

**Influencing habitat selection and use through conspecific
attraction and supplementary feeding**

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Bellbirds (*Anthornis melanura*) are one of two endemic honeyeaters in New Zealand. They are still common in many parts of the country, but also rare and absent in some areas where they were abundant before. Together with tui (*Prosthemadera novaeseelandia*) bellbirds are responsible for avian pollination of several native plants in New Zealand.

Habitat fragmentation and geographical constraints prevent bellbirds from re-occupying formerly inhabited areas. After translocations birds often disperse; some just disappear, some are thought to fly back to their source site and probably many die. Supplementary feeding provides energy rich food, which helps to ensure birds are well-nourished until they can discover natural food sources at the release sites. Conspecific song playback as an attractant for many bird species can be used as public information about high habitat value and additionally lure birds to good food sources and nest sites.

Artificial feeding stations were set up at 18 locations in Kennedy's Bush, Port Hills, Canterbury, New Zealand. Feeders filled with sugar water were available for five to six consecutive days and during observation hours the effect of song playback was tested.

Variation in bird numbers resulting from experimental treatments was recorded using five-

minute bird counts prior to treatments and additional counts every minute of observation time. Bellbird numbers varied strongly with habitat types, showing highest numbers for dense and tall bush areas and close to creeks and lowest for open areas besides pasture and in post-flowering flax fields. Bellbird numbers increased when song was broadcast, with the strongest effect in areas where bellbird numbers were moderate or low, but not in areas where bellbirds were absent. Feeding stations were not observed to be used by bellbirds.

The strong response in bellbird numbers to conspecific song playback proved the attractiveness of song for bellbirds. Nevertheless, its function as a lure for bellbirds to artificial feeding stations was not shown. This contrasting result indicates that the use of bellbird song as an enticement for bellbirds has to be investigated further.

Keywords: bellbird; *Anthornis melanura*; supplementary feeding; sugar water; song; broadcast; intraspecific attraction; public information; habitat selection; Kennedy's Bush

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Arrangement of thesis

This thesis comprises five chapters, with chapters three and four representing stand-alone papers with an introduction, method, result and discussion section. A general methods chapter precedes these chapters to avoid overlap. Additional general introduction and general discussion chapters integrate the papers into a thesis format. References and appendices are positioned at the end of the thesis.

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1. General introduction

1.1. Purpose of study

a) Threats for honeyeaters (*Meliphagidae*) in New Zealand

Worldwide, habitat loss is one of the most important threats for all kinds of species. Human usage of land often ends in a highly altered landscape. 75% of New Zealand was covered in forest before human settlement. When the first Polynesian settlers arrived around 1000 years ago, human interference with the forest started. Within 850 years this impact, together with habitat loss due to climate change, volcano eruptions and natural fires, reduced the area of woodland by one third. The loss of dry conifer-broadleaf forest habitat and hunting are regarded as the reasons for moa (Fam.: *Dinornithidae*) extinctions (McGlone, 1989). Between the arrival of European settlers and today the decline went even further, down to natural forest coverage of only one quarter of the land mass. Forest clearance was mainly undertaken for farming purposes, because sheep and cattle required great areas of pasture, and also for timber harvesting (Ministry of Agriculture and Forestry, 2002). Introduced mammalian browsers like common brushtail possums (*Trichosurus vulpecula*), deer (*Cervidae*) and goats (*Capra hircus*) placed additional pressure on the remaining forest (O'Donnell & Dilks, 1994). Since these browsers were absent before European settlement, forests in New Zealand were not adapted to mammalian browsing (McGlone, 1989). As woodlands declined, other habitats were also reduced. Drainage of wetlands, for example, provided use of areas that were previously unsuitable for farming or housing (Merton, 1992).

Not only has there been loss of habitats as a whole, but also human alteration of forest has had an impact on remaining habitat quality and suitability. Birds often need specific landscape structures for different purposes like foraging, mating and breeding (Cody, 1985), and forest alteration may reduce or remove these structures. Silviculture, for example, has a major impact on forest birds. Onley (1983) found significantly fewer bellbirds (*Anthornis melanura*) in logged forest in high country and flat terrace country than in unlogged forest. Logging can be divided into coupe-logging and selective logging. Whereas the first has an effect on most forest birds, due to the decline in total amount of forest available (Spurr, Warburton & Drew, 1992), selective harvesting of only old mature trees affects the most important avian seed dispersers. Many bird species do not switch to other food sources or nest sites after their main food and/or nesting trees are logged. As a consequence such bird species disappear from these areas (O'Donnell & Dilks, 1994). For example, New Zealand pigeon (*Hemiphaga novaeseelandiae*), tui (*Prosthemadera novaeseelandiae*) and bellbird have a clear preference for old stands (Warburton, Kingsford, Lewitt, & Spurr, 1992). The latter two are also the most important avian pollinators in New Zealand.

Many New Zealand forest birds are also important seed dispersers. New Zealand's native flora has a high percentage of trees (33%) with nearly three quarters of them dispersed by birds (Anderson, Kelly, Robertson, Ladley & Innes, 2006). However, the number of bird species adapted to this task is very low with only 12 indigenous species responsible for most dispersal. For example, large fruits with a diameter of more than 12 mm are probably exclusively dispersed by New Zealand pigeon (Lee, Clout, Robertson & Wilson, 1991).

Extinction of avian species and population declines caused by habitat loss and alteration and predation of mammalian predators therefore has a negative feedback effect on the New Zealand flora, leading to additional habitat change.

A second major threat to New Zealand birds is predation by introduced predators such as cats (*Felis catus*), weasels (*Mustela spp.*) and stoats (*Mustela erminea*) and rats (*Rattus spp.*). Mammalian predators were absent in New Zealand before first human settlement. Polynesian settlers brought in kiore (*Rattus exulans*), the Polynesian rat, which not only preys on eggs and small birds but also on larger ground-nesting birds and possibly preyed on moas (Fleming, 1969). Dogs (*Canis lupus*), which were first introduced by Polynesian settlers and also later by Europeans, are also recorded preying on birds (SCN, 1951). More mammalian predators came with European settlers, and because New Zealand's endemic species did not co-evolve with these predators, they lacked appropriate mammalian anti-predator responses (Blackburn, Cassey, Duncan, Evans & Gaston, 2004). This led to the extinctions of many native species in New Zealand and major declines in other species. Atkinson and Bell (1973) found the decline of many bird species in New Zealand coincided with the spread of rats. Bellbirds, for example, disappeared from many areas where they were common when first European settlers arrived (e.g. bellbirds in Northland and Auckland (Buller, 1873, as cited in Craig & Douglas, 1984a, p. 7)). On the other hand, Massaro, Starling-Windhof, Briskie & Martin (2008) compared parental bellbird behaviour with behaviour of Australian honeyeaters, which co-evolved with a broader range of predators, and found some similarities that seem to be adaptations to minimize predation risks. However, this adaptation by bellbirds took place over 700 years and bellbirds on offshore islands without the long exposure to predation risk did not show the risk-reducing behaviours.

Reestablishment and assuring survival of native and especially endemic species are important issues in conservation. Predator control and landscape restoration of altered habitats as well as protection of existing healthy habitats provide suitable habitats and build the foundation for recolonization of habitats.

b) Translocation of honeyeaters

Translocation is an important issue for New Zealand conservation management. New Zealand has a unique flora and fauna, because it has been relatively isolated from other landmasses for 80 million years. This long period of isolation allowed many endemic species to evolve independently from ancestral species. Isolation favours the evolution of unique species, but also may increase vulnerability to threats. Endemic island species face the greatest risk of extinction. Merton (1992) noted that 90 % of recorded avian extinctions had occurred on islands and more than 50 % of threatened species were island species, even though islands comprise only 3 % of the world's land mass. Since New Zealand has many endemic species, and many were lost before and during the first hundred years of European arrival, conservationists started taking early action against loss of species.

Translocation as a conservation tool, which is defined by Griffith, Scott, Carpenter and Reed (1989) as one or more “intentional releases of animals or plants into the wild to establish or reestablish, or augment a population,” has a long history in New Zealand. The first records of translocation attempts by Richard Henry are from the 1880's. He wanted to move kakapo (*Strigops habroptilus*) to Resolution Island. Henry not only faced problems in establishing a kakapo population on Resolution Island, but also in catching and transporting the birds (Hill & Hill, 1987). Other translocations followed, but they were all not successful as for example

early translocations of North Island saddlebacks (*Philesturnus carunculatus rufusater*) failed most likely because the release sites were not suitable in regard to predator presence.

Important issues for successful translocations are safe capture techniques, transfer boxes suitable for the focal species, fast transit and soft release techniques (caging release birds for several days at the release site) (Saunders, 1995). Additionally, suitable habitats are needed with sufficient food sources, constant predator control and, if possible, predator eradication (Armstrong, 2008). Predator control might be one of the most important issues, because many failures of early translocations and bird declines are reported to have been caused by predation (Stead, 1932; Atkinson & Bell, 1973; Armstrong, 2008).

By the 1960's translocation methods were developed which allowed the successful translocation of North Island saddlebacks to Middle Chicken Island (Merton, 1965a, 1965b); these methods were applied shortly afterwards, in 1964, to the South Island saddleback (*Philesturnus carunculatus carunculatus*) after a rat invasion on Big South Cape Island (Atkinson & Bell, 1973). Many more translocations followed this first successful attempt. Up to the early 1990's, 415 translocations involving 51 species were conducted. From 1990 onwards translocations of 42 bird species, one mammal species, two tuatara species, three frog species, one fish species, 13 invertebrate species and 11 plant species were undertaken. For some species more than one translocation was attempted, either as intentional introductions or as reintroductions. Definitions are given by IUCN (1987) for "introduction" as a release outside the species' historically known native range and "reintroduction" as freeing individuals of a species into an area where they were historically found but later disappeared or were eradicated from.

Many translocation efforts adapt translocation methodology to match the specific needs of the species and the local circumstances. Experimental studies often address specific translocation issues like the importance of familiarity of released birds as, for example, Armstrong, Lovegrove, Allen and Craig (1995) did for Whiteheads (*Mohoua albicilla*), North Island robins (*Petroica australis longipes*) and North Island saddlebacks. With most bird species, aggression against familiar neighbours is much lower than against strangers (dear enemy hypothesis). The dear enemy phenomenon is defined by Fisher (1954) as the tendency to act less aggressively against familiar conspecifics intruding the territory of an individual or pair than against unfamiliar individuals of the same species. Reasons for this behaviour are regarded as reduction of costs with already established territories. Neighbouring intruders do already have territories on their own and might be a competitor for the mate, but not for the territory. Strangers compete for both. Additionally, the chance of wrongly estimating the likelihood of being winner or loser in this competition is greater for strangers than for neighbours which were already opponents in the past (Temeles, 1994). However, birds have to establish new territories after they have been translocated and Armstrong's (1995) and Armstrong and Craig's (1995) findings support the idea that familiarity before translocation is not important for a successful establishment of a new population at the target site. During the first two to five weeks, Armstrong et al. (1995) observed very little aggression between translocated North Island robins. After this introduction time, familiarity at the new site was the important factor for aggressiveness. Aggression declined with the time birds were neighbours. Translocation of established breeding pairs (Armstrong et al., 1995) showed that even pair bonds did not last after translocation and that pair members ended up in different places and found new mates.

Supplementary feeding experiments are also often related to translocations. Armstrong and Perrott (2000) tested whether the decline of stitchbird numbers at the release sites on Mokoia Island was related to food shortages. Supplementary feeding at the release sites was used to ensure sufficient intake of carbohydrates. However, food supply had no significant effect on survival rates of the stitchbirds and population size continued to decline. Armstrong et al. (2002) subsequently found an infection of *Aspergillus fumigatus* responsible for the decline on Mokoia. This fungus occurs mostly in modified habitats and is more common on Mokoia than on Tiritiri Matangi Island, the source population for the translocated stitchbirds. However, stitchbird survival on Tiritiri Matangi was limited by supplementary feeding. This indicates that generally survival of stitchbirds without intensive management is not likely. Jamieson (2004) analysed reproductive success in relation to malnourishment of translocated takahe (*Porphyrio hochstetteri*) and found no diet-related explanation of poor reproductive success of takahe.

Another topic of research in translocations is hard versus soft release, with soft release comprising acclimatisation to the new site before release, usually in cages and with supplementary feeding. Hard release on the other hand means immediate transportation and release after capture in the source population. Bright and Morris (1994) experimentally tested soft release of dormice against hard release and found dormice released immediately after arrival at the release site dispersed further and returned less often to the nest boxes at the release side. Focusing on birds, Lovegrove and Veitch (1994) successfully used a soft release technique for translocating saddlebacks from Stanley Island to Kapiti Island in 1988 which is stated by Saunders (1995) as one of the important developments of translocation efforts. Additionally Wanless et al. (2002) recommend soft release as “the conservative and precautionary method of choice for avian reintroductions and translocations.” Contrastingly,

Castro, Alley, Empson and Minot (1995) held stitchbirds in an aviary for up to 15 days at the capture site and tested immediate release versus delayed release at the release site. Birds held in captivity for two weeks at the release site disappeared faster than birds who were released immediately after arrival at the release site. As all birds were held in captivity after capture, this study did not compare both extremes (soft release versus hard release) but a modified hard release versus soft release. Bird health was monitored prior to release and supplementary feeding during the time in captivity enabled the stitchbirds to gain sufficient energy resources. Altogether, the overview of Armstrong (2008) about translocations of birds in New Zealand shows that both hard and soft release can be successful and as stitchbird releases at Karori Wildlife Reserve show, survival can be sometimes higher for soft release and sometimes vice versa. However, soft release has besides the primary goal of acclimatisation to the release site, the clear advantage of monitoring health condition of individuals.

After release, translocated birds often leave the release site and disperse. Song playback as a management tool to attract and establish colonial seabird populations after translocations is highly recommended and has been successfully applied to many species. Podolysky (1990) tested the attractiveness of conspecific song playback for first year breeders of Laysan albatrosses (*Diomedea immutabili*). Song playback was used in addition to visual stimuli versus no stimuli or only visual stimuli, and the use of song playback was associated with a significant increase in visitation rates. In New Zealand, Miskelly and Taylor (2004) reported a successful long-term translocation of chicks of common diving petrels (*Pelecanoides urinatrix*), which were translocated to Mana Island and hand-fed till they fledged. Petrel calls and calls of other seabirds were broadcast nearly every night for ten years. Of the fledged chicks, 17 % returned to the island for breeding together with unbanded petrels. Offspring of these returning petrels were raised by parental birds without human assistance. Likewise Bell,

Bell and Bell (2005) described the successful establishment of a new colony of fluttering shearwater (*Puffinus gavia*) on Maud Island, Marlborough Sounds, New Zealand. Chicks were translocated from Long Island and placed in artificial burrows where they were hand-fed twice a day until they fledged. Every year, shearwater calls were broadcast nightly between September and January. These are all examples for successful translocation projects where vocalisation broadcast was involved.

Recent studies on song broadcasting with territorial birds (Ward & Schlossberg, 2004; Ahlering, Johnson & Faaborg, 2006; Hahn & Silverman, 2007) have indicated that conspecific attraction might have an influence in habitat choice not only for colonial seabirds but also for some territorial birds (discussed later in this chapter). Recently conducted translocations used song playback of conspecifics for non-colonial birds. For example, Molles et al. (submitted) successfully released North Island kokako (*Callaeas cinerea wilsoni*) at Ngapukeriki, North Island, New Zealand in 2005. Continuous intense predator control was undertaken at the release site and broadcasting of kokako song was used to attract kokako to the release area. Released birds were monitored for nearly 10 months, including observations of kokako interaction with the broadcasting speakers. During this time pair bonding and breeding success was observed. Further long-term monitoring will show if a sustainable population can establish.

Bellbird translocations

Bellbird translocations before 2001 were all unsuccessful. Translocations of bellbirds were made from an unknown source to the Waitakeres (1931, 15 birds), from Tiritiri Matangi to Whangaparoa Peninsula in 1983 (unknown number of birds), and from Cuvier Island to Whangaparoa Peninsula (1984, 38 birds) (McHalick, 1999). Unfortunately, not much information is available about these failed attempts. When bellbirds were translocated from Kaingaroa State Forest to Waiheke Island in 1988 (11 birds) and 1989 (10 birds) all birds were released immediately (hard release), but these reintroduction attempts were also not successful. A second attempt to reintroduce bellbirds to Waiheke Island was made in 1990 (30 birds) and 1991 (59 birds) using a soft release in which the birds were held in aviaries for several days at the release site and supplementary feeding was available for the first two weeks after release. Many sightings were recorded for the first few weeks after release, but after six months only occasional sightings were noted and no bellbirds were seen after five years (Armstrong, 2008). However, the latest release of bellbirds, in the Karori Wildlife Sanctuary, seems to have been successful. Between 2001 and 2003 94 bellbirds were released, with the first breeding success (24 fledglings) in the 2002/2003 breeding season. Despite limited survival of females and an excess of males, 29 fledglings were found in the 2005/2006 breeding season. A supplemental translocation of females was conducted in July 2007 to balance sex ratio, but the sex ratio is still 17 males : 6 females. This might be due to the sex ratio of nestlings and further research is scheduled to determine whether supplementary feeding can skew the sex ratio of nestlings towards female chicks (Karori Reservoir Wildlife Sanctuary Trust (Inc.), 2008).

Knowledge about special requirements of the focal species is essential for translocation. This comprises knowledge of their biology and ecology, including the awareness of interactions with other species such as competitors, predators or species involved in mutualisms.

To date, translocations of honeyeaters in New Zealand have been conducted only for bellbirds, but there is a reintroduction of tui to Banks Peninsula scheduled for 2009. Tui will be translocated from Maud Island, Marlborough Sounds in the North of the South Island and be brought to the south-eastern flanks of Banks Peninsula. Experience and knowledge from former bellbird translocations and information gained from this study will be used to help plan tui reintroduction.

1.2. Habitat selection and habitat use

Finding a suitable habitat to live in is difficult, not only for birds, but also for conservation managers choosing areas for translocations. Loss of habitat, habitat fragmentation and constant change of habitat due to human impacts handicap birds – and their rescuers – as they try to find optimal patches for nesting, foraging and social interactions.

I follow the definitions of Hall, Krausman and Morrison (1997) who describe “habitat” as all resources and conditions influencing the occupancy of an organism in an area. Presence of a species, population or individual is dependent on biological and physical criteria and these criteria build the habitat. “Habitat use” then is the usage of any of these components, whereas “habitat selection” is the process by which an animal chooses what components to use. Selected components can be arranged in a hierarchical order with first order being the

geographical range, and the second order individual home range within the geographical range. The third order would then be the usage of components within the home range and finally the fourth order is represented by the part of the home range component actually used by the individual (e.g. if third order represents a foraging site, fourth order would be the food consumed) (Johnson, 1980).

The choice of habitat is a multi-faceted decision that a bird has to make. Many factors may influence the selection of breeding, mating and foraging sites. Some factors of habitat selection in birds are structural landscape features as water, cliffs, maturity of forest or bush or grassland or heath, density and tallness of bush, proximity of foraging and nesting opportunities, food availability, predator occurrence, ease of defence, likelihood of offspring survival, microclimate changes, and distance to human settlements. These manifold factors show that it is very costly for a bird to explore the whole area to check all these factors – or at least the factors important for the individual. Therefore, it is very likely that birds rank important indicators and use additional information to estimate habitat value. Public information about habitats can be provided by conspecifics and heterospecifics. Their presences or absences and their density (Forsman, Hjernquist, Taipale & Gustafsson, 2008) are often used as indicators of suitability of an area. This will be examined later in this chapter.

Inherited and learned knowledge about habitats also influence habitat selection. Evolutionary constraints determine the range where a species occurs. Inherited behavioural traits (e.g. nesting in holes) are usually responsible for some aspects of habitat selection; others might be experience or exploration (Hutto, 1985). The selection of the specific area and territory is

mainly related to learned behaviour. Habitat imprinting during the first few weeks of life is the first part of learning about habitat quality by using conspecifics' (in this case parental) breeding success. On the other hand, habitat does also influence behaviour. Klopfer and Ganzhorn (1985) outline a broad range of foraging and social behaviours varying with different habitats. For example, mockingbirds (*Mimus polyglottos*) often use aerial hawking techniques in areas of tall grass but less in areas with short grass. In other species, diet changes with the availability of food items. Fegley (1988) compared relative feeding height of bellbirds in natural forest compared with pine forest and found bellbirds foraging on the ground more often in the pines.

Some long-standing theories about habitat selection are addressed in other studies (Pimm, Rosenzweig & Mitchell, 1985). One of the most popular theories is density-dependent habitat selection (Fretwell & Lucas, 1970). In uniform habitats, low population densities lead to high fitness levels which decrease as density increases. Ideal distribution occurs when fitness in all habitats is equal. For ideal despotic distributions the habitat offers higher- and lower-quality patches. Individuals can be excluded from good areas in better patches by occupants of these areas defending their territories (Goss-Custard & Sutherland, 1997). This system leads very quickly to the theory of avoidance of competition: high-value habitats are preferred until competition reaches a level where the level of resources per individual in those habitats is equal to that in other habitats. For an individual, it is time to leave the patch when its potential fitness in the high-value habitat drops below the potential fitness in the "average" habitat.

Habitat selection in Honeyeaters

The family of honeyeaters is endemic to the south-west Pacific with only two monospecific genera, *Anthornis* and *Prosthemadera*, endemic to New Zealand. Honeyeaters occupy all habitat types available in the Australasian region, but are usually not found in alpine zones. Some species are limited to particular habitats, while others occur in a broad spectrum of habitats (Higgins, Peter, & Steele, 2001).

Bellbirds are found within a broad altitude range from sea level up to more than 1200 m (Higgins et al., 2001). Bellbird counts at different altitudes between 1974 and 1976 and 1976/1977 showed highest bellbird numbers for beech-podocarp forest at a moderate altitude between 320 and 430 m all year round. Lower altitudes of 230 m and 70-90 m showed a decline of bellbird numbers towards lowland. Still, high altitude > 820 m showed lowest bellbird numbers (Gill, 1980; Dawson, Dilks, Gaze, McBurney & Wilson, 1978). Even though bellbirds sometimes occur in subalpine shrub above tree-line (CSN, 1972), they are more commonly found in dense and tall forest, where they forage in all levels (Gravatt, 1971; O'Donnell & Dilks, 1994). When forest remnants are available bellbirds can also be seen in urban areas (Baker, 1986; Guest & Guest, 1987). Still, tall dense forest with a tall, dense and diverse understory that includes many native plants is preferred by bellbirds (Gill, 1980).

North et al. (2003) derived rules describing habitat use on the Port Hills for bellbirds and separated habitat into four classifications. Primary habitat meets all foraging, nesting and other social needs and comprises at least ten hectares with tall trees (greater than eight metres tall) and at least five preferred food species. Secondary habitats are smaller, with patch sizes between one and ten hectares, but otherwise fulfil the same criteria as primary habitats and

meet foraging and nesting requirements for several breeding pairs. The maximum distance from a secondary habitat to a primary patch is 500 m. Primary nest sites (and secondary nest sites) can have fewer foraging trees, but still require tall trees (more than eight metres high). All nest sites have to be within 500 m of patches of primary or secondary habitat quality.

Movement

Movement of birds is usually related to searching for food, escaping from extreme weather (migratory birds) and finding new breeding areas. Strategies of movement in birds, such as patch departure times, were traditionally considered to be related to optimal foraging theories. These theories assume a free distribution and are dependent on bird density and resource availability at the local patch and in the surrounding environment. More recent studies also include individual knowledge, site fidelity and conspecific cues in modeling movement strategies. Hancock and Milner-Gulland (2006) tested the influence of density-dependence and conspecific cues by modeling optimal foraging strategies for different stages of heterogeneously distributed resources, different bird densities and different knowledge of individuals about food availability in all patches. They found optimal foraging strategies sufficiently explained by density dependence and the marginal value theorem only when bird densities were high or patchiness of resources was low or individuals had knowledge about the food distribution within the whole area and not only about the local patch. If this knowledge was missing, the use of conspecific cues like following departing intraspecific individuals became important. In this case individuals would stay longer in a patch than density dependent habitat selection would predict. Public information is discussed later in this chapter.

Movement of bellbirds

Movement of bellbirds is most conspicuous when food resources are scarce. Especially over the winter, habitats which were suitable for a high number of bellbirds during food rich seasons cannot nourish the same amount of individuals. If food is still available for several birds, some will stay in the area and others will disperse to areas with better food supplies. Even though some birds leave the area in search of food during the non-breeding season, it is very likely that these birds return before the next breeding season starts, because bellbirds are highly site faithful and return to the same breeding territory every year (Higgins et al., 2001). North et al. (2003) outlined rules for habitat use during the breeding season and found that bellbirds appeared to limit foraging and social interactions to within 500 m of the nest. Outside the breeding season, movement increases, probably as birds travel farther to search for food. Male bellbirds are reported to forage in wider areas and move more often than females on Tiritiri Matangi Island (Craig, Stewart & Douglas, 1981), but the opposite was found on Poor Knights Island (Sagar, 1985).

Foraging and supplementary feeding

New Zealand's honeyeaters have a broad range of food sources. Besides their nectar intake they also feed on honeydew, fruit and insects. O'Donnell and Dilks (1994) showed the variation in bellbird diet across seasons with peaks for invertebrates in August (90 % of the diet) and flowers in October with strong preferences for rata (*Metrosideros spp.*) and fuchsia (*Fuchsia excorticata*). Fruit consumption peaked in June (16 % of the diet) with a wide range of species, but mainly rimu (*Dacrydium cupressinum*), *Coprosma spp.* and *Pseudopanax*. Honeydew was an all-year food source with a low but constant observed proportion of 2-5 % of the diet. Bellbirds forage in all levels of forest including the ground. The preferred foraging

level depends on the habitat. Bellbirds in pine forest were observed to feed on the ground twice as often as within a native forest (Fegley, 1988).

During the breeding season, bellbirds are territorial and forage alone, but during mating and incubation males sometimes feed their mates (Stead, 1932). After the breeding season bellbirds usually feed solitarily, but often many bellbirds are seen to forage in the same tree, defending small territories within the tree. In contrast, females are often observed to join multi-species flocks of insectivorous birds outside the breeding season (Gravatt, 1971). Sagar (1985) also reported females and juveniles forming feeding flocks on Aorangi Island, Poor Knights Islands, outside the breeding season.

Supplementary feeding for honeyeaters is usually conducted by setting up sugar water feeders. As male bellbirds are dominant at food sources, female bellbirds are often excluded from these feeders. Craig and Douglas (1984a) report only males feeding from artificial food sources on Tiritiri Matangi and Little Barrier Island. When food sources are limited, feeders may also be defended by individuals, as Molles (personal comment, 18.11.2008) observed on Tiritiri Matangi.

1.3. Territoriality

Territoriality is closely related to habitat selection, because territorial birds have to find a patch which is not already used by a conspecific or other competitor or have to usurp a territory already used by another individual or pair. Territoriality is usually shown by aggressive responses against other individuals involving displacing, chasing, or striking and

some weaker responses as vocalising and displaying. Establishing and defending a territory is most likely an approach to secure availability of sufficient resources such as food, nest sites and mates. Therefore aggressiveness against intruders is expected to be highest when resources are most valuable (Jaeger, 1981; Brunton et al., 2008). When population densities are high, territories are usually smaller than in times or areas of low population density (Goss-Custard & Sutherland, 1997). In some species, territories have defined boundaries, and aggression against intruders often increases with closer proximity to the centre of the territory, the nests or main perches. This behaviour might be related to the increasing value of core areas of the territory, such as for central-place foragers (Giraldeau & Ydenberg, 1987).

Territoriality in honeyeaters

Armstrong (1991) observed aggressive behaviour in New Holland honeyeaters (*Phylidonyris novaehollandiae*) and white-cheeked honeyeaters (*Phylidonyris nigra*) directed mainly towards unfamiliar conspecific intruders, less often towards neighbours and rarely towards mates. Aggressive responses were strongest when food availability was low. Outside the breeding season, Paton (1985) found New Holland honeyeaters only defending their territory when other birds fed on food sources within their territory; in contrast, Armstrong observed aggressive behaviour against intruders also before foraging started during the breeding season.

With some Australian honeyeaters, territory sizes changed depending on flower density and nectar availability (Ford, 1981; Paton, 1985; McFarland, 1986). Outside of the breeding season, territory sizes are related to energy needs of the individual, including energy requirements for defending the territory, and the accessible energy in the patch. Higher

abundance of nectar results in smaller territories, most likely to reduce defense costs (Ford, 1981). Hixon, Carpenter and Paton (1983) experimentally tested territory size and time budgeting for rufous hummingbirds (*Selasphorus rufus*). They found the same results for territory size as Ford, McFarland and Paton did for honeyeaters. Additionally, Hixon et al. concluded that territory size and time budgeting is related to the hummingbirds' maximization of their daily net energy gain.

Many studies about territorial behaviour in birds address foraging territories and are conducted outside the breeding season. This excludes some factors such as nest defense or mate defense and allows a focus on foraging tactics and influence of food abundance and competitors. Nevertheless, many birds show territorial behaviour only during the breeding season and therefore other factors besides foraging have to be included to explain territorial behaviour within breeding season.

Bellbirds are often found in aggregations with some territorial overlap. Even though flowering resources are often used by more than one pair, during times of scarcity of nectar these areas are often defended against neighbours by males (Anderson & Craig, 2003).

Bellbirds are highly territorial during the breeding season, leaving their territories only momentarily to access water for drinking and bathing or food sources outside their defended areas (Sagar, 1985). Males are usually responsible for defending the territory (Craig, 1984), but females also show aggressive responses during the courtship and chick-rearing periods, especially against intrusion of neighbouring females. This is very likely to secure parental care and avoid polygyny as well as to ensure access to a food supply for chicks (Brunton, Evans, Cope & Ji, 2008). Even though bellbirds generally move over larger areas after the

breeding season, some studies found bellbirds territorial over the entire year (Sagar, 1985). Outside the breeding season, dispersed nectar sources lead to territorial defence in bellbirds, whereas access to food follows a hierarchical order when high nectar abundance is located in a single tree (Craig & Douglas, 1986). Resident males are of highest rank within this hierarchy, followed by resident females or very dominant non-resident males. Juvenile bellbirds are lowest in the hierarchical order. Male bellbirds usually also exclude their mates from feeding territories (Craig & Douglas, 1984b), but some occasions have been reported where the female was chased by another male and the resident male then chased the intruder and left his mate feeding. However, this probably has to be regarded more as a defence of the territory against the intruder than a support of the mate (Craig, 1985).

In bellbirds, aggressive behaviour and territorial defence usually comprises wing noise, displaying, chasing and singing (Craig & Douglas, 1986), but occasionally fighting also takes place (Wilson & Wilson, 1999). Wing noise is produced only by adult birds, particularly males, using a notch in the ninth primary feather. This notch is smaller in female feathers and absent in juveniles (Craig, 1984). Interspecific aggression towards smaller birds at food sources is reported for stitchbirds (*Notiomystis cincta*), silvereyes (*Zosterops lateralis*) (personal observation, March 2008) and other small passerines. However, bellbirds are often displaced by tui (Craig et al., 1981; Craig, 1984). Tui have similar wing slots to bellbirds and also use them to create a wing noise to chase and display to other species (Craig, 1984).

Territorial behaviour and territory size for bellbirds depends on many factors such as food availability, stage of reproduction cycle, availability of nest sites and individual fitness.

Interaction with conspecifics and competition are part of population dynamics and this study will show if bellbirds are attracted to conspecifics, even though they respond with aggression.

1.4. Conspecific attraction

In the early 18th century Daniel Defoe recorded the use of conspecific cues by fowlers to attract ducks and lure them into funnel nets. What worked for hunting birds might also be a useful tool for conservation (Reed & Dobson, 1993). Colonial birds are widely known to use conspecifics to identify suitable breeding sites (Kotliar & Burger, 1984; Serrano, Forero, Donazar & Tella, 2004). A greater amount of conspecifics provides a higher number of mate choices, a lower predation rate and gives advantages for foragers to locate potential food sources. These effects are positively correlated with density increase. Therefore individuals in small populations have a lower chance of reproductive success and survival than individuals in large populations (“Allee” effect). Many studies have addressed Allee effects and found advantages of large populations in levelling out competition pressure (Highsmith, 1982; Bertness & Grosholz, 1985; Donahue, 2006).

Besides the Allee effect, conspecifics cues providing information about habitat quality and social attraction are recorded for a broad variety of different taxa (Reed, 1999). Observed aggregations of territorial birds led to the assumption that they are attracted to their conspecifics. This idea was first stated more than 50 years ago (reviewed in Stamps, 1988). The use of the performance of conspecifics as an information source about habitat quality is

also known as public information. Brown, Brown and Danchin (2000) found the breeding success of cliff swallows in the previous year being used as a conspecific cue for choosing a nest site in the current year. This resulted in an increase of colonies with high breeding success due to the return of successful breeders and immigration of first year breeders and other sites' failures of the previous year. Doligez, Danchin, Clobert and Gustafsson (1999) found similar results for the non-colonial collared flycatcher (*Ficedula albicollis*), but with a difference between the two sexes. Females were attracted to sites with high patch reproductive success whereas male dispersal was positively related to patch reproductive success. This might indicate that males also respond to competition pressure and not entirely to breeding success. With species for which habitat quality of colony sites varies between years, breeding success of previous years seems to have no influence of habitat selection in subsequent years (Erwin, Nichols, Eyster, Stotts & Truitt, 1998).

Time constraints for the choice of breeding habitats are most important for migratory birds as they do not have the opportunity to evaluate potential breeding sites all year round. Finding a suitable breeding site is crucial for reproductive success. Especially first-year breeders, but also breeders who failed in the previous year need public information to identify suitable habitats. Successful breeders of the previous year tend to use their own reproductive success and return to their former breeding patch (Doligez et al., 1999). Despite the potential negative effects of competitors for the access to food sites or mates, aggregations offer some advantages including higher breeding success, for non-colonial birds as well as colonial birds.

Some studies (Mountjoy & Lemon, 1991; Ward & Schlossberg, 2004; Ahlering et al., 2006) have experimentally shown that not only colonial birds, but also territorial birds use conspecific cues to identify suitable breeding and foraging sites. These studies on conspecific attraction in passerines did not only use visual decoys, but also song playback of the focal species.

Reproductive success of conspecifics as part of performance-based attraction is an example for the use of public information (Serrano et al., 2004; Doligez, Part, Danchin, Clobert & Gustafsson, 2004). However, with synchronized breeding periods, information about breeding success cannot be assessed by juveniles. Nocera, Forbes and Giraldeau (2006) tested the use of public information by juveniles using incidental public information by playing conspecific song of breeding males during pre- and post-breeding periods. For bobolinks (*Dolichonyx oryzivorus*), a social species, song playback in the post-breeding period of the previous year showed a positive correlation to the choice of breeding sites for first-year breeders. The same song playback during the pre-breeding period showed no effect. Contrastingly, the Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*) – a more solitary species – showed no response to the playback for their choice of breeding sites.

Despite public information about conspecific breeding success, the mere presence of conspecifics is also an attractant for some species. Abundance of conspecifics is an indicator for habitat quality even though the cues for settlement of the residents are not known to the immigrant (Serrano et al., 2004). Mountjoy and Lemon (1991) experimentally assessed if the broadcast of starling song near nest boxes attracts female starlings to these boxes and holds off male starlings from these sites. They found both sexes were drawn to the nest boxes.

Females were attracted to all kind of songs and males only to relatively simple songs. This could indicate that males considered simple song to signal the presence of a competitor they could potentially outcompete.

Providing conspecific cues and, in passerines especially, conspecific song playback might be a management tool to direct birds to suitable habitats. Hahn and Silverman (2007) tested this for black-throated blue warblers (*Dendroica caerulescens*) by providing song playback in selected breeding areas. In comparison to the previous year without playback, nest sites and territories were shifted towards the speakers in the year of song broadcast, even though no sign of change in suitability of habitats was apparent. Former territories were still available, but preferences had obviously changed towards sites close to the speakers. This shows that broadcasting of conspecific song is a strong attractant for black-throated blue warblers and also might be used to move territories towards safe areas before habitat alteration or destruction takes place. Schlossberg and Ward (2004) recommend considering the use of conspecific attraction and especially the use of song playback for conservation purposes. However, they emphasise on the potential risk of drawing birds away from good habitats or luring them to low quality habitats. Song playback can have a non-target influence on heterospecifics and therefore this influence has to be estimated and taken into account before song playback is used in sensitive areas (Fletcher, 2008).

Conspecific attraction by song playback is assumed for both New Zealand honeyeaters and playback of bellbird and tui song are used to lure individuals to mist nets for banding purposes. Song playback was already successfully used in New Zealand for translocating North Island kokako (see Translocation section). However, whether New Zealand honeyeaters

can also be attracted to particular habitats has not been experimentally assessed yet, but as both species are often found in aggregations, conspecific song playback might be a useful management tool for providing artificial public information about habitat quality.

1.5. Aim and objectives

One major problem after translocation of birds is dispersal from release sites. Even though habitats are of high quality and offer sufficient food sources, translocated birds often leave the release site soon after release. This study was conducted to identify if habitat selection and habitat use of honeyeaters can be influenced by supplementary feeding and conspecific song playback.

Objectives of this study are:

- to identify potential factors influencing habitat choice of bellbirds.
- to investigate if supplementary feeding can influence habitat choice and lead bellbirds into specific areas.
- to investigate if conspecific song playback attracts bellbirds to specific sites.
- to investigate if conspecific song playback increases the chance of feeder discovery by bellbirds.

2. General methods

2.1. Bellbird biology and ecology

Bellbird and tui are the only honeyeaters in New Zealand (Driskell et al., 2007). Bellbirds are smaller than tui with a length of 17-20 cm and a wingspan of 22 cm. They have a low sloping forehead and a short and slightly curved bill. Plumage is of olive green with prominent pale yellow tufts in the fore-flanks. Both sexes of adult bellbirds have red irides. Body measurements of male and female bellbirds show an overlap for some characteristics. Reliable discriminators are head and bill length and tail length, both remarkably longer for males (Craig, Douglas, Stewart & Veitch, 1982). However, sexes can also be determined by plumage, which does not vary seasonally. Male bellbirds show a designated distinctive shape in their tail with a rather narrow base and it is flared and deeply notched at the tip. Adult males also show a dark olive green with iridescent purple sheen to their head and bluish black wings and tails. The adult females are duller than males and show a more olive brown plumage with only a little contrast between body, head, wings and tail. A striking attribute for females is a short white moustachial stripe on their cheeks. Both sexes of juveniles also look distinctively different from adults possessing brown irides and lacking a yellowish patch on the fore-flank. Both juvenile sexes are duller than adult females and they have a pale yellowish moustachial stripe. The juvenile male can be separated from juvenile females by its greater contrast between body, head, wings and tail (Higgins et al., 2001).

Even though bellbirds are omnivorous, a major part of their diet is nectar. Due to the specialised feeding behaviour of honeyeaters, bellbirds are important for the pollination of

many native plants in New Zealand, such as kowhai (*Sophora tetraptera*) and puriri (*Vitex lucens*). Favourite nectar plants for honeyeaters are fuchsia, flax (*Phormium ssp.*), five finger (*Pseudopanax spp.*), kowhai and rata (Schmechel, 2004). Besides nectar, the honeyeaters' diet includes fruit, insects and honeydew (Gaze & Clout, 1983; O'Donnell & Dilks, 1994). Merton (1966) noted the importance of insects in bellbird diet when he compared feeding behaviour of several forest bird species in autumn. Additionally, Gravatt (1971) and O'Donnell and Dilks (1994) considered bellbirds to be more insectivorous than tui or stitchbirds. St. Paul (1975) described the bellbird diet as varying seasonally with a predominance of nectar and fruit in spring and summer, and a peak of insects (mostly cicadas (Fam. *Cicadidae*)) in January, while in autumn and winter the diet contained mainly fruit. The diet of chicks comprises mostly insects (Stead, 1932) whereas the diet of non-breeding adults varies with sex, for males mostly consisting of fruit and nectar and for females also having a high proportion of insects (Gravatt, 1971). Fruit is primarily eaten as whole but sometimes squashed to extract extra juice. Williams and Karl (1996) found bellbirds preferred indigenous fruit, mainly from Hall's totara (*Podocarpus hallii*) and karamu (*Coprosma robusta*).

Both honeyeater species are highly mobile in both time and space, following the patchy availability of flowering, nectar-bearing food plants. Unlike tui, which forage in family groups, bellbirds are mostly solitary foragers. Several bellbirds may forage at the same time in the same tree, but they each defend their foraging territory within the tree (Heather & Robertson, 2005). In different studies on different islands throughout New Zealand, the movement between males and females varied significantly between sexes. Craig et al. (1981) and Craig and Douglas (1984a) described males as moving further and more often than females on Tiritiri Matangi, although Sagar (1985) found that males defended territories

throughout the year with females and juveniles moving around between seasons and being more mobile outside breeding season. In Christchurch, bellbirds were found to spend the summer in the bush and in the winter move to coastal areas and lower altitudes (Landcare Research, 2008) where they are often located in plantations or in urban areas.

Despite the fact that a favourite food source of bellbirds is flax, which usually grows in open areas, bellbirds are more often seen in denser bush, particularly native bush. Williams and Karl (2002) found that bellbirds were ten times more frequent in kanuka (*Kunzea ericoides*) than in gorse (*Ulex europaeus*). High nectar abundances of flowering plants attract insects and this provides an additional food source for bellbirds. Therefore, gorse, with low nectar production (Sandrey, 1985), can be regarded as a poor habitat for bellbirds whereas kanuka shrub, with high numbers of insects and high nectar abundance, is a relatively good habitat.

In contrast to many other passerine species, female and male bellbirds are both very active singers. Both sexes sing frequently over the whole day, all year long. However, males show a wider repertoire of songs with different song structures and outside the breeding season they are more active singers as well as countersingers (Brunton & Li, 2006). During the breeding season the frequency of female bellbird song is three times higher than male bellbird singing (Brunton & Li, 2006). Behavioural observations during bellbird song studies conducted on Tiritiri Matangi in the 1980s by Craig and Douglas (1986) and between 2002 and 2007 by Brunton and Li (2006) and Brunton et al. (2008) lead to suggestions about the role of male and female bellbird song. Since bellbirds form gender-specific foraging flocks and access to foraging sites follows hierarchical orders (Craig & Douglas, 1984a, 1984b), the role of male song throughout the non-breeding season is regarded as being for food resource defence

rather than mate attraction. Even though females also sing all year round, female singing is most frequent in the breeding season and Brunton et al. (2008) found female response to song playback of neighbouring females highest during courtship and chick rearing, but low during incubation. Female response to non-neighbour female song was significantly lower with regards to approaching the song source and in countersinging. This indicates that, contrary to the dear enemy hypothesis, which states that response to neighbours should be less aggressive than to strangers (Sinervo & Brandt, 2007), neighbouring females are a greater threat to bellbird females than are strangers. Brunton et al. (2008) associate this with competition over food and mates, as neighbouring females are very likely to be in the same stage of breeding, whereas strangers moving around are less likely to breed and directly compete for resources. Aggressive use of female song against conspecifics might also be used to prevent polygyny of the mate to secure exclusive paternal care. Polygyny often leads to abandonment of the female and no incident of successful chick rearing by a solo bellbird parent has ever been reported. In summary, bellbird song has several functions: finding mates during courtship, male defence of the territory, securing biparental care for offspring and defence of food resources in females.

2.2. Study area

The Port Hills near Christchurch comprise the western flank of Banks Peninsula, Canterbury, South Island, New Zealand. The Port Hills are derived from the northern rim of an ancient volcanic cone and range from sea level to peaks of 350 m to 500 m in altitude. They separate Lyttelton Harbour from the Canterbury Plains and are an important recreation area for Christchurch residents. The 13,700 ha Port Hills Ecological District can be entered by car through Dyers Pass and Gebbies Pass and a road along the summit connects these access

roads. Public car parks at several reserves allow easy access to mountain bike and walking tracks. Whereas the northern slopes are mostly residential areas, other parts are used for farming and forestry. The vegetation on the Port Hills ranges from open tussock to some native bush remnants and larger areas of regenerating second growth forest. Whereas the steepest slopes are found in the north-eastern part of the hills, the slopes to the west are moderate and form the rolling hills towards the Canterbury Plains (Christchurch City Council, 2008).

The fieldwork for this study was conducted in Kennedy's Bush on the Port Hills. Kennedy's Bush is an 86.5 ha scenic reserve/recreation area controlled by Christchurch City Council. Kennedy's Bush ranges from 200 m altitude to 440 m and is covered by patches of second growth hardwood forest with mahoe (*Melicytus ramzjlorus*), kanuka and fuchsia with a few extant podocarps like totara (*Podocarpus totara*) and matai (*Prumnopitys taxifolia*) and, in open patches, gorse (Freeman, 1999) and other cultivated plant varieties, e.g. *Phormium tenax* 'Variegatum' (Crutchley, personal communication, 05.02.2008). The upper boundary of Kennedy's Bush is defined by the Summit Road. From there it stretches down a valley towards Halswell. Several walking tracks start from Summit Road and the shorter loop tracks, like the Totara Trail, are favourite walks for weekend trips. The longer and more challenging Orongomai Trail, which follows the two brooks creeping through the area, and return tracks, like the Holdsworth Track, are less frequently walked.

Observation sites

Experimental stations were set up in different patches; some in open areas, like the flax field on Holdsworth Track, some in clearings, such as the junction of Fantail and Quarry Trail Track or a bush edge at the Sign of the Bellbird, and some were in denser bush parts, like the bottom of Orongomai Trail (Fig. 2.1).

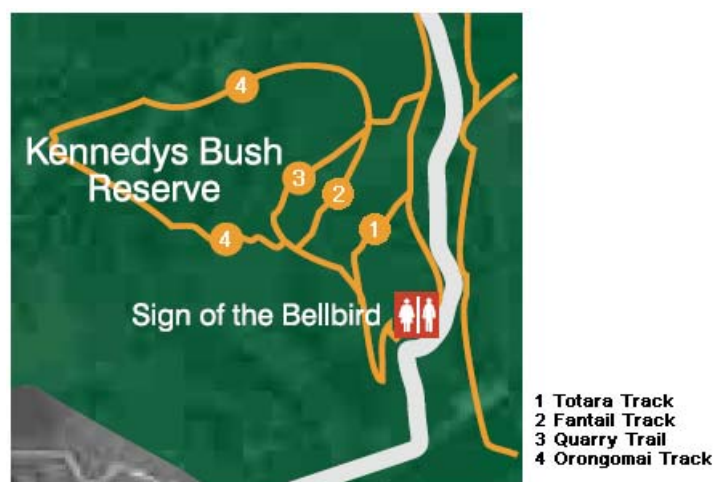


Figure 2.1: Walking tracks within Kennedy's Bush Scenic Reserve; all tracks start and end at the Sign of the Bellbird (modified map from Christchurch City Council, 2005)

Eighteen locations were chosen within Kennedy's Bush scenic reserve with a minimum distance of 150 m between locations (Fig. 2.2). This spacing minimized territorial overlap, even though most of the experiment was undertaken in the post breeding period when birds were no longer defending breeding territories. The first location was chosen close to the Sign of the bellbird, but hidden from public view. Since I wanted to minimize potential damage to the vegetation, existing tracks and trap lines of Christchurch City Council were used to walk to the observation spots. From the first location I walked on these tracks and trap lines until a distance of 150 m (measured with a GPS handheld unit: Garmin gecko 201) was reached. The

next location was determined by the next site reached that fulfilled the following criteria:

- Keeping the distance of at least 150 m to all other locations,
- soft ground, so that the poles for feeding stations could be relatively easy driven into the soil,
- at least one shrub or small tree close to the feeding station to place the speaker in,
- more or less easy access to avoid injuries in bad weather conditions and,
- whenever possible, some concealment from visitors in the reserve.

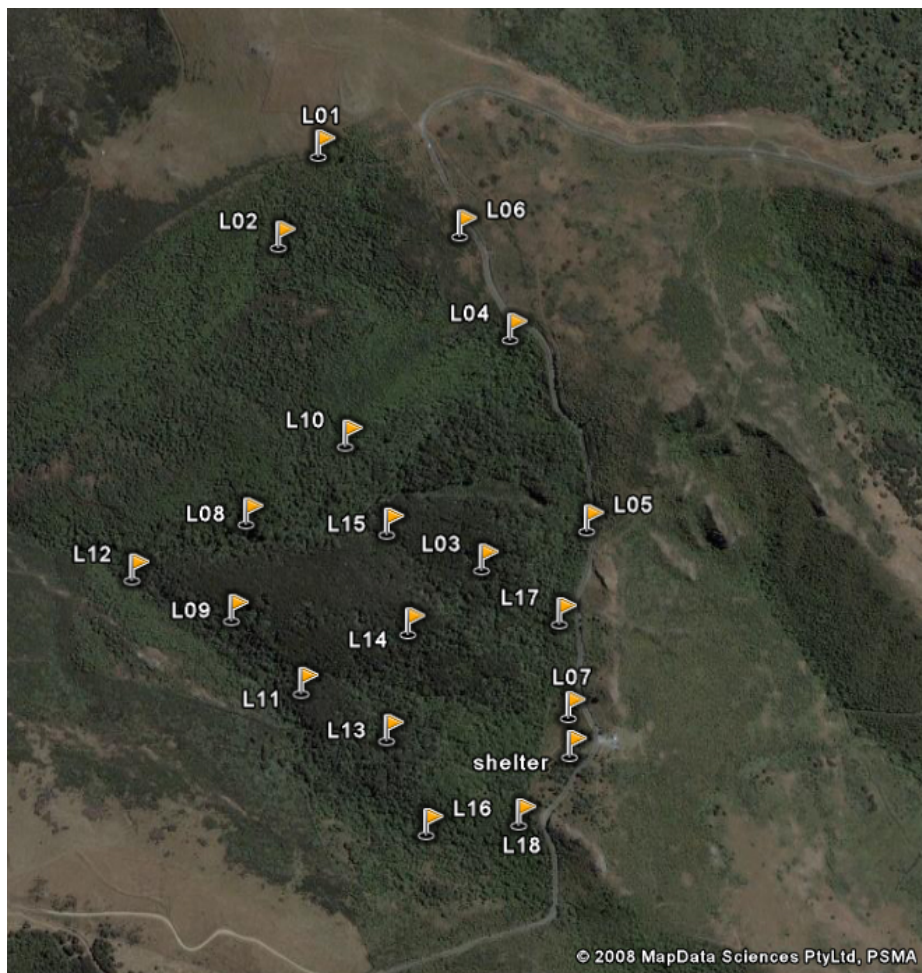


Figure 2.2: Observation sites in Kennedy's Bush; numbers refer to location numbers as stated in table 2.1; shelter is the "Sign of the Bellbird"

Close to tramping tracks the sites were within 15 m of the track. On trap lines, the sites were within 2 m of the track. The locations varied in vegetation, bush density and proximity to the brooks running through Kennedy's Bush. Locations with close proximity to creeks were location 11 and location 09 (approximately 15 m to water), location 08 (approximately 10 m to the brook) and location 10 (4 m to the brook). All other locations were at least 20 m away from water. In some locations it was not possible to search for water sources beyond 20m because the bush was very dense. Table 2.1 shows location numbers, a short description of the locations, information about vegetation and GPS coordinates. These were only approximate values, because the GPS handheld unit used was accurate to only +/- 50-60 m.

Table 2.1 Locations of feeding stations and observation areas

No.	location	GPS coordinates & height	vegetation within 25m
01	in the open, near paddock with cattle, just above bush, at north end of Kennedy's Bush	S: 43°37'25.37" E: 172°37'13.37" h: 430 m	grass, some gorse, flax, cabbage tree (<i>Cordyline australis</i>)
02	dense bush in gully at north end of Kennedy's Bush	S: 43°37'29.97" E: 172°37'10.59" h: 368 m	mahoe, tree daisy (<i>Olearia spp.</i>), fern, gorse, <i>Sambucus spp.</i>
03	bush at old track west of Holdsworth Track	S: 43°37'46.30" E: 172°37'24.79" h: 458 m	mahoe
04	shrubby bush edge at Holdsworth Track	S: 43°37'34.64" E: 172°37'26.79" h: 458 m	gorse, five finger, tree daisy, broom, lemonwood (<i>Pittosporum eugenioides</i>), tree daisy, lacebark (<i>Hoheria spp.</i>)
05	bush between mid of Holdsworth Track and Summit Road	S: 43°37'44.32" E: 172°37'32.14" h: 449 m	mahoe, five finger, tree fuchsia
06	flax field at Holdsworth Track, north end	S: 43°37'29.41" E: 172°37'23.26" h: 457 m	flax

No.	location	GPS coordinates & height	vegetation within 25m
07	clearing at Sign of the Bellbird	S: 43°37'53.77" E: 172°37'30.86" h: 443 m	mahoe
08	small clearing at a creek on Orongomai Track (north)	S: 43°37'43.97" E: 172°37'8.34" h: 295 m	mahoe, totara, matai, <i>Coprosma spp.</i> , tree daisy, liane
09	bush at western Orongomai Track, near creek	S: 43°37'48.85" E: 172°37'7.31" h: 277 m	mahoe, lemonwood, five finger, kanuka
10	small clearing in northern gully of Orongomai Track, close to creek	S: 43°37'40.03" E: 172°37'15.27" h: 368 m	mahoe, five finger, tree daisy, lilies, fern
11	bush in gully on Orongomai Track, near creek	S: 43°37'52.54" E: 172°37'12.18" h: 294 m	mahoe, kanuka
12	bush in slope west of Orongomai Track	S: 43°37'46.80" E: 172°37'0.36" h: 237 m	mahoe, kanuka
13	bush at junction of Orongomai Track and Quarry Trail	S: 43°37'54.92" E: 172°37'18.16" h: 353 m	mahoe
14	clearing at junction of Fantail Track and Quarry Trail	S: 43°37'49.53" E: 172°37'19.65" h: 365 m	lacebark, mahoe, five finger, <i>Coprosma spp.</i> , Broadleaf (<i>Grisilinia</i>)
15	bush at northern start of Orongomai Track	S: 43°37'44.48" E: 172°37'18.17" h: 330 m	five finger, mahoe, lemonwood, kanuka
16	bush at junction of Totara Track and Fantail Track	S: 43°37'59.68" E: 172°37'20.92" h: 385 m	mahoe, kanuka
17	bush at connecting Track between Kennedy's Bush Tracks and Summit Road	S: 43°37'48.82" E: 172°37'30.35" h: 439 m	flax, <i>Coprosma spp.</i> , tree daisy
18	bush south of Sign of the Bellbird	S: 43°37'59.20" E: 172°37'27.39" h: 450 m	five finger, <i>Olearia paniculata</i>

2.3. Bird count method

Five-minute point counts using the methods of Dawson and Bull (1975) were used to collect data about relative bellbird abundance at 18 locations within Kennedy's Bush (chapter 3 for details). At each experiment station an initial five-minute bellbird count was conducted before the experiment started. These pre-counts had, in contrast to the experiment, no song playback involved. Counts were carried out daily from 21.02.2008 till 23.02.2008 between 1100 and 1600 hours. All birds heard or seen within distances up to 100 m were counted. The distance between observer and bird was estimated in bands of 0-25 m, 25-50 m and 50-100 m. For some counts minimum numbers were noted as bird numbers were often difficult to estimate when the number was high or bird song was very common. The same five-minute bird count technique was used to repeat counts throughout the experimental period prior to starting new treatments.

2.4. Supplementary feeding and song playback

a) Pre-trials

Initially, I tried to determine the amount of time bellbirds need to discover an artificial food source. During pre-trials in November 2007 in the Marlborough Sounds, bellbirds discovered artificial feeders within two to four days without any use of song playback. As food availability was higher at the Port Hills in the summer of 2008 and the locations for the feeding stations were often in denser bush, two artificial feeders were presented in Kennedy's Bush for three weeks from 25.01.2008 till 15.02.2008. The feeders, with no song playback, were located in an area of moderate food resources with kanuka, mahoe, five finger and lemonwood available nearby. The feeders were monitored every two days between 1000 and

1600 hours for 45 to 60 minutes on each visit. The bellbird density in each area was moderate with some bellbirds seen or heard within 100 m during five-minute bird counts, but always fewer than ten bellbirds. No bellbird visits were noted at any feeding station, and few were seen in close proximity (within 5 m).

Pre-trials with three stations of food with song playback and one control station with no food and no song playback were conducted between 16.02.2008 and 22.02.2008 to determine the potential variation of bellbird visits over one observation period. All three song playback stations were observed twice daily and the control station once per day over one week between 0745 and 1630 hours for one hour per observation. During the subsequent experiment run from 24.02.2008 to 05.04.2008 between 0749 and 1730, conspicuousness, the probability that a bird is detected by an observer during a specific observation time (McKinlay, 2001), was noticeably higher than during the pre-trial. Conspicuousness in bellbirds is known to change over the time and is lowest in the breeding season from September to January (Freeman, 1999).

b) Experimental design

• Station design

Each station consisted of a wooden platform, 1.5 m high with a feeder attached on top of the platform. With treatments that had song playback involved, a speaker (large speaker: model SME-AFS, Saul Mineroff Electronics, Inc., Elmont, NY, USA; small speaker: model 40-168, Radio Shack Corporation, Fort Worth, TX, USA) connected to a mp3-player (DSE, A5368) was placed in a shrub or tree at a height of 1-2 m at a distance of 1-2 m from the feeding

station. For all but one treatment at each of three locations the large speaker was used. The small speaker was used for treatment “song” at location 01 and treatment “song and food” at locations 05 and 17.

White clothes-pegs were used to mark the 5 m radius and pink clothes-pegs for the 15 m radius around each feeding station. Each station had three white pegs set up at intervals of 90° around the feeder (excluding the direction of the observer). The pegs were attached to small branches and leaves. Four pink pegs were similarly attached at greater distances of 15 m. Where visibility was limited small pieces of white paper towels were added to the pegs to allow easier identification of the observation radius. The observer sat at a distance of 5 m from the feeding station.

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Figure 2.3: Feeder built from two soda bottles © by Heidi Stevens

The feeders were made of recycled material. Two soft-drink plastic bottles were used for each feeder. One bottle formed the sugar water reservoir and the second bottle formed the spout.

The top of this bottle was cut off at two-thirds of its height. The lower part was notched with a small half-round opening of approximately 2 cm in diameter (Fig. 2.3).

The reservoir bottle with the sugar water (for food treatments) was then placed into the cut bottle until the opening of the sugar water bottle levelled the half round opening. Turning the feeder filled the spout bottle up to the opening. The feeders sat in brackets screwed on to the platform which allowed ease of change of feeders and also secured the feeders from falling off the platform due to wind or other animal interference. Small perches were attached to the platform to allow bellbirds to sit while feeding on the sugar water (Fig. 2.4).



Figure 2.4. Feeding station at location L12

• Food preparation

For treatments involving food, the reservoir bottle was filled with 25 % (by mass) sugar water. Bergquist (1989) observed tui avoiding nectar resources with a sugar concentration of less than 7 %. As tui and bellbirds often aggressively compete over food resources, I assumed sugar water concentrations for tui were suitable for bellbirds. Tui most frequently used flowers with high sugar concentrations of up to 27 %. The sugar concentration of the feeders Bergquist used in her survey measured between 10 and 15 %. As my study was conducted when food availability was high, I chose a higher sugar water concentration than Bergquist.

Feeders were rinsed with hot water (approximately 70-80 °C). 250 g of sugar were dissolved in 750 ml of boiled tap water. After cooling down to approximately 40-50 °C, this solution was then poured into the upper feeder bottle. When the sugar water reached ambient temperature, the bottle was screwed for transportation. Before use, the cap was removed, the spout bottle attached and then the feeder turned over and locked into the brackets. After the use over three days, feeders were cleaned with antibacterial dishwashing liquid and thoroughly rinsed with clear water.

• Song preparation

Bird songs were recorded on 24.01.2008, 31.01.2008 and 06.02.2008 in Kennedy's Bush, Port Hills, Christchurch by Dr. Laura Molles using an Audio-Technica 815B shotgun microphone and Sound Devices 722 digital recorder. Recordings were collected between 0715 and 1630. To stimulate singing, playback of bellbirds recorded on Maud Island was played on 24.01.2008, and playback of bellbirds from Kennedy's Bush was played on the remaining recording days. Songs and calls were collected from adult male (most tracks), adult female,

and juvenile singers. Suitable recordings were bandpass filtered (700-9000 Hz) to reduce background noise and volume was normalised to a peak volume of -3 dB. A total of 58 tracks ranging in length from 7 to 30 seconds were prepared.

For treatments involving playback, each song track was played twice during the observation period to provide 40 minutes of song as well as 20 tracks of silence (20 seconds each). The silence was included to mimic natural bird song behaviour as birds do not sing uninterrupted for a whole hour. All tracks were played in random order for 45 minutes (cp. Ward & Schlossberg, 2004).

2.5. Approvals

All experimental work of this study was approved by Lincoln University Animal Ethics Committee (No. 229), by Christchurch City Council (Kay Holder) and by the Department of Conservation (National permit number: CA-22365-RES).

2.6. Data analysis

The statistical models were performed in GenStat, Release 11; graphs were created in Microsoft Office Excel 2003.

3. Bellbird abundances

3.1. Introduction

a) Bird count methods

Bird counts can be divided into two general types. A census is a complete bird count that does not need a correction for absolute bird numbers. Incomplete bird counts only record a fraction of the total bird population and need a correction factor to estimate absolute numbers (Gregory, Gibbons, & Donald, 2004). Both types of bird count methods are used to estimate and compare bird densities and distributions between sites and/or over time. This study addresses the question of how and why bellbirds are attracted to specific areas. To estimate bellbird density and compare it between the observation sites of this study, knowledge about relative bellbird numbers at the different locations is needed. Several methods are available to count heard and/or seen birds within specific areas. Each method has some advantages and disadvantages over others. In the following some bird count methods are described:

- ***Five-minute bird counts***

This method is also known as point count or point transect. Points are constricted randomly selected in a defined area. Restrictions are for example a minimum distance between observation points of at least 200 m (Dawson et al., 1978) or 300 m (Flade, Schwarz & Fischer, 2003) or accessibility. At each point all birds heard or seen during a five-minute interval are counted. The distance between the bird to be counted and the observer is traditionally not limited and not recorded. Nonetheless, some derived methods of five-minute bird counts limit the distance and/or record distance bands for all sightings. Repeated

observations have to be conducted at each point over several years to allow statements about the trends in population size. This method is used in many bird surveys in Europe and the USA (e.g. National Bird Counts in France and Hungary, Breeding Bird Survey in the USA (Spurr, 2004)).

- ***Line transects***

The US Christmas Bird Count conducted by the Audubon Society is a well-known example of a line transect bird count. All birds found along a defined route of a specific length are counted. As with the five-minute bird count every bird heard or seen is counted. In New Zealand this method is also called a “slow-walk” transect count (Spurr, 2004). Variations of this technique are to count all birds seen along the route up to some specified distance on either side of the observer. Buckland et al. (2001) defines a variation of line transects where the observed band to each side of the walking line is limited to a specified width (“strip transect”). This strip transect ignores all birds outside the determined band width and counts all birds heard or seen within the band. Another version is the “curved-line” transect count (following landscape or existing tracks). These transects use existing paths and game trails. They are especially useful for dense forest and areas with difficult accessibility (Hiby & Krishna, 2001).

- ***Mapping***

Territory, or spot mapping, records all birds showing some territorial or breeding behaviour in a determined area. This data is then used to plot distribution and size of territories on a map.

For territorial mapping, defined areas are divided into small grids – often 1 km x 1 km – and

depending on the availability of observers, a subset of the total number of grids is randomly picked. The chosen grids are surveyed by walking along routes, which have to allow coverage of nearly all the terrain.

b) Five-minute bird count versus alternative methods

This study was conducted between January and April 2008. Change of abundances and attraction of bellbirds to playback and supplementary feeding were the focus of this study.

The breeding season of bellbirds starts in September and ends in January, so nest building and territorial behaviour had already ended when the study began. Therefore, an absolute count of bellbird numbers using mapping of breeding pairs was not possible.

Because some experiment locations were only 150 m apart, line transects for bellbird counts would not have been independent. Another criterion against the use of line transect for bird counts in this study was the difficulty of the terrain. The dense bush prevents observers from concentrating on the bird count while walking safely through the wood. Counting at spots without walking at the same time makes it easier to detect birds and/or estimate their distance.

The five-minute bellbird counts were conducted in this study to obtain information about bellbird distribution within Kennedy's Bush Scenic Reserve. Five-minute counts do not give information about absolute bird numbers, but allow the comparison of areas and can be used to estimate variation in relative density over time. The information about bellbird numbers at different locations was used to establish relationships between habitat factors and bellbird abundances.

3.2. Methods

a) Five-minute count

Pre-experimental bellbird counts were conducted daily from 21.02.2008 till 23.02.2008 between 1100 to 1600 hours at 18 locations within Kennedy's Bush. The locations (chapter 2.2 Table 1) where five-minute counts took place were used for bird counts and for the experimental data collection. During the experimental part of this study additional five-minute counts were conducted before each new experimental treatment started at a location (details: Appendix 1, Table 7.1).

b) Statistical analysis

The bellbird distribution was measured by bellbird numbers per location during the initial bird count (chapter 2.3). Three distances, up to 25 m, 25-50 m and 50-100 m were initially used to determine the relative bellbird density for all experimental stations. For locations with very high bellbird numbers, individuals in the farthest distance class of 50-100 m could not be accurately counted as bellbird song close to the observer was too intense to hear the additional bellbirds further out. I did not use data for the farthest distance class in the analyses. The bellbird numbers of the two distance bands of 0-25 m and 25-50 m were summed up for each counting event and this data of all five-minute bird counts (initial counts and counts during the experiment) was then used to perform a Generalized Linear Model (GLM) with a negative binomial distribution to analyse if any long-term effects of the five-day long treatments existed.

Habitat factors were analysed using a Generalized Linear Mixed Model (GLMM) with a negative binomial error distribution, since the collected data was not normally distributed and most likely had correlated factors. The sum of all available five-minute counts, five per location (initial count and four pre-treatment counts during the experiment), was used to analyse the potential factors that drive bellbird habitat choice within Kennedy's Bush. The tested factors were: distance to creeks (< 20 m or > 20 m), canopy height (< 4 m or > 4 m), bush density (open, moderate or dense), and distance from the shelter "Sign of the bellbird." Distance from shelter was included as a proxy for disturbance by humans. Parts of the area are highly visited by tourists and locals for recreation purposes. The lower part of Kennedy's Bush is relatively quiet but the upper part, especially the shelter itself, is frequented up to 24 hours on fine days in the summer (Cruchley, personal communication, 05.02.2008).

3.3. Results

a) Distribution of bellbirds in different habitats within Kennedy's Bush

The highest bellbird densities were for locations 8 - 11 and location 15 within a distance of 50 m (Fig. 3.1). As there was only one pre-count prior to the experiment, we cannot fit a statistical model to the data. The graph shows a great variation over all 18 locations and section 3.3b addresses the factors which might drive to this distribution.

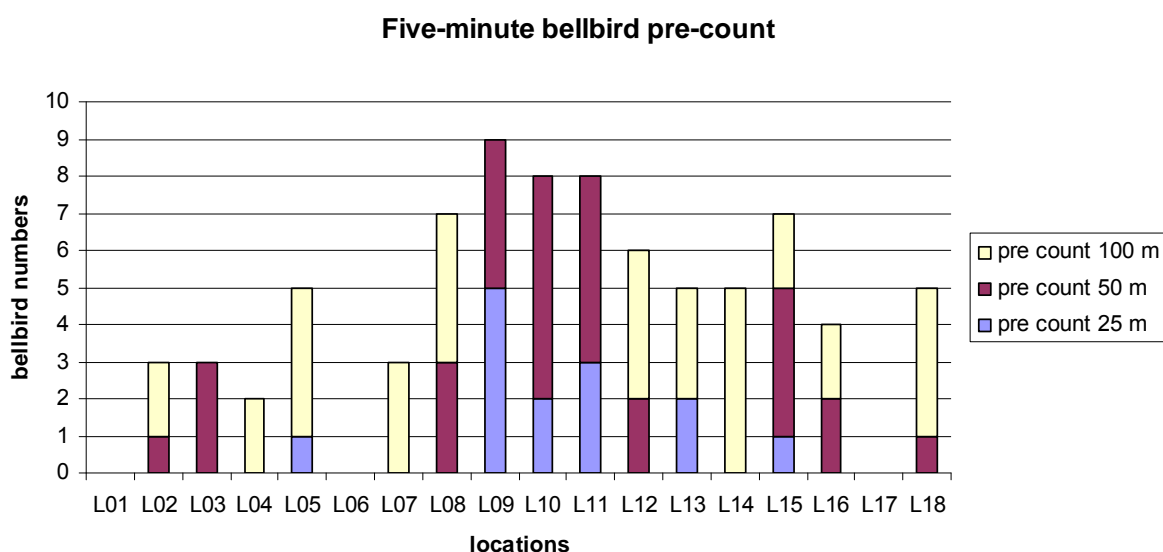


Figure 3.1: Five-minute bellbird pre-count; bellbird numbers at feeding location before experiment started. L09, L10 and L11 bellbird numbers within 50-100 m could not be estimated. L14 had at least five bellbirds within 50-100 m.

Taking all five-minute bird counts into account, no time patterns could be found for changes in bellbird numbers, neither for bellbird counts over time of day nor for counts over the season. The correlation coefficient between time of day and bellbird numbers was 0.02 and for sampling dates and bellbird numbers was 0.07.

b) Significant factors influencing habitat choice

One GLM was undertaken for each potential factor driving habitat selection. All factors could not be fitted into one model as replication was too low for a robust test. However, from the resulting P-values from the four individual models some conclusions can be derived. For example, the distance to creek ($F = 4.52$, $df = 1,16$, $P = 0.03$) was the only significant criterion among the four factors tested. However, the standard error for “close-range” to

creeks was very high (Fig. 3.2), due to the fact that there were only four values for locations near the creek.

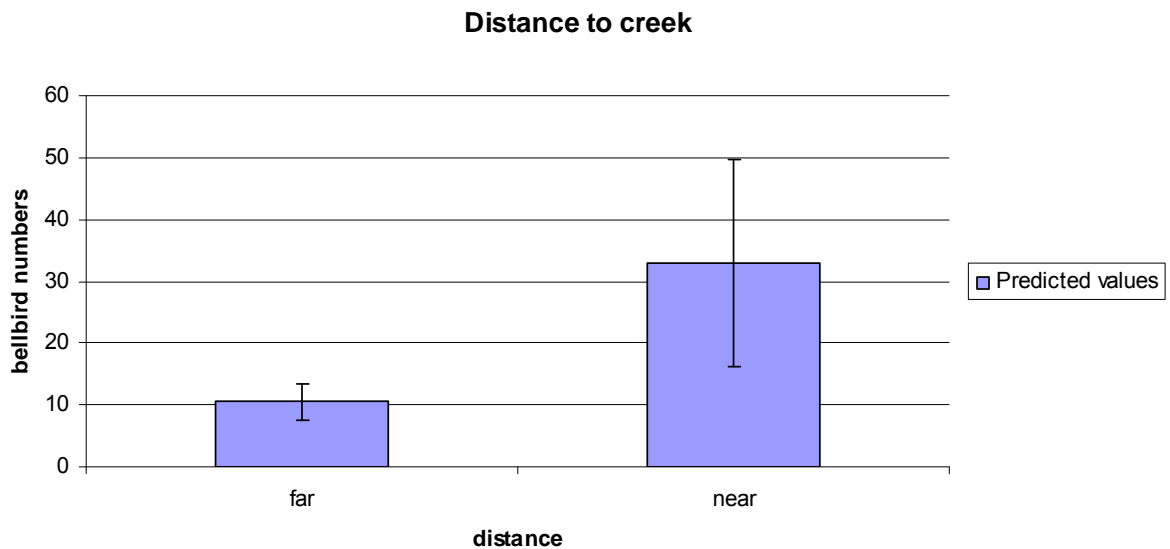


Figure 3.2: Distance to creek; predicted (Wald post-hoc test) mean number of bellbirds at locations near (<20 m) and far (>20 m) creeks, $P = 0.03$; error bars indicate s.e.

Canopy height showed a tendency for higher numbers of bellbird in high canopy areas than in lower-height bush (Fig. 3.3) but this was not statistically significant ($F = 3.00$, $df = 1,14$, $P = 0.13$).

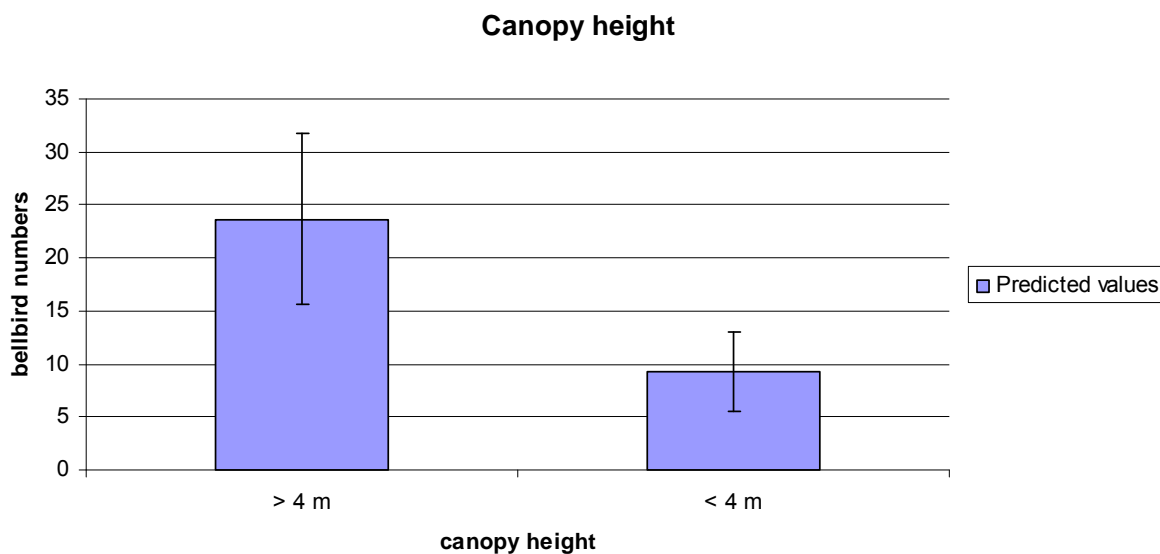


Figure 3.3: Canopy height; predicted (Wald post-hoc test) mean number of bellbirds at locations with high (>4 m) and low (<4 m) canopy, $P = 0.13$; error bars indicate s.e.

Bush density was not significant ($F = 1.93$, $df = 2,15$, $P = 0.29$) with moderate and dense bush having similar predicted values, but open habitats having very low numbers of birds (Fig. 3.4). However, even when moderate and dense bush were lumped together, the difference between open areas and bush areas was not significant ($F = 3.82$, $df = 1,16$, $P = 0.12$).

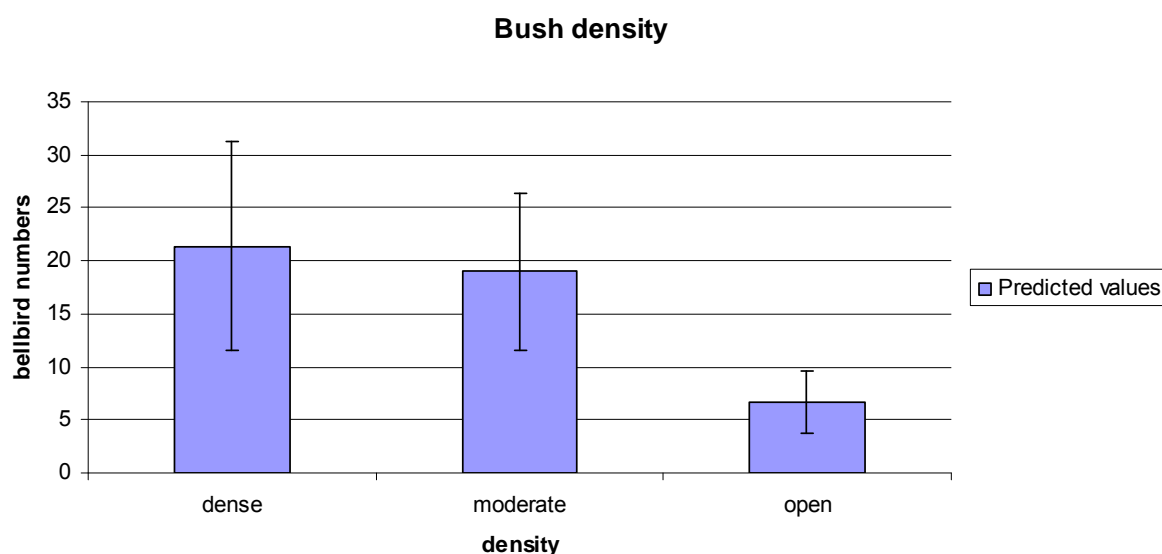


Figure 3.4: Bush density; predicted (Wald post-hoc test) mean number of bellbirds at locations with dense bush, moderate density and locations in the open, $P = 0.29$; error bars indicate s.e.

Finally, the distance to the shelter “Sign of the Bellbird” also showed no influence at all on bellbird numbers ($F = 0.1566$, $df = 1,16$, $P = 0.69$).

3.4. Discussion

In this study five-minute bellbird counts were used to determine the bellbird distribution within Kennedy's Bush on the Port Hills. This method allows the comparison of areas and density changes over the time, but does not give any information about absolute bellbird numbers within an area. Areas of relatively high and low bellbird densities were defined by this method and used for determination of factors influencing their distribution. As no breeding pairs were counted, the information about habitat choice is limited to areas used for foraging. Breeding territories could not be determined.

The density of bellbirds was highest in close proximity to fresh water. Even though nectar feeding birds, like *Meliphagidae* or hummingbirds (Fam. *Trochilidae*) obtain their water mostly from the nectar they consume and sometimes have an excessive intake of water through nectar (Nicolson, 2006), in hot dry summers they need additional water intake to maintain a sufficient water balance. Territories close to creeks or other water supply are, therefore, more suitable than drier areas. The data gained from this study were not sufficient to provide strong evidence for this assumption as there were only four locations which were in close proximity to creeks, but these four sites had very high count numbers for all conducted bird counts over the whole pre-experiment and experiment time and these values were significantly higher ($P = 0.03$) than for other sites. Therefore, presence of water is very likely to be one of the influencing factors of habitat choice for bellbirds. Potentially the distance to water was correlated to other factors, e.g. all creek locations had high canopy or might have had a higher abundance of insects, but because there were only four locations close to creeks and insect abundances was not recorded, this question cannot be statistically approached.

Canopy height is potentially another factor for habitat use of bellbirds. Even though canopy height was not a statistically significant predictor of bellbird numbers, the predicted and observed values suggest a preference for high canopy (Fig. 3.3). Several studies have been undertaken in New Zealand to show the vertical distribution of some forest birds. Spurr et al. (1992) caught bellbirds mostly with high mist nets at a height of 12-18 m, Fitzgerald, Robertson and Whitaker (1989) used mist nets up to a height of 13.5 m and also caught the majority of bellbirds in the upper part of the nets with a mean of around 10 m. Murphy and Kelly (2003) recorded bellbirds feeding just below the canopy in 12.8 % of all observations and in the upper and middle levels of the trees in 77.6 % of the observations. As their research

was conducted in mountain beech forest we can assume that the middle level of tree height was still reasonably high as mountain beech grow up to a height of 20 m (Cookson, 2008). Contrastingly, Gravatt (1971) observed bellbirds feeding much more at lower levels. These differences might be related to food availability.

Bush density only differed in bird numbers for the comparison of habitats outside versus inside the bush. Still, this variation was not significant. Open areas showed considerably fewer bellbirds than locations within the bush, whereas bush sites of moderate and high bush density showed little difference. Bush density was also not significant when it was analysed with a GLM. Open areas provided less natural food during the experimental time than locations within the bush and all bush sites, with both moderate density and high density, provided equally sufficient food sources. This explains why there was no difference detected between sites within the bush. Nevertheless, North et al. (2003) state that bellbirds prefer tall trees with a dense understory. Bellbird preference for native forest with high abundance of fruit and insects is also emphasized by Clout and Gaze (1984). They report highest bellbird numbers for forest where scale insects (*Ultracoelostoma assimile*), which produce honeydew, can be found. As bellbirds feed in all height levels and insects make up a huge part of the diet, dense understory might provide a good food source and is therefore preferred. This is supported by the findings of Williams and Karl (2002) who found bellbirds ten times more frequently in insect-rich kanuka forest than in gorse shrub habitat (chapter 2). However, this question can only be addressed by observation of bellbird feeding behaviour and qualitative and quantitative recording of food availability.

The distance to the shelter “Sign of the Bellbird” was tested, because I assumed this could be regarded as an indicator of levels of human disturbance. The Orongomai Track is less frequently visited by trampers than the area around the Sign of the Bellbird and the short tracks at the top of Kennedy's Bush. People who walk these long tracks usually stay on the tracks and mostly do not enter the bush. Nevertheless, the model for distance to shelter gave no evidence that bellbirds are sensitive to human activity. Most likely bellbirds are relatively tolerant of disturbance by humans. Predator control is equally conducted over the whole area and therefore has probably no effect on the bellbird distribution within Kennedy's Bush.

There was no influence of time on the bellbird numbers at the observation stations. Five-minute bird counts during this study varied, but showed no correlation with time of day or over the time period of the total experiment. This indicates that the experiment (chapter 4) conducted within the same period was also not affected by time of the day or by observation date.

Five-minute bird count was a suitable method to compare bellbird distribution within Kennedy's Bush. The identification of habitat factors driving habitat choice for bellbirds would have required a wider range of recorded factors. Additionally, a higher number of locations would have been needed to insure sufficient numbers of replications for a statistical analysis of potential factors.

4. Combined feeding and song playback experiment

4.1. Introduction

Conspecific attraction is well documented for colonial birds (Kotliar & Burger, 1984; Danchin et al., 1998; Serrano et al., 2004), but several studies (Ward & Schlossberg, 2004; Ahlering, 2006) have shown that conspecific cues also have a strong effect on habitat choice for some territorial birds. Public information from more experienced conspecifics gives useful information about habitat values, especially for newly dispersed first-year breeders without established territories (Doligez et al., 2004; Nocera et al., 2006). Classical habitat selection theories emphasise the importance of competition and its avoidance to individuals when finding and establishing appropriate territories, but searching for habitat is very costly and conspecific cues might help to reduce these costs. As not all territorial species which were included in studies about conspecific attraction showed a positive response towards conspecifics, e.g. the Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*) which is a relatively solitary living species (Nocera et al., 2006), this phenomenon has to be tested for individual species or at least for taxonomic families or genera.

One factor in habitat value is food availability. Supplementary feeding increases the value of a habitat and often lures birds into an area or keeps them there, even though natural food sources may decline (Bergquist & Craig, 1988; Bell, 2006). Many long-term studies of bellbirds, tui and stitchbirds (formerly thought to be honeyeaters) included supplementary feeding (Armstrong, 1992; Bergquist & Craig, 1988; Bergquist, 1989; Armstrong & Perrott, 2000) and showed a strong acceptance of sugar water by all three species.

The experiment in this study was conducted to show if bellbirds can be attracted to suitable habitats by supplementary food and/or the use of conspecific song playback. The song playback was also meant to assist bellbirds in locating feeders. These two techniques may help to draw and keep bellbirds and other honeyeaters to areas where they are scarce or absent and the habitats are still of good value. The expectation was that both supplementary food and song playback would have a significant effect on the presence of bellbirds and would increase their numbers.

4.2. Methods

a) Experimental set-up and protocol

The experiment included four different treatments that examined the role of supplementary feeding and song playback.

- Treatment one (food and playback) comprised a feeder filled with a 25 % sugar water solution. A speaker was placed within 1 m of the feeder in a tree or shrub (1-2 m above the ground), connected to an mp3-player. Recordings were played over the whole observation period and included 40 minutes of song (details: chapter 2).
- Treatment two (food only) comprised the same set up as treatment one except with no song playback.
- Treatment three (playback only) consisted of an empty feeder and the use of song playback.
- Treatment four (no food, no playback) comprised an empty feeder with no song playback.

The experiment took place at 18 locations within Kennedy's Bush (chapter 2 Table 2.1). Each of the 18 patches was used only once for each treatment, meaning that 18 of 24 possible sequences of four treatments were performed (Appendix 2, Table 7.2). Between subsequent treatments there was a break of at least one day to reduce effects of previous treatments on current treatments. When a location was in use for a treatment, its feeding station was observed once a day for 45 minutes between 0749 and 1730 hours on five to six consecutive days. The order of personal observations of feeding stations (Appendix 2, Table 7.2) stayed the same over one replicate even though the starting time varied due to additional tasks, such as five-minute bird counts and changes of sugar water on some days as well as different walking times because of track conditions. Both observers monitored two treatments per station, which were randomly assigned. Since the field assistant was not available over the whole experiment period, one station (location 01) was monitored for three replicates by me. Feeding stations were available for the birds 24 hours per day, whereas playback was started manually by observer only for the observational time.

For every observation observer, location, date and starting time of observation were noted (Appendix 3, Table 7.4). Records of fruiting and flowering plants showed that all locations within the bush had natural food sources available within 25 m. Only locations 01 and 06 had low availability of flowers and fruit.

To identify potential observer biases or variation, six observations were conducted by both observers at the same time and location. These comparisons took place between 22.02.2008 and 24.03.2008 and were undertaken for 10 to 45 minutes between 0840 and 1510 hours at locations where song playback was used.

b) Monitoring of feeding stations and playback response

For feeding events, the sex and age (adult or juvenile) of the visiting bird were recorded, together with arrival time at the feeder and the duration of time spent on the perch (Appendix 3, Table 7.5, observation at feeder). To measure reaction to song playback, the times of first five arrivals of bellbirds within 15 m were recorded. Whether the bird was heard and/or seen for each observation was also recorded for these individuals. Additionally, the number of bellbirds heard and/or seen within 5 m and 15 m of the feeder were counted every minute for the whole observation time of 45 minutes (Appendix 3, Table 7.5, minute-count in surrounding area (within 15 m)). For these observations sex was only occasionally noted because the distance and the sometimes high number of birds did not allow a definite determination of the sex. Also, the sex could not be determined for birds only heard but not seen.

c) Statistical analysis

The experimental data collected was not normally distributed and most likely had correlated factors; therefore a Generalized Linear Mixed Model (GLMM) with a negative binomial error distribution was used for the statistical analysis. Time was included as a random effect with treatment and location being fixed effects. In total, 398 observation periods of 45 minutes were undertaken, allotted to five to six observations per station for treatments one (food together with song playback), two (food only) and four (no food and no song playback). For locations 01, 05 and 17 five additional observations were undertaken for the song only

treatment (treatment 3), because of the use of the small speaker for five observations at each of these stations. Significance of the fixed effects was determined by Wald tests where each factor was individually dropped from the full model.

A mixed-model ANOVA with the treatment effect nested in location was used for the analysis of the first arrivals of bellbirds at the observation locations. The total number of observations for the first arrival was 398. On occasions when no bird was seen or heard within the observation time of 45 minutes, a maximum time of 2700 seconds = 45 minutes was used for these observations. Time was measured in seconds and then log transformed ($\log(x+1)$). Predicted values from the model were used in post-hoc tests for comparison of means using a Least Significant Difference (LSD) test at $\alpha=0.05$ level of significance.

Five-minute bellbird count data for a distance of up to 50 m (including the initial counts at each station and all five-minute counts prior to the start of each new treatment) was used to analyse the long-term effect of the experiment on bellbird numbers. The data was examined using a Generalized Linear Model (GLM) with a negative binomial distribution due to the fact that this data also was not normally distributed. Five five-minute counts were conducted at each station to add up to a total of 90 five-minute counts.

Potential observer biases were analysed using a correlation matrix with a total of 12 observations.

4.3. Results

Observer biases were not included in the statistical model because paired observer data was highly correlated ($r = 0.912$).

No data was recorded for feeding events as there were no bellbirds directly observed using the feeder!

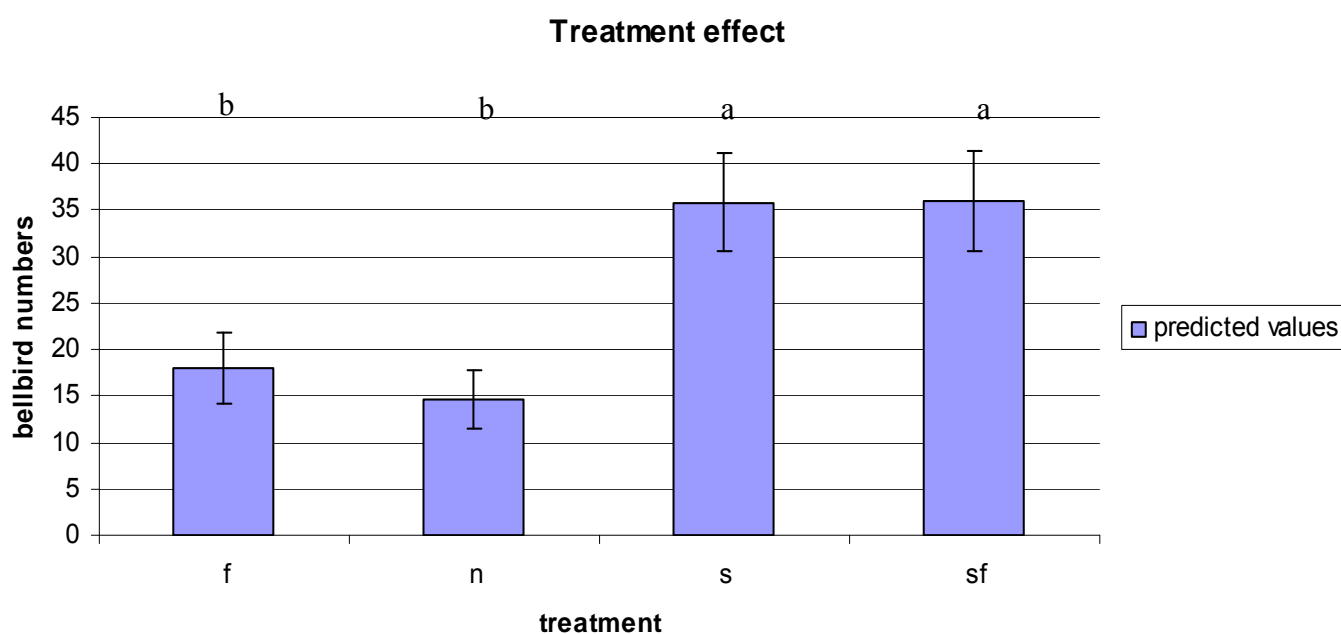


Figure 4.1: Treatment effect; predicted values for different treatments; *f* = food only, *n* = no food and no song playback, *s* = only song playback, *sf* = song playback and food; groups *a* and *b* are significantly different (Fishers LSD at $\alpha = 0.05$); error bars indicate *s.e.*

The data comparing bellbird visitation rates within 15 m radius for the four different treatments of the experiment showed a significant difference between treatments ($F = 8.89$, $df = 71, 326$, $P < 0.001$). Pairwise comparisons (Fisher's LSD at $\alpha = 0.05$) of different treatments indicated that both treatments with song playback had significantly more visits than both treatments without use of song playback (Fig. 4.1). Visitations by both sexes were recorded,

but because of high numbers of individuals during some trials and the high number of birds only heard, sex was not always recorded and therefore was excluded from the analysis.

Location as a fixed effect was included in the final model because there was a significant location by treatment interaction ($P < 0.001$ Fig. 4.2).

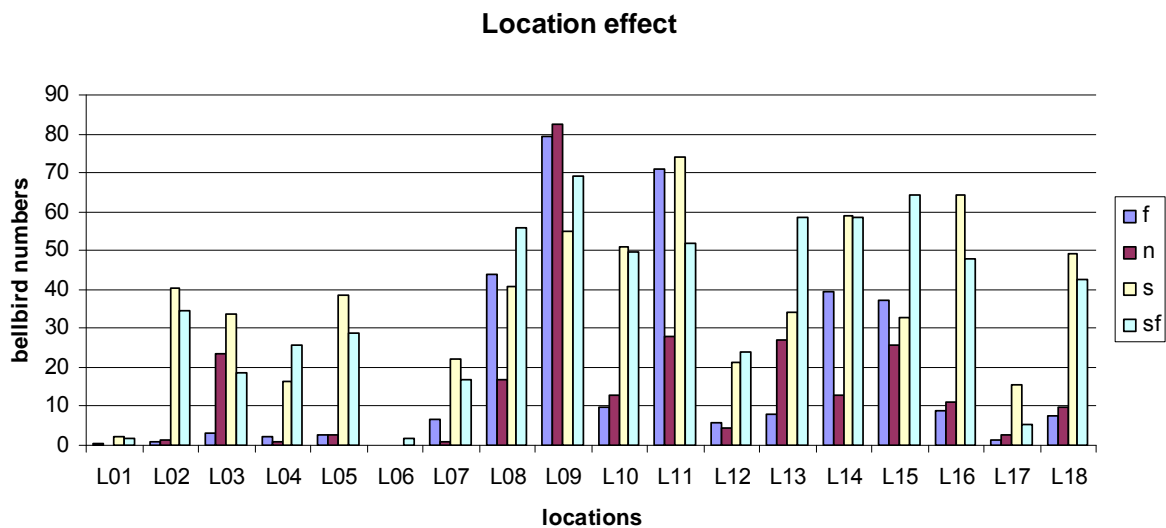


Figure 4.2: Location effect; *f* (blue) = food only, *n* (pink) = no food and no song playback, *s* (black) = only song playback, *sf* (turquoise) = song playback and food; effect of song was more pronounced for locations with low bellbird numbers (locations 1-8, 10, 14 and 16-18)

First arrivals of bellbirds

Within each location, the treatment had also a significant effect on time of first arrival of bellbirds ($F = 5.37$, $df = 3, 51$, $P = 0.003$). Differences between both treatments involving song playback were not significant, similar to the non-significance of differences between both treatments without playback. Only comparison of treatments using playback with treatments without playback showed a significant treatment effect (Fig. 4.3).

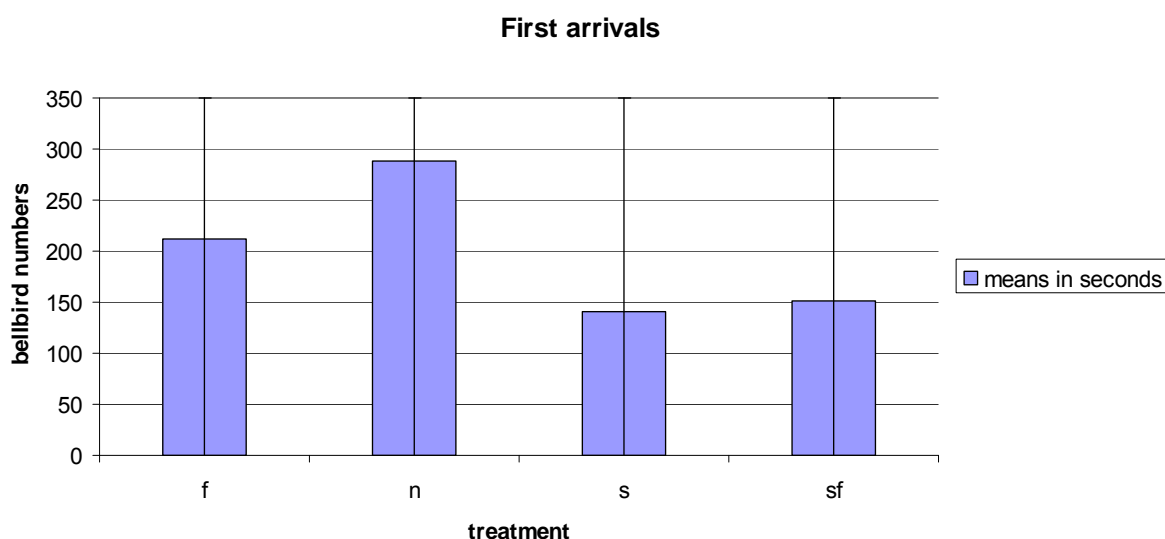


Figure 4.3: First arrivals; comparison of first bellbird arrival for treatments f = food only, n = no food, no song playback, s = song playback only, sf = food and song playback; data in means of seconds over all locations; error bars indicate s.e. with a range from 0 to 2700 seconds.

Long-term effect

Five-minute bird counts varied over the time, but showed for all stations:

- a. increases in bellbird numbers from the initial count to the count before the first treatment started,

- b. increases between the second and third treatment,
- c. declines between the first and second treatment, and
- d. declines between third and fourth treatment.

This pattern occurred regardless of the treatment order (Fig. 4.4). The peak value was reached before the first treatment started; the lowest number of bellbirds was counted during the initial count. Disregarding the apparent overlap of standard error, all stations presented the same pattern (Appendix 2, Table 7.3). The GLM showed no significance for date as an effect on bellbird numbers ($F = 4.942$, $df = 4,89$, $P = 0.293$).

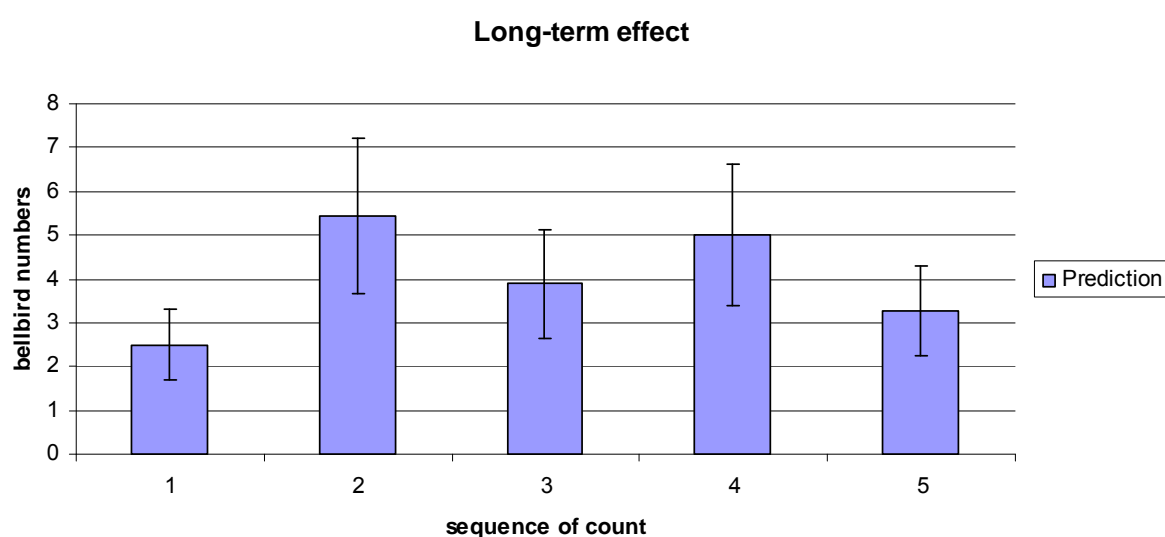


Figure 4.4: Long-term effect using 5-minute counts; predicted values for the GLM; sequence of count: 1 = initial count, 2 = count before the first treatment was started, 3 = prior to second treatment, 4 = prior to third treatment, 5 = prior to fourth treatment; error bars indicate s.e.

4.4. Discussion

Counts of bellbird visits and data of first arrivals showed no significant differences in bellbird numbers between food and no food treatments, both with and without song playback. Since there was no effect of feeder status (filled versus unfilled) on bellbird visitation to experimental stations, no information was gained about whether supplementary food can draw bellbirds to an area. Song playback, on the other hand, had a major effect in attracting bellbirds, but as the feeders were not used, they probably were not detected by the bellbirds and therefore, in this experiment, song playback did not help to discover the feeders during the experiment. One reason why feeders were not detected might have been the short time of six days for which the feeders were available. During pre-experimental trials two feeding stations were out for three weeks, but without using song playback. These feeders had artificial flowers attached to attract bellbirds, but were not detected. Some feeding stations on Maud Island were coloured bright red and were also not detected, whereas some feeders without any bright colour or flowers attached were out for only a few days before they were used by bellbirds. On Maud Island, the time before a feeder was discovered increased with the distance to established feeding stations at human dwellings. I assume that bellbirds with experience of artificial feeders are more likely to discover new feeding stations than bellbirds without this knowledge. Additionally, introducing feeding stations before the breeding season might help birds to discover artificial food supplements, as during the breeding season the diet of bellbirds, especially of female bellbirds, changes to include more insects and chicks are usually exclusively fed insects (Stead, 1932). Furthermore, bellbirds are opportunistic feeders. When food availability is high, searches for new food sources are probably very limited. Therefore, the best time to introduce feeders is when food availability is low, but still high enough that bellbirds would not leave the area in search for better foraging sites.

On the other hand, some observations during the experiment showed that feeders might have been discovered if they had been available for a longer time. I observed some silvereyes landing on top of the feeder, but not feeding from them. These approaches suggested that feeding events would start soon, but feeders were not out long enough to enable these birds to discover the food. Another event, which supports the hypothesis that song playback helps to discover food sources, was observed at location 17. Of several flax bushes in the area, only one still had a few flowers left by the start of the experiment, but bellbirds were scarce in this area and no flax feeding events were initially observed. After a few days of playback, three bellbirds were observed feeding on the last nearly dried out flax flower. Once they had discovered this last flower, they came and went for the whole observation period when playback was used. During an observation week with no playback when bellbirds already had discovered the last flower, no bellbird was seen at this plant during observation hours.

Playback of conspecific songs of bellbirds had a major effect in attracting bellbirds to the observation stations. Birds arrived within a few minutes of playback, sometimes even within less than a minute. The effect of song playback was smaller in locations with high bellbird numbers than locations with low pre-count numbers. In some cases (location 09 and 11), the number of bellbirds even declined when song playback was used in areas of high bellbird numbers (Fig. 4.2). A possible explanation for this decline may be that the additional noise of the playback prevented the observers from locating bellbirds and hindered the estimation of the distance between bird and speaker. If fewer birds were in the area or no additional playback was used, these observations could have been carried out easier. Other causes could have been a stronger attraction of bellbirds to live bellbird song (because live birds are interactive) near the experimental station but outside of the observation radius. Alternatively, there might be a reduced sensitivity to conspecific song when bellbird numbers were high. As

most of the song used for the experiment came from the area where reaction to song playback was lowest, and mostly male song playback was used, it is not unlikely that birds reacted less to the known neighbour song than they would have to the song of a stranger. This assumption is supported by the dear enemy hypothesis, which states that reactions to unknown conspecifics are stronger than to neighbouring conspecifics (chapter 1). Nevertheless, birds are expected to react very strongly to songs of neighbours that come from an unfamiliar site; an even stronger response is expected when they are confronted with their own song, which may have occurred. To my knowledge the dear enemy hypothesis has not been tested for male bellbirds. However, Brunton et al. (2008) found female bellbirds reacted stronger to conspecific song of neighbours than to unfamiliar females, especially during the breeding season. Aggressiveness is usually stronger in males than in females, but during the breeding season, breeding success is dependent on parental care and food availability. Therefore females become most aggressive against female neighbours because neighbours most likely also have chicks and compete for local food sources. Security of parental care, especially preventing polygyny, is also very important, because no female bellbird has been reported to have raised her chicks successfully alone (chapter 2). However, in this area so many bellbirds were seen and heard during all observations that sex could not be recorded. Whether males or females responded strongest at these particular sites can therefore not be answered.

Another potential reason for a small effect of song playback may be that the carrying capacity for this habitat was reached. Bellbird density may have become the limiting factor for the habitat and even though playback suggested a very high habitat value, competition was too high to attract more bellbirds.

Bellbirds are territorial all year round. As mainly solitary feeders (Heather & Robertson, 2005) they defend food resources against conspecifics and establish feeding territories. While this study was conducted after the breeding season the response to playback was very strong, especially in areas with high levels of natural food resources. These food resources might have drawn many bellbirds into this area and allowed establishment of small – but sufficient – foraging territories. The strong response of bellbirds is very promising for conspecific song playback use with tui, which seem to be more social foragers and are often reported to forage in family groups (Bergquist, 1989).

Throughout the experiments, more male than female bellbirds were observed (personal observations), especially at locations with moderate to high bellbird numbers. Because song playback mainly contained male bellbird song and male bellbirds usually are dominant over female bellbirds and chase them away from food sources, playback might have deterred females away from the experimental locations. However, this issue was not addressed with systematic data collection and must be regarded as anecdotal.

No conclusion about a long term effect can be drawn from this experiment, as song playback for 45 minutes over five to six consecutive days had no impact on the bellbird numbers during the following week. Five minute counts prior to the treatments varied over the time, but showed the same pattern (but with strong variation and great overlap of error bars) for all locations regardless of the treatment at this time (Appendix 2, Table 7.3). It is unlikely that bellbirds had left the area because of the song playback, even if song playback suggested that carrying capacity for the area was exceeded. For example, at location 09 (with consistently high bellbird numbers,) treatment two had song playback and food involved, but bellbird

numbers still increased. Most likely the playback used was not consistent enough to drive birds away.

The variation in bellbird numbers over different locations was very likely related to different habitat types (chapter 3.3 b). This variation shows the preference of bellbirds for proximity to water and tall canopy height. The preference for tall trees is also reported by North et al. (2003) and Williams and Karl (2002). Means over all treatments for each station of the fitted model data showed a high correlation with pre-experimental bellbird counts for these locations. This indicates that the location effect is a major factor, even though treatment itself is already significant.

5. General Discussion

5.1. Overall outcome

Observational five-minute counts before and during the experimental period showed a difference in bellbird numbers amongst the 18 randomly chosen locations. Bird numbers did not show any time patterns during the day or over the season when observations were conducted. Presumably, the difference between the 18 locations can be explained by some habitat factors. Even though the data of this study was not comprehensive enough to statistically prove the significance of the proximity to water as an important factor for habitat choice, the very high numbers at all locations close to creeks can be regarded as an evidence for the importance of having water close to bellbird territories. In my study, tall trees and dense bush were not significantly related to bellbird numbers, but these habitat characteristics are reported by many studies as important factors for habitat choice with bellbirds. These questions were not the main focus of this study and to address them, count locations would have to include more different habitat types in sufficient numbers, and more habitat factors would have to be recorded and statistically addressed. Additionally, the length of the study could be increased to cover and compare different seasons.

No conclusions could be drawn from supplementary feeding in this experiment as no feeding event at the feeders was recorded during the observations. It is most likely that the feeders were not detected by bellbirds, because similar feeders are accepted and highly used by bellbirds in other areas such as Tiritiri Matangi Island (Fig. 5.1) and Karori Wildlife Sanctuary. Other studies including sugar water feeders for supplementary feeding were all long-term studies or comprised areas where artificial feeders were already established. We did

not foresee the very long discovery time and the pre-trial on Maud Island suggested that feeders would have been discovered over the time of the experiment. However, lower food availability or potential previous bellbird experience with artificial feeders might have influenced the ability of bellbirds to detect the feeders on Maud Island.

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Figure 5.1: Bellbirds at a feeder on Tiritiri Matangi Island, April 2008; © by Christina Joelle Painting

Conspecific song proved to be a strong attractant for bellbirds. Bellbirds often responded within a few minutes, sometimes within seconds, to the playback. In areas where bellbirds were absent or very rare before playback – these were areas with a lack of natural food

sources during the time of the experiment – it sometimes took a few days before bellbirds responded to the playback. However, even though these areas offered no other attractant than the song playback, after playback for a few days single bellbirds could be observed for very short periods. Although, song playback did not help bellbirds to detect the feeders, it obviously attracted bellbirds to different areas. Therefore, feeder might have been discovered if the feeders had been available for a longer time and/or song playback had been broadcasted more often during the day.

Bellbirds responding to the playback often countersang with the playback and usually also approached the speaker. This shows that the response was clearly to the playback and not influenced or induced by the observer.

5.2. Recommendation for translocations of honeyeaters

Conspecific attraction experiments and observations of habitat choice have shown that patchy distributions of territorial birds are often not related to habitat quality alone. Habitats of similar quality are often not occupied by similar population sizes and some might be not used at all. Quite often even territorial birds can be found in aggregations. Against the theory of density dependent loss of fitness and increased competition, birds are often attracted to areas which are already used by conspecifics. These preferences are very likely related to conspecific cues about habitat quality. If a bird species is absent or very rare in suitable habitats and additionally is regarded as a threatened or potentially threatened species, conservation efforts should be undertaken to secure survival of the species and re-establish the population in areas where this species was common before. If species can re-occupy a

habitat without transfer of individuals by conservationists, this alternative has to be preferred. However, if a self-introduction does not happen within decades, translocation might be an option. New Zealand's conservationists, with their long history of translocations (chapter 1.1 b) are very experienced using this management tool. Nevertheless, methods for translocations of particular species have to be adapted to the special needs of the particular species.

a) Supplementary feeding

Food supplements mean a continuous and reliable food source. If the translocated birds have learned that they can rely on this food source this might add to the value of the new habitat. Supplementary feeding also insures that the energetic needs of the translocated birds are met. However, artificial feeding stations have to be familiar to the translocated birds. As my feeding experiment shows, feeders may have to be introduced in the source area long before translocation. A good time to introduce feeders is when natural food sources are limited and the focal birds are actively searching for food. This may increase the chance of feeder discovery.

Whereas a hard release (release immediately after catching and transporting to the release site) would definitely require an introduction of feeders before translocation, soft release (holding in aviary for several days) might offer the option to introduce artificial feeders during the cage stage. My pre-trials on Maud Island showed that once an artificial feeder is discovered it is highly used, so if the translocated birds learn within the few days of caging what their feeders look like, the chance of locating the same feeders at the release site can be regarded as very high.

b) Conspecific attraction

Conspecific attraction has been tested for some species and Danchin, Heg and Doligez (2001) state that in all studies where conspecific attraction is shown for territorial birds, it is most likely occurring through the use of public information to address habitat quality. Naive birds tend to use conspecific cues more intensely than experienced birds (Muller, Stamps, Krishnan & Willits, 1997), but after translocation more experienced breeders might also use this information source for evaluating a habitat. If translocation is conducted at the end of the breeding season, the inclusion of juvenile song in playbacks might be used by translocated birds as public information about breeding success in the release habitat (Nocera et al., 2006). Additionally, it might be important for juvenile birds to use song recorded at their natal sites. Even though Armstrong et al. (1995) found no difference in dispersal, breeding success and mating behaviour between familiar bird groups and unfamiliar groups, song playback from the natal site might have an attractive effect on juveniles as potential first year breeders as they often return to their natal sites for breeding. Stamps and Swaisgood (2007) point out that natal dispersers prefer habitats containing similar stimuli to their natal habitats due to natal habitat preference induction. Since New Zealand's honeyeaters often return to their natal sites for the breeding season, there is a great chance that stimuli similar to stimuli at the natal sites will help to influence habitat choice and support establishment at the release site.

5.3. Future research

a) Song

Identification of song patterns of New Zealand's honeyeaters used for different purposes, e.g. mate attraction, territory defense or food source defense, could help to increase the success of using conspecific song playback for translocations. Song related to mate attraction, for example, is probably more attractive during mating and courtship season than in other seasons and song related to food defense might be strongly related to evaluation of foraging sites. Nocera et al. (2006), for example, used song of breeding males in the post-breeding period to attract juveniles to breeding sites in the following year. Long-term studies of conspecific attraction – and especially attraction by conspecific song – of New Zealand's honeyeaters could prove the usefulness of this management tool for translocation purposes.

b) Supplementary feeding

My study shows that one problem of supplementary feeding using artificial feeders is the knowledge of the focal birds about these feeders. If birds do not know that they can expect food at these sites, they will not use them. Identifying the most attractive feeder design would help to increase the chance of detecting an artificial food supply. Knowledge about how honeyeaters detect potential food sources could help to increase the chance of honeyeaters discovering artificial feeders. Visual cues might not be the only option to advertise food.

Olfaction is regarded as poor within most birds, but we are often stunned by how honeyeaters discover their food sources of nectar. Our knowledge about food discovery of bellbirds and

tui is very limited and my pre-trial with visual cues of colour and flowers did not show any response to either. Birds known to have excellent senses of smell are kiwi, tubenosed seabirds and New World vultures. These species need olfaction to find their food. Marine birds also often use their olfaction skills for navigation.

Bird species known to use olfaction have either large olfactory lobes, a distinctive olfactory nerve or a complex nasal passage (Evans & Heiser, 2004). I could not access any information about the olfactory morphology of bellbirds or honeyeaters, but I assume that if the olfactory system was somehow outstanding or investigated at all I would have come across this information. However, new findings of Steiger, Fidler, Valcu and Kempenaers (2008) suggest that olfaction in birds might be more important than previously thought. If honeyeaters also possess a well developed olfactory sense, adding olfactory cues might help honeyeaters to discover artificial food sources. Still, our knowledge about how honeyeaters discover their food sources is not extensive and further research could fill this gap.

Conspecific song proved to be a strong attractant for bellbirds. Also, feeders might have been discovered if they were out for longer and visual or olfactory cues had been added. High usage of artificial feeders at other locations within New Zealand shows that artificial food sources are accepted by bellbirds. Further research on supplementary feeding should therefore include factors such as the most accepted feeder design and season of feeder introduction.

6. References

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7. Appendices

Appendix 1: Bird count

Table 7.1: Bird count timetable

location	date	time	location	date	time
L01	23/02/08	11:15	L18	3/03/08	14:33
L02	23/02/08	12:20	L03	9/03/08	12:30
L03	22/02/08	12:25	L05	9/03/08	13:30
L04	23/02/08	13:55	L07	9/03/08	14:20
L05	23/02/08	14:40	L08	9/03/08	08:33
L06	23/02/08	13:00	L09	9/03/08	09:40
L07	22/02/08	10:55	L10	9/03/08	09:40
L08	22/02/08	15:55	L11	9/03/08	10:30
L09	21/02/08	15:00	L12	9/03/08	08:45
L10	22/02/08	15:00	L13	9/03/08	11:30
L11	21/02/08	13:50	L14	9/03/08	11:37
L12	21/02/08	15:55	L15	9/03/08	10:40
L13	21/02/08	12:50	L16	9/03/08	12:25
L14	22/02/08	13:20	L17	9/03/08	14:27
L15	22/02/08	14:05	L18	9/03/08	13:25
L16	21/02/08	12:00	L02	16/03/08	08:15
L17	22/02/08	11:35	L06	16/03/08	08:13
L18	21/02/08	11:05	L07	16/03/08	10:07
L01	24/02/08	10:35	L08	16/03/08	12:03
L02	24/02/08	11:45	L09	16/03/08	14:12
L03	24/02/08	15:50	L10	16/03/08	11:10
L04	24/02/08	13:45	L11	16/03/08	13:54
L05	24/02/08	14:55	L12	16/03/08	12:58
L06	24/02/08	12:45	L13	16/03/08	13:07
L07	24/02/08	16:45	L14	16/03/08	09:25
L08	24/02/08	14:23	L15	16/03/08	10:18
L09	24/02/08	12:22	L16	16/03/08	12:06
L10	24/02/08	15:26	L17	16/03/08	09:11
L11	24/02/08	11:23	L18	16/03/08	11:07
L12	24/02/08	13:22	L01	25/03/08	14:05
L13	24/02/08	10:18	L02	25/03/08	14:22
L14	24/02/08	16:31	L03	25/03/08	10:15
L01	2/03/08	12:40	L04	25/03/08	13:27
L02	2/03/08	13:47	L05	25/03/08	12:00
L03	2/03/08	09:34	L06	25/03/08	13:01
L04	2/03/08	11:40	L11	25/03/08	10:25
L05	2/03/08	10:38	L12	25/03/08	09:31
L07	2/03/08	08:28	L13	25/03/08	08:29
L08	2/03/08	11:35	L14	25/03/08	09:20
L09	2/03/08	12:42	L15	25/03/08	08:24
L10	2/03/08	10:30	L16	25/03/08	11:32
L15	2/03/08	09:30	L17	25/03/08	11:05
L16	2/03/08	13:58	L18	25/03/08	12:31
L17	2/03/08	08:35	L01	31/03/08	09:48
L06	3/03/08	13:55	L04	31/03/08	08:50
			L05	2/04/08	10:10

Appendix 2: Supplementary feeding / playback experiment

Table 7.2: Observation order; 18 replications run over 18 locations (Loc + number), showing observer (a and c) and order of monitoring (1 to 7). After each replication observation order (sequence) changed.

one week observation per treatment at each station

	Loc 1	Loc 2	Loc 3	Loc 4	Loc 5	Loc 6	Loc 7	Loc 8	Loc 9	Loc 10	Loc 11	Loc 12	Loc 13	Loc 14	Loc 15	Loc 16	Loc 17	Loc 18
T1	w1 a 1	w4 a 1	w5 a 3	w5 c 6	w2 c 3	w1 a 3	w1 a 7	w3 c 1	w3 a 2	w4 a 4	w1 c 2	w3 a 1	w5 a 1	w3 c 4	w3 c 3	w3 a 5	w4 c 2	w5 c 5
T2	w2 c 5	w1 a 2	w2 c 2	w6 a 2	w5 a 5	w4 c 1	w2 c 1	w1 c 5	w2 a 5	w3 c 2	w5 c 3	w4 a 6	w1 c 1	w1 c 7	w4 a 3	w5 c 4	w5 a 4	w3 a 6
T3	w6 a 1	w2 c 6	w1 a 6	w2 c 4	w1 a 5	w5 a 6	w3 a 7	w4 a 5	w1 c 3	w2 a 3	w3 a 3	w5 c 2	w4 c 6	w5 a 2	w2 a 2	w4 c 5	w2 a 1	w4 c 4
T4	w5 a 7	w5 c 7	w3 c 5	w1 a 4	w3 c 6	w2 c 7	w4 c 3	w2 a 4	w4 c 7	w1 c 6	w4 a 7	w1 c 4	w3 a 4	w4 a 2	w5 c 1	w2 a 6	w3 c 7	w2 a 7
Sequences:																		
T1	1	3	4	3	2	1	1	3	3	4	1	2	4	2	2	2	3	4
T2	2	1	2	4	4	3	2	1	2	3	4	3	1	1	3	4	4	2
T3	4	2	1	2	1	4	3	4	1	2	2	4	3	4	1	3	1	3
T4	3	4	3	1	3	2	4	2	4	1	3	1	2	3	4	1	2	1

Loc = Location

T = treatment

T1: filled feeder / no playback

T2: filled feeder and playback

T3: empty feeder / no playback

T4: empty feeder and playback

w1; w2; w3 week 1; week 2; week 3

a observer Astrid

c observer Chrissie

1;2;3 observation at time of day (first, second, third observation of the day)

Table 7.3: Long-term effect; Predicted values from the GLM for each location; last treatments before 5-minute count: z = no treatment (initial count and first pre-treatment count), n = no food and no song playback, f = food only, s = song playback only, sf = food and song playback

		Treatment before count	Prediction	s.e.	Treatment before count	Prediction	s.e.
\Location		L01			L02		
Time\	1	z	0.183	0.198	z	1.328	0.702
	2	z	0.211	0.234	z	1.797	1.109
	3	f	0.201	0.221	sf	1.613	0.937
	4	sf	0.209	0.231	n	1.754	1.067
	5	s	0.195	0.213	f	1.507	0.845
\Location		L03			L04		
Time\	1	z	2.499	1.148	z	0.183	0.198
	2	z	4.115	2.480	z	0.211	0.234
	3	n	3.405	1.816	s	0.201	0.221
	4	sf	3.938	2.303	n	0.209	0.231
	5	s	3.044	1.527	f	0.195	0.213
\Location		L05			L06		
Time\	1	z	1.615	0.811	z	0.183	0.198
	2	z	2.285	1.382	z	0.211	0.234
	3	n	2.015	1.131	f	0.201	0.221
	4	f	2.221	1.320	s	0.209	0.231
	5	s	1.864	1.002	sf	0.195	0.213
\Location		L07			L08		
Time\	1	z	0.702	0.450	z	4.449	2.058
	2	z	0.868	0.605	z	11.456	8.029
	3	f	0.807	0.545	sf	7.598	4.257
	4	sf	0.854	0.591	s	10.327	6.796
	5	n	0.769	0.510	f	6.170	3.167
\Location		L09			L10		
Time\	1	z	4.738	2.232	z	4.569	2.129
	2	z	13.315	9.698	z	12.189	8.675
	3	n	8.409	4.837	s	7.927	4.487
	4	sf	11.829	8.059	n	10.924	7.288
	5	f	6.709	3.522	sf	6.391	3.309
\Location		L11			L12		
Time\	1	z	4.387	2.022	z	2.611	1.192
	2	z	11.095	7.716	z	4.392	2.657
	3	f	7.431	4.143	s	3.600	1.916
	4	n	10.031	6.556	f	4.193	2.457
	5	s	6.057	3.096	sf	3.204	1.600
\Location		L13			L14		
Time\	1	z	3.582	1.606	z	3.825	1.724
	2	z	7.374	4.726	z	8.343	5.463
	3	sf	5.497	2.940	sf	6.042	3.259
	4	s	6.869	4.195	f	7.711	4.791
	5	n	4.679	2.314	s	5.079	2.527

\Location Time\	Treatment before count			s.e.	Treatment before count		
	Prediction				Prediction		s.e.
	L15				L16		
1	z	4.387	2.022	z	2.721	1.235	
2	z	11.095	7.716	z	4.672	2.838	
3	n	7.431	4.143	s	3.795	2.016	
4	f	10.031	6.556	f	4.451	2.614	
5	sf	6.057	3.096	n	3.361	1.672	
	L17				L18		
1	z	1.024	0.583	z	2.015	0.962	
2	z	1.325	0.851	z	3.046	1.824	
3	n	1.210	0.742	s	2.615	1.423	
4	s	1.298	0.825	sf	2.941	1.722	
5	f	1.142	0.682	n	2.383	1.231	

