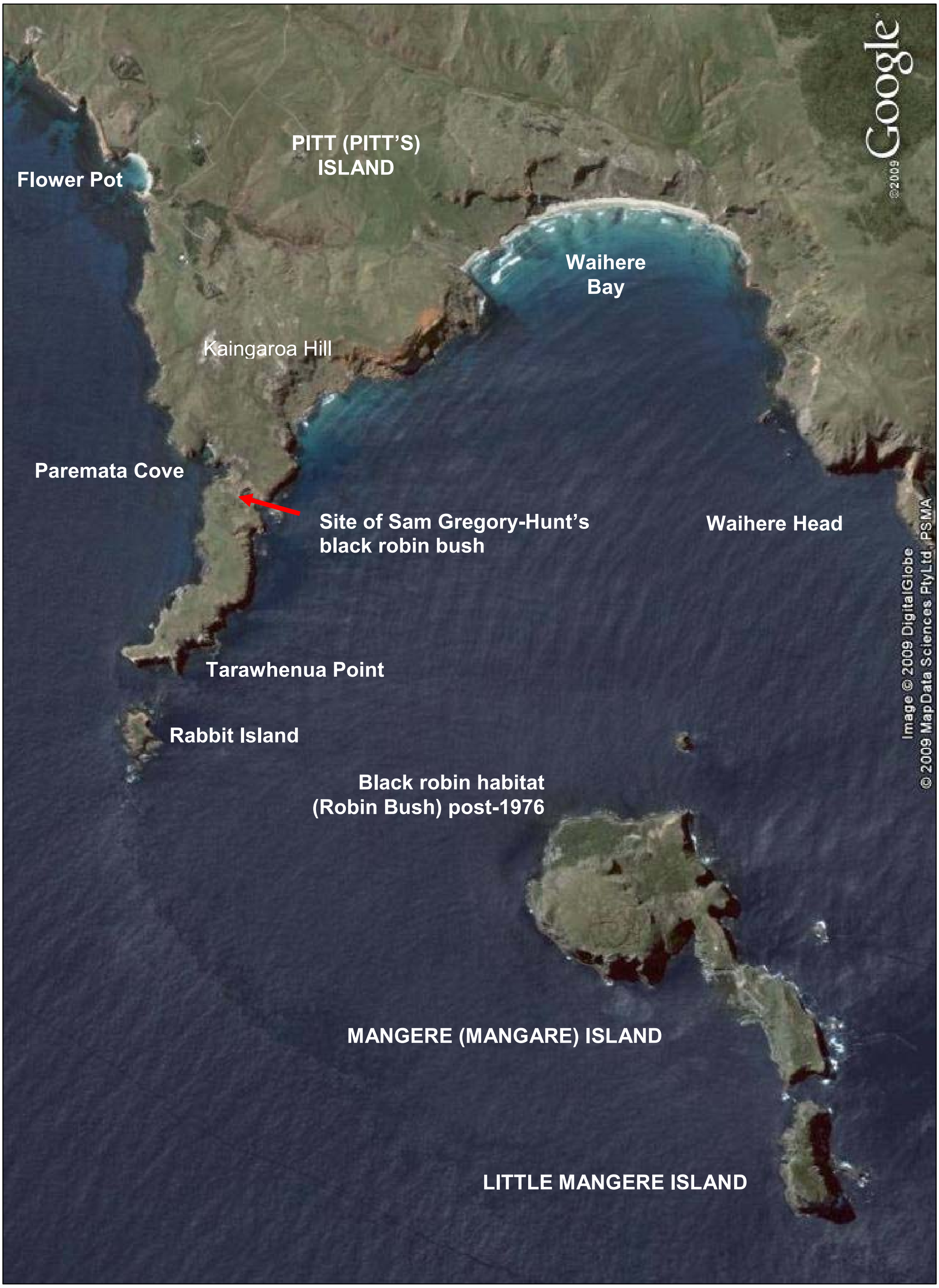


Figure 3A Site on Pitt Island in which Sam Gregory-Hunt was working with his father when he saw '15-16 black robins' in summer 1938-39 (Kenneth Lanauze, pers. comm.).

*Source: Google™ Earth*

Figure 3B Photograph of Paremata Cove (the Boat Harbour), Pitt Island, c.1888. Mangere Island is out of view at the far left (see *Figure 3C*). The peninsula leading to Tarawhenua Point (upper right) retains forest cover but, as is evident from the bush in the foreground, may be lacking an understorey. I am indebted to Bill Carter for drawing my attention to this photograph.

*Photo: Te Papa (http://collections.tepapa.govt.nz)*

Figure 3C Photograph of Paremata Cove (the Boat Harbour), Pitt Island, c.1888, with Mangere Island on the distant horizon. The bush in which Sam Gregory-Hunt believes he saw black robins in summer 1938-39 was a remnant of the bush visible on the hillside at the right of the picture.

*Photo: Te Papa (http://collections.tepapa.govt.nz)*

# APPENDIX FOUR

## Supplementary Figures and Tables for Chapter Six

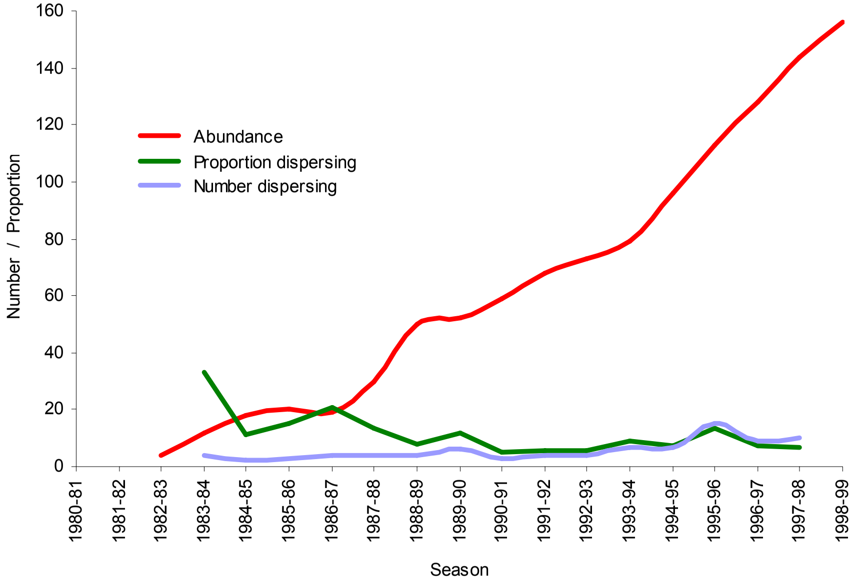


Figure 4A Trends in the numbers and proportions of black robins in all age- and sex-classes dispersing naturally to the Woolshed Bush from the Top Bush (Rangatira Island) relative to post-breeding abundance in the latter, 1980-81 to 1998-99.

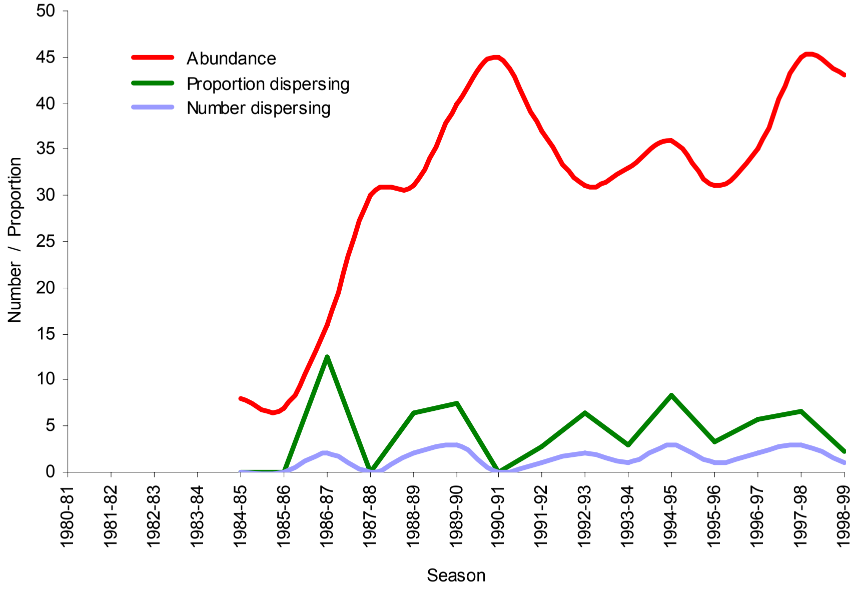


Figure 4B Trends in the numbers and proportions of black robins in all age- and sex-classes dispersing naturally to the Top Bush from the Woolshed Bush (Rangatira Island) relative to post-breeding abundance in the latter, 1980-81 to 1998-99.

Table 4A Micro-climate data-logger sites on Mangere and Rangatira Islands, 1 October 2004 to 17 February 2006

| **Logger** | **Island** | **Sub-habitat** | **Installation site** | **Aspect** | **Substrate and Vegetation** |
|---|---|---|---|---|---|
| 1 | Rangatira | West Woolshed Bush | West Woolshed Bush track, 30m west of Annex junction | $3^{o}$ slope, $80^{o}$ mN aspect | Soil<br>Plagianthus canopy 6–8m<br>Myrsine/Melicytus sub-canopy<br>Macropiper/Myrsine understorey<br>Open forest structure |
| 2 | Rangatira | Central Woolshed Bush | South Cross track, 15m along from Summit track junction | $5^{o}$ slope, $350^{o}$ mN aspect | Soil<br>Plagianthus/Myrsine canopy 10+m<br>Myrsine/Melicytus/supplejack sub-canopy,<br>Open forest structure |
| 3 | Rangatira | East Woolshed Bush | Lower Long Drop track, 30m north of G+G track junction | *Slope / aspect not measured* | Soil<br>Plagianthus canopy 6–8m<br>Melicytus sub-canopy<br>Dense forest structure |
| 4 | Rangatira | Top Bush | Upper Long Drop track, 70m down from Rangatira Trig track junction | *Slope / aspect not measured* | Soil<br>Olearia/Plagianthus canopy 6–8 m<br>Melicytus sub-canopy<br>Macropiper understorey<br>Dense forest structure |
| 5 | Rangatira | Top Bush | Upper Marlesh track, 100m from Summit track junction; 5m downhill from CP #213 | $5^{o}$ slope, $360^{o}$ mN aspect | Soil<br>Olearia/Plagianthus canopy 7–10m<br>Melicytus/Macropiper/Myrsine sub-canopy<br>Dense forest structure |

Table 4A continued

| Logger | Island | Sub-habitat | Installation site | Aspect | Substrate and Vegetation |
|---|---|---|---|---|---|
| 6 | Rangatira | Top Bush | Fran & Rua track, opposite Swamp track junction | $5^{o}$ slope, $122^{o}$ mN aspect | Soil<br>Plagianthus canopy 8–10m<br>Melicytus sub-canopy<br>Macropiper/Pseudopanax understorey<br>Moderate density forest |
| 7 | Mangere | Robin Bush | Mid track, at MD 20 tag | $10^{o}$ slope, $40^{o}$ mN aspect | Boulder field<br>Olearia canopy 6–8m<br>Melicytus sub-canopy<br>Mod–open density forest |
| 8 | Mangere | Robin Bush | Main track, at Rocky Road track junction | $40^{o}$ slope, $45^{o}$ mN aspect | Boulder field<br>Plagianthus/Olearia canopy 6m<br>Melicytus sub-canopy<br>Moderate density forest |
| 9 | Mangere | Robin Bush | 20m downhill from Main track south (below MS 240 tag) 100m from southern bush entrance; by 10 Downing Street robin nest box | $45^{o}$ slope, $60^{o}$ mN aspect | Boulder field<br>Olearia canopy 6–10m<br>Melicytus sub-canopy<br>Moderate density forest |

Table 4B Pre- and post-breeding census counts by age-class and sex in the three black robin populations on Mangere and Rangatira Islands, 1980-81 to 2001-02. Sex assignments are accurate for almost all adults. The sex of yearlings and juveniles dying before breeding (32.9% of the total) is estimated from nestling weights or post-fledging behaviour. The line drawn after 1989-90 represents the transition from intensive management to post-management monitoring. Population figures for 2007-08 to 2008-09 are the most reliable estimates available from the eight seasons following the complete cessation of full-population monitoring in 2001-02 (second line). Age-classes are unknown for these seasons.

| | **PRE-BREEDING** | | | | | | | | | | | | | **POST-BREEDING** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Mangere** | | | | **Woolshed Bush** | | | | **Top Bush** | | | | | **Mangere** | | | | **Woolshed Bush** | | | | **Top Bush** | | | | |
| | **Adult** | | **Yearling** | | **Adult** | | **Yearling** | | **Adult** | | **Yearling** | | | **Adult** | | **Juvenile** | | **Adult** | | **Juvenile** | | **Adult** | | **Juvenile** | | |
| **Season** | **M** | **F** | **M** | **F** | **M** | **F** | **M** | **F** | **M** | **F** | **M** | **F** | **Total** | **M** | **F** | **M** | **F** | **M** | **F** | **M** | **F** | **M** | **F** | **M** | **F** | **Total** |
| 1980-81 | 2 | 2 | | 1 | | | | | | | | | **5** | 2 | 3 | 2 | 2 | | | | | | | | | **9** |
| 1981-82 | 2 | 2 | 1 | 2 | | | | | | | | | **7** | 3 | 4 | 1 | 4 | | | | | | | | | **12** |
| 1982-83 | 3 | 4 | 1 | 2 | | | | | | | | | **10** | 2 | 3 | | 1 | 2 | 2 | | | | | | | **10** |
| 1983-84 | 2 | 3 | | 1 | 1 | 2 | | | | | | | **9** | 2 | 3 | 1 | 1 | 1 | 2 | 6 | 3 | | | | | **19** |
| 1984-85 | 2 | 3 | 1 | 1 | 1 | 1 | 3 | 2 | | 1 | 2 | 1 | **18** | 4 | 1 | 1 | 1 | 3 | 4 | 8 | 3 | 2 | 1 | 1 | 4 | **33** |
| 1985-86 | 2 | 1 | 1 | | 3 | 2 | 7 | 4 | 1 | 2 | 2 | 2 | **27** | 3 | 2 | | 1 | 8 | 4 | 2 | 6 | 2 | 4 | 1 | 0 | **33** |
| 1986-87 | 3 | 2 | | 1 | 6 | 4 | 1 | 3 | 2 | 3 | 1 | 3 | **29** | 3 | 2 | 2 | 3 | 7 | 4 | 5 | 3 | 3 | 4 | 3 | 6 | **45** |
| 1987-88 | 3 | 2 | 2 | 3 | 6 | 4 | 2 | 2 | 3 | 3 | 5 | 4 | **39** | 5 | 4 | 2 | 1 | 6 | 7 | 9 | 8 | 6 | 6 | 8 | 10 | **72** |
| 1988-89 | 5 | 4 | 2 | 1 | 5 | 6 | 10 | 6 | 4 | 5 | 5 | 5 | **58** | 6 | 4 | 1 | 3 | 14 | 6 | 14 | 16 | 10 | 8 | 10 | 3 | **95** |
| 1989-90 | 4 | 4 | 2 | 3 | 12 | 6 | 10 | 11 | 6 | 7 | 7 | 7 | **79** | 6 | 7 | 5 | 3 | 21 | 17 | 9 | 5 | 13 | 14 | 8 | 5 | **113** |
| 1990-91 | 5 | 6 | 5 | 3 | 18 | 17 | 4 | 2 | 9 | 12 | 6 | 6 | **93** | 8 | 8 | 3 | 5 | 20 | 17 | 16 | 6 | 11 | 15 | 11 | 8 | **128** |
| 1991-92 | 8 | 7 | 2 | 4 | 18 | 16 | 10 | 6 | 7 | 11 | 7 | 4 | **100** | 10 | 9 | 4 | 3 | 26 | 20 | 10 | 12 | 14 | 13 | 7 | 3 | **131** |
| 1992-93 | 9 | 8 | 4 | 3 | 26 | 14 | 7 | 10 | 10 | 9 | 3 | 2 | **105** | 11 | 10 | 6 | 13 | 32 | 22 | 12 | 7 | 10 | 9 | 5 | 7 | **144** |
| 1993-94 | 9 | 9 | 5 | 12 | 23 | 21 | 9 | 7 | 9 | 9 | 4 | 5 | **122** | 13 | 21 | 7 | 1 | 29 | 23 | 13 | 14 | 11 | 11 | 6 | 5 | **154** |
| 1994-95 | 12 | 21 | 6 | 1 | 22 | 22 | 7 | 5 | 7 | 7 | 4 | 4 | **118** | 17 | 19 | 3 | 6 | 27 | 27 | 25 | 17 | 9 | 10 | 7 | 10 | **177** |
| 1995-96 | 15 | 17 | 3 | 4 | 22 | 24 | 19 | 14 | 8 | 7 | 3 | 6 | **142** | 18 | 20 | 8 | 10 | 37 | 36 | 22 | 18 | 11 | 12 | 4 | 4 | **200** |
| 1996-97 | 15 | 19 | 8 | 7 | 34 | 26 | 10 | 11 | 8 | 9 | 9 | 5 | **161** | 22 | 24 | 11 | 3 | 44 | 35 | 24 | 25 | 14 | 11 | 1 | 9 | **223** |
| 1997-98 | 20 | 20 | 11 | 2 | 35 | 29 | 19 | 14 | 10 | 6 | 5 | 9 | **180** | 28 | 22 | 8 | 10 | 50 | 39 | 30 | 25 | 15 | 15 | 5 | 10 | **257** |
| 1998-99 | 22 | 17 | 5 | 7 | 41 | 31 | 22 | 18 | 10 | 9 | 8 | 7 | **197** | 25 | 22 | 17 | 7 | 61 | 43 | 31 | 21 | 18 | 14 | 11 | | **270** |
| 1999-00 | 18 | 19 | 13 | 4 | | | | | | | | | **54** | 29 | 21 | 5 | 3 | | | | | | | | | |
| 2000-01 | 26 | 19 | 5 | 3 | | | | | | | | | **53** | 28 | 18 | 12 | 8 | | | | | | | | | |
| 2001-02 | 21 | 15 | 9 | 8 | | | | | | | | | **53** | 28 | 21 | 8 | 6 | | | | | | | | | |
| … | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2007-08 | | | | | ~ 87 individuals | | | | ~ 16 individuals | | | | | | | | | | | | | | | | | |
| 2008-09 | ~ 30 individuals | | | | | | | | | | | | | | | | | | | | | | | | | |

Table 4C Proportions of juveniles produced in each black robin population raised to independence by Chatham Island tomtit or black robin foster-parents during the intensive management phase, 1980-81 to 1989-90. Foster-parents were not necessarily located in a juvenile's natal population (% per foster-site).

| | | Foster-raised | | | % by foster-site | |
|---|---|---|---|---|---|---|
| | *n* Produced | % | By Tomtit | By Robin | Natal | Other |
| Mangere | 62 | 54.8 | 14 | 20 | 11.8 | 88.2 |
| Rangatira | 143 | 51.7 | 12 | 62 | 79.7 | 20.3 |
| Woolshed Bush | 75 | 57.3 | 7 | 36 | 76.7 | 23.3 |
| Top Bush | 68 | 45.6 | 5 | 26 | 83.9 | 16.1 |
| All sub-populations | 205 | 52.7 | 26 | 82 | 58.3 | 41.7 |