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**Home Range Characteristics of the
Australian Brushtail Possum in New Zealand:
Is Density a Driver?**

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

at
Lincoln University
by
Belinda Isobel Whyte

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Abstract of a thesis submitted in partial fulfilment of the
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Home Range Characteristics of the Australian Brushtail Possum in New
Zealand: Is Density a Driver?

by

Belinda Isobel Whyte

There is conflicting research regarding whether density is a driver of the home range characteristics of the Australian brushtail possum (*Trichosurus vulpecula*). This species transmits bovine tuberculosis (bTB) to livestock in New Zealand. Therefore, variations in movement patterns between populations of different densities, or changes in movement patterns due to density reduction (i.e., pest control), may result in variations or changes in bTB transmission risk. The first objective of this study was to investigate whether the home range characteristics of possums varied between two low-density populations within pine (*Pinus radiata*) habitat, and one high-density population within oak (*Quercus robur*) and sycamore (*Acer pseudoplatanus*) habitat, using GPS and VHF-tracking. Possum home range characteristics did not vary between the two low-density populations. However, these possums displayed considerably larger home range sizes and home range overlap with conspecifics than those in the high-density population. In addition, the low-density populations used more dens and changed these more often. Across all sites, there were generally no intersexual differences in home range characteristics. The second objective of this study was to test whether possums change their home range characteristics (i.e., exhibit spatial perturbation) in response to density reduction. Experimental density reductions were undertaken at the high-density site and one of the low-density sites. Comparisons of the home range characteristics of the same possums before and after reduction were then compared, using GPS and VHF-tracking. Density reduction was not carried out at the second low-density site, but movement patterns were still monitored. Possums displayed spatial perturbation at the high-density manipulated site by increasing their home range size and overlap following density reduction. Females at this site also increased the number of dens they used and changed their dens more often. There were no other intersexual differences in the occurrence or magnitude of perturbation at this site. In contrast, possums at the two low-density sites did not change their home range characteristics, as density at these sites remained constant between the pre-and-post monitoring periods, even though a number of individuals

were removed at one of these sites. This thesis also presents a theoretical model that predicts whether species are likely to display perturbation after a disturbance event, such as density reduction, depending on the distribution pattern of the population. The predictive capacity of this model was assessed against a range of case studies and this model predicts that possums distribute themselves predominantly based on the availability of resources. Overall, this PhD research suggests that the home range characteristics of possums are density-dependent and that possums will exhibit spatial perturbation in response to density reduction. This might mean that bTB transmission risk is not uniform across populations and could increase in some cases following density reduction, due to increases in home overlap and consequently contact rates. Therefore, control should continue to include low-density possum populations that are infected with bTB or are in vector risk areas. Furthermore, efficient density reductions of bTB infected populations should be carried out that reduce populations to very low densities across the entirety of sites (i.e., avoiding patchiness in control effort), to prevent potential increases in bTB transmission.

Keywords: bovine tuberculosis, control, den site, density-dependent, GPS-tracking, high-density, low-density, pasture use, resources, socio-spatial perturbation, spatial perturbation, *Trichosurus vulpecula*, VHF radio-tracking.

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Photos of some of the possums studied during this research

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Chapter 1:

General Introduction

1.1 Chapter summary

This chapter presents the theoretical framework underpinning this thesis – density as a driver of home range characteristics and consequently the occurrence of spatial perturbation in response to density reduction. Firstly, the potential drivers of home range characteristics are discussed, followed by the concept of spatial perturbation and how this relates to disturbance events, such as density reduction. The biology and ecology of the Australian brushtail possum (*Trichosurus vulpecula* Kerr) in New Zealand is then discussed, including what is currently known about the home range characteristics of this species and the incidence of spatial perturbation following density reduction. The chapter then concludes with a description of the objectives and layout of the thesis. A glossary of some of the terms used in this chapter is provided in Table A.1 in Appendix A.

1.2 Drivers of home range characteristics

William Burt originally defined a home range in 1943 as the area that an animal traverses in its 'normal' activities of food gathering, mating and caring for young. Under this definition, a home range does not include occasional, potentially exploratory, forays (Burt, 1943). Moreover, a home range should not to be confused with a 'territory', which is the area that an individual defends within its home range (Burt, 1943). There are potentially many drivers of home range characteristics in animals. Food availability, is considered to be a strong determinant of home range size at the population level (Coleman and Downs, 2010). Individuals likely increase their home ranges in habitats of low productivity to meet their energy requirements and decrease their home ranges in areas of high productivity as their energy needs are more easily met (the habitat-productivity hypothesis; Harestad and Bunnell, 1979). In support of this, home range characteristics of European badgers (*Meles meles*) in the United Kingdom appears to be determined by the availability of resources, with individuals changing their home ranges in response to seasonal changes in food availability (Palphramand et al., 2007).

Population density can also determine home range characteristics, with individuals in high-density populations generally having smaller home ranges than individuals in low-density populations (Sutherland, 1996). Eurasian red squirrels (*Sciurus vulgaris*) in Italy, for instance, respond to fluctuations in the density of members of their sex by adjusting their home range size, showing an inverse relationship between core area size and density (Romeo et al., 2010). The home ranges of roe deer (*Capreolus capreolus*) in two populations in Sweden have also been recorded to decrease with

increasing population density (Kjellander et al., 2004), as have the home ranges of bobcats (*Lynx rufus*) in North America (Benson et al., 2006). However, other species have shown no relationship between density and home range characteristics, such as fox squirrels (*Sciurus niger*) in the United States (Sheperd and Swihart, 1995). Moreover, it is often difficult to separate changes in density from that of food availability, as the two may be positively related (Benson et al., 2006). This may mean that variations in home range characteristics between different density populations are due to differences in food availability (as discussed above), not density. Therefore, testing whether density is a driver of home range characteristics is best achieved by manipulating densities whilst resources remain constant.

Home range characteristics can also be influenced by the social and territorial behaviour of individuals. For example, dominance hierarchies can determine the access of individuals to resources (Wehi et al., 2006) and therefore their use of space. Territoriality usually results in the uniform distribution of home ranges within the landscape, owing to direct aggression between individuals, or indirect detection of occupation, such as scent marking (Moorcroft, 2008; Reece et al., 2011). The home range characteristics of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*), for instance, is influenced by social organisation, as individuals avoid areas where adjacent neighbouring groups are present (Gibson and Koenig, 2012). This mediates their use of these border areas.

Individuals may also adjust their home range characteristics due to breeding. For example, home range overlap between conspecifics has been shown to increase during the breeding season in the Mongolian gerbil (*Meriones unguiculatus*) (Wang et al., 2011) and the Arizona gray squirrel (*Sciurus arizonensis*) (Cudworth and Koprowski, 2010). Home range size has also been shown to increase during the breeding season in giant kangaroo rats (*Dipodomys ingens*) in California (Cooper and Randall, 2007) and raccoons (*Procyon lotor*) in America (Byrne and Chamberlain, 2011).

Predation pressure may also influence the home range characteristics of animals. A study on bank voles (*Myodes glareolus*) in Finland has shown that adults decrease their home ranges in summer to most likely better protect their nestlings from predation by common shrews (*Sorex araneus*) (Liesenjohann et al., 2011). Atlantic salmon (*Salmo salar*) have been shown to decrease their territory size in response to experimental increases in predation risk (Kim et al., 2011). Wild guinea pigs (*Cavia aperea*) also temporarily shift their home ranges to areas of greater cover to decrease predation risk and then return to their original home ranges when this cover is removed (Asher et al., 2004).

Animals can also change their home range characteristics in response to environmental events or stress, such as travelling less in winter to save energy (Coleman and Downs, 2010). Greater guinea pigs (*Cavia magna*), for example, have been recorded altering their home range size in response to changes in water levels (Kraus et al., 2003). In addition, following a wildfire in Kenya, vervet monkeys (*Cercopithecus aethiops*) changed their ranging behaviour to incorporate burned

areas, which they had not previously occupied before the fire (Jaffe and Isbell, 2009). The home ranges of western bluebirds (*Sialia mexicana*) in northern Arizona are also greater in areas where fires have occurred (Hurteau et al., 2010). Floods in stream systems in Massachusetts have also resulted in the displacement of wood turtles (*Glyptemys insculpta*) by up to 17 kilometres (Jones and Sievert, 2009). Furthermore, human-induced disturbance events can alter home ranges. For example, male Eurasian red squirrels are strongly affected by patch size and shape (as determined by fragmentation of the landscape), and increase their home range size as patch size increases (Verbeylen et al., 2009).

These drivers of home range characteristics are likely not mutually exclusive. For instance, Tome's spiny rats (*Proechimys semispinosus*) in Panama vary their home range size between wet and dry seasons, with larger home ranges during the wet season (Endries and Adler, 2005). This is thought to be due to both resources being more abundant and breeding. In addition, home ranges can vary between individuals of the same species and also within individuals over time (Powell and Mitchell, 2012). For example, male home ranges are typically larger than female home ranges (Harestad & Bunnell 1979; Coleman & Downs 2010). A study in Australia on the mountain brushtail possum (*Trichosurus cunninghami*), for instance, showed that males had double the size of home ranges than females (Martin et al. 2007). These differences might be due to female home ranges only needing to encompass resources to raise offspring, but male home ranges also needing to gain access to receptive females (Coleman & Downs 2010). This is supported by the fact that males usually have larger home ranges than females in polygynous and promiscuous species (Clutton-Brock 1989; Fisher & Lara 1999; Martin et al. 2007). A study on a small antelope in Ghana, the oribi (*Ourebia oureb*), has also shown that female home range size varies inversely with food abundance and quality (Brashares and Arcese, 2002). In contrast, male home range size changes in relation to females, with males travelling greater distances when females have larger home ranges. Studies on badgers have also shown that the home range configuration of males can be driven by female distribution in space (Molina-Vacas et al., 2009).

1.3 Disturbance events and perturbation of home range characteristics

Disturbance events¹ can occur due to either natural causes (e.g., a disease outbreak) or human-induced causes (e.g., culling), and animals often change their home range characteristics in response to these disturbance events. For example, foxes (*Vulpes vulpes*) in the United Kingdom surviving an outbreak of sarcoptic mange increased their home ranges in response to the death of neighbours, with ranges following the outbreak three times larger than before (Baker et al., 2000). White-tailed

¹ Defined in this thesis as an event that results in a loss or reduction of biomass (e.g., loss of vegetation due to fire, or the removal of individuals due to culling)

deer (*Odocoileus virginianus*) in the United States of America have also been recorded changing their home ranges in response to hunting (Henderson et al., 2000).

This change in home range characteristics in response to a disturbance event is defined in this thesis as 'spatial perturbation' (Tuytens et al., 2000). Disturbance events affecting territorial species may also result in the disruption of the social organisation and behavioural patterns of populations, resulting in 'social perturbation' (Carter et al., 2007). Spatial and social perturbation are likely inextricably linked, and therefore probably occur concurrently, resulting in 'socio-spatial perturbation' (Tuytens et al., 2000). Appendix A theorises the probable mechanisms behind the occurrence and nature of these perturbations, and presents a model that predicts whether a given population of animals will likely exhibit perturbation following a disturbance event.

1.3.1 Studies investigating perturbation due to density reduction

The most detailed research on spatial and social perturbation following density reduction has involved European badgers in the United Kingdom. These badgers live in mixed-sex groups of up to 35 animals that defend a territory (Kruuk, 1978; Tuytens et al., 2000). Culling of badgers has occurred for many years to reduce the transmission of bovine tuberculosis (caused by the bacterium *Mycobacterium bovis*; bTB) from these animals to cattle. One study by Tuytens et al. (2000) assessed a badger population using VHF radio-tracking, before and after a culling operation removed 90% of the population (Carter et al., 2007). This study recorded a decrease in the home range size of individuals following density reduction, as well as an increase in the home range size and overlap of social groups. Woodroffe et al. (2006a) also investigated the response of badger social groups to culling within 13 study areas that were subjected to different levels of culling. These study areas were part of the Randomised Badger Culling Trial (RBCT) that commenced in 1998, which aimed to measure the effect of badger culling on bTB infection in cattle. They assessed the geographical extent of home ranges using colour-marked baits and the retrieval of subsequent colour-marked faeces. They recorded larger social group home ranges in the areas subjected to culling than control areas. Furthermore, the home ranges of social groups in non-culling areas increased with increasing proximity to culling areas. A greater number of overlaps between the home ranges of social groups were also recorded in culling areas. A subsequent VHF radio-tracking study also monitored the response of badgers within the RBCT to culling operations that removed 34–43% of the population (Riordan et al., 2011). In contrast to the Tuytens et al. (2000) study, surviving individuals showed a 44% increase in home range size in response to culling and a 73% increase in the overlap of summer home ranges. Further genetic work on the RBCT has also shown greater dispersal of badgers following culling (Pope et al., 2007).

A number of studies have also researched spatial perturbation following density reduction in white-tailed deer in the United States. Henderson et al. (2000) investigated the effects of a 50%

population reduction of deer in South Carolina using VHF radio-tracking. Deer were experimentally removed and the responses of remaining adult females were compared to females in a non-treatment area. Home range size of study animals in the treatment area increased by 30% on average following experimental removal, whereas, the home ranges of females in the non-treatment area did not change. In contrast, other studies on female deer in Huntington Wildlife Forest in New York have recorded no changes in home range characteristics of females following the removal of family groups (McNulty et al., 1997; Oyer and Porter, 2004). The difference between these studies was considered to be due to habitat and climate variations, with the aforementioned study investigating urban deer in Newcomb, New York, and the latter studies investigating forest deer in South Carolina (Henderson et al., 2000).

Spatial perturbation following density reduction has also been observed in a number of rodent species in New Zealand. A study on feral house mice (*Mus musculus*) recorded individuals extending their home ranges into areas where neighbours were removed, within three nights of the removal (Fitzgerald et al., 1981). It was concluded that these movement changes were due to this species being territorial and excluding other mice of the same sex from their home range. Another study on ship rats (*Rattus rattus*) recorded individuals promptly expanding their home ranges into areas where conspecifics had been removed (Innes and Skipworth, 1983). This was thought to be due to an inverse relationship between home range size and population density. Norway rats (*Rattus norvegicus*) surviving density reduction have also been recorded expanding their home ranges in response (Taylor and Thomas, 1989).

The influence of population density on home ranges have also been investigated in a nine year study of the bobcat (*Lynx rufus*) in Mississippi (Benson et al., 2006). Bobcats had been harvested for a number of years immediately prior to this study, but this was discontinued at the commencement of the research. Bobcats responded to the resultant increase in population density by decreasing their home range size. Female-female dyads also increased their home range overlap as density increased. Wiggins et al. (2010) monitored the home ranges of the Tasmanian pademelon (*Thylogale billardierii*) and the red-necked wallaby (*Macropus rufogriseus rufogriseus*) in Tasmania following density reduction. Although home range size did not change following reduction, utilisation of agricultural habitat increased and the location of home ranges shifted. Larsen and Boutin (1995) monitored the response of North American red squirrels (*Tamiasciurus hudsonicus*) to the removal of their neighbours. Individuals were recorded shifting their territory boundaries in response to density reduction. As discussed previously, foxes in the United Kingdom have been recorded increasing their home ranges in response to a disease outbreak of sarcoptic mange that reduced population density (Baker et al., 2000). Foxes live in territorial social groups and this spatial perturbation only occurred once neighbouring groups had died out.

1.4 The Australian brushtail possum in New Zealand

1.4.1 Background

The Australian brushtail possum is a marsupial with a thick bushy prehensile tail, a pointed snout, long fox-like tapering ears, and two general colour forms of grey and black (King, 2005). Possums are cat-sized, weighing 2 – 4 kilograms, with males and females similar in size and weight (Clout and Ericksen, 2000; King, 2005). They are solitary, nocturnal, arboreal and polygynous (Clout and Ericksen, 2000; Day et al., 2000a). The main breeding season occurs from March to November (Fletcher and Selwood, 2000), although births can happen at any time of the year (Fletcher and Selwood, 2000; J. Bothwell, Lincoln University, personal communication, 2013; personal observation). Social interaction is generally limited to the breeding season (King, 2005; Spurr and Jolly, 1999). Daytime dens are preferentially located aboveground in tree holes or perching epiphytes, but can also be located on the ground in dense vegetation or in holes underground (Cowan, 1989). Possums only require cover and a varied food supply; thus, they are found in almost all habitats (King, 2005). They are opportunistic herbivores that mainly feed on leaves, but also readily eat meat, preying on native animals and invertebrates, and scavenging deer (*Cervus* spp. and *Dama dama*) and pig (*Sus scrofa*) carcasses (King, 2005; Nugent et al., 2000). Pasture also constitutes a significant proportion of the diet of possums when it is available (Nugent et al., 2000).

Possums were first introduced into New Zealand from Australia in the 1800s to establish a fur trade and were a protected resource until 1921 (Montague, 2000). No other species of possum is present in New Zealand and this species has adapted well to the new diets and habitats of New Zealand, with less parasites, predators and competitors, than brushtail possums in Australia (King, 2005). They have now colonised 98% of the country (Montague, 2000) and are arguably considered to be New Zealand's most serious mainland vertebrate pest (Wilson, 2004). They eat the eggs, nestlings and adults of native bird species, such as the kōkako (*Callaeas cinerea*), fantail (*Rhipidura fuliginosa*), and kererū (*Hemiphaga novaeseelandiae*), potentially contributing to the decline of a number of native bird species (Brown et al., 1993; Nugent et al., 2000). The fact that many of New Zealand's birds are ground nesters has likely increased their vulnerability to predation by possums, as predation by this species has been shown to be higher on ground nests than arboreal nests (Whyte, 2002; Whyte et al., 2005). Possums also eat a large proportion of native vegetation, causing dieback in forests (e.g., canopy-dominant southern rata, *Metrosideros umbellata*) and even local extinctions of some plants (e.g., mistletoes) (Wilson, 2004). In addition, the possum competes for food with other native species. For example, there is dietary overlap between possums and the endangered kōkako, and this may have contributed to the decline of this species (Leathwick et al., 1983). Possums also have the potential to disperse seeds and have been implicated in the spread of introduced weeds into native forests (Wilson, 2004).

On top of all these ecological impacts, possums also transmit bTB to farmed cattle and deer. This disease is easily transmitted, debilitating, chronic and sometimes fatal (Coleman and Caley, 2000). Possums are now considered to be the primary wildlife reservoir of bTB in New Zealand livestock and the single greatest barrier to the eradication of this disease on the New Zealand mainland (Coleman and Caley, 2000). The social behaviour of possums (such as overlapping home ranges and the sharing of den sites) likely promotes the spread of bTB (Green, 1984). Millions of dollars are therefore spent every year reducing the number of possums, in an attempt to limit their impacts (Montague, 2000). For example, possums were controlled over 2.5 million hectares of New Zealand in 2012 for bTB control alone, at a cost of NZ\$56 million (AHB, 2012).

Infection of bTB in possums is characterised by microscopic and gross (visible) lesions (Coleman and Caley, 2000). As the majority of lesions in wild possums have historically been found within the lungs, it is believed that the respiratory tract is one of the main routes of bTB infection in possums through inhalation of infectious droplets (Jackson, 1995; Jackson et al., 1995a; Morris and Pfeiffer, 1995). However, other studies suggest that possums can also become infected via the percutaneous route (Cooke et al., 2003; Jackson et al., 1995a). As lesions can come to the surface of the skin, burst, and release their contents (Coleman, 1988; Jackson et al., 1995b), possums may become infected through direct contact with these lesions, during fighting, copulation, sniffing, or investigating dead possums (G. Nugent, Landcare Research, personal communication, 2010). Possums may also become infected through contact with infected excreta, such as urine and faeces (Corner and Presidente, 1980). In addition, oral transmission has been shown to occur in offspring due to the suckling of infected mothers (pseudo-vertical transmission; Jackson et al., 1995b; Morris and Pfeiffer, 1995).

Some research shows that adults are more likely to be infected with bTB than immature possums (Pfeiffer et al., 1995), whereas other research has shown no difference in prevalence between ages (Caley et al., 2001; Jackson et al., 1995a). Males typically record a higher prevalence of bTB infection than females (Caley et al., 2001; Jackson et al., 1995a; Pfeiffer et al., 1995; Tompkins et al., 2009) and this is especially apparent in juveniles (Coleman, 1988). This might be due to males foraging more widely and juvenile males dispersing over several kilometres from their natal range (Coleman, 1988), increasing their chances of coming in contact with infected possums or excreta.

In cattle it is probable, based on lesion distributions in naturally infected cattle and experimental studies, that bTB transmission is via the respiratory and oral routes (Phillips et al., 2003; Pollock and Neill, 2002). However, it is still unclear by what route farmed deer and cattle become infected with bTB from possums, but due to their exploratory behaviour towards possums, transmission is likely to be via aerosols or direct contact with discharges (Paterson, 1993; Paterson and Morris, 1995; Sauter and Morris, 1995).

1.4.2 Previous research on home ranges

The home ranges of possums in New Zealand have been studied in a range of habitats (Glen et al., 2012). Home range size varies considerably depending on habitat and density, from as little as less than a hectare to greater than 30 hectares (Cowan and Clout, 2000). These differences in home ranges may be driven by population density, as the home ranges of individuals tend to be larger in low-density populations compared to high-density populations (Arthur et al., 2002; Cowan and Clout, 2000). Low-density populations are defined in this thesis as those with less than five possums per hectare; high-density populations are defined as those with equal to or greater than five possums per hectare. This cut-off point is considered to be representative for the whole of New Zealand, as habitats generally considered to be low-density habitats, namely plantation pine (*Pinus radiata*) and beech (*Nothofagus* spp.) forest, typically do not have densities of greater than five possums per hectare (Efford, 2000). Males appear to have larger home ranges than females (Cowan and Clout, 2000; Green, 1984). The home ranges of individuals also typically overlap with one another considerably, both within and between sexes (Crawley, 1973; Paterson et al., 1995). The extent of a possum's home range may not always be used and seasonal movements to food sources often occur (Cowan and Clout, 2000). Possums also often move onto the pasture to feed, some moving significant distances from forest habitat to reach these areas (Green and Coleman, 1986). Possum density is greatest in the forest-pasture margin (Efford, 2000) and the nearer possums den to these margins the more likely they are to move onto pasture to feed (Green and Coleman, 1986). Previous research on home range characteristics of possums has generally been limited to VHF radio-tracking and trapping (Cowan and Clout, 2000), but more recently GPS technology has allowed more precise and detailed investigations of the spatial ecology of this species (Blackie et al., 2010; Pech et al., 2010).

1.4.3 Previous research on spatial perturbation following density reduction

It is probable that possums disperse and re-aggregate after populations have been reduced to very low densities (Sweetapple and Nugent, 2009). For example, live-capture trapping of two populations subjected to density reduction has suggested that home range sizes of both sexes increase following control (Morgan et al., 2007). In addition, research using GPS-tracking technology has shown that the removal of mothers results in juvenile offspring substantially expanding their home ranges in response (Blackie, 2010b). One VHF radio-tracking study on brushtail possums in Australia anecdotally recorded neighbours expanding their denning ranges into areas of experimentally removed individuals, where they occupied their vacated dens (Clinchy et al., 2001). A VHF radio-tracking study by Ji et al. (2003) recorded possums using more den sites in populations recovering from density reduction than populations not subjected to density reduction. However, this study had very low sample sizes and therefore statistical tests could not be conducted. Caley et al. (1998) also

showed that den sharing greatly reduces following density reduction, likely due to a greater availability of den sites. Home range overlap between males and females has been recorded to increase following density reduction, as determined by VHF radio-tracking (Ramsey et al., 2002).

There are other studies, however, that have recorded contradictory results to the above studies. One study examining the reinvasion of possums into controlled areas using a trap-based index and VHF radio-tracking, recorded no changes in home range size (Efford et al., 2000). Although, during the first year following removal, many possums close to the removal boundary shifted their range centre, with this effect reducing with increasing distance from the boundary. Another live-capture trapping study recorded both no apparent change in movements and greatly increased range of movements following density reduction (Brockie et al., 1997). Ramsey et al. (2002) also recorded an increase in male home ranges following density reduction during a live-capture trapping study, but no change for females. Other research has investigated the 'vacuum effect', whereby neighbouring possums re-colonise areas where density reduction has occurred, most likely to take advantage of excess food and available den sites (Barlow, 1993; Efford et al., 2000). However, research has either shown that this effect is largely confined to home range adjustments by individuals with ranges overlapping the area of reduced density (Efford et al., 2000), or shown no vacuum effect at all (Pech et al., 2010). An additional study by Monks & Ramsey (2005) investigated changes in home range size of possums following a poisoning operation using VHF radio-tracking. However, they were unable to get any useful data from before poisoning and immediately following poisoning, due to equipment failure.

These possum studies have generally all focussed on home range size and shifts, but there are other density-dependent home range characteristics that have not been investigated in detail, such as home range overlap (with the exception of overlap between males and females in the Ramsey et al. (2002) VHF radio-tracking study), habitat use and den use. These studies have also generally used now outdated and therefore less accurate monitoring techniques (e.g., trap-based indices with imperfect detection probabilities and VHF radio-tracking). Further research on possums that investigates a variety of home range variables using more advanced GPS technology, would therefore allow more accurate testing of the occurrence of spatial perturbation following density reduction.

1.4.4 Influence of density and home range characteristics on possum management

It is important to understand variations in home range characteristics due to density, so that optimal pest management strategies can be developed. If certain density populations have larger home range sizes and overlap (e.g., low-density sites), this might mean that contact rates amongst possums and therefore bTB transmission rates are greater in these populations. These areas may therefore need to be a priority for control, if bTB infected possums are present or populations are within bTB vector

areas. Furthermore, a lower density of ground-based control devices (e.g., bait stations and traps) may be able to be used in these areas, due to individuals being more likely to come in contact with devices. Knowing this could consequently reduce management costs. Behavioural changes of possums surviving density reduction, can also substantially affect the ability of managers to control and monitor populations following initial density reduction (Arthur et al., 2002). For example, increases in home range size following density reduction may mean that encounter rates with traps and baits increase in follow-up operations (Arthur et al., 2002), resulting in overestimates of densities when compared to pre-control monitoring. It could also mean that less traps or bait can be used at lower densities in follow-up control operations to achieve the desired outcome, reducing control costs. Moreover, badger culling strategies in the United Kingdom have sometimes resulted in increases in the incidence of bTB in badgers (Woodroffe et al., 2006b). This may be due to social perturbation causing an increase in contact rates between survivors, and long-distance movement and dispersal, resulting in increases in bTB transmission (Carter et al., 2007; Donnelly et al., 2003; Macdonald et al., 2006; Riordan et al., 2011; Tuytens et al., 2000; Woodroffe et al., 2009). If this also occurs in possums following density reduction, this suggests that control operations should aim to remove the majority of a population, rather than partially reduce densities, to prevent potential increases in transmission risk.

1.5 Thesis outline

1.5.1 Aims and objectives

The aim of this study was to investigate whether population density is a driver of home range characteristics in brushtail possums and whether this is consistent between sexes. To achieve this aim, the study had the following objectives:

1. Observe whether possum home range characteristics differs between sites of varying habitat and density (Chapter 3)
2. Investigate whether experimental density reduction results in survivors exhibiting spatial perturbation of home ranges, with respect to:
 - a. Den site use (Chapter 4)
 - b. Other home range characteristics (Chapter 5)

These objectives were achieved by monitoring home range characteristics of possums at three sites (of differing population density and habitat) for five weeks (addressing Objective 1), then reducing the densities of two of these sites and monitoring home ranges at all three sites for another five weeks (addressing Objectives 2a and 2b). Experimental density reduction was not undertaken at one of these sites to observe if movements changed without density reduction. However, it is acknowledged that this site is not a strict experimental control, due to differences in habitat,

population density and the year of monitoring, as explained further on in this thesis. Home range characteristics were determined using GPS-tracking and den use was determined using VHF radio-tracking. Den use was monitored at only two of the three sites (one low-density and one high-density site).

1.5.2 Chapter descriptions

Chapter 2: General methods

This chapter provides detailed descriptions of the three sites used in this study, as well as detailed information on the important aspects of the methodology used to collect the data for Chapters 3 – 5. Specifics of the methodology used for each objective are contained within the relevant chapters.

Chapter 3: Observational study – differences in possum home range characteristics between sites of varying habitat and population density

One of the sites in this study had a high-density possum population and the other two sites had low-density populations. Habitat type varied between the low-density sites and the high-density site (as discussed in detail in Chapter 2: General Methodology). This chapter compares the home range characteristics of possums (the time taken for home ranges to be fully revealed, home range size, home range overlap and pasture use) between the three sites. Den use (den type, number of dens and changes between dens) is also compared between two of these sites. This chapter addresses Objective 1 of this thesis.

Chapter 4: Experimental study – spatial perturbation of possum den site use following density reduction

In this chapter, changes in possum den site use (den type, number of dens and changes between dens) at one of the sites where density reduction was carried out is assessed. Den site use at the non-manipulated site is also discussed. This chapter addresses Objective 2a of this thesis.

Chapter 5: Experimental study – spatial perturbation of possum home range characteristics following density reduction

To address Objective 2b of this thesis, this chapter assesses whether possums at the two manipulated sites changed their home range characteristics (time taken for home ranges to become fully revealed, home range size, home range shift, home range overlap and pasture use) following density reduction. Home range characteristics at the non-manipulated site are also discussed.

Chapter 6: Synthesis and conclusions

This chapter synthesises the three data chapters of the thesis in the context of the theoretical underpinnings presented in the General Introduction (density as a driver of home range characteristics and the occurrence of spatial perturbation due to density reduction). The implications for future research and management are then discussed. The chapter concludes with a discussion of the implications of this research and recommendations for future research.

Appendices

Appendix A theorises the mechanisms behind spatial perturbation following a disturbance event and presents a model that predicts whether a given species is likely to exhibit perturbation. Appendix B describes the methodology and results of the population size and density reduction estimates used in Chapters 3 – 5, and referred to in Chapter 2: General Methods. Appendix C contains the Lincoln University standard operating procedure for the anesthesia of possums using halothane, which was developed as a result of this research. Appendix D presents descriptions of the dens used by each of the possums at the three sites.

General comments

The three data chapters of this thesis (Chapters 3 – 5) have been written as stand-alone manuscripts, with the intention that these will all be published. Due to this, there is some repetition between chapters. However, every attempt has been made to keep this to a minimum. All chapters of this thesis are written in the format of the New Zealand Journal of Ecology for consistency. The status of publications arising from this thesis (i.e., in preparation, in review, in press or published) is presented in Table 1.1).

Table 1.1 Manuscript status of thesis chapters

Thesis chapter	Title	Authors	Journal	Status
3	Differences in possum home range characteristics between sites of varying habitat and population density	Whyte, BI; Ross, JG; Blackie, HM	Wildlife Research	In press
4	Changes in possum den site use following density reduction: Implications for conservation and bovine tuberculosis control	Whyte, BI; Ross, JG; Blackie, HM	Proceedings of the 25th Vertebrate Pest Conference	Published
4	Changes in Australian brushtail possum (<i>Trichosurus vulpecula</i>) den site use following density reduction	Whyte, BI; Ross, JG; Buckley, HL	New Zealand Journal of Ecology	In press
4 and 5	Innovative developments for long-term vertebrate pest control in New Zealand ²	Blackie, HM; MacKay, JWB; Allen, WJ; Smith, DHV; Barrett, B; Whyte, BI; Murphy, EC; Ross, J; Shapiro, L; Ogilvie, S; Sam, S; MacMorran, D; Inder, S; Eason, CT	Pest Management Science	In press
5	Spatial perturbation of possums due to density reduction: Implications for control	Whyte, BI; Ross, JG; Blackie, HM	Austral Ecology ³	In preparation
Appendix A	Development of a theoretical model to predict occurrence of spatial perturbation	Whyte BI	Journal of Animal Ecology ³	In preparation

² Invited review paper with research group

³ Intended journal for submission

Chapter 2:

General Methodology

2.1 Study sites

2.1.1 Overview

The three sites in this study were located in Hororata (Sites 1 and 3) and Whitecliffs (Site 2), in the Canterbury region of the South Island of New Zealand (Plate 2.1). All three sites were in close proximity to each other, with a maximum distance between sites of 13 kilometres (between Sites 1 and 2). Research at Sites 1 – 3 was conducted in January – April 2011 (summer), September – December 2011 (spring) and January – April 2012 (summer), respectively. For the purposes of each chapter, the names of each of the three sites varied, as detailed in Table 2.1.

Canterbury has a dry, temperate climate, with a mean annual air temperature in the location of the study sites of 11.9 °C, and mean winter minimum and mean summer maximum temperatures of 1.4 °C and 24.2 °C, respectively⁴ (NIWA, 2012). The Whitecliffs Ecological District consists of hill country and plains at 300 – 900 metres above sea level, between the Waimakariri and Rakaia Rivers (McEwen, 1987). The district receives a mean annual rainfall of 866 millimetres (NIWA, 2012). Hororata is located within the High Plains Ecological District, an area of coalesced fans of outwash gravels and alluvial deposits, fringing the eastern foothills of the Southern Alps, at 150 – 600 metres above sea level (McEwen, 1987). The Hororata area receives a mean annual rainfall of 838 millimetres (NIWA, 2012). Both districts have warm summers, with occasional hot foehn northwesterlies giving temperatures above 32.0 °C, and cool winters, with frequent frosts and occasional snowfalls (McEwen, 1987). These districts have been modified from lowland short tussockland, native forest and scrub, into patches of native forest, farmland (intensive sheep, cattle and crops) and extensive pine plantations (McEwen, 1987).

Known introduced mammals at the sites were possums, rats (*Rattus* spp.), mice (*Mus musculus*), hedgehogs (*Erinaceus europaeus occidentalis*), rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus occidentalis*), ferrets (*Mustela furo*) and feral cats (*Felis catus*). Although not confirmed, there were also likely to be stoats (*Mustela erminea*) and weasels (*Mustela nivalis*).

⁴ Based on data from a weather station in Darfield, approximately 18 kilometres from all three sites, as no temperature information is available in the specific locations of the study sites



Plate 2.1 Location and satellite images of the three study sites. From top to bottom: Site 1 in Hororata (entire fragment), Site 2 in Whitecliffs (entire fragment) and Site 3 in Hororata (area within red polygon). All sites are located in the Canterbury region of the South Island of New Zealand.

Table 2.1 Description of the site names used within the thesis chapters. N/A = not applicable as data not collected.

Chapter	Site 1	Site 2	Site 3
3 (home range characteristics between sites of varying habitat and density)	High-Density Site	Low-Density Site 1	Low-Density Site 2
4 (spatial perturbation of den site use following density reduction)	Manipulated Site 1	N/A	Non-Manipulated Site
5 (spatial perturbation of home range characteristics following density reduction)	Manipulated Site 1	Manipulated Site 2	Non-Manipulated Site
Appendix B (population size and density reduction estimates)	Manipulated Site 1	Manipulated Site 2	Non-Manipulated Site

2.1.2 Site 1

Site 1 was approximately a fifteen-hectare forest fragment located at Terrace Station in Hororata (43°32'50.03"S, 171°54'35.96"E). The fragment was situated within a cattle, sheep and crop farm, and was bordered by pasture and crops on all sides. The site was generally flat with an elevation of approximately 215 metres. The dominant canopy species at the site were English oak (*Quercus robur*) and sycamore (*Acer pseudoplatanus*), with some macrocarpa (*Cupressus macrocarpa*), poplar (*Populus* sp.) and pine (*Pinus radiata*). The understory was dominated by perennial grass species, oak and sycamore saplings, with some gorse (*Ulex europaeus*) and *Pittosporum* spp. in the bush-pasture margins. Surrounding pasture and crop species consisted of Italian ryegrass (*Lolium multiflorum*) and kale (*Brassica oleracea*), respectively. No large-scale density reduction of possums (e.g., poisoning) had previously been conducted at the site, only sporadic trapping and shooting. Possum density at this site was high, at approximately seven possums per hectare (refer to Appendix B for more detailed information on density assessments).

2.1.3 Site 2

Site 2 was approximately a fifteen-hectare forest fragment located on a cattle farm in Whitecliffs (43°25'37.70"S, 171°54'33.80"E). Topography at the site was undulating and moderately steep, with an elevation of approximately 360 metres. The site was surrounded by pasture on all sides and consisted of a pine plantation, with gorse and blackberry (*Rubus fruticosus*) in the gullies and at the forest edge. Pasture species were Italian ryegrass and white clover (*Trifolium repens*). No large-scale

density reduction of possums had previously been conducted at the site, only occasional shooting. Possum density at this site was low, at approximately two possums per hectare.

2.1.4 Site 3

This site consisted of a 15-hectare end of a 60-hectare forest block, located in Hororata (43°30'50.64"S, 171°53'23.33"E). The site was undulating, with moderately steep sections. The elevation at the site was approximately 315 metres. The site consisted of plantation pine, with gorse and blackberry in gullies and at the bush-pasture margins. The site was a commercially owned plantation, and was surrounded by a cattle and sheep farm. All sides of the site were bordered by pasture consisting of Italian ryegrass. No large-scale density reduction of possums had been undertaken at the site for 5 – 10 years, only occasional shooting of possums. Possum density at the site was low, at approximately one possum per hectare.

2.2 Research tasks

2.2.1 Site reconnaissance

To address the objectives of this study, it was established that the sites would ideally meet the following requirements:

1. Be forest fragments, to prevent adjacent possums reinvading the study area following density reduction
2. Not have had possum control for a minimum of five years, to prevent monitoring possums when they are potentially still changing their movement patterns in response to density reduction
3. Be of similar habitat and starting population density (ideally high-density), to prevent the potentially confounding factors of habitat and density
4. Be of similar size of 15-20 hectares, to prevent the potentially confounding factor of site size and because this size was considered manageable for the research

The suitability of sites was established by examining aerial photography in Google Earth, and consulting with local landowners, organisations and government departments, such as the Animal Health Board and the Department of Conservation. Potential sites were visited and if they showed promise, possums were live-capture trapped and marked, to estimate the likely densities of the population. The suitability of the site for the research was also assessed at this time (e.g., the ability to take GPS fixes through the canopy). Sites in Canterbury were originally investigated, but this was extended to sites throughout New Zealand when it became difficult to find suitable sites. Overall, it was very difficult to find sites that met all of the criteria (in particular, same habitat and starting density, and no control within the past few years). The sites chosen in this study achieved the most

requirements. Approximately six months was spent undertaking site reconnaissance activities, with approximately fifty sites investigated and a dozen sites live-capture trapped.

2.2.2 Site set-up

The first task at each site was to set up a grid of fifty live-capture traps (resulting in a density of three traps per hectare), which involved carrying traps using a tramping pack, and many trips back and forth between a field vehicle. Each trap site was marked with flagging tape and a GPS coordinate taken using a handheld GPS (Garmin® GPSMAP 60CX, Kansas City, USA), to allow the traps to be re-located and their positions mapped. This task generally took a couple of days to complete at each site.

2.2.3 Possum monitoring

Following set-up of the site, monitoring of possums was carried out in accordance with the timeline outlined in Figure 2.1. Firstly, a pre-reduction density assessment was undertaken for a week using live-capture trapping and mark-recapture techniques (as per Section 2.6.1). VHF and GPS-collars were fitted to study animals during this time. Possums were then monitored for five weeks, which involved VHF-tracking each possum to their den site three times per week. Descriptions of each den were recorded in a field notebook, and den locations were marked with flagging tape and their GPS coordinates taken using the handheld GPS. To allow tracking of all the possums, fieldwork was required generally 3 – 5 times per week, depending on the number of possums to track and their locations. The exception was at Site 2, where possums were only tracked every 1 – 2 weeks during the monitoring period, to check survivorship and that their collars were still fitted. However, den descriptions and locations were still recorded at this site. A mid-experiment density reduction was then undertaken for a week at Sites 1 and 2 using live-capture trapping (trapping was still undertaken at Site 3, but individuals were not removed), as per Section 2.5.1. An additional twenty traps were set-up and used for these density reduction events at all three sites, increasing the density of traps to five per hectare. Then the possums were monitored for another five weeks. Finally, a post-reduction density assessment was undertaken using the original fifty live-capture traps, which also provided the opportunity to remove GPS and VHF-collars from any study animals that were caught.

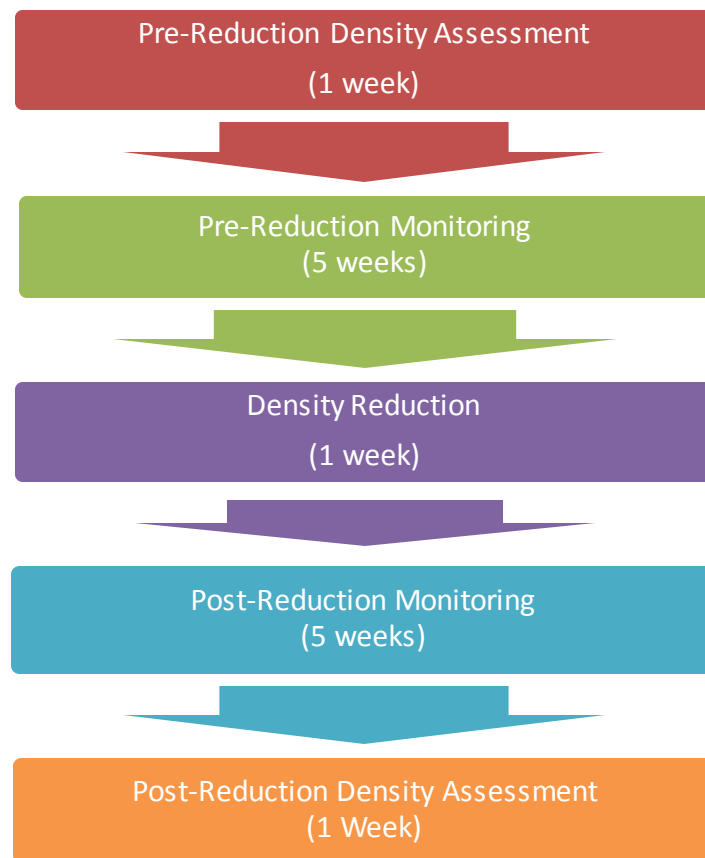


Figure 2.1 Timeline for possum monitoring at each of the three sites

2.2.4 Site clean-up

After the completion of work at each of the three sites, Feratox[®] (cyanide capsules; Connovation Limited, Auckland, New Zealand) operations were carried out across the entirety of the sites to retrieve collared individuals, and for pest management for the landowners and the local community, as per Section 2.5.2. This involved pre-feeding the site using non-toxic bait for a week, followed by application of toxic bait for a week. The age (adult or juvenile), identification (if known) and location of each possum killed was recorded. After the control operation, additional live-capture and leg-hold trapping was undertaken to retrieve any outstanding study animals, which took an additional 2–3 weeks per site. Traps and flagging tape were also removed from each site during this time. In total, a minimum of 15 weeks was spent at each site to complete site set-up, possum monitoring and site clean-up.

2.3 Animal handling procedures

2.3.1 Live-capture cage trapping

Possoms at the three sites were caught using either treadle (Trappers Cyanide Limited, Canterbury, New Zealand) or trigger (Grieve Wrought Iron Limited, Christchurch, New Zealand) live-capture cage traps. Traps were baited with apple and their entries blazed with a mixture of flour, icing sugar and

cinnamon, to entice possums into the traps (NPCA, 2009). Traps were set overnight and all efforts were undertaken to check these traps within 12 hours following sunrise, in accordance with the New Zealand Animal Welfare Act 1999. When the traps were not in use, they were left un-set in the field. Traps were dispersed evenly throughout the site, to ensure representative trapping of the entire sites. Approximately 2600 trap nights, which is the setting of one trap for one night (Parmenter et al., 2003), were carried out in total at the three sites during this study. A further few hundred trap nights were also carried out at additional sites throughout the Canterbury region for site reconnaissance purposes. The Lincoln University Animal Ethics Committee (Application Number 373) approved all research for this PhD.

2.3.2 Anesthetising

All caught possums were anaesthetised using gaseous halothane prior to handling, to ensure that the possums did not become too stressed or injured, and to prevent injury to the researchers from the study animals. Anaesthetising was carried in accordance with the Lincoln University standard operating procedure (#91 – Anaesthesia of Possums using Halothane), approved by the Lincoln University Animal Ethics Committee (see Appendix C).

2.3.3 Tagging and collection of demographic data

During both density assessment trapping events at each site, each caught possum was anaesthetised, ear-tagged in both ears with a unique metal identification tag, and weighed using a plastic bag and a 5-kilogram spring scale. The sex of each possum was determined via visual examination of external genitalia. Females were considered adults if their pouch was invaginated (Clout, 1977; Clout and Efford, 1984; Gilmore, 1969) and males were considered adults if their testis length was greater than 18 millimetres (Clinchy, 1999; Issac, 2005). The breeding status of females was also recorded, such as whether they had a joey or backrider, or whether they were feeding. In addition, a description of each possum (e.g., colour, scars or injuries) was recorded. GPS and VHF-collars were then attached to a certain number of animals. Approximately 240 possums were caught at the three sites in total (due to live-capture cage trapping and Feratox® operations), with approximately 25 additional individuals caught at other sites during site reconnaissance activities.

2.3.4 Handling, trapping and collaring effects

The trapping, handling and fitting of GPS-collars to possums has been shown to affect the movement behaviour of individuals, with changes most pronounced during the first night following trapping and handling, and persisting for at least four nights (Dennis and Shah, 2012). However, the wearing of collars over the long term does not appear to inhibit the movement behaviour of possums or affect their health (Blackie, 2010b; Dennis and Shah, 2012). It is recommended generally, however, that

tracking devices should weigh no greater than 5% of the body mass of an animal to prevent adverse effects on their behaviour (Kenward, 2001). Suitability of study animals was therefore established at the time of fitting by first weighing the individuals. In addition, monitoring periods did not start until a week following trapping, to allow individuals sufficient time to return to their normal movement patterns. The health of possums was also checked during each subsequent re-capture through visual examination and by weighing individuals to establish if they had lost weight. No significant losses in bodyweight or any other long-term adverse effects were recorded due to the wearing of collars.

2.4 Global Positioning System (GPS) and Very High Frequency (VHF) collars

The GPS was developed in 1973 by the United States Department of Defence and allows estimations of locations ('fixes') by measuring the time it takes for signals to travel from satellites in space of known positions to GPS receivers (Tomkiewicz et al., 2010). Fixes provide details of longitude, latitude, altitude, the time of the fix, and the speed and direction of travel (Zogg, 2002). In the mid-1990s, animal tracking devices based on GPS were developed to allow the study of such things as movement behaviour (Dennis et al., 2010). Only recently, however, have technological advances allowed the development of tracking devices for animals less than seven kilograms, such as possums (Blackie, 2010a; Dennis et al., 2010; Recio et al., 2011). GPS technology has generally superseded traditional VHF radio-tracking methods, as a higher frequency of automated pre-scheduled data can be collected, from larger and previously inaccessible areas, at any time, and with higher accuracy and no observer measurement biases (Blackie, 2010b; Recio et al., 2011).

A total of fifty adult possums were fitted with GPS-collars (Sirtrack Limited, Havelock North, New Zealand; Plate 2.2) at the three sites in this study. Juvenile possums were not studied, due to their movement potentially being confounded by dispersal behaviour. The GPS-collars weighed no more than 135 grams and had fabric, belt-like, straps to allow attachment to the possums. These straps were adjustable to an individual's size and were secured by plastic bolts. The collars were fitted around the neck of the possum using the 'three-finger rule', whereby the collars were loose enough to allow placement of three fingers between the possum and the collar, both at the back of the neck and under the chin (Blackie et al., 2010). This allowed sufficient room for growth and movement, as well as averting rubbing and limbs getting caught in the collar, but preventing the collar from being loose enough to slip over the possum's head (Blackie, 2010b). The batteries on the majority of the collars could be replaced and this was undertaken when possums were caught mid-experiment during the density reduction operations, to ensure sufficient battery life for the monitoring periods.

The GPS-collars had an accuracy that resulted in approximately 50% of the readings being within five metres of their true location and 90% being within eight meters (Sirtrack, New Zealand, personal communication). The ability of collars to take fixes under the canopy at each of the sites

was also confirmed manually prior to undertaking the research. They were also integrated with a duty cycle to prevent fixes being attempted during daylight hours (when the possums are denning) to conserve battery power. The fix configuration was determined at the time of manufacturing, with a trade-off between obtaining as much data as possible and having sufficient battery life for the duration of the project. The majority of collars were programmed to take eight fixes per night, with hourly intervals between fixes. The time fixes were taken was determined by the time the collars were first turned on (using a magnet), with generally a four-hour delay until the first fix. Collars were generally set to take their first fix at 9:00 pm New Zealand Standard Time (NZST).

GPS fixes were stored in the non-volatile internal memory of the collar and data were downloaded by attaching the collar to a computer using a serial port. Possums were therefore required to be re-caught to collect the data. A high retrieval rate of possums was achieved in this study, with only one of the 50 GPS-collared possums being unable to be re-caught at the completion of the research. For each successful fix, the following data were recorded: date and time in Universal Time Coordinates (UTC), latitude, longitude, altitude, speed of the animal from last recorded location (kilometres per hour), heading, number of satellites used to obtain each location and the Horizontal Dilution of Precision (HDOP) (Sirtrack®, 2010).

Ten additional possums at Site 1 were fitted with VHF-collars (Sirtrack Limited, Havelock North, New Zealand; Plate 2.2) around their necks. These were used as they were already available for the research and allowed the sample sizes for the den site monitoring to be increased; other home range characteristics (e.g., size and overlap) were not established for these possums. These collars weighed approximately 35 grams and were fitted to possums using cable ties, which could be adjusted to an individual's size using the three-finger rule as per above. In addition, each of the GPS-collars mentioned above also contained VHF units. VHF units send out radio waves that can be heard using a VHF receiver, allowing the location of an animal to be established by following the strength of the signal. Each VHF unit on the VHF and GPS-collars was programmed with a unique frequency, to allow accurate tracking of each individual to their den site. The VHF units were turned on at the time of fitting using a magnet and remained on continuously, allowing tracking at any time of the day or night. Although these units did not have replaceable batteries, they generally had sufficient battery life for the duration of the entire experiments. An Australis 26k™ VHF receiver and a yagi™ multi-directional antenna (Titley Scientific, Australia) were used for VHF radio-tracking.

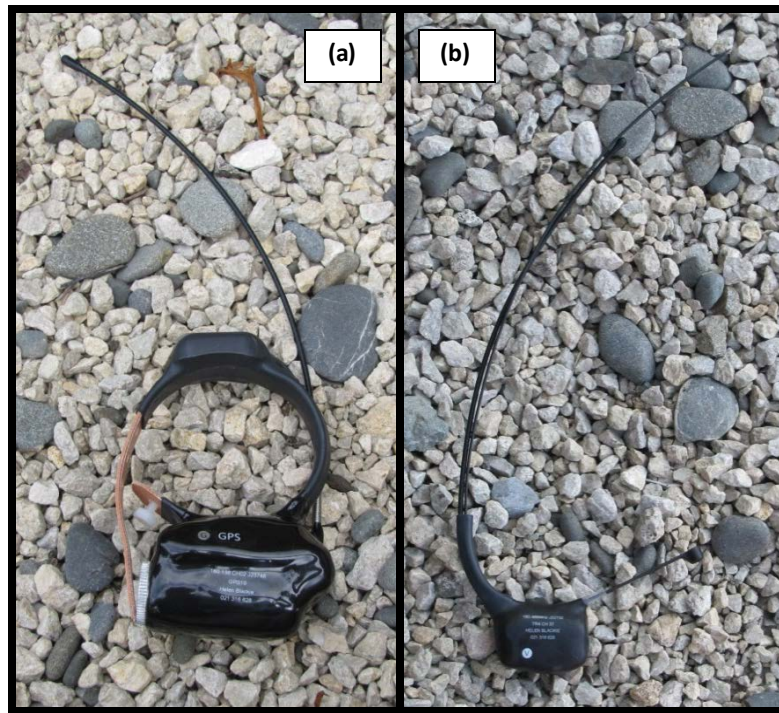


Plate 2.2 Example (a) GPS and (b) VHF-collars fitted to possums in this study

2.5 Density reduction operations

2.5.1 Mid-experiment density reduction

After the five-week pre-reduction monitoring periods, the populations at Sites 1 and 2 were reduced to lower densities by live-capture cage trapping throughout the sites for a week. All non-collared individuals caught during this time were humanely euthanised (by overdosing with halothane) and any collared individuals caught were released. Individuals were still trapped mid-experiment at Site 3 to ensure consistency in methods and to prevent potential biases due to not trapping; however, these individuals were not removed during this operation and were released as soon as they were found.

2.5.2 Final density reduction

The final density reduction was undertaken using Feratox[®] (cyanide capsules), under Lee Shapiro (Connovation Limited, Auckland) and Belinda Whyte's Controlled Substance Licences, and with permission from the Ministry of Health (application numbers 11/30/BNL/CHRP and 12/04/BNL/CHRP). Feratox[®] results in possums dying in a quick and humane manner (Gregory et al., 1998). They also die close to the bait stations, allowing the animals to be retrieved. The bait consisted of 3 – 6 capsules of Feratox[®] within 200 grams of the non-toxic pre-feed Ferafeed[®], contained in bait bags that were stapled to trees (NPCA, 2009). Signage relating to the poisoning operation was erected in accordance with the National Possum Control Agencies protocol (NPCA,

2009) and Ministry of Health requirements. To maximise bait uptake, pre-feeding was carried out at each site the week prior to using the Feratox[®], using bait with just the Ferafeed[®] and no cyanide capsules (NPCA, 2009; Warburton et al., 2009). This pre-feed was stapled to trees at the same location and manner as the toxic bait. The outward appearance of the toxic and non-toxic bait was similar and therefore unlikely to be distinguished by the possums. The total number of possums removed during both the mid-experiment density reductions and the final density reductions are presented in Table 2.2.

Table 2.2 Number of individuals removed at the three study sites during the mid-experiment and final density reductions. A = Adults, J = Juveniles, M = Males, F = Females, U = Unknown sex and T = Total removed.

Site	Mid-Experiment Density Reduction						Final Density Reduction						Total					
	A	J	M	F	U	T	A	J	M	F	U	T	A	J	M	F	U	T
Site 1	63	5	29	31	8	68	65	7	28	44	-	72	128	12	57	75	8	140
Site 2	12	2	9	5	-	14	13	5	10	8	-	18	25	7	19	13	0	32
Site 3	-	-	-	-	-	-	17	9	15	11	-	26	17	9	15	11	0	26

2.6 Population size assessments

2.6.1 Mark-recapture operations

To estimate how much the size of each population was reduced following density reduction, mark-recapture operations were carried out at the beginning ('pre-reduction mark-recapture event') and the end ('post-reduction mark-recapture event') of each study. Each of these events involved live-capture cage trapping possums for four to five consecutive nights, and recording which individuals were recaptured and which were new individuals. Fifty traps were used (resulting in a density of three traps per hectare), which were distributed evenly throughout each of the sites, to ensure that all individuals had access to a trap and therefore did not differ in their probability of capture (Otis et al., 1978). Trap types, locations and lures were all consistent between both mark-recapture events at each site. Density assessments at Site 3 were undertaken within the 15-hectare study area, not the entire 60-hectare fragment. The home ranges of the study animals were all within this 15-hectare study area and therefore it was considered that assessing only this area would provide the most accurate estimate of density.

The behaviour of individuals in the post-reduction mark-recapture events may have been influenced by their trapping experiences in the pre-reduction mark-recapture events. For example, individuals may have become 'trap-shy' after the first event and therefore not caught in the second event. However, research has shown that possums are not intrinsically un-trappable and that previous capture is unlikely to have a long-lasting effect on the trappability of individuals (Morgan et al., 2007). As such, it was considered that analysing each trapping event independently did not bias these estimates.

The resulting data were analysed in the computer program 'Program MARK' (Version 6.1), which gave an estimate of population sizes (Cooch and White, 2011; Lettink and Armstrong, 2003; Pryde, 2003). This program is the most comprehensive and widely used software for the analysis of

marked individuals (Cooch and White, 2011). Generally, the proportion of marked animals will be high when population size is low and the proportion will be low when population size is large (Begon et al., 1996). Due to the short timeframe for each mark-recapture operation (less than one week), it was assumed that the population was closed, remaining generally constant in both size and composition, and not subject to animals leaving and entering the population through births, deaths, emigration and immigration (Cooch and White, 2011; Lettink and Armstrong, 2003; Otis et al., 1978; Pryde, 2003).

Four different pre-defined Closed Population Estimation models were run for each mark-recapture event, to account for potential biases in estimates due to variations in the behaviour of individual possums (

Table 2.3). The four models for each event were then ranked by Program MARK using Akaike Information Criteria (AIC), whereby the weights of all models in the set sum to one and the model with the highest Akaike Weight is considered to have the best fit for the available data (Burnham and Anderson, 2002). Population estimates were derived through model averaging, to account for potential relevant information in models ranked below the best model (Anderson, 2008; Burnham and Anderson, 2002). Models were constructed for the total population, each age class (adult and juvenile) and each sex (male and female). Density reduction was subsequently estimated by calculating the percent difference between the pre-reduction population estimate and the post-reduction estimate. This work was peer-reviewed by a biometrician, Dr Darryl MacKenzie of Proteus Wildlife Research Consultants. Detailed results of the population size and density reduction estimates are presented in 'Appendix B: Population size and density reduction estimates'.

There is another capture-recapture program that estimates the density of possums directly from live-capture trapping (Efford, 2004). This program was developed to account for 'edge effects', whereby animals move on and off a trapping grid due to random spacing of traps and the home range size of individuals (Efford et al., 2005). Program MARK was chosen over this program, however, as the traps in this study were generally placed in grids and the entire study area was trapped; therefore, edge effects likely did not occur. Furthermore, spatial variation was of less interest in this study, with the change after density reduction being the main focus. It was also more important to account for behavioural changes in the trapping probabilities of individuals, which Program MARK addressed.

Table 2.3 List of models used to estimate population size in Program MARK (Otis et al., 1978; White, 2010)

Model	Description
M (o)	Equal capture probabilities among individuals (null model)
M (b)	Behavioural response after initial capture (capture probabilities vary with trap experience – i.e., “trap-happy” or “trap-shy” individuals)
M (t)	Time-specific variation in trapping probabilities (capture probabilities vary through time, e.g., due to weather changes)
M (tb)	Both time-specific variation and behavioural response after initial capture

2.6.2 WaxTag® surveys

WaxTag® surveys were also carried out at Site 1 as another method to estimate changes in possum abundance following density reduction (NPCA, 2008). WaxTags® were stapled to trees along survey lines to allow the identification of species, such as possums, through bite marks on the wax. A Bite Mark Index (BMI) was then calculated based on the percentage of WaxTags® that received possum interference (NPCA, 2008). Monitoring was conducted at the beginning of the experiment (pre-reduction) and then immediately following density reduction (post-reduction). However, regardless of the removal of 79 individuals (approximately 50% of the population), this index was not substantially different between events (pre-reduction BMI: 86%; post-reduction BMI: 79%). This was most likely due to contagion, whereby individual possums move along the whole survey line biting a large proportion of WaxTags®, causing an overestimation of population densities (Thomas et al., 2007). This technique was therefore not deemed a useful indicator of density change and was not employed at the following two study sites.

2.7 Analysis of GPS data

This section addresses specific GPS data analysis techniques used in this study that are considered to require in-depth discussion.

2.7.1 Data quality screening

A possible source of error and bias with GPS fixes is the inaccurate recording of an animal’s true location. One method of evaluating fix inaccuracies is to undertake stationary tests of GPS-collars (e.g., Pech et al., 2010). However, stationary tests may not reflect the accuracy of animal-deployed

collars, due to differences in vegetation obstruction and animal behaviour, such as movement rates (Augustine et al., 2011). Accuracy of animal-deployed collars may even differ between individuals (Augustine et al., 2011). As such, using stationary collars to assess the accuracy of animal-deployed collars is considered to be theoretically unsound (Augustine et al., 2011).

Another method is to assess the dimensional nature of fixes (D'Eon and Delporte, 2005). The dimension of a fix is determined by the number of satellites used, with three satellites required to achieve a 2-D fix (longitude and latitude) and four satellites required to achieve a 3-D fix (longitude, latitude and altitude) (Dassault et al., 2001; Rempel and Rodgers, 1997). If fewer than three satellites are available, a location cannot be calculated (Bjørneraas et al., 2010). Some studies use only 3-D fixes to reduce location inaccuracy; however, the removal of 2-D data can result in the elimination of a significant amount of data that may in fact be accurate (Bjørneraas et al., 2010; D'Eon and Delporte, 2005; Recio et al., 2011).

Location error can also be evaluated by assessing the Dilution of Precision (DOP) (D'Eon and Delporte, 2005). When the GPS satellites used to make a fix are close together, the geometry is weak and the DOP value associated with the fix is high, and when the satellites are far apart the opposite occurs (Langley, 1999). Generally, the lower the DOP value, the greater the number of satellites used to take the fix and the higher the positional accuracy (Langley, 1999). Many studies in the past have removed fixes that have an HDOP above a certain value, although this value is not 'standardised' across studies, ranging from 5 – 10 (Blackie, 2010b; Dassault et al., 2001; Hansen, 2010; Recio et al., 2010). However, inconsistencies have also been shown between DOP and location error, with high values not necessarily being correlated with location inaccuracies (Bjørneraas et al., 2010; D'Eon and Delporte, 2005; Hulbert and French, 2001; Recio et al., 2011).

The use of the above methods may therefore result in the removal of accurate data that may in itself cause biases in the dataset (D'Eon and Delporte, 2005). This may reduce the statistical power of the analyses (Bjørneraas et al., 2010) and may result in over- or underestimation of home ranges. Animal home range analyses are also largely robust to GPS measurement error and there is still not a strong argument that complex analyses are necessary to account for location errors in ecological studies (Frair et al., 2010). Appropriate location accuracy must be defined in relation to the objective of the study, which limits error but does not hide the pattern being studied (Bjørneraas et al., 2010; Recio et al., 2011). There is unlikely to be a consistent 'best' method for estimating home ranges (Fieberg and Börger, 2012). Comparative studies should more importantly use standardised sampling regimes and estimation methods (Fieberg and Börger, 2012). This will limit biases when comparing between individuals and populations.

The manufacturer of the collars used in this study recommends that HDOP values greater than 10 be viewed with caution (Sirtrack®, 2010). Therefore, these 'high HDOP' fixes (i.e., those with greater than 10 HDOP) were identified in the dataset. These values were then visually assessed

against previous and subsequent fixes to determine if a possum could reasonably reach these locations between fix intervals (Yockney et al., 2013). Overall, the proportion of high HDOP fixes (i.e., those >10) was very low (<5%) compared to the total dataset and no fixes were identified as being behaviourally unrealistic. In addition, high HDOP values were all within a few hundred metres of the centre of the associated home ranges. As such, it was considered that all fixes provided an acceptable level of accuracy and that removing these values would more likely introduce biases to the dataset than eliminate them. These methods of sampling and estimation were the same for all individuals, ensuring accurate comparisons between individuals and populations (Fieberg and Börger, 2012).

2.7.2 Incremental area analyses

Prior to undertaking home range analyses, tests are necessary to confirm that home ranges are fully revealed within the timeframe of monitoring, to prevent biases when comparing between individuals (Laver and Kelly, 2008; Metsers et al., 2010; Recio et al., 2010). Many studies adopt the approach of using estimates of the minimum number of locations reported in the literature for a particular species, using this value as cut-off point as to whether home ranges are revealed or not (Laver and Kelly, 2008). For example, Seaman et al. (1999) recommend that a minimum of 30 locations per animal are used to assess home ranges using kernel estimates (see information below on Kernel Density Estimates), but preferably greater than 50 locations. However, in a review of home range studies, Laver & Kelly (2008) state that minimum sample sizes should not be used as an egalitarian limit, as analyses are sensitive to the number of locations and individual behaviour can result in variability within a population. Instead, area-observation plots should be used for each individual, where one can examine how the range area changes as successive locations are added (Kenward et al., 2008; Laver and Kelly, 2008).

Area-observation plots (incremental area analyses) were therefore conducted for this study in Ranges8 (Version 2.7), which is a computer program that allows viewing, editing and analysis of spatial data, particularly animal movement data (Blackie, 2010b; Kenward et al., 2008). Locations were added incrementally to determine if a sufficient number of locations were obtained to define the 95% home range area (Asari et al., 2010; Kenward et al., 2008; Metsers et al., 2010; Recio et al., 2010). Home ranges were considered to be revealed if an asymptote was reached (i.e., additional fixes did not increase home range size), which was established visually (Laver and Kelly, 2008; Recio et al., 2010).

2.7.3 Serial autocorrelation

Serial autocorrelation is the correlation of a variable with itself over successive time intervals, resulting in a lack of independence between data points (Swihart and Slade, 1985). This phenomenon

can occur in home range analyses, as an animal's position in time is non-random and dependent on its previous location, particularly if short time intervals between successive observations are used (Blackie, 2010b; De Solla et al., 1999; Swihart and Slade, 1985). This lack of independence can interfere with statistical testing and the robustness of analyses (De Solla et al., 1999), resulting in such things as underestimates of home range size (Swihart and Slade, 1985). However, substantial controversy has arisen in the literature about the effects of autocorrelation (Blundell et al., 2001). Hawkins (2012) states that spatial autocorrelation is the exact issue that ecologists are trying to understand, and if this is part of nature then it makes little sense to claim it represents bias. Fieberg (2007) also contends that autocorrelation has drawn attention away from the more important consideration of obtaining a representative sample of locations. That aside, the level of autocorrelation will depend on the duration of the study and the sampling rate of location data (Fieberg, 2007). Autocorrelation can be reduced by increasing the duration of the study, or by decreasing the sampling rate, essentially allowing sufficient time between observations so that the animal can relocate to any other point within its home range (Fieberg, 2007). The choice of home range estimator can also influence autocorrelation, with Kernel Density Estimates (KDE) generally being the least sensitive to autocorrelation (Blundell et al., 2001; De Solla et al., 1999). This is because these analyses are non-parametric and therefore do not require sequential data points to be independent of each other (De Solla et al., 1999). KDE also provide accurate estimates of home range sizes and therefore this analysis technique is commonly used in the literature (Kenward et al., 2008; Laver and Kelly, 2008; Seaman and Powell, 1996; Worton, 1995).

To reduce autocorrelation in this study, location data were collected for a number of weeks and fixes were taken no less than one hour apart, which was considered sufficient time for an animal to move anywhere within their home range if they chose to do so. This is supported by previous studies of possums that have reported independence of data when hourly fix intervals were employed (Pech et al., 2010). In addition, KDE were used to determine the home ranges of individuals, to reduce the sensitivity of analyses to autocorrelation.

2.7.4 Home range estimation

Data were first converted from GPS World Geodetic System (WGS1984) coordinates to New Zealand Map Grid. Home ranges were then analysed in Ranges8 using KDE. This method estimates home ranges by smoothing each data point to determine a utilisation distribution (Sawyer, 2012; Seaman et al., 1999; Van Winkle, 1975; Worton, 1995). Contours are produced that estimate the probability of including a particular proportion of locations; typically a 95% contour is chosen, which delineates the area where 95% of an individual's GPS fixes are encompassed (Kenward et al., 2008). In this study, the 95% contour was calculated for each possum to determine their home range boundaries, while at the same time excluding outliers (Blackie, 2010b). The 50% contour was also calculated to

determine an animal's core area (Blackie, 2010b; Laver and Kelly, 2008). These two contour levels are often used in studies (Grovenburg et al., 2009; Hansen, 2010; Jacques et al., 2009; Laver and Kelly, 2008), including possums in New Zealand (Blackie et al., 2010; Pech et al., 2010).

It is recommended that KDE analyses are undertaken using fixed smoothing and Least Squares Cross Validation (LSCV) bandwidth, to more accurately estimate home ranges (Seaman et al., 1999). However, LSCV often results in under-smoothing and the creation of numerous small perimeters around individual data points, which do not appear to have any behavioural relevance (Jones et al. 1996; Blundell et al. 2001; Kie et al. 2010). This was also the case when LSCV was employed in this study (Plate 2.3a). This fragmentation may be due to large data sets leaving out travel corridors between areas (Fieberg and Börger, 2012), which may have been the case with this data-rich study. Analyses using fixed smoothing with reference bandwidth solve this fragmentation issue and therefore more accurately estimate home ranges (Blundell et al., 2001; Jones et al., 1996; Kie et al., 2010). When reference bandwidth was employed with the home ranges in this study, fragmentation also substantially reduced (Plate 2.3b). As such, the home ranges presented in this study were all analysed using this method.

Minimum Convex Polygons (MCP) are also used to calculate home range sizes of animals, including possums in New Zealand (e.g., Blackie, 2010b; Glen et al., 2012; Paterson et al., 1995). MCP are the smallest polygons that can be drawn around a set of location points; typically 100% MCP are used, meaning that 100% of all locations are encompassed (Kenward et al., 2008). However, this method suffers from a number of limitations, including being heavily influenced by outlying locations, and is therefore not considered to accurately estimate home range size (Kenward et al., 2008; Laver and Kelly, 2008). For this reason, KDE's were chosen as the main method of analysis for this study. Some studies use KDE but also include MCP, to allow comparisons to previous studies that have employed this method (Laver and Kelly, 2008). However, this is not recommended as the sensitivity of this method to such factors as sampling duration and the treatment of outliers, may result in spurious comparisons between studies (Laver and Kelly, 2008). However, 100% MCP's can allow the identification of the full extent of movements of an individual, in particular occasional longer-distance forays (Blackie, 2010b). This may be an important consideration in this study; for example, possums may respond to the removal of neighbours by conducting long-distance forays to determine the location of conspecifics. As such, 100% MCP were calculated for each of the possums in this study in Ranges8, using a harmonic mean peel centre (Blackie et al., 2010). In addition, to further investigate long-distance forays, home range length was calculated in the GIS program ESRI® ArcMap™ (Version 9.3; ESRI, 2008), by measuring the maximum distance across each 100% MCP.

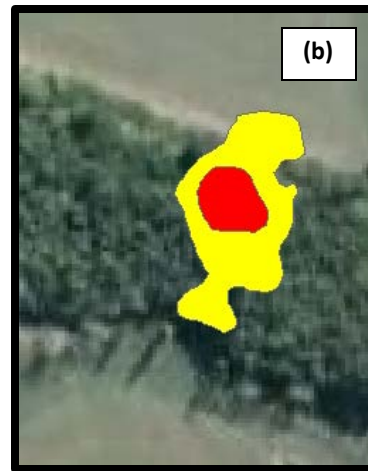
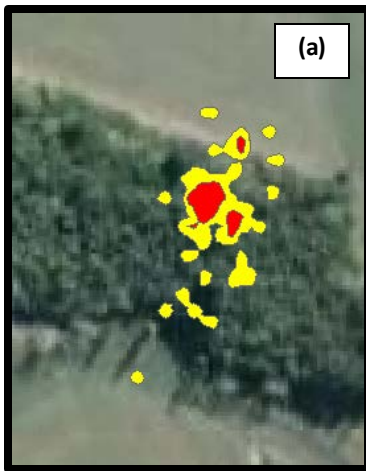


Plate 2.3 95% (yellow area) and 50% (red area) Fixed Kernel Density Estimates (KDE) of one example possum using (a) least square cross validation bandwidth versus (b) reference bandwidth

Chapter 3:

Observational Study – Differences in Possum Home Range Characteristics Between Sites of Varying Habitat and Population Density

3.1 Abstract

In New Zealand, the Australian brushtail possum transmits bovine tuberculosis (bTB) to livestock in some areas. Therefore, variations in home range characteristics between populations, such as pasture use and home range overlap, may mean that bTB transmission risk among possums, and between possums and livestock, is not uniform between sites. Being able to predict how home ranges vary may allow optimal control operations to be developed that aid in the local eradication of bTB. Previous studies on possums have shown that home ranges differ depending on habitat and population density. However, direct comparisons between these studies are not feasible due to the use of differing monitoring techniques, some of which are now outdated and imprecise. Therefore, the primary objective of this study was to use GPS-tracking and similar methodology to observe and compare variations in possum home range characteristics, in three sites over five weeks. The first site was located in a 15-hectare oak and sycamore forest fragment with a high-density possum population, which was monitored in summer 2011. The second site was within a 15-hectare pine and gorse forest fragment with a low-density possum population, and was monitored in spring 2011. The final site was within a 15-hectare area of a 60-hectare pine and gorse forest fragment, and this site was monitored in summer 2012. The secondary objective was to observe whether possum home range characteristics varied between males and females. Regardless of differences in fragment characteristics, and season and year of monitoring, possum home range characteristics did not vary between the two low-density sites. However, compared to the high-density population, these populations exhibited considerably larger home range sizes and overlap between pairs of collared possums. In addition, the low-density populations used more dens and changed these more often. Across all sites, there were generally no intersexual differences in home range characteristics. This research shows how home ranges can vary between populations, depending on habitat and population density. This may mean that bTB transmission is not uniform across sites. Further research into the drivers of home range characteristics would therefore be beneficial, so that pest management strategies can better target areas with potentially greater bTB transmission risk.

3.2 Introduction

Observational studies allow us to gain a better understanding of patterns and processes in nature (Wardle et al., 2000). They also provide the knowledge from which explanatory models and hypotheses can be generated (Coulson, 2012; Underwood et al., 2000). Consequently, progress in ecological research has been due to a combination of field observations and controlled experiments (Eberhardt and Thomas, 1991). Observational studies also enhance our understanding of population variation and therefore how behavioural differences might affect our ability to monitor, conserve and control populations.

The Australian brushtail possum (*Trichosurus vulpecula* Kerr) was introduced into New Zealand in the 1800s to establish a fur trade (King, 2005). This possum is a cat-sized, nocturnal, arboreal and polygynous marsupial, weighing 2–4 kilograms, with males and females similar in size and bodyweight (Clout and Ericksen, 2000; King, 2005). Possum home ranges have previously been studied in New Zealand and Australia in a range of habitats including native forest, scrublands, plantations and farmland (Cowan and Clout, 2000). These observational studies have shown that home ranges vary depending on habitat and population density. For example, Crawley (1973) conducted a live-capture trapping study of possums in a podocarp-mixed broadleaf forest with a high population density of between 6–11 individuals per hectare. The mean home range sizes of both males and females in this study were less than one hectare. A more recent study using Global Positioning System (GPS) technology recorded mean female home ranges within a podocarp-broadleaf forest of 0.5 hectares, with a very high population density of approximately 14 individuals per hectare, estimated using the total number of individuals killed during an intensive ground control operation (Blackie et al., 2010). In contrast, a live-capture trapping study of possums in dry grasslands in the South Island has recorded individuals as having home ranges of 36–54 hectares in populations with a density of less than one individual per hectare (Rouco et al., 2013). Another study using live-capture trapping within a beech forest (*Nothofagus*) with a low population density of less than one possum per hectare, recorded home range lengths of up to 1 kilometre long (Clout and Gaze, 1984).

These differences in home ranges may be driven by population density, as individuals in low-density populations often exhibit larger home ranges than those within high-density populations (Arthur et al., 2002; Cowan and Clout, 2000). However, it is difficult to separate population density and food availability as regulators of home range characteristics, as the two may be positively related (Benson et al., 2006). In addition, direct comparisons between these studies are not possible due to the use of differing monitoring and analyses techniques. Some of these studies also used now outdated trapping and VHF radio-tracking techniques, which are less accurate than modern GPS-tracking technology.

Being able to predict how the behaviour of pest populations will vary depending on habitat and density is important for the development of optimal pest management strategies. Possums have now become the greatest wildlife barrier to the eradication of bovine tuberculosis (*Mycobacterium bovis*, bTB) from livestock in New Zealand, as they transmit this disease to cattle and farmed deer (AHB, 2012; Coleman and Caley, 2000). In addition, possums have also caused the decline of a number of native bird species, by both competition and direct predation (Nugent et al., 2000; Sadleir, 2000). Variations in home range characteristics between populations, such as pasture use and home range overlap, may mean that bTB transmission risk among possums, and between possums and livestock, is not uniform between sites. Absence of data on how possum ranging behaviour varies in response to habitat and density, may also mean that individuals are more difficult to target in control operations, due to having unpredictable movement patterns.

The primary objective of this study was to observe whether possum home range characteristics differed among two low-density sites within pine habitat and one high-density site within oak and sycamore habitat. Time taken for home ranges to become fully revealed (i.e., until additional location fixes do not increase home range size), home range size, home range overlap (between each pair of collared possums), den use and pasture use were therefore determined at these sites using GPS-tracking technology. The latter four variables were chosen as they are all potentially density and/or habitat dependent. These behaviours may also play a role in bTB transmission risk among possums, and between possums and livestock. The first variable (time taken for home ranges to become fully revealed) was chosen as this may increase with increasing home range size – this relationship does not appear to have been previously investigated in possums or any other species. The secondary objective of this study was to observe whether possum home range characteristics varied between males and females, because previous research has suggested that males have larger home ranges than females (Glen et al., 2012; e.g., Paterson et al., 1995; Yockney et al., 2013). This research builds on previous observational studies of possums, by providing more accurate comparisons between sites, through the use of GPS-tracking and similar methodology. Moreover, this study investigates a range of home range parameters that have not previously been researched together. This study also appears to be the first to quantify home range overlap and pasture use of possums for multiple populations.

3.3 Methods

3.3.1 Study sites

High-Density Site and Low-Density Site 1 were 15-hectare forest fragments in Hororata (43°32'50.03"S, 171°54'35.96"E) and Whitedcliffs (43°25'37.70"S, 171°54'33.80"E), respectively, in Canterbury, New Zealand. Low-Density Site 2 was the 15-hectare end of a 60-hectare forest fragment in Hororata (43°30'56.38"S, 171°53'23.74"E), Canterbury. The habitat at High-Density Site consisted

of English oaks (*Quercus robur*) and sycamores (*Acer pseudoplatanus*), with surrounding paddocks of pasture species and kale (*Brassica oleracea*). The habitat at both low-density sites was predominately plantation pine (*Pinus radiata*) and gorse (*Ulex europaeus*), with surrounding paddocks of pasture species. The density at each of the sites was seven, two and one possum per hectare, respectively. These densities were estimated using mark-recapture events and pre-defined Closed Population Estimation models in Program Mark (Version 6.1) (Cooch and White, 2011; Lettink and Armstrong, 2003; Pryde, 2003). No large-scale possum control had been carried out at these sites for at least five to ten years, only sporadic trapping and shooting. Therefore, differences in possum density were likely to be due to variations in resource levels between sites.

3.3.2 Data collection

Possums were monitored at the three sites as follows: High-Density Site during January – February 2011 (summer), Low-Density Site 1 during September–October 2011 (spring) and Low-Density Site 2 during January – February 2012 (summer). As the main breeding season for possums in New Zealand is approximately March – November (Fletcher and Selwood, 2000), it is possible that breeding occurred at Low-Density Site 1 during monitoring. However, breeding can occur at any time of the year (Fletcher and Selwood, 2000; J. Bothwell, Lincoln University, personal communication, 2013), and adult females were observed with joeys and backriders during the monitoring periods at all three sites.

Adult possums were caught using treadle (Trappers Cyanide Limited, Canterbury, New Zealand) and trigger (Grieve Wrought Iron Limited, Christchurch, New Zealand) live-capture cage traps. Following live-capture, possums were anaesthetised using gaseous halothane to allow handling under sedation. All research was carried out with the approval of the Lincoln University Animal Ethics Committee (Approval Number 373) and all anaesthetising followed the Lincoln University Standard Operating Procedure (Number 91 – Possum Anaesthesia using Halothane; Appendix C).

All possums were weighed and fitted with either VHF-collars or GPS-collars that also contained VHF units (Sirtrack Limited, Havelock North, New Zealand). The VHF units allowed the possums to be radio-tracked to determine the location of their den sites, possum survival and to ensure that the collars were still fitted. The GPS-collars were generally programmed to obtain eight hourly location fixes per night between sunset and sunrise. Collars were not programmed to take fixes during the day when possums were most likely in dens. Collars were fitted with a three-finger gap between the collar belt and the skin, to prevent rubbing, but also to ensure that the collar could not slip over the possum's head (Blackie, 2010b). The VHF-collars weighed 35 grams, and the GPS-collars weighed no more than 135 grams. Possums were weighed at the time of fitting to ensure that collars weighed no more than 5% of each possums total bodyweight, to prevent adverse effects on the behaviour of the study animal (Kenward, 2001). At High-Density Site, seventeen possums were

fitted with GPS-collars (8 males and 9 females) and ten possums were fitted with VHF-collars (5 males and 5 females). Sixteen possums (8 males and 8 females) were fitted with GPS-collars at both the low-density sites. No possums were fitted with VHF-collars at these two sites.

Possums were monitored for five weeks to establish home range characteristics, as this was considered sufficient time for home ranges of possums to become revealed based on the results of similar research (H. Blackie, Lincoln University, personal communication, 2010). The GPS-collars collected location fixes throughout the entire monitoring period at all three sites. Possums at High-density Site and Low-Density Site 2 were tracked to their den sites three times per week using an Australis 26k™ VHF receiver and a yagi™ multi-directional antenna (Titley Scientific, Australia). All den site locations were recorded on a handheld GPS (Garmin® GPSMAP 60CX, Kansas City, USA). Possums at Low-Density Site 1 were only tracked sporadically to check for mortality and accidental collar removal; den use was therefore unable to be analysed at this site.

3.3.3 Data analyses

To ensure location accuracy of the GPS-collar data, fixes with Horizontal Dilution of Precision (HDOP) values greater than 10 (Sirtrack®, 2010) were visually assessed against previous and subsequent fixes, to determine if a possum could reasonably reach these locations between fix intervals (Yockney et al., 2013). Overall, the proportion of high HDOP fixes (i.e., those >10) was very low (<5%) and no fixes were identified as being behaviourally unrealistic. The mean number of fixes obtained per possum was then calculated for each population, to determine whether there were differences in sampling effort between individuals.

Prior to undertaking home range analyses, incremental area analyses are recommended to confirm that home ranges are fully revealed within the timeframe of monitoring and therefore comparisons are not biased (Laver and Kelly, 2008; Metsers et al., 2010; Recio et al., 2010). Home ranges were considered to be fully revealed if 95% of a home range was obtained within the monitoring timeframe (i.e., additional location fixes did not increase home range size) (Asari et al., 2010; Metsers et al., 2010; Recio et al., 2010). This was determined by carrying out incremental area analysis of 95% Kernel Density Estimates (KDE) in Ranges8 (Kenward et al., 2008; Laver and Kelly, 2008) and visually establishing if an asymptote was reached (Laver and Kelly, 2008; Recio et al., 2010). This information was then collated to determine the percentage of possums at each site that fully revealed their home ranges within the monitoring period, as well as the mean number of fixes required for home ranges to be fully revealed. These incremental area analyses were then used to determine which individuals home range analyses (size, overlap and pasture use, as detailed below) were conducted on.

Home range size was estimated in Ranges8 (Version 2.7) using 95% and 50% KDE, and 100% Minimum Convex Polygons (MCP) (Kenward et al., 2008). Analyses using fixed kernels with Least

Squares Cross Validation (LSCV) bandwidth is recommended for KDE (Seaman et al., 1999). However, this technique often results in under-smoothing and the creation of numerous small perimeters around individual data points, which do not appear to have any behavioural relevance (Blundell et al., 2001; Jones et al., 1996; Kie et al., 2010). This was also the case when LSCV was employed in this study. Analyses using fixed smoothing with reference bandwidth solve this excessive fragmentation issue and therefore more accurately estimate home ranges in these circumstances (Blundell et al., 2001; Jones et al., 1996; Kie et al., 2010). Consequently, reference bandwidth was employed in this study, which also eliminated the excessive fragmentation (see Section 2.6.4: Home range estimation in Chapter 2: General Methods). MCPs were also calculated to identify longer distance forays that are excluded using KDE, using a harmonic mean peel centre (Blackie et al., 2010; Kenward et al., 2008). Home range length was calculated in the GIS program ESRI® ArcMap™ (Version 9.3; ESRI, 2008), by measuring the maximum distance across each MCP.

Home range overlap between collared individuals was calculated in Ranges8 for the 95% and 50% KDE, giving the number of overlaps and percent overlap in home range area (Kenward et al., 2008). For the percent overlap analyses, as the whole population was unable to be collared, the total area of an individual's home range that overlapped with the home ranges of all other possums in the population was unable to be calculated. Instead, the percent overlap between each pair of collared possums was established. This was only carried out when overlap between possums occurred (i.e., zero overlaps were not included in the analysis). This analysis is therefore considered to provide a relative comparison of the degree of overlap between any two possums at each of the sites (when overlap occurs). The percentage of home range that did not overlap with any other collared possum (the 'exclusive area') was also calculated for each study animal, by exporting the data into ArcMap™ and carrying out overlay procedures (Hoset et al., 2008). To assess pasture use, the percentage of 95% KDE fixes within pasture habitat was calculated. Percentages were used instead of absolute numbers for the home range overlap and pasture use analyses to prevent biases due to varying home range sizes and fix configurations of the collars. Den site data were collated to establish 'den type' (aboveground versus ground), the 'number of dens' and the 'number of den changes'.

Count data (i.e., number of fixes, number of fixes until home range revealed, number of home range overlaps, number of dens and number of den changes) were all analysed using generalised linear models, with a Poisson error structure and logarithmic link function (Crawley, 2007). Proportional data (i.e., percent home range overlap, exclusive area, pasture use and den type) were all analysed using generalised linear models with a binomial error structure and logit link function (Crawley, 2007). Continuous data (KDE, MCP and home range length) were analysed using linear models, with a normal (Gaussian) error structure and an identity link function (Crawley, 2007). Continuous data were either natural log or square-root transformed when the model residuals

exhibited heteroscedasticity. Poisson and binomial models that exhibited overdispersion were re-run using quasi-Poisson/binomial linear models (Crawley, 2007).

All models were run in the statistical program R (Version 2.15.1, Woodroffe et al., 2006b) with the following combinations of fixed effects: (1) a null model with intercept only; (2) a model that considered site (High-Density Site, Low-Density Site 1 or Low-Density Site 2); (3) a model that considered bodyweight (which was measured in kilograms); (4) a model that considered sex (male or female); and (5) a model that considered the interaction between site and sex. All model sets were ranked using sample size corrected Akaike Information Criterion (AICc), with the exception of the quasi-Poisson/binomial models, which were ranked using sample size corrected Quasi-AICc (QAICc) (Anderson, 2008; Bolker, 2009; Burnham and Anderson, 2002). The weights of all models in each set summed to one and the model with the highest Akaike Weight was considered to be the closest to reality (i.e., had the best fit for the available data) (Anderson, 2008; Burnham and Anderson, 2002). Support for each model was evaluated by assessing the change in AICc/QAICc from the best model ($\Delta\text{AICc}/\Delta\text{QAICc}$) (Anderson, 2008; Burnham and Anderson, 2002). Models with a change of approximately less than two from the best model have substantial empirical support, models with a change of 4 – 7 have considerably less support and models with a change of greater than 10 have essentially no support (Burnham and Anderson, 2002). Each model set was assessed for ‘pretending variables’, whereby the addition of a variable does not change the deviance and therefore the fit of the model, skewing and biasing Akaike weights, but none were identified (Anderson, 2008).

3.4 Results

3.4.1 Sample sizes

At High-Density Site, Low-Density Site 1 and Low-Density Site 2, the home ranges of three, one and one of the possums, respectively, could not be analysed due to the GPS-collars malfunctioning within the monitoring timeframe. The reason for this was unclear, but was due to either the hardware of the collars malfunctioning or the collar batteries going flat. One possum at High-Density Site was also unable to be located during the monitoring period or at the completion of the study. In addition, one possum was excluded from the analyses at Low-Density Site 2 due to having a home range that did not include the study area, even though she was originally trapped in this area (see Possum 9 den descriptions in Appendix D). The home range of this female possum was within the surrounding agricultural matrix, largely within shelterbelts. She had a much larger home range size than the other possums at this site (95% contour = 76 hectares; 50% contour = 15 hectares). It was unclear why her behaviour differed to the other possums (i.e., she was not a dispersing male juvenile). Due to these possums being unable to be analysed and due to some home ranges not being fully revealed within the monitoring timeframe (due to possums exhibiting ‘unstable’ home ranges), home ranges could only be calculated for eight possums (5 males and 3 females), eleven possums (7 males and 4

females) and twelve possums (7 males and 5 females) at High-Density Site, Low-Density Site 1 and Low-Density Site 2, respectively (Table 3.1).

For the den site analyses, two possums at High-Density Site were unable to be analysed due to the batteries of one VHF-collar and one GPS-collar going flat. In addition, one possum at this site was unable to be located during the monitoring period, as detailed above. At Low-Density Site 2, the female mentioned above that ranged outside the study area was excluded from the analyses. This resulted in den use at High-Density Site and Low-Density Site 2 only being analysed for 24 possums (10 males and 14 females) and 15 possums (8 males and 7 females), respectively.

Table 3.1 The total number of possums at the three sites that were fitted with GPS-collars, the number of collars that were unable to be analysed, the number of home ranges that were not fully revealed within the monitoring timeframe and the resultant number of possums for which home range analyses were conducted.

GPS-collared possums	High-Density Site			Low-Density Site 1			Low-Density Site 2		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
Number collared	17	8	9	16	8	8	16	8	8
Number unable to be analysed	4	2	2	1	0	1	2	1	1
Number where home range was not revealed	5	4	1	4	2	2	2	1	1
Resultant number analysed	8	5	3	11	7	4	12	7	5

3.4.2 Number of fixes

Model comparisons revealed that the 'Bodyweight' model had the best fit to the number of fixes data (Akaike Weight of 0.66; Table 3.2). However, the 'Null' model was very close to being within two $\Delta AICc$ values of this model (Akaike Weight of 0.23; Table 3.2). This suggests that there was no influence of site, sex or the bodyweight of individuals on the number of fixes taken (Figure 3.1).

Table 3.2 Akaike weights ($\Delta\text{AICc}/\Delta\text{QAICc}$) from the linear models investigating number of fixes, number of fixes until home ranges fully revealed, home range size, home range overlap, pasture use and den use, for possums at the three sites. Site is a categorical variable with three categories, sex is a categorical variable with two categories (male or female) and bodyweight (BW) is a continuous variable, which was measured in kilograms. Bold numbers indicate models within a set that have a ΔAICc of less than two. KDE = Kernel Density Estimates and MCP = Minimum Convex Polygons. Level of empirical support for models: substantial = ΔAICc of 0 – 2, considerably less = ΔAICc of 4 – 7, essentially none = ΔAICc of >10.

Response variable	Null	Site	BW	Sex	Sex*Site
<i>Number of fixes</i>	0.23 (2.1)	0.02 (6.7)	0.66 (0.0)	0.09 (4.0)	0.00 (11.0)
<i>Number of fixes until home ranges revealed</i>	0.40 (0.0)	0.30 (0.6)	0.15 (1.9)	0.12 (2.4)	0.02 (6.4)
<i>Home range size</i>					
95% KDE	0.00 (13.1)	0.95 (0.0)	0.00 (12.8)	0.00 (13.9)	0.05 (6.1)
50% KDE	0.00 (11.7)	0.97 (0.0)	0.00 (11.9)	0.00 (13.1)	0.02 (7.4)
100% MCP	0.02 (7.9)	0.93 (0.0)	0.01 (8.3)	0.01 (10.0)	0.03 (6.6)
Length	0.08 (4.5)	0.80 (0.0)	0.04 (6.1)	0.03 (6.6)	0.05 (5.5)
<i>Home range overlap</i>					
95% KDE percent overlap	0.03 (6.6)	0.82 (0.0)	0.04 (6.1)	0.02 (7.4)	0.09 (4.3)
50% KDE percent overlap	0.00 (19.6)	0.98 (0.0)	0.00 (19.1)	0.00 (21.6)	0.02 (7.4)
95% KDE number of overlaps	0.00 (52.9)	0.96 (0.0)	0.00 (46.0)	0.00 (53.7)	0.04 (6.6)
50% KDE number of overlaps	0.00 (60.8)	0.58 (0.0)	0.00 (54.9)	0.00 (54.9)	0.42 (0.7)
95% exclusive area	0.00 (28.8)	0.97 (0.0)	0.00 (26.3)	0.00 (30.9)	0.03 (6.7)
50% exclusive area	0.00 (17.8)	0.99 (0.0)	0.00 (17.7)	0.00 (20.2)	0.01 (8.9)
<i>Percentage of fixes within pasture</i>	0.00 (16.7)	0.93 (0.0)	0.00 (15.2)	0.00 (15.0)	0.07 (5.2)
<i>Den use</i>					
Den type	0.00 (98.3)	0.00 (94.7)	0.00 (99.9)	0.00 (11.4)	1.0 (0.0)
Number of dens	0.00 (16.9)	0.00 (10.6)	0.00 (16.7)	0.09 (4.7)	0.91 (0.0)
Number of den changes	0.00 (40.3)	0.00 (26.1)	0.00 (41.4)	0.00 (17.2)	1.0 (0.0)

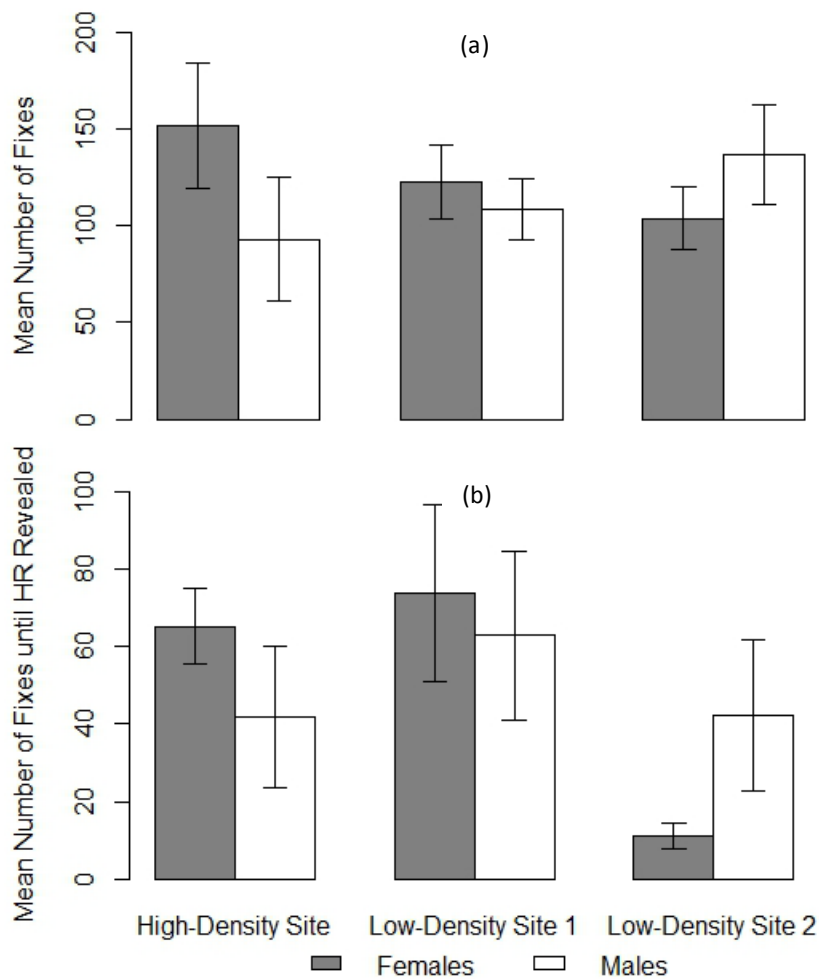


Figure 3.1 Mean number of GPS fixes taken (a) per individual and (b) for home ranges to be fully revealed, for possums at the three sites. Error bars are \pm the standard error. HR = Home Range.

3.4.3 Number of fixes until home range revealed

The total percentage of possums that fully revealed their home ranges during the monitoring period at High-Density Site, Low-Density Site 1 and Low-Density Site 2, were 62%, 73% and 86%, respectively (Table 3.1). The model comparisons gave equal support to the null, 'Site' and 'Bodyweight' models, as they were all within two Δ AICc values (Akaike Weights of 0.40, 0.30 and 0.15, respectively; Table 3.2). This suggests that there was no support for differences in the number of fixes until home ranges were fully revealed due to site, sex or bodyweight (Figure 3.1).

3.4.4 Home range size

The linear model sets for the home range size parameters (95% and 50% KDE, MCPs and home range length) all showed that the model containing 'Site' had the strongest support, with Akaike Weights of between 0.80 and 0.97 (Table 3.2). There was weak support for the other models in these sets. These results are due to both male and female possums at High-Density Site having substantially smaller home ranges than possums at the two low-density sites (Plate 3.1, Plate 3.2 and Figure 3.2). Furthermore, home ranges were similar between the two low-density sites. There was also more variability in home range sizes at the low-density sites than High-Density Site.



Plate 3.1 95% Kernel Density Estimates (larger polygons) and 50% Kernel Density Estimates (smaller polygons) for the eight possums at High-Density Site (depicted by different colours).



Plate 3.2 95% Kernel Density Estimates (larger polygons) and 50% Kernel Density Estimates (smaller polygons) for the (a) eleven possums (depicted by different colours) at Low-Density Site 1 and (b) twelve possums at Low-Density Site 2. The home ranges of some possums are concealed by the home ranges of others.

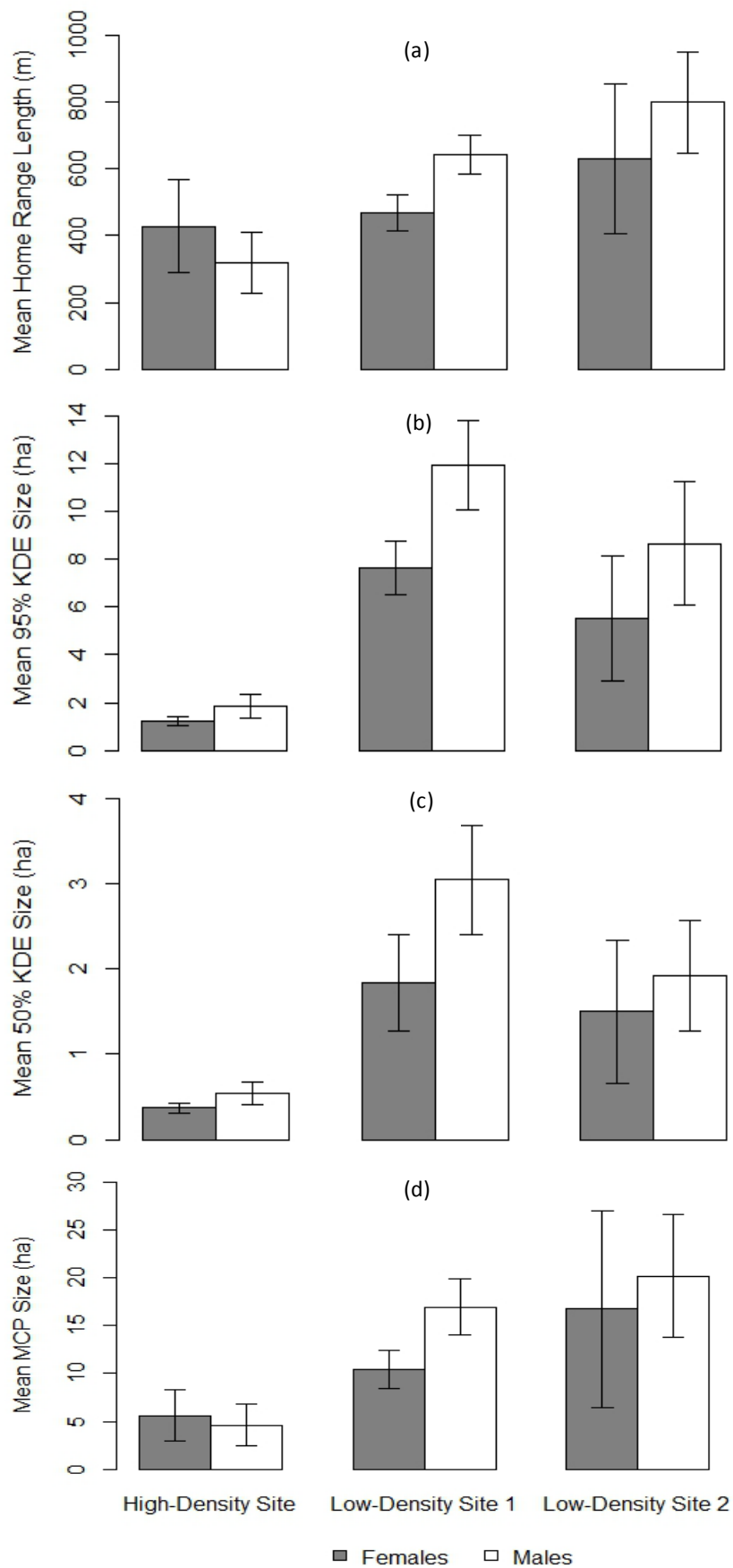


Figure 3.2 Mean (a) home range length, (b) 95% Kernel Density Estimates (KDE) size, (c) 50% KDE size and (d) Minimum Convex Polygons (MCP) size. Error bars are \pm the standard error.

3.4.5 Home range overlap

For all the home range overlap model sets (percent overlap, number of overlaps and exclusive area, for the 95% and 50% KDE), 'Site' again had the strongest support (Akaike Weights of 0.58 – 0.99) and there was generally very weak support for the other models (Table 3.2). These results are due to both males and females at High-Density Site exhibiting substantially less home range overlap than possums at the two low-density sites (Figure 3.3, Figure 3.4, Plate 3.1 and Plate 3.2). Of particular note was the lack of 50% KDE home range overlap between pairs of collared possums at High-Density Site. Home range overlap was similar between the two low-density sites.

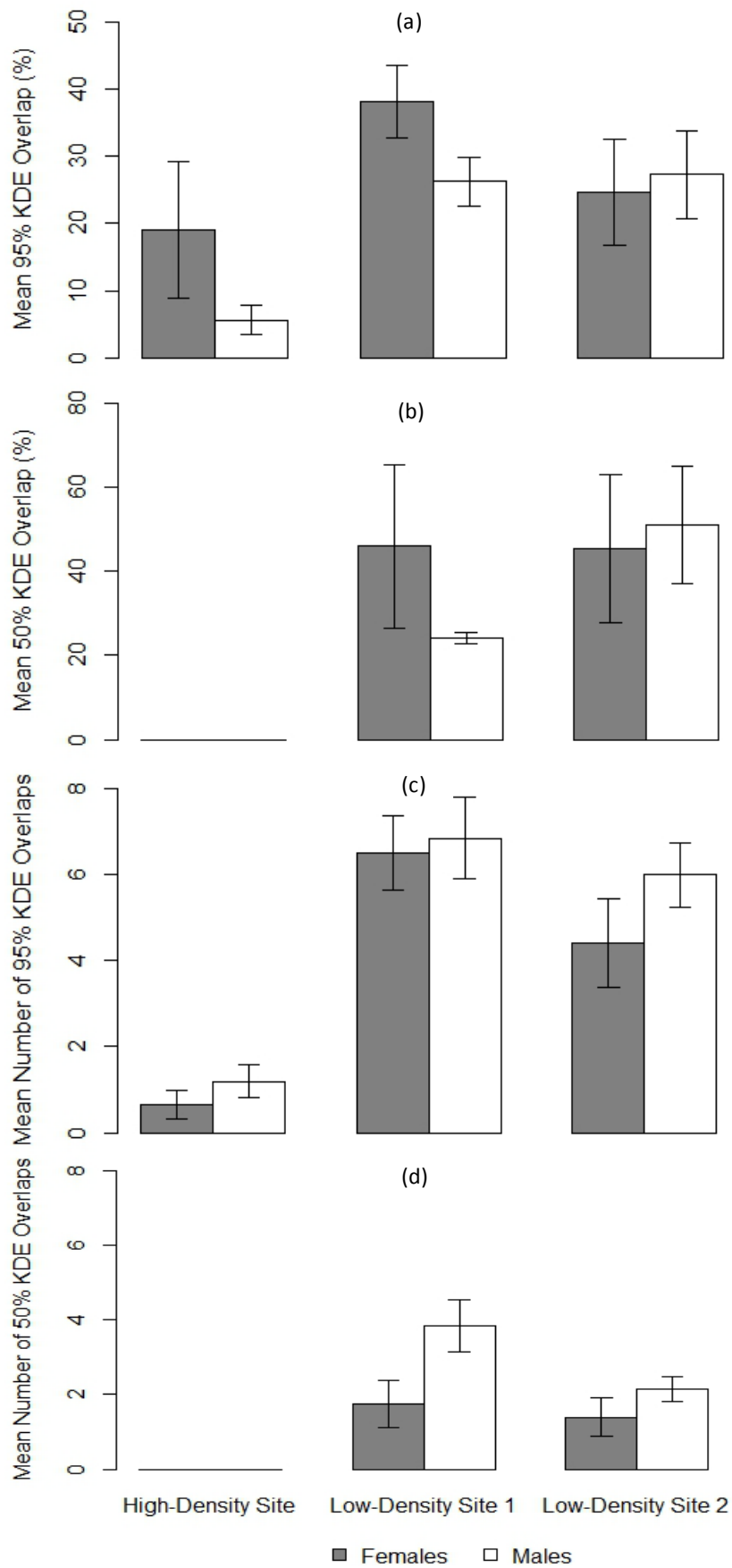


Figure 3.3 Mean (a) percent overlap of 95% Kernel Density Estimates (KDE), (b) percent overlap of 50% KDE, (c) number of 95% KDE overlaps and (d) number of 50% KDE overlaps, for possums at each of the three sites. Error bars are \pm the standard error.

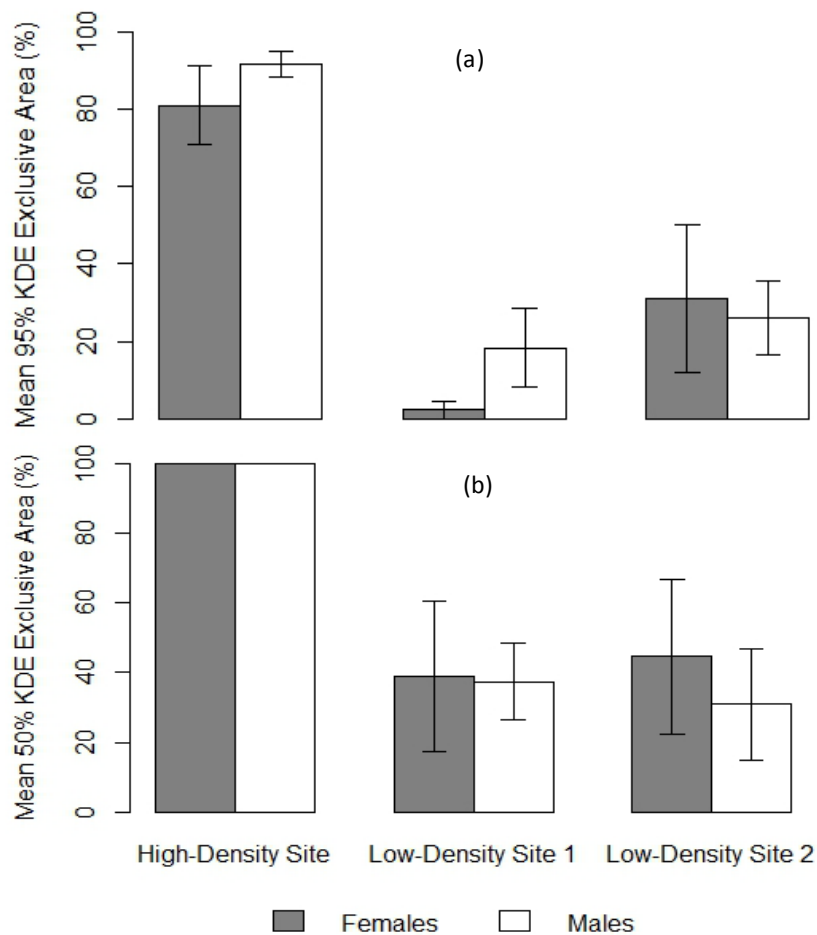


Figure 3.4 Mean exclusive area for (a) the 95% Kernel Density Estimates (KDE) and (b) the 50% KDE, for possums at each of the three sites. Error bars are \pm the standard error. Means without error bars had no variation.

3.4.6 Pasture use

The linear model set for the percentage of fixes within pasture also recorded the 'Site' model as having the strongest support (Akaike Weight of 0.93; Table 3.2). There was little support for the other models. This was due to both male and female possums at Low-Density Site 1 spending substantially more time in pasture than possums at the other two sites (Figure 3.5).

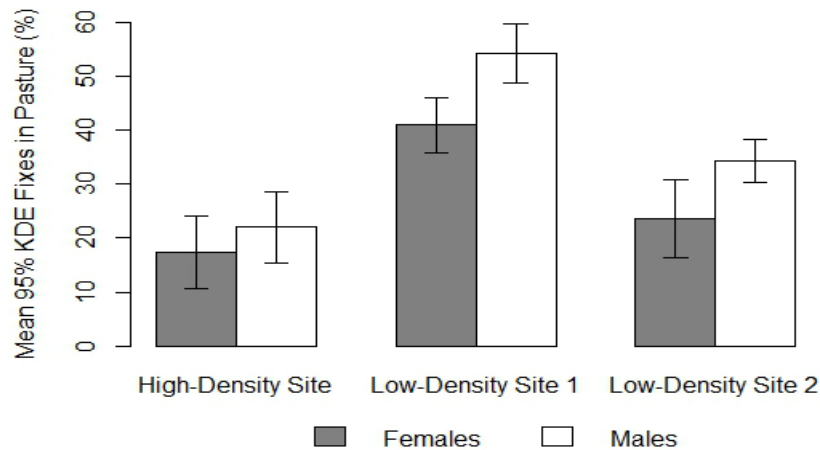


Figure 3.5 Mean percentage of 95% Kernel Density Estimates (KDE) fixes in pasture for possums at each of the three sites. Error bars are \pm the standard error.

3.4.7 Den use

The 24 individuals monitored at High-Density Site were radio-tracked on 290 occasions to a total of 42 den sites. The 15 possums at Low-Density Site 2 were radio-tracked on 197 occasions to 55 den sites. At the high-density site, all the dens of females were located in the core area of their home ranges. In contrast, the dens of males at this site were located within core areas on average 37% of the time ($\pm 12\%$ Standard Error, SE). For the low-density site, female and male possums denned in core areas 43% ($\pm 27\%$) and 27% ($\pm 14\%$) of the time, respectively.

Den type

At High-Density Site, female and male possums denned predominantly aboveground in trees (Figure 3.6). The reverse was true at Low-Density Site 2, where both sexes denned predominantly on the ground in gorse and other shrubby vegetation (Figure 3.6). Although den use was not quantified at Low-Density Site 1, incidental tracking identified that possums at this site denned solely on the ground in gorse and other vegetation.

The linear model set recorded the 'Sex*Site' model as having the entirety of support for the available data (Akaike Weight of 1.0; Table 3.2). This was due to females at High-Density Site denning solely aboveground, compared to males at this site that sometimes denned on the ground, and both males and females at Low-Density Site 2 that denned predominantly on the ground. These results did not support differences in den type due to the bodyweight of individuals.

Number of dens

For the number of dens, the linear model set showed that the 'Sex*Site' model had the strongest support (Akaike Weight of 0.91; Table 3.2). This was due to two reasons. Firstly, females at High-Density Site used fewer dens than males at this site, and also fewer than both males and females at Low-Density Site 2 (Figure 3.6). Secondly, males at Low-Density Site 2 used more dens than females at this site, and also more than both males and females at High-Density Site (Figure 3.6). These results show that the number of dens did not vary due to the bodyweight of individuals.

Number of den changes

The linear model set for the number of den changes showed that the 'Sex*Site' model had the entirety of support for the available data (Akaike Weight of 1.0; Table 3.2). Again, this was due to females at High-Density Site changing their dens less often, and males at Low-Density Site 2 changing their dens more frequently, than other possums at the two sites (Figure 3.6). These results also suggest that the bodyweight of individuals did not influence the number of den changes.

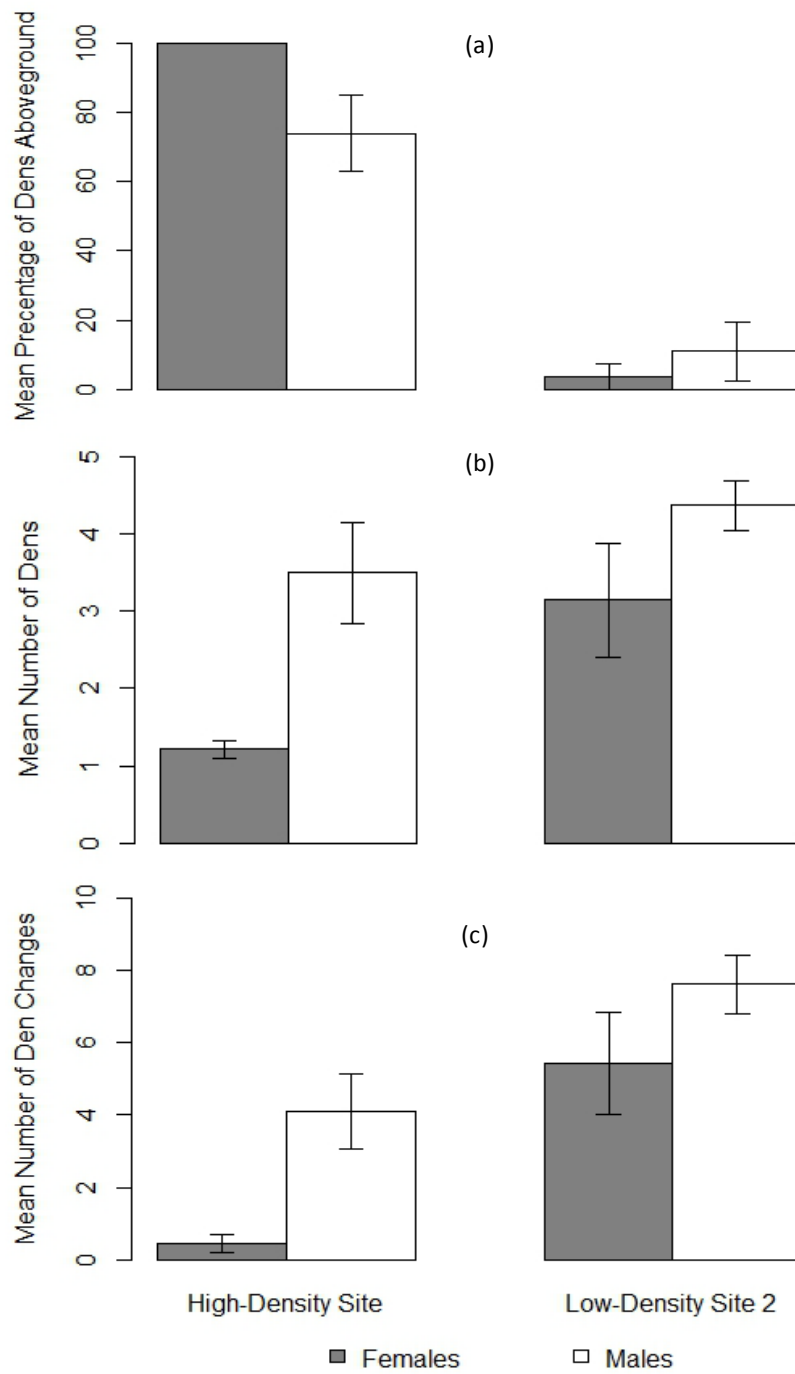


Figure 3.6 Mean (a) percentage of dens aboveground, (b) number of dens and (c) number of changes between dens, for possums at High-Density Site and Low-Density Site 2. Error bars are \pm the standard error. The mean with no error bars is due to there being no variation in the dataset (i.e., all females denned aboveground).

3.5 Discussion

Possum home range characteristics did not vary between the two low-density pine and gorse sites. However, home range characteristics differed between these two sites, and the high-density oak and sycamore site. This was regardless of monitoring being undertaken at the three sites during different seasons and years, as well as two of the sites being entire fragments and one site being part of a larger fragment. Possums at the low-density sites had considerably larger home range sizes and exhibited greater home range overlap between pairs of collared possums, than the possums at the high-density site. There was also more variability in home range size at the low-density sites and many of these possums regularly travelled outside the study site into adjacent forest fragments. In addition, the low-density populations used more dens and changed these more often. This may have been due to a positive relationship between number of dens and home range size (Ji et al., 2003). For example, possums at these sites may have required more dens to prevent long forays back to den sites at the end of the night. Dens at the low-density sites were also predominantly located on the ground, as opposed to dens at the high-density site, which were mostly located aboveground. This is a reflection of the pine habitat at the low-density site not providing preferential tree holes or suitable boughs for denning (Cowan, 1989), meaning that possums had to den on the ground in gorse and other vegetation. In contrast, the oaks and sycamores at the high-density site provided an abundance of these types of den sites.

One site recorded greater pasture use than the other two sites (Low-Density Site 1). The reason for this was unclear, but may be due to variations in resource availability at this site. For example, although the forest and pasture habitat was the same between the two low-density sites, Low-Density Site 2 was close to a farm house, where possums had been observed feeding on garden vegetation. In contrast, Low-Density Site 1 was completely within a rural setting with no dwellings nearby, meaning that possums could only feed in the pasture or the forest. Alternatively, the difference in pasture use at this site may be due to the different season of monitoring (this site was monitored in spring and the other two sites were monitored in summer).

There was no difference between the three sites in the number of GPS fixes obtained during the monitoring period, confirming that sampling effort was consistent between the sites. There was also no difference in the number of fixes until home ranges were fully revealed between sites, even though possums at the low-density sites had substantially larger home ranges. This suggests that individuals move further in the same relative time period, the greater their home range size. In addition, there were no intersexual differences in home range characteristics between males and females at the two sites. The exception to this was female possums at the high-density site, who

denuded more often aboveground, and used fewer dens and changed these less often, than males at this site, and both males and females at Low-Density Site 2.

Behavioural plasticity is the ability of an individual to vary its behaviour in a given situation (Mills et al., 2010). This study confirms that possum home range size is not fixed and that behavioural plasticity can occur. Furthermore, the variation in home range overlap observed at these sites suggests that possums may also exhibit plasticity with respect to territorial behaviour. Knowledge of the limiting conditions for territoriality is important to understand variations in spatial behaviour within and between species (Powell, 2000). Food availability appears to be the limiting resource stimulating territorial behaviour in many animals (Powell, 2000). A territory must be economically defensible (Brown, 1964) and there are likely to be thresholds for when territoriality occurs; when productivity is low, the cost of defending a territory outweighs the benefits, and when productivity is high, there is enough of the resource that territoriality is not necessary (Carpenter and Macmillen, 1976). For example, black bears (*Ursus americanus*) and nectivorous birds interchange rapidly between territorial and non-territorial behaviour when food availability moves across this territorial threshold (Powell, 2000).

As this was an observational study, it was not clear what the driver was for the difference in home range characteristics at the low-density sites. This may have been due to less social pressure from conspecifics at these sites compared to the high-density site (i.e., home range characteristics were density-dependent), resulting in less movement constraints (Arthur et al., 2002). This is plausible, given that dominant possums often prevent subordinates from accessing limited resources (Day et al., 2000a; Green, 1984), likely resulting in more competition in high-density populations. In support of this, possums have been recorded changing their home range characteristics as densities decrease, when habitat and resources have not changed (Clinchy et al., 2001; see also Chapter 5 of this thesis; Clout, 1977). Large home ranges in possums (>40 hectares) have also been recorded in low-density habitats with seemingly abundant den sites and food resources, and where possums were in excellent condition, also indicating high levels of resources (H. Blackie, Lincoln University, personal communication, 2012). Alternatively, home range differences at the low-density sites may have been due to the habitat at these two sites providing lower amounts of resources (i.e., home range characteristics are resource-dependent), resulting in the need to roam further to meet energy demands (Arthur et al., 2002; Benson et al., 2006; Harestad and Bunnell, 1979; Kerle, 1984). Certainly, the pine trees at the low-density sites in this study appeared to provide less preferential tree holes and food than the oaks, sycamores and kale at the high-density site. It is also possible that both density-dependent and resource-dependent processes determine the home range

characteristics of possums; especially because it is likely that when densities decrease, resource availability per individual increases.

The greater home range overlap between pairs of collared possums at the low-density sites may have been due to these sites providing insufficient resources for the threshold of territoriality to be stimulated (Carpenter and Macmillen, 1976). In contrast, productivity at the high-density site may have been sufficient for territoriality to occur, explaining the lower levels of home range overlap at this site, although it is noted that individuals may still be territorial towards each other even if their home ranges overlap. Moreover, percent overlap was similar between the 95% and 50% KDE at the low-density sites, whereas the percent 95% KDE overlap at the high-density site appeared to be greater than the 50% KDE. This may be due to possums exhibiting partial territoriality at this site (Day et al., 2000a), defending only the core areas where the most important resources are located (Powell, 2000). Such resources for possums in this study could have included dens; for example, females denned in core areas 100% ($\pm 0\%$ SE) of the time at the high-density site, but only 43% ($\pm 27\%$ SE) of the time at the low-density site. This is supported by related research that has shown that individuals expand their 50% KDE contours following the removal of conspecifics, but not their 95% KDE (see Chapter 5 of this thesis).

The home range overlap analyses may have been influenced by which animals were tracked because only a sample of each population were collared and analysed. For example, no home range overlap was recorded at the high-density site for the 50% KDE. Had a larger number of possums been able to be collared at this site, this may have resulted in additional study animals exhibiting overlap with each other. This is shown by the analysis of a different set of individuals at this site for Chapter 5 of this thesis, where some overlap for this contour was recorded (male mean = 39.6%, $\pm 22.8\%$ SE; female mean = 0.4%, $\pm 0.4\%$ SE). However, these analyses still allow a relative comparison between sites, with the high-density site showing much less home range overlap than the other two sites.

Variation in home ranges of pest populations can substantially affect the ability of managers to control and monitor populations (Arthur et al., 2002). Having knowledge of variations in behaviour may allow predictions of how populations will behave depending on habitat and density, allowing the development of optimal pest management strategies. For example, variation in home range overlap between possum populations may mean that bTB transmission risk is not uniform between sites. There may be greater bTB transmission risk among possums, and between possums and livestock, in populations where possums display larger home ranges. Therefore, these sites should become a priority for possum control. Furthermore, the movements of pests determine vulnerability to control and information on this behaviour may help with the effective placement of traps and bait

stations (Cowan and Clout, 2000). For example, a lower density of control devices, such as traps and bait-stations, may be able to be used in areas where individuals exhibit larger home ranges. In addition, individuals with larger home ranges, which potentially come in contact with more detection devices, may inflate population estimates when carrying out post-control monitoring. This may need to be factored into the results of monitoring.

In New Zealand, the Animal Health Board (AHB) is the organisation responsible for managing and controlling bTB (AHB, 2012). To assist with this task, the AHB uses a spatially explicit model, to simulate bTB dynamics within possum populations and to predict the effect of differing control strategies on disease persistence (the Spatial Possum Model; SPM) (Ramsey and Efford, 2010; Ramsey and Efford, 2005). However, there are a number of parameters in this model that are estimated or based on limited field data (Ramsey and Efford, 2010; Ramsey and Efford, 2005). The results of this and future studies could therefore also be used to update and consequently increase the predictive capacity of the model. For example, the SPM uses home range size to determine the amount of overlap and therefore contact rates between possums, and subsequently transmission risk. Home ranges are established using a negative relationship between an index of home range size (home range scalar; σ) and population density, resulting in variable bTB transmission risk in different density populations (Ramsey and Efford, 2005). However, although many high-density sites were used to fit this relationship, low-density sites were under-represented due to a lack of studies of these populations at the time (Barron, 2012). As a result, the fitted relationship (which is an exponential decay with an intercept) does not predict the larger home range sizes (>8 hectares) that have been observed in populations with low densities of <1 possum per hectare (e.g., Rouco et al., 2013 and this study) (Barron, 2012). This potentially results in underestimations of bTB transmission. The parameters of this relationship have therefore recently been adjusted to produce more realistic larger home ranges at low possum densities (Barron, 2012). To assess the accuracy of this alteration, home range sizes and possum density estimates from this study were plotted against this adjusted relationship (Figure 3.7). These data appear to support the proposed new parameters, as the σ values of the two low-density sites all fall in close proximity to the new fitted curve. In addition, the σ value for the high-density site is in close proximity to the other high-density sites used to determine the original relationship. This highlights the direct relevance of this research to managing possums and bTB in New Zealand. Moreover, these results appear to cross-validate the accuracy of the density assessments undertaken in this research. The results of this and future research could also be used to update other key parameters in the model. For example, this study could allow assessment of the current assumption in the SPM that possum home ranges are randomly distributed in space, rather than aggregated or uniformly distributed.

The results of this observational study allow a number of research hypotheses to be generated. For example, it is predicted that home range characteristics are density-dependent, rather than resource-dependent. The best way to test this hypothesis would be to manipulate the densities of possum populations whilst keeping resource levels constant and observe whether home range characteristics change (see Chapters 4 and 5 of this thesis). This experimental manipulation of densities has been achieved in a number of other studies, which have recorded changes in the home range characteristics of various species following density reduction (white-tailed deer, *Odocoileus virginianus*, Henderson et al., 2000; e.g., red squirrels, *Tamiasciurus hudsonicus*, Larsen and Boutin, 1995; European badgers, *Meles meles*, Tuytens et al., 2000; Tasmanian pademelon, *Thylogale billardierii* and red-necked wallaby, *Thylogale billardierii*, Wiggins et al., 2010). In addition, populations can be tested to see if home range characteristics are resource-dependent by experimentally increasing food supply, whilst keeping density constant. For example, experimental increases in the food supply (sunflower seeds) of eastern chipmunks (*Tamias striatus*), when population density was held constant, resulted in a decrease in the home range size of individuals (Mares et al., 1982). However, when food supplies were held constant, but population density was reduced, home range sizes did not change. This type of experimental manipulation appears to be rare in the literature, with most studies comparing between groups that receive food supplementation and those that do not, with studies sometimes confounded by density effects (e.g., Hubbs and Boonstra, 1998; López-Bao et al., 2010; Santangeli et al., 2012). Identification of whether possum home ranges are density-dependent would allow management of this species to be more targeted. For instance, if home ranges are density-dependent, it is likely that all low-density populations will exhibit large home range sizes, regardless of habitat. This may mean that all low-density possum populations infected with bTB or within bTB vector areas should be a priority for control, due to potentially higher bTB transmission in these areas. These studies would also benefit from being long-term, to investigate seasonal and annual variations in home range characteristics between populations.

Finally, research into the limiting conditions for territoriality in possums would also be useful. This might be achieved by measuring productivity levels in a range of different sites and observing whether contact rates (or some other measure of territoriality) between possums vary. This information would be useful in more definitively assessing the variations in bTB transmission risk between sites of differing population density and habitat. Again, long-term monitoring would be valuable to investigate seasonal and annual variations in territoriality between populations.

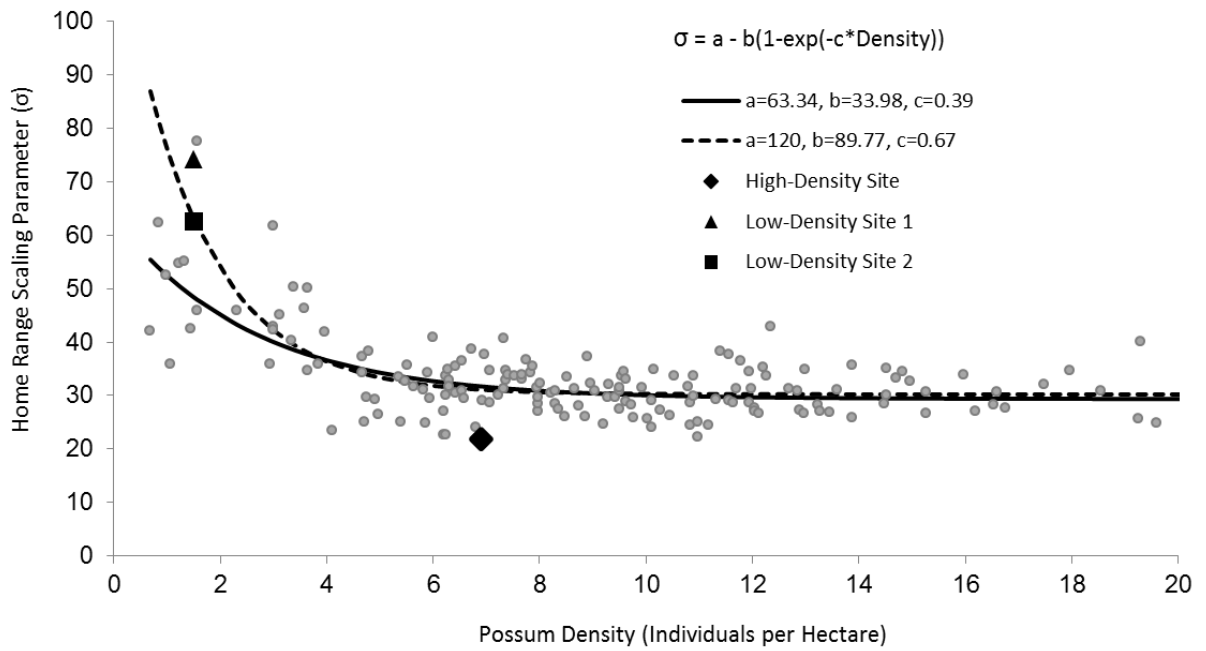


Figure 3.7 The relationship between possum home range index (home range scalar; σ) and possum density, as used in the Animal Health Board Possum Spatial Model. The circles and the solid line are the original data and fitted relationship for the model (Ramsey and Efford, 2005). The dashed line is the new fitted relationship (Barron, 2012). The square, triangle and diamond are the data from the three sites in this study, as detailed in the legend of the graph.

Chapter 4:

Experimental Study – Spatial Perturbation of Possum Den Site Use Following Density Reduction

4.1 Abstract

Some mammals change their home ranges following density reduction, thereby exhibiting spatial perturbation. Den availability for the brushtail possum may be density-dependent, meaning that possums might change their den use in response to density reduction. Furthermore, possums in New Zealand transmit bovine tuberculosis (bTB) to livestock in some areas. Possums share dens and these may be a potential source of infection, due to possums excreting bTB whilst in dens. It is therefore important to understand changes in denning behaviour and consequently bTB transmission risk. However, changes in possum den use due to density reduction have not previously been investigated in detail. This un-replicated study monitored den use of a population subjected to approximately a 50% density reduction event. Possums were radio-tracked to determine den type, the number of dens used and the number of times possums changed dens, before and after density reduction. A second non-manipulated site of different habitat and where density reduction was not undertaken, was also monitored. There was no difference between monitoring events for males at the manipulated site, but female possums increased their den use. However, den use was more dependent on the sex of the individual than density reduction, with males using more dens than females and changing their dens more often overall. In contrast, den use did not differ between monitoring events or sexes at the non-manipulated site. Increases in den use may result in increases in bTB transmission risk amongst possums, and between possums and livestock. Therefore, in bTB vector areas or areas where possums are infected with bTB, density reductions need to reduce populations to very low densities, to prevent any potential increases in transmission risk. Differences in denning behaviour were also recorded between the two sites, indicating that denning behaviour is habitat-dependent and that bTB transmission risk may not be uniform between sites.

4.2 Introduction

Mammals have been recorded altering their spatial distribution in response to changes in population density (e.g., Henderson et al., 2000; Wiggins et al., 2010; Woodroffe et al., 2006a). However, the mechanisms of this spatial perturbation are not always clear, and may vary within and between

species. It may be that spatial perturbations are dictated by the underlying spatial distribution of populations (Wiggins et al., 2010). For instance, the distribution of European badgers (*Meles meles*) in the United Kingdom appears to be influenced by the availability of resources, as individuals change their home ranges in response to seasonal changes in food availability (Palphramand et al., 2007) and they are territorial (Kruuk, 1978). Following culling, surviving badgers have been recorded increasing their home-range size and home range overlap with conspecifics (Riordan et al., 2011), potentially due to the altering of resource availability. In contrast, other populations that are considered to distribute themselves predominantly based on natal philopatry rather than resources, such as female white-tailed deer (*Odocoileus virginianus*) in the United States, have not been recorded exhibiting spatial perturbation following density reduction (McNulty et al., 1997; Oyer and Porter, 2004).

In New Zealand, the Australian brushtail possum (*Trichosurus vulpecula* Kerr) is a cat-sized, solitary, nocturnal, arboreal and polygynous marsupial, weighing 2 – 4 kilograms, with males and females similar in size and bodyweight (Clout and Ericksen, 2000; Day et al., 2000a; King, 2005). Possums preferentially choose dens in hollows of trees with large diameters, over dens on the ground (Cowan, 1989; Ji et al., 2003). Male and female possums will also defend their dens if challenged by other possums (Day et al., 2000a). Therefore, in some habitats, den availability for possums may be a limited resource that is density-dependent (Caley et al., 1998; Clout, 1977; Fairweather et al., 1987). Density reduction may consequently result in possums changing their den use to take advantage of a greater availability of better quality den sites following the removal of dominant individuals. This may explain why possums have been observed increasing their home ranges following density reduction (Brockie et al., 1997; Morgan et al., 2007; Ramsey et al., 2002; Chapter 5 of this thesis). Alternatively, individuals may change their den use as a consequence of moving into new areas (Ji et al., 2003) for other reasons, such as newly available food resources or territories.

One study has previously recorded possums in populations recovering from density reduction using more dens than possums in populations not subjected to density reduction (Ji et al., 2003). However, this study had very low sample sizes and therefore statistical tests could not be conducted. Another study in Australia recorded neighbours expanding their denning ranges into areas of experimentally removed individuals (Clinchy et al., 2001). These possums then occupied the unoccupied dens of the removed individuals. However, both these studies did not comprehensively compare den use of the same individuals before and after a density reduction, to explicitly test whether density reduction results in changes in den use.

Experimental manipulations of population densities not only contribute to our understanding of the mechanisms of spatial perturbation, but allow us to evaluate the use of culling as a pest management strategy. The possum was introduced into New Zealand to establish a fur trade (King, 2005). This species has now become the greatest wildlife barrier to the eradication of bovine tuberculosis (*Mycobacterium bovis*, bTB) from livestock, as they transmit this disease to cattle and farmed deer (AHB, 2012; Coleman and Caley, 2000). The density of possum populations are consequently reduced (i.e., 'controlled') over 2.5 million hectares of New Zealand, at a cost of NZ\$56 million per annum (AHB, 2012). Although the incidence of bTB in livestock in New Zealand has been reduced, infected herds remain, attributed to 'hot spots' of infection in possum populations. Therefore, it is important to obtain a thorough understanding of possum behaviour and bTB dynamics, as this may help identify ways to increase control effectiveness.

How possums use dens may be an important consideration in controlling bTB. For example, a study by Paterson et al. (1995) suggested that bTB infection in possums was correlated with denning areas rather than foraging areas. Infected possums were limited to those denning in certain areas of the study site, regardless of individuals having overlapping foraging areas. Cattle grazing in these possum denning areas were also more susceptible to bTB infection than those grazing in possum foraging, non-denning, areas (Paterson et al., 1995). Transmission of bTB may therefore be closely associated with possum denning, through the excretion and transmission of bTB by possums whilst in dens (Coleman and Caley, 2000; Green and Coleman, 1987; Ji et al., 2003; Paterson et al., 1995). This may be accentuated by the fact that possums change their dens frequently, use many per year and often share or use others' dens sequentially (Coleman and Caley, 2000; Cowan and Clout, 2000; Cowan, 1989; Ji et al., 2003; Pfeiffer, 1994). Possums have also been recorded sharing their dens with dead possums (Caley et al., 1998; Day et al., 2000b; Fairweather et al., 1987). Research has shown that bTB can survive within dens for up to a month (Jackson et al., 1995c). One study estimated that, given a bTB bacilli survival period of less than 10 days, possums at their site had a minimum 50% chance of occupying dens within this survival time (Cowan, 1989). If denning behaviour changes following density reduction (for example, if possums increase the total number of dens they use following control), then this may increase exposure to this disease for both possums and consequently livestock.

The first objective of this study was to therefore investigate whether possums change their denning behaviour following density reduction, specifically the type of den used (ground versus aboveground), the total number of dens used and the number of changes between dens. If possum den site use is density-dependent, it is expected that den use will change following density reduction. If not, then den use is not expected to change. The second objective was to assess

whether there were intersexual differences in any changes in den site use. As males commonly use more dens than females (Clout, 1977; Cowan, 1989), they were predicted to exhibit a greater degree of spatial perturbation following density reduction, by altering the number of dens they used and changes between dens to a greater degree than females.

These objectives were achieved by radio-tracking individual possums at a site before and after density reduction, using Very High Frequency (VHF) collars. Den use of individuals was then compared between these two monitoring periods ('pre-reduction' and 'post-reduction'). A second site where density reduction was not undertaken was also monitored, but was not treated as an experimental control, due to differences in habitat, population density and year of investigation (although monitoring at both sites was undertaken in the summer season). However, comparisons between these two sites allow investigation into the variations in denning behaviour due to these site-level differences. In addition, if similar changes in den use occur at this second site, this would suggest that other factors are potentially determining den use changes at this time of year (e.g., breeding).

4.3 Materials and methods

4.3.1 Study sites

The manipulated site, where density reduction was undertaken, was a 15-hectare forest fragment in Hororata, Canterbury, New Zealand (43°32'50.03"S, 171°54'35.96"E), consisting of predominantly English oaks (*Quercus robur*) and sycamores (*Acer pseudoplatanus*). The non-manipulated site was a 15-hectare end of approximately a 60-hectare forest fragment in Hororata, Canterbury, New Zealand (43°30'56.38"S, 171°53'23.74"E). The vegetation at this site consisted of plantation pine (*Pinus radiata*), and gorse (*Ulex europaeus*) at the forest edge. These two sites were located approximately 3.5 kilometres apart. The population density at the manipulated site was high at seven possums per hectare. The densities at the non-manipulated site were low at one possum per hectare. No large-scale possum control had been carried out at these sites for at least five to ten years, only sporadic trapping and shooting. Differences in possum density were therefore likely to be due to variations in resource levels between sites.

4.3.2 Data collection

Research at the manipulated site was conducted between January and April 2011 (summer) and research at the non-manipulated site was conducted exactly one year later. Study possums were caught using treadle (Trappers Cyanide Limited, Canterbury, New Zealand) and trigger (Grieve Wrought Iron Limited, Christchurch, New Zealand) live-capture cage traps. These possums

were then anaesthetised using gaseous halothane to allow handling under sedation. All research was carried out with the approval of the Lincoln University Animal Ethics Committee (Approval Number 373) and all anaesthetising followed the Lincoln University Standard Operating Procedure (Number 91 – Possum Anaesthesia using Halothane; Appendix C). Possums were weighed and fitted with either VHF or Global Positioning System (GPS) collars that also contained VHF transmitting units (Sirtrack Limited, Havelock North, New Zealand). Both these collar types allowed the possums to be radio-tracked to their individual den sites. Twenty-seven adult possums (13 males and 14 females) were fitted with collars at the manipulated site and sixteen adults (8 males and 8 females) were fitted with collars at the non-manipulated site. Collars were fitted with a three-finger gap between the collar belt and the skin, to ensure there was enough room so that rubbing did not occur, but that the collar would not slip over the possum's head (Blackie, 2010b). The VHF-collars weighed 35 grams and the GPS-collars weighed no more than 135 grams. Possums were weighed at the time of fitting to ensure that collars weighed no more than 5% of each possums total bodyweight, to prevent adverse effects on the behaviour of the study animal (Kenward, 2001).

This study followed a Before-After (BA) design (Smith, 2002), with possums at the manipulated and non-manipulated sites monitored before and after density reduction. Density reduction at the manipulated site was undertaken for a week using live-capture cage trapping. This method was used over other techniques, such as poisoning, to ensure that the collared animals were protected and not accidentally culled. Any collared individuals caught in the traps were released and any non-collared individuals were euthanised. A week of trapping was also conducted at the non-manipulated site, but individuals were released after capture and not euthanised. This was to ensure consistency in methods between sites and to remove possible behavioural biases due to trapping itself. Although no density reduction was undertaken at the non-manipulated site, the monitoring periods before and after this trapping week are still referred to in the remainder of this chapter as 'pre-reduction' and 'post-reduction'.

Possum den use was monitored for five weeks prior to density reduction and five weeks following density reduction, as this was considered sufficient time for den site locations to become revealed based on the results of similar research (H. Blackie, Lincoln University, personal communication, 2010). Monitoring involved tracking each individual to their den site approximately three times per week using an Australis 26k™ VHF receiver and a yagi™ multi-directional antenna (Titley Scientific, Australia). Den site locations were recorded on a handheld GPS (Garmin® GPSMAP 60CX, Kansas City, USA). Data was then collated to establish the type of dens occupied (i.e., aboveground versus on the ground), the total number of dens used, as well as the number of times individuals changed between dens, before and after density reduction.

4.3.3 Data analysis

Population sizes at each of the sites before and after density reduction were estimated using mark-recapture techniques and Closed Population Estimation models in 'Program MARK', Version 6.1 (Cooch and White, 2011; Lettink and Armstrong, 2003; Pryde, 2003). The 'number of dens' and the 'number of den changes' before and after density reduction were analysed using generalised linear mixed-effects models, which accounted for non-normal count data by using a Poisson error structure and logarithmic link function (Crawley, 2007). Models could not be run for 'den type', due to a lack of variation in the dataset for each site; the majority of dens were aboveground for the manipulated site and the majority were on the ground for the non-manipulated site. Individual possum identity was included in each model as a random effect, as well as their change between events (i.e., before and after density reduction) to account for any temporal autocorrelation. All models were run in the statistical program R (Version 2.15.1, Woodroffe et al., 2006b) with the following combinations of fixed effects: (1) a null model with intercept only; (2) a model that considered event (pre-reduction and post-reduction); (3) a model that considered bodyweight (which was measured in kilograms); and (4) a model that considered sex (male and female); as well as other models that considered the higher level interactions among these variables. These models were all ranked using sample size corrected Akaike Information Criterion (AICc) (Anderson, 2008; Burnham and Anderson, 2002). The weights of all models in the set sum to one and the model with the highest Akaike Weight is considered to have the best fit for the available data (Burnham and Anderson, 2002). Support for each model was evaluated by assessing the change in AICc from the best model (ΔAICc) (Anderson, 2008; Burnham and Anderson, 2002). Models with a change of approximately less than two from the best model have substantial empirical support, models with a change of 4 – 7 have considerably less support and models with a change of greater than 10 have essentially no support (Burnham and Anderson, 2002). Each model set was assessed for 'pretending variables', whereby the addition of a variable does not change the deviance and therefore the fit of the model, skewing and biasing Akaike weights, but none were identified (Anderson, 2008). Due to differences in habitat type and possum densities between the two sites, and due to the study not being replicated in the same year, the data from the two sites were analysed separately.

4.4 Results

4.4.1 Sample sizes and population density assessments

At the manipulated site, the batteries of one VHF-collar and one GPS-collar went flat during the monitoring period. One GPS-collar was found detached from a possum and wedged up high in a tree hole; this was only discovered when tree climbers were bought into the site to check the den at the

completion of the study. One GPS-collared possum was also unable to be located at this site during the monitoring period and one possum was accidentally shot. At the non-manipulated site, one possum was excluded from the analyses due to roaming well outside the study area, as detailed in Chapter 3, and one possum was accidentally overdosed with halothane. This resulted in 22 possums at the manipulated site (9 males and 13 females) and 14 adults at the non-manipulated site (8 males and 6 females) being analysed.

Possoms at the manipulated site were radio-tracked on 598 occasions to 64 den sites; possums at the non-manipulated site were radio-tracked on 405 occasions to 69 den sites. The population density of the manipulated site (\pm Standard Error; SE) before and after density reduction was estimated to be seven (\pm 1.27) and three (\pm 0.26) possums per hectare, respectively. This resulted in approximately a 50% density reduction. As expected, the density of adults at the non-manipulated site was similar pre-reduction (1.5 possums per hectare; \pm 0.00 SE) to post-reduction (1.5 possums per hectare, \pm 0.10 SE).

4.4.2 Den type

Descriptions of each of the dens used by each possum are presented in Appendix D. Males at the manipulated site primarily denned aboveground in trees, both before and after density reduction (Figure 4.1). Females at this site always denned aboveground. Conversely, both male and female possums at the non-manipulated site denned predominantly on the ground in gorse and other vegetation, both before and after density reduction (Figure 4.1). The percentage of possums that denned aboveground did not appear to vary between events at either site (Figure 4.1). As discussed in the methods, mixed-effects models were unable to be run for this variable due to a lack of variation in the data for each site.

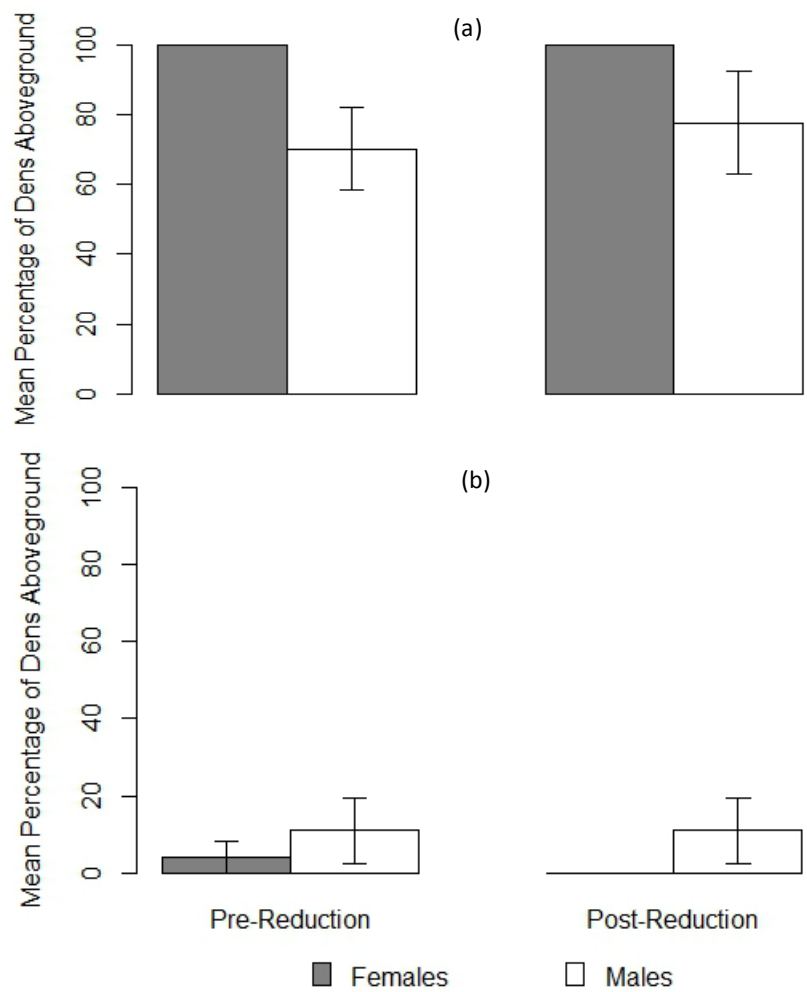


Figure 4.1 Mean percentage of dens aboveground, before and after density reduction, for possums at the manipulated site (a) and the non-manipulated site (b). Error bars are \pm the standard error. Means without error bars had no variation (i.e., possums either denned solely aboveground or solely on the ground).

4.4.3 Number of dens

Individuals at the non-manipulated site used a greater number of dens on average than those at the manipulated site, both before and after density reduction (Figure 4.2). The model sets, which analysed event (pre-reduction and post-reduction), sex and bodyweight, showed that the model containing 'Sex' had the highest Akaike Weight for the manipulated site (0.89; Table 4.1). This was due to males using more dens than females, irrespective of the monitoring event. There was also minor support for the 'Event*Sex' interaction model at this site (Akaike Weight of 0.10; Table 4.1). This was due to females using more dens following density reduction. Den number did not appear to vary between events for males. In contrast, the 'Null' model had the majority of support for the non-manipulated site data (Akaike Weight of 0.52; Table 4.1). This indicates that event, sex or the bodyweight of individuals did not influence the number of dens used at this site.

Table 4.1 Akaike weights ($\Delta AICc$) from the linear models investigating number of dens and number of den changes, for possums at the manipulated and non-manipulated sites. Event is a categorical variable with two categories (pre-reduction and post-reduction), sex is a categorical variable with two categories (male or female) and bodyweight (BW) is a continuous variable. Bold numbers indicate models within a set that have a $\Delta AICc$ of less than two. Level of empirical support for models: substantial = $\Delta AICc$ of 0 – 2, considerably less = $\Delta AICc$ of 4 – 7, essentially none = $\Delta AICc$ of >10 (Burnham and Anderson, 2002).

Response variable	Null	Event	BW	Sex	Event *Sex	Event *BW
<i>Number of dens</i>						
Manipulated Site	0.00 (10.5)	0.00 (13.0)	0.00 (10.6)	0.89 (0.0)	0.10 (4.5)	0.00 (14.7)
Non-Manipulated Site	0.52 (0.0)	0.14 (2.6)	0.10 (3.2)	0.21 (1.8)	0.01 (8.1)	0.01 (8.7)
<i>Number of den changes</i>						
Manipulated Site	0.00 (12.0)	0.00 (9.7)	0.01 (8.9)	0.61 (0.0)	0.37 (1.0)	0.01 (9.3)
Non-Manipulated Site	0.41 (0.0)	0.27 (0.9)	0.10 (2.9)	0.20 (1.4)	0.02 (6.2)	0.01 (7.7)

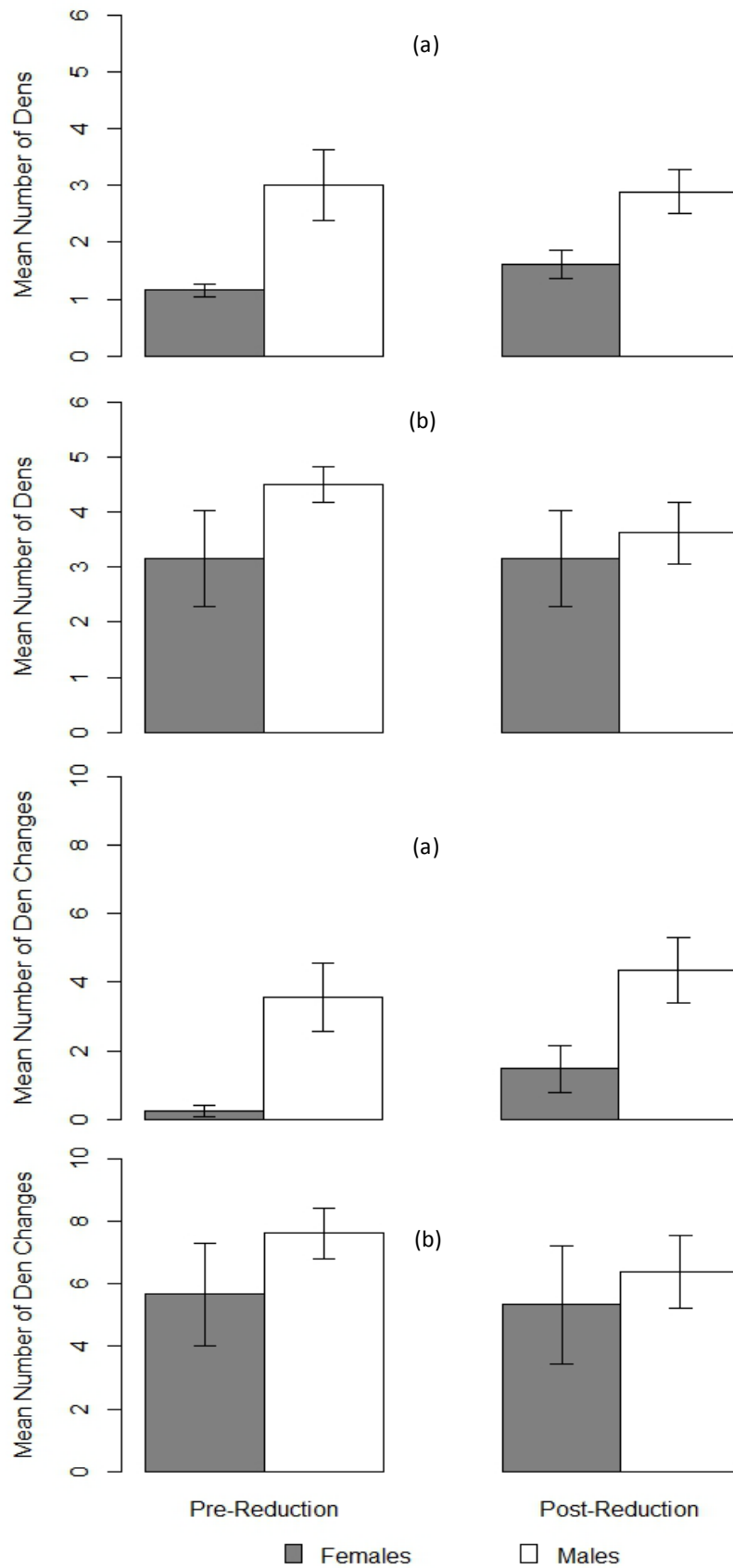


Figure 4.2 Mean number of dens and changes between dens, before and after density reduction, for possums at the manipulated site (a) and the non-manipulated site (b). Error bars are \pm the standard error.

4.4.4 Number of den changes

Possoms at the non-manipulated site changed their dens more often on average than those at the manipulated site, both before and after control (Figure 4.2). The model comparisons for the manipulated site, which analysed event, sex and bodyweight, showed that the model 'Sex' and the 'Event*Sex' interaction model had the majority of support (Akaike Weights of 0.61 and 0.37 respectively; Table 4.1). As the $\Delta AICc$ for the second model was less than two, there was equal support for both these models and they accounted for 98% of the total weighting of the model set. This was due to male possums changing their dens more frequently than females, irrespective of the monitoring event, and females changing their dens more frequently following density reduction (Figure 4.2). Males did not differ in the number of den changes between monitoring events. In contrast, the 'Null' model had the highest Akaike Weight for the non-manipulated site (0.41; Table 4.1). This suggests that there was no support for differences in den changes due to event, sex or the bodyweight of individuals at this site.

There were also some observations made in the field at the manipulated site with regard to den changes. Some female possums that did not change their dens at all prior to density reduction moved to a new den within 1 – 2 weeks after density reduction and stayed there for the remainder of the monitoring period. Other male and female possums that never moved before density reduction were among those that made the most changes following density reduction. Moreover, after density reduction, one male on a number of occasions followed another male possum around, denning in the same dens he had used the previous day. This behaviour was not observed in the pre-reduction monitoring period. It also appeared that some possums moved from potentially lower quality dens (i.e., exposed ground-level dens) to higher quality dens (i.e. sheltered aboveground dens). For example, one possum denned for the entirety of the pre-reduction period in a tree hollow situated at the base of a tree, where the possum could be visually observed during every tracking event. During the second week following density reduction, this possum then moved to a den approximately 40 metres high in another tree and remained there for the remainder of the study. Following density reduction, possums were also recorded in dens that had recently been vacated due to the previous occupant moving to a new den. All these changes may not have influenced the statistical models, as the number of changes overall between events was not dramatically different. These behavioural changes were not observed at the non-manipulated site, with possums generally showing the same denning behaviour before and after density reduction.

4.5 Discussion

Female possums at the manipulated site exhibited spatial perturbation following density reduction by increasing the number of dens they used and the number of changes they made between dens. Males, however, did not significantly vary their den use between monitoring events. Behavioural observations in the field of both males and females also implied recognition of density reduction and changes in den use because of this, such as possums moving to 'higher-quality' dens (i.e., from dens on the ground to dens aboveground). Den use may therefore be density-dependent at this site in line with previous anecdotal evidence recording an increase in total den use of possum populations following density reduction (Ji et al., 2003). However, den use at High-Density site was more dependent on the sex of the individual than density reduction, with males using more dens than females and also changing their dens more often. The fact that only females changed their den use in response to density reduction, and that males used more dens and changed them more often than females overall, suggests that females may be more territorial of den sites than males. This may be due to dens being a preferential resource for females, who prioritise resources required to raise offspring (Coleman & Downs 2010). In contrast, males likely prioritise access to receptive females (Coleman & Downs 2010) and not den sites, and therefore potentially have less need for stable den use. There was no difference in den use between the two monitoring events or sexes at the non-manipulated site, where density reduction was not undertaken.

The density of possums at the manipulated site was substantially greater than that at the non-manipulated site. There were also differences in den use between possums at the two sites. The majority of possums denned aboveground at the manipulated site, whereas possums predominantly denned on the ground at the non-manipulated site. Possums at the manipulated site also appeared to have more stable den use, as they used fewer dens and changed their dens less often. As den site choice is likely habitat-dependent (Green and Coleman, 1987), these differences may be due to the oaks and sycamore trees at the manipulated site providing a greater proportion of preferential aboveground tree holes, than the pine trees and gorse at the non-manipulated site. Males also used more dens and changed them more often than females at the manipulated site, but not at the non-manipulated site. The reason for this was unclear, but may have been due to a lack of 'high-quality' den sites at the non-manipulated site.

A captive study on possums has shown that males rarely share dens with other males in either the non-breeding or breeding season, and that female pairs frequently share dens, with the occurrence of this similar between the breeding and non-breeding seasons (Day et al., 2000b). However, mixed-sex pairs share their dens more frequently during the breeding season compared to

the non-breeding season (Day et al., 2000b). The main breeding season for possums in New Zealand is approximately March – November, although this varies by region (Fletcher and Selwood, 2000). The breeding season may therefore have occurred within the duration of both field experiments. This may have resulted in the changes in den use at the manipulated site, rather than density reduction. However, during the breeding season, male possums accompany females and sometimes share their dens with them (Winter, 1976, as cited in Day et al., 2000a). Therefore, if breeding did occur, one would have expected males to change their den use significantly, but this was not the case. The low-density non-manipulated site was also monitored during the same season as the high-density manipulated site and these sites were in close proximity to each other; yet spatial perturbation was not observed at the non-manipulated site. In addition, adult females were observed with joeys and backriders during the monitoring period at all three sites in the overall study, suggesting continuous breeding in the Canterbury region. It is therefore considered unlikely that the changes observed at the manipulated site were due to breeding. As it appears breeding happens all year round (Fletcher and Selwood, 2000; J. Bothwell, Lincoln University, personal communication, 2013; personal observation), this means that it would be difficult to design a study to account for the effects of breeding.

The population in this study was reduced by approximately 50%. Had a larger reduction been achieved, it is possible that this would have resulted in more pronounced changes in den use. Further research where possum populations are reduced by up to 90%, which is the level commonly achieved in control operations (P. Livingston, Animal Health Board, Wellington, personal communication, 2011), would test this theory. However, the 50% reduction in this study allowed an assessment of partial density reductions. This can occur in New Zealand due to trapping by fur harvesters, who have been recorded in one study pulling out of operations when trap-catch rates drop to only 26% on average (Jones et al., 2012).

As discussed previously, bTB transmission between possums may be closely associated with denning, through the excretion and transmission of bTB by individuals whilst they are in dens (Coleman and Caley, 2000; Green and Coleman, 1987; Ji et al., 2003; Paterson et al., 1995). Therefore, the potential increase in bTB transmission risk shown in this study due to partial density reduction, highlights the need for extremely efficient initial control that reduces populations to very low densities across entire sites (to prevent patchiness in control effort). Furthermore, the Animal Health Board, which is the organisation responsible for managing and controlling bTb, uses a model to simulate bTB transmission amongst possums and the effect of differing control strategies on disease persistence (Ramsey and Efford, 2010; Ramsey and Efford, 2005). These results could potentially be incorporated into this model, to predict likely changes in den use and therefore

transmission risk due to control (in particular, inefficient control). This study also highlights that bTB transmission risk may not be uniform between habitat types, due to differences in den use. For example, if bTB infected possums were present at the sites in this study, transmission risk may have been greater at the non-manipulated site, due to possums using more dens and changing these dens more often.

Although this study was un-replicated, it nonetheless allows us to hypothesise that den site changes in possums may occur in response to density reduction. Future research should involve replication in locations with similar population densities and habitats, and experimental controls where density reduction is not carried out. It is possible that spatial perturbation might not occur in habitats where preferential den sites are few or there are low levels of competition (i.e., low-density populations), or in contrast, where preferential dens are abundant, due to density reduction not changing the availability of preferential dens. Therefore, measurements of den availability would also be useful, with studies undertaken in habitats with a range of den availability levels. A den-quality index could also be incorporated, to measure the availability of 'higher-quality dens', which could also be used to assess whether individuals change the quality of their den following density reduction. This index could include parameters considered to be important drivers in den site selection, such as hollow characteristics (Gibbons et al., 2002; Isaac et al., 2008), tree species (Cowan, 1989; Gibbons et al., 2002), and exposure to wind and rain (Caley, 1996). Furthermore, research could be extended to investigating juveniles, as they are known to become infected with bTB (Coleman, 1988; Jackson et al., 1995a). Longer-term studies would also allow an assessment of whether any changes are permanent, or whether den use returns to pre-reduction levels. This would also allow investigation into any seasonal or annual variations in spatial perturbation.

In conclusion, investigating the responses of individuals to experimental density reduction improves our understanding of the spatial organisation of populations (Blackie et al., 2010). As behavioural changes of pests can substantially affect the ability of managers to control and monitor populations post-control (Arthur et al., 2002), these types of studies can also identify areas where control strategies could be improved. This study suggests that density reduction might result in changes in den use and that pest control operations need to remove the majority of possums across entire sites to reduce bTB transmission risk. Furthermore, this study implies that bTB transmission risk may not be uniform between habitat types, due to differences in denning behaviour. Further manipulative and non-manipulative studies would be useful to test these hypotheses.

Chapter 5:

Experimental Study – Spatial Perturbation of Possum Home Range Characteristics Following Density Reduction

5.1 Abstract

Population density can be a driver of home range characteristics, with density reduction resulting in changes in movement patterns (i.e., spatial perturbation). This likely occurs due to individuals taking advantage of newly available resources and reduced movement constraints from conspecifics. However, not all species change their spatial behaviour following density reduction. There has been conflicting research investigating this behaviour in the Australian brushtail possum (*Trichosurus vulpecula* Kerr). Knowledge of perturbation is particularly important for this species because possums transmit bovine tuberculosis (bTB) to livestock in New Zealand, and understanding changes in home ranges is important for control of possums and bTB. The primary objective of this study was to test whether possums change their home range characteristics, such as home range size, following density reduction. The secondary objective was to investigate whether there were intersexual differences in spatial perturbation. These objectives were addressed by carrying out experimental density reductions of two populations, and comparing the home range characteristics of the same possums before and after reduction, using GPS-tracking. The first site was a 15-hectare oak and sycamore forest fragment with a high-density possum population, which was monitored in summer 2011. The second site was a 15-hectare pine and gorse forest fragment with a low-density possum population, which was monitored in spring 2011. A third site where no density reduction was carried out was also monitored. This site was monitored in summer 2012, and consisted of a 15-hectare area of a larger 60-hectare pine and gorse fragment, with a low-density possum population. Possums at the first manipulated site increased their home range size and overlap following reduction. However, pasture use and the time taken for home ranges to become fully revealed did not change. Possums also did not shift the centre of their home ranges. There were no intersexual differences in movement changes. In contrast, possums at the other two sites did not change any of these home range characteristics. This was due to density at both of these sites remaining constant between the pre-and-post monitoring periods, even though a number of individuals were removed at one of these sites. There was no difference in home range characteristics between males and females at any of the sites. This research suggests that the home range characteristics of possums

are density-dependent. This study provides an experimental framework for which additional research could be based to confirm these findings. This study also highlights the need for efficient reductions that reduce populations to very low densities across entire sites (i.e., avoiding patchiness in control effort), to prevent potential increases in bTB transmission, due to increases in home ranges.

5.2 Introduction

Population density can be a driver of home range characteristics in some mammals, with density reduction resulting in changes in movement patterns (i.e., spatial perturbation; Tuytens et al., 2000). For instance, it has been shown in a number of rodent species, including mice (*Mus musculus*), ship rats (*Rattus rattus*) and Norway rats (*Rattus norvegicus*), that individuals quickly expand their home ranges once their neighbours are removed (Fitzgerald et al., 1981; Innes and Skipworth, 1983; Taylor and Thomas, 1989). North American red squirrels (*Tamiasciurus hudsonicus*) have also been recorded shifting their territory boundaries in response to the removal of neighbours (Larsen and Boutin, 1995). However, some studies on white-tailed deer (*Odocoileus virginianus*) in the United States have not recorded spatial perturbation following density reduction (McNulty et al., 1997; Oyer and Porter, 2004). Therefore, further information on changes following density reduction may help clarify the occurrence and mechanisms of spatial perturbation in mammals.

The incidence of perturbation is likely to be determined by the mechanisms of spatial distribution of the population (Wiggins et al., 2010). The removal of a significant number of individuals from a population almost certainly results in an increase in the availability of resources, such as food and den sites. Density reduction may also remove movement constraints towards resources that are imposed by conspecifics (Efford et al., 2000). Therefore, if populations distribute themselves predominantly based on resources, their home range characteristics will likely be density-dependent, with survivors of density reductions exhibiting spatial perturbation to take advantage of newly available resources (Wiggins et al. 2010). For example, the movement behaviour of European badgers (*Meles meles*) in the United Kingdom appears to be influenced by the availability of resources, as their home ranges change in response to seasonal changes in food availability (Palphramand et al., 2007) and they are territorial (Kruuk, 1978). Following density reduction, surviving badgers increase their home range size and overlap with conspecifics, thereby exhibiting spatial perturbation (Riordan et al., 2011; Woodroffe et al., 2006a). However, if a population does not predominantly distribute itself based on resources, individuals may not exhibit spatial perturbation following density reduction (Wiggins et al., 2010). This might explain why female white-tailed deer have not been recorded changing their home ranges following density reduction,

as they are considered to distribute themselves predominantly based on natal philopatry, rather than available resources (McNulty et al., 1997; Oyer and Porter, 2004).

The Australian brushtail possum (*Trichosurus vulpecula* Kerr) in New Zealand is a nocturnal, polygynous and arboreal marsupial that weighs 2–4 kilograms, with males and females similar in size and bodyweight (Clout and Ericksen, 2000; Day et al., 2000a; King, 2005). This species exhibits a social hierarchy, with dominant individuals preventing subordinates from accessing limited resources, such as dens (Biggins and Overstreet, 1978; Green, 1984; Jolly and Spurr, 1996; Wehi et al., 2006). The distribution of possums may therefore be based on resource availability, such as food and mates, meaning that individuals that survive density reduction might exhibit spatial perturbation. However, female possums also exhibit natal philopatry, with the home ranges of females inherited from their mothers (Ji et al., 2001; Stow et al., 2006). This might mean that females do not exhibit spatial perturbation following density reduction.

To date, there has been limited and conflicting research on spatial perturbation in possums following density reduction. Live-capture trapping of two populations subjected to density reduction has suggested that home range sizes of both sexes increase following control (Morgan et al., 2007). VHF radio-tracking of male and female brushtail possums in Australia has shown that individuals expand their ranges into areas where others been removed (Clinchy et al., 2001). Den site use has also been recorded to increase following density reduction (see Chapter 4 of this thesis). In contrast, one study examining the reinvasion of possums into controlled areas using a trap-based index and VHF radio-tracking, recorded shifts in the home range location of males and females following density reduction, but no change in home range size (Efford et al., 2000). Another live-capture trapping study recorded both no apparent change in movements and greatly increased range of movements following density reduction (Brockie et al., 1997). Ramsey et al. (2002) recorded an increase in male home ranges following density reduction during a VHF radio-tracking study, but no change for females. These conflicting results highlight the need to robustly research whether spatial perturbation occurs in possums following density reduction, using more accurate and modern experimental techniques.

There are home range characteristics other than size that are potentially density-dependent and therefore may change in response to density reduction. For example, changes in home range overlap have been recorded in badgers surviving various levels of population density reduction (e.g., Riordan et al., 2011; Tuytens et al., 2000). Possum home ranges overlap extensively (Brockie et al., 1987; Paterson et al., 1995) and the extent of overlap may vary depending on the social hierarchy of individuals. Therefore, density reduction may result in changes in home range overlap between survivors. There is some evidence of this from the Ramsey et al. (2002) VHF radio-tracking study, as

they also recorded an increase in home range overlap between males and females following density reduction. Changes in habitat use have been recorded in other mammals following density reduction, such as increases in the use of agricultural habitat by the red-necked wallaby (*Macropus rufogriseus rufogriseus*) and the Tasmanian pademelon (*Thylogale billardierii*) (Wiggins et al., 2010). As possums have a preference for pasture plants in their diet and are known to spend significant amounts of time in pasture when this habitat is available (Coleman et al., 1985; Green, 1984; Nugent et al., 2000), density reduction may also result in changes in pasture use. However, there have been no studies published on changes in possum habitat use due to density reduction. There are other home range characteristics that do not appear to have been previously investigated in any species, such as the time taken for home ranges to become fully revealed (i.e., the point at which the addition of extra location fixes does not increase home range size). In possums, male and female adults generally show site fidelity and exhibit stable home ranges (Cowan and Clout, 2000). Therefore, changes in movement patterns and home range size due to density reduction may affect how long it takes for a possum to reveal their full home range.

Movement changes following density reduction may occur due to survivors noting the removal of the physical presence of conspecifics, including reductions in vocalisations. However, marsupials (including possums) scent mark to provide information about their identity, social status and territories, with this potentially determining the relative spacing of individuals (Biggins and Overstreet, 1978; Croft and Eisenberg, 2006; Kerle, 2001). Conspecifics can therefore determine the current occupancy of home ranges by the rate of scent fade-out (Croft and Eisenberg, 2006). As such, the removal of individuals from a population and subsequent dissipation of their scent markings may instead initiate possums to move into these areas (Blackie et al., 2010). If possums respond to the removal of the physical presence of other possums, one would expect spatial perturbation to occur within a few days of density reduction. In contrast, if possums respond to the dissipation of scent markings, perturbation may be delayed until such time as scents can no longer be detected. However, there does not appear to be any information available in the literature on how long scent markings of marsupials last, to allow a prediction of when this will occur. Scent markings of other mammals are known to last for less than 24 hours to a few months after deposition (Gosling and Roberts, 2001). It is also possible that movement occurs after recognition of both the direct removal of conspecifics and their scent markings.

Being able to predict whether and how a pest species will exhibit spatial perturbation following density reduction is important for the development of optimal pest management strategies. Specifically, it allows density reduction to be evaluated as a control method. For example, badgers are culled in the United Kingdom, as they transmit bovine tuberculosis (*Mycobacterium*

bovis; bTB) to livestock. It has been suggested that culling of badgers may result in some counter-productive effects (i.e., increases in bTB prevalence), due to increases in home range overlap between badgers following density reduction and therefore contact rates (Riordan et al., 2011). In New Zealand, the possum, which was introduced in the 1800s to establish a fur trade (King, 2005), also transmits bTB to livestock. This species is now considered to be the greatest wildlife barrier to the eradication of this disease (AHB, 2012; Coleman and Caley, 2000). It is therefore important to establish whether density reduction of this pest species allows management goals to be achieved. For example, if bTB infected possums surviving density reduction increase their home ranges as badgers do, this may mean that bTB transmission risk amongst possums, and between possums and livestock, may also increase. Moreover, not having knowledge of how possums respond to density reduction may mean that survivors are then more difficult to target in follow-up control operations, due to having unpredictable movement patterns.

The primary objective of this study was to investigate whether possums exhibit spatial perturbation of home range characteristics following density reduction. Although females exhibit natal philopatry (Ji et al., 2001; Stow et al., 2006), previous studies have indicated that they still display spatial perturbation following density reduction (Clinchy, 1999; Efford et al., 2000; Morgan et al., 2007). As such, male and female possums in this study were both predicted to exhibit density-dependent home range characteristics and therefore display spatial perturbation. Specifically, it was hypothesised that following density reduction, males and females would (1) take longer for their home ranges to become fully revealed (due to changing their movement patterns) compared to before reduction, (2) increase their home range sizes (to take advantage of newly available resources and less movement constraints), (3) shift the centre of their home ranges (to take advantage of newly available resources and less movement constraints), (4) increase their home range overlap with conspecifics (in line with the observations of badgers) and (5) increase their use of pasture (to take advantage of newly available resources and less movement constraints). The secondary objective of this study was to assess whether there was a difference in the magnitude of spatial perturbation between males and females.

Both these objectives were addressed by carrying out experimental density reduction of two possum populations, and comparing the home range characteristics of the same possums before and after density reduction. A third site where no density reduction was carried out was also monitored. This site was not an experimental control, due to differences in habitat, population density and the year of monitoring (although the season of monitoring was the same as the first manipulated site). However, comparisons between this site and the others are still useful. For example, if spatial perturbation occurs at this site, even though density reduction was not

undertaken, this would suggest other factors are potentially determining movement changes during this time of year (e.g., breeding). Possum home range characteristics at all sites was determined using GPS-tracking technology.

5.3 Methods

5.3.1 Study sites

The two sites where density reductions were carried out ('Manipulation Site 1' and 'Manipulation Site 2') were 15-hectare forest fragments in Hororata (43°32'50.03"S, 171°54'35.96"E) and Whitecliffs (43°25'37.70"S, 171°54'33.80"E), Canterbury, New Zealand. The site where density reduction was not carried out ('Non-Manipulated Site') was a 15-hectare end of a 60-hectare forest fragment in Hororata (43°30'56.38"S, 171°53'23.74"E), Canterbury. The habitat at Manipulated Site 1 consisted of English oaks (*Quercus robur*) and sycamores (*Acer pseudoplatanus*), with surrounding paddocks of pasture plant species and kale (*Brassica oleracea*). The habitat at both Manipulated Site 2 and Non-Manipulated Site was predominately plantation pine (*Pinus radiata*) and gorse (*Ulex europaeus*), with surrounding paddocks of pasture plant species. The population density at Manipulated Site 1 was high at seven possums per hectare. The densities at Manipulated Site 2 and Non-Manipulated Site were low at two and one possum per hectare, respectively. These densities were estimated using mark-recapture events and pre-defined Closed Population Estimation models in Program Mark (Version 6.1) (Cooch and White, 2011; Lettink and Armstrong, 2003; Pryde, 2003). No large-scale possum control had been carried out at any of the sites for at least five to ten years, only occasional trapping and shooting. Differences in possum density were therefore likely to be due to variations in resource levels between sites.

5.3.2 Data collection

Possums were monitored at the three sites during January – April 2011 (summer), September – December 2011 (spring) and January – April 2012 (summer), respectively. Adult possums were caught using treadle (Trappers Cyanide Limited, Canterbury, New Zealand) and trigger (Grieve Wrought Iron Limited, Christchurch, New Zealand) live-capture cage traps. Following live-capture, possums were anaesthetised using gaseous halothane to allow handling under sedation. All research was carried out with the approval of the Lincoln University Animal Ethics Committee (Approval Number 373) and all anaesthetising followed the Lincoln University Standard Operating Procedure (Number 91 – Possum Anaesthesia using Halothane; Appendix C). All possums were weighed and fitted with GPS-collars that also contained VHF units (Sirtrack Limited, Havelock North, New Zealand). The VHF units allowed the possums to be radio-tracked regularly to check possum

survival and to ensure that the collars were still fitted. VHF radio-tracking was undertaken using an Australis 26k™ VHF receiver and a yagi™ multi-directional antenna (Titley Scientific, Australia). The GPS-collars were generally programmed to obtain eight hourly location fixes per night between sunset and sunrise (as possums are nocturnal). Collars were not programmed to take fixes during the day when possums were most likely in dens. Seventeen possums (8 males and 9 females) were fitted with GPS-collars at Manipulated Site 1. Sixteen possums (8 males and 8 females) were fitted with GPS-collars at both Manipulated Site 2 and Non-Manipulated Site. Collars were fitted with a three-finger gap between the collar belt and the skin, to prevent rubbing, but also to ensure that the collar would not slip over the possum's head (Blackie, 2010b). The collars weighed no more than 135 grams. Possums were weighed at the time of fitting to ensure that collars weighed no more than 5% of each possums total bodyweight, to prevent adverse effects on the behaviour of the study animal (Kenward, 2001).

This study followed a Before-After (BA) design (Smith, 2002), with possums at all three sites monitored before and after density reduction. Density reduction at the two manipulated sites was undertaken for a week using live-capture cage trapping. This method was used over other techniques, such as poisoning, to ensure that the collared animals were protected and not accidentally culled. Any collared individuals caught in the traps were released and any non-collared individuals were humanely euthanised (by overdosing with halothane). A week of trapping was also conducted at Non-Manipulated Site, but all individuals were released after capture. This was to ensure consistency in methods between sites and to remove possible behavioural biases due to trapping itself. Although no density reduction was undertaken at Non-Manipulated Site, the monitoring periods before and after this trapping week are still referred to in the remainder of this chapter as 'pre-reduction' and 'post-reduction'. Possums were monitored for ten weeks in total, five weeks before and after density reduction at all three sites. This timeframe was considered sufficient for the home ranges of possums to become revealed, based on the results of similar research (H. Blackie, Lincoln University, personal communication, 2010).

5.3.3 Data analyses

Home range size, length, shift and overlap, and pasture use were calculated for each possum for both the pre-reduction and post-reduction monitoring periods. Before these analyses were undertaken, the GPS-collar data were evaluated for location accuracy. Fixes with Horizontal Dilution of Precision (HDOP) values greater than 10 (Sirtrack®, 2010) were visually assessed against previous and subsequent fixes, to determine if a possum could reasonably reach these locations between fix intervals (Yockney et al., 2013). Overall, the proportion of high HDOP fixes was very low (<5%) and no fixes were identified as being behaviourally unrealistic. The mean number of fixes obtained per

possum was then calculated for each monitoring event, to determine whether there were differences in sampling effort between individuals.

Prior to undertaking home range analyses, incremental area analyses are recommended to confirm that home ranges are fully revealed within the timeframe of monitoring and therefore comparisons are not biased (Laver and Kelly, 2008; Metsers et al., 2010; Recio et al., 2010). Home ranges were considered to be fully revealed if 95% of a home range was obtained within the monitoring timeframe (i.e., additional location fixes did not increase home range size) (Asari et al., 2010; Metsers et al., 2010; Recio et al., 2010). This was determined by carrying out incremental area analysis of 95% Kernel Density Estimates (KDE) in Ranges8 (Kenward et al., 2008; Laver and Kelly, 2008) and visually establishing if an asymptote was reached (Laver and Kelly, 2008; Recio et al., 2010). This information was then collated to determine the percentage of possums at each site that fully revealed their home ranges within the monitoring period, as well as the mean number of fixes required for home ranges to be fully revealed. However, with respect to the remaining home range estimations, the aim was to assess changes in home range utilisation. Therefore, limiting analyses to only possums that revealed the extent of their home ranges may have resulted in the removal of potentially useful data. As such, possums with an equal sampling effort between events (i.e., there was a similar number of fixes before density reduction as after density reduction, to ensure unbiased comparisons), were also included in these analyses.

Home range size was estimated in Ranges8 (Version 2.7) using 95% and 50% (core) KDE, and 100% Minimum Convex Polygons (MCP) (Kenward et al., 2008). Analyses using fixed kernels with Least Squares Cross Validation (LSCV) bandwidth is recommended for KDE (Seaman et al., 1999). However, this technique often results in under-smoothing and the creation of numerous small perimeters around individual data points, which do not appear to have any behavioural relevance (Blundell et al., 2001; Jones et al., 1996; Kie et al., 2010). This was also the case when LSCV was employed in this study. Analyses using fixed smoothing with reference bandwidth solve this excessive fragmentation issue and therefore more accurately estimate home ranges in these circumstances (Blundell et al., 2001; Jones et al., 1996; Kie et al., 2010). Consequently, reference bandwidth was employed in this study, which also eliminated the excessive fragmentation (see Section 2.6.4: Home range estimation in Chapter 2: General Methods).

One hundred percent MCP were calculated to identify longer distance forays that are excluded using KDE, using a harmonic mean peel centre (Blackie et al., 2010; Kenward et al., 2008). Home range length was calculated in the GIS program ESRI® ArcMap™ (Version 9.3; ESRI, 2008), by measuring the maximum distance across each MCP. Home range shift was also assessed in ArcMap™, by determining the centroid of the 50% KDE before reduction and following reduction,

and calculating the distance between these two points (Janmaat et al., 2009; Rasiulis et al., 2012). To estimate the timing of any changes in movement patterns at Manipulated Site 1, 95% KDE, 50% KDE and MCP home ranges were also calculated for each week of the two monitoring periods (a total of 10 weeks). The weekly percent utilisation of the total home range of the given monitoring period was then calculated, to allow relative comparisons in home range size across individuals and between weeks. The idea being that a peak in utilisation might indicate a point of change in movement patterns. Some weekly values were greater than 100% for the kernel density estimates, due to the smoothing function of this technique resulting in greater weekly sizes than that for the entire monitoring period.

Home range overlap between collared individuals was calculated in Ranges8 for the 95% and 50% KDE, giving the number of overlaps and percent overlap in home range area (Kenward et al., 2008). The area of a home range that did not overlap with any other collared possum (the 'exclusive area') was also calculated for each study animal, by exporting the data into ArcMap™ and carrying out overlay procedures (Hoset et al., 2008). For the percent overlap analyses, as the whole population was unable to be collared, the total area of an individual's home range that overlapped with the home ranges of all other possums in the population was unable to be calculated. Instead, the percent overlap between each pair of collared possums was established. This was only carried out when overlap between possums occurred (i.e., zero overlaps were not included in the analysis). This analysis is therefore considered to provide a relative comparison of the degree of overlap between any two possums at each of the sites (when overlap occurs). To assess pasture use, the percentage of 95% KDE fixes within pasture habitat was calculated.

Count data (i.e., number of fixes, number of fixes until home range revealed and number of home range overlaps) were all analysed using generalised linear mixed-effect (GLMM) models, with a Poisson error structure and logarithmic link function (Crawley, 2007). Proportional data (i.e., percent home range overlap, exclusive area and pasture use) were all analysed using GLMM models with a binomial error structure and logit link function (Crawley, 2007). Continuous data (home range size, home range shift and weekly home range utilisation – as >100% utilisation could be achieved) were analysed using linear mixed-effect models, with a normal (Gaussian) error structure and an identity link function (Crawley, 2007). Individual possum identity was included in each model as a random effect, as well as their change between events (i.e., before and after density reduction) to account for any temporal autocorrelation. Continuous data were natural log transformed when the model residuals exhibited heteroscedasticity.

Models for all response variables were run in the statistical program R (Version 2.15.1, Woodroffe et al., 2006b) with the following combinations of fixed effects: (1) a null model with

intercept only; (2) a model that considered event (before or after density reduction); (3) a model that considered bodyweight (which was measured in kilograms); (4) a model that considered sex (male or female); and (5) a model that considered the interaction between sex and event (to allow an assessment of any variations in spatial perturbation between sexes). An exception to this was the home range shift analyses, which produced only one measurement for each individual and not a value for each event. The model set for this variable was therefore run with a 'Site' fixed effect instead of an 'Event' fixed effect. This allowed comparisons in home range shift between all three sites. Another exception was the weekly home range analyses, where the model set was run with models 1 – 4 above, as well as a week model (Weeks 1 – 5) and models investigating interactions between week, event and sex.

All model sets were ranked using sample size corrected Akaike Information Criterion (AICc), where the weights of all models in the set sum to one and the model with the highest Akaike Weight is considered to have the best fit for the available data (Anderson, 2008; Burnham and Anderson, 2002). Support for each model was evaluated by assessing the change in AICc from the best model (ΔAICc) (Anderson, 2008; Burnham and Anderson, 2002). Models with a change of approximately less than two from the best model have substantial empirical support, models with a change of 4 – 7 have considerably less support and models with a change of greater than 10 have essentially no support (Burnham and Anderson, 2002). Each model set was assessed for 'pretending variables', whereby the addition of a variable does not change the deviance and therefore the fit of the model, skewing and biasing Akaike weights, but none were identified (Anderson, 2008). Due to differences in habitat type and initial possum densities between sites, and since the study was not replicated in the same year, the data from the three sites were analysed separately (with the exception of home range shift as discussed above).

5.4 Results

5.4.1 Sample sizes and density reduction estimates

At Manipulated Site 1, Manipulated Site 2 and Non-Manipulated Site, the home ranges of five, three and three⁵ of the possums, respectively, could not be analysed due to the GPS-collars malfunctioning within the monitoring timeframe. The reason for this was unclear, but was due to either the hardware of the collars malfunctioning or the collar batteries going flat. One possum at Manipulated Site 1 was accidentally shot and one possum at Non-Manipulated Site was accidentally overdosed with halothane. At Manipulated Site 1, one collar also detached from a possum and

⁵ One of these was the possum that roamed outside the study area, as detailed in Chapter 3, which would have therefore been excluded from the analyses in any case.

became stuck in a tree (this was not discovered until the completion of the study), and one possum was unable to be located during or after the monitoring period. An unauthorised trapper also killed six of the possums at Manipulated Site 2 mid-way through the study.

Due to these possums being unable to be analysed, incremental area analysis (to determine whether home ranges were revealed within the monitoring timeframe) was only assessed for nine possums (3 males and 6 females), seven possums (4 males and 3 females) and twelve possums (7 males and 5 females) at Manipulated Site 1, Manipulated Site 2 and Non-Manipulated Site, respectively. For the subsequent home range analyses, a number of these possums could not be analysed due to having an uneven sampling effort (i.e., number of fixes) between monitoring periods. One male possum was also removed from the Non-Manipulated Site analyses due to being a statistical outlier; this possum had an atypical increase in home range size (537%) due to completely shifting its home range during the post-reduction monitoring period. The final home range analyses were therefore conducted on eight (3 males and 5 females), five (3 males and 2 females) and eight possums (4 males and 4 females) at the three sites, respectively (Table 5.1).

The population density at Manipulated Site 1 (\pm Standard Error; SE) before and after density reduction was estimated to be seven (\pm 1.3 SE) and three (\pm 0.3 SE) possums per hectare respectively, resulting in approximately a 50% density reduction. Unexpectedly, the estimated density at Manipulated Site 2 was similar before (1.5 possums per hectare; \pm 0.0 SE) and after (1.3 possums per hectare; \pm 1.9 SE) reduction, even though approximately twenty possums were removed (which includes the six possums taken by the trapper at approximately the same time as the mid-experiment density reduction). The density of adults at Non-Manipulated Site was similar pre-reduction (1.5 possums per hectare; \pm 0.0 SE) to post-reduction (1.5 possums per hectare, \pm 0.1 SE), as expected. Appendix B provides more detailed results of these density assessments.

Table 5.1 The total number of possums at the three sites that were fitted with GPS-collars, the number that were unable to be analysed, the number with uneven sampling effort between monitoring periods and the resultant number of possums for which home range analyses were conducted.

GPS-collared possums	Manipulated Site 1			Manipulated Site 2			Non-Manipulated Site		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
Number collared	17	8	9	16	8	8	16	8	8
Number unable to be analysed	8	5	3	9	4	5	4	1	3
Number with uneven sampling effort	1	0	1	2	1	1	4 ⁶	3 ⁶	1
Resultant number analysed	8	3	5	5	3	2	8	4	4

5.4.2 Number of fixes

The model comparisons for the three sites all recorded the ‘Null’ model as having the best support, either due to this model having the largest weighting, or being within two $\Delta AICc$ of the best model (Table 5.2). This suggests that there was no influence of event (pre-reduction versus post-reduction), sex or the bodyweight of individuals on the frequency of fixes taken at any of the sites (Figure 5.1).

⁶ One of these includes the male possum that was a statistical outlier (see ‘Sample size and density reduction estimates’ section for more information)

Table 5.2 Akaike weights ($\Delta AICc$) from the linear mixed-effects models investigating the number of fixes, the number of fixes until home ranges were fully revealed, home range size and pasture use, for possums at the three sites. Event and sex are categorical variables with two categories (pre-reduction and post-reduction, and male or female) and bodyweight (BW) is a continuous variable, which was measured in kilograms. Bold numbers indicate models within a set that have a $\Delta AICc$ of less than two. KDE = Kernel Density Estimates and MCP = Minimum Convex Polygons. Level of empirical support for models: substantial = $\Delta AICc$ of 0 – 2, considerably less = $\Delta AICc$ of 4 – 7, essentially none = $\Delta AICc$ of >10.

Response variable	Manipulated Site 1					Manipulated Site 2					Non-Manipulated Site				
	Null	Event	BW	Sex	Sex* Event	Null	Event	BW	Sex	Sex* Event	Null	Event	BW	Sex	Sex* Event
<i>Number of fixes</i>	0.29 (0.39)	0.27 (0.48)	0.08 (2.99)	0.35 (0.00)	0.02 (6.20)	0.74 (0.00)	0.12 (3.67)	0.07 (4.61)	0.07 (4.72)	0.00 (18.50)	0.26 (1.41)	0.53 (0.00)	0.14 (2.63)	0.05 (4.56)	0.01 (7.38)
<i>Number of fixes until home ranges revealed</i>	0.99 (0.00)	0.00 (10.59)	0.00 (11.39)	0.00 (11.47)	0.00 (102.92)	0.93 (0.00)	0.02 (7.79)	0.02 (8.21)	0.03 (6.78)	0.00 (48.03)	0.55 (0.00)	0.19 (2.08)	0.14 (2.74)	0.12 (3.04)	0.00 (11.20)
<i>Home range size</i>															
95% KDE	0.26 (1.99)	0.69 (0.00)	0.02 (6.92)	0.02 (6.93)	0.00 (10.07)	0.99 (0.00)	0.00 (14.63)	0.00 (10.59)	0.00 (11.15)	0.00 (128.46)	0.73 (0.00)	0.08 (4.50)	0.14 (3.34)	0.05 (5.30)	0.00 (19.62)
50% KDE	0.06 (4.98)	0.72 (0.00)	0.00 (10.08)	0.01 (8.45)	0.20 (2.55)	1.00 (0.00)	0.00 (14.84)	0.00 (14.91)	0.00 (16.06)	0.00 (130.63)	0.76 (0.00)	0.09 (4.28)	0.09 (4.34)	0.06 (5.03)	0.00 (18.11)
100% MCP	0.10 (4.41)	0.89 (0.00)	0.01 (9.73)	0.01 (9.74)	0.00 (13.89)	0.99 (0.00)	0.00 (15.00)	0.01 (10.44)	0.01 (9.51)	0.00 (129.51)	0.72 (0.00)	0.17 (2.91)	0.06 (5.05)	0.06 (4.96)	0.00 (17.69)
Length	0.71 (0.00)	0.18 (2.74)	0.05 (5.13)	0.05 (5.31)	0.00 (15.46)	0.99 (0.00)	0.00 (14.91)	0.00 (13.13)	0.01 (8.80)	0.00 (128.70)	0.75 (0.00)	0.12 (3.65)	0.06 (5.15)	0.07 (4.66)	0.00 (17.89)
<i>Pasture use</i>															
Percentage of fixes within pasture	0.63 (0.00)	0.15 (2.91)	0.07 (4.29)	0.14 (2.99)	0.00 (12.93)	0.82 (0.00)	0.01 (8.99)	0.07 (5.03)	0.10 (4.22)	0.00 (48.93)	0.62 (0.00)	0.10 (3.66)	0.21 (2.20)	0.07 (4.36)	0.00 (14.45)

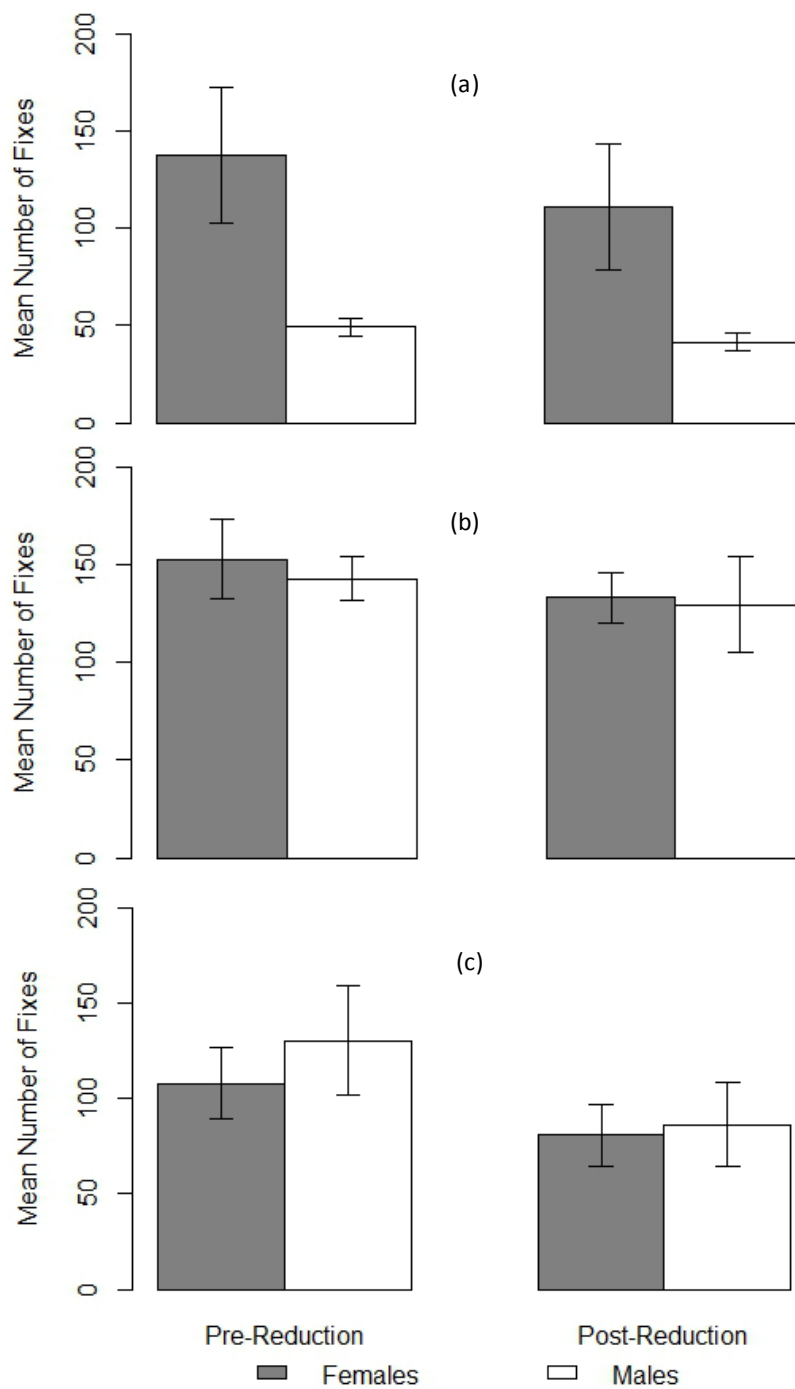


Figure 5.1 Mean number of GPS fixes taken per individual before and after density reduction at (a) Manipulated Site 1, (b) Manipulated Site 2 and (c) Non-Manipulated Site. Error bars are \pm the standard error.

5.4.3 Number of fixes until home range revealed

At Manipulated Site 1, fewer possums fully revealed their home ranges within the pre-reduction monitoring period than the post-reduction (44% and 56% of all possums, respectively) period. At Manipulated Site 2, the same percentage of possums fully revealed their home ranges in the pre-reduction and post-reduction monitoring periods (83% of all possums). At Non-Manipulated Site, 83% and 58% of possums revealed their home ranges in the pre-reduction and post-reduction monitoring period, respectively. The model sets for the number of fixes until home ranges were fully revealed, all recorded the 'Null' model as having the best fit for the three sites (Table 5.2). This implies that there was no support for difference in this variable due to event, sex or the bodyweight of individuals, at any of the sites (Figure 5.2).

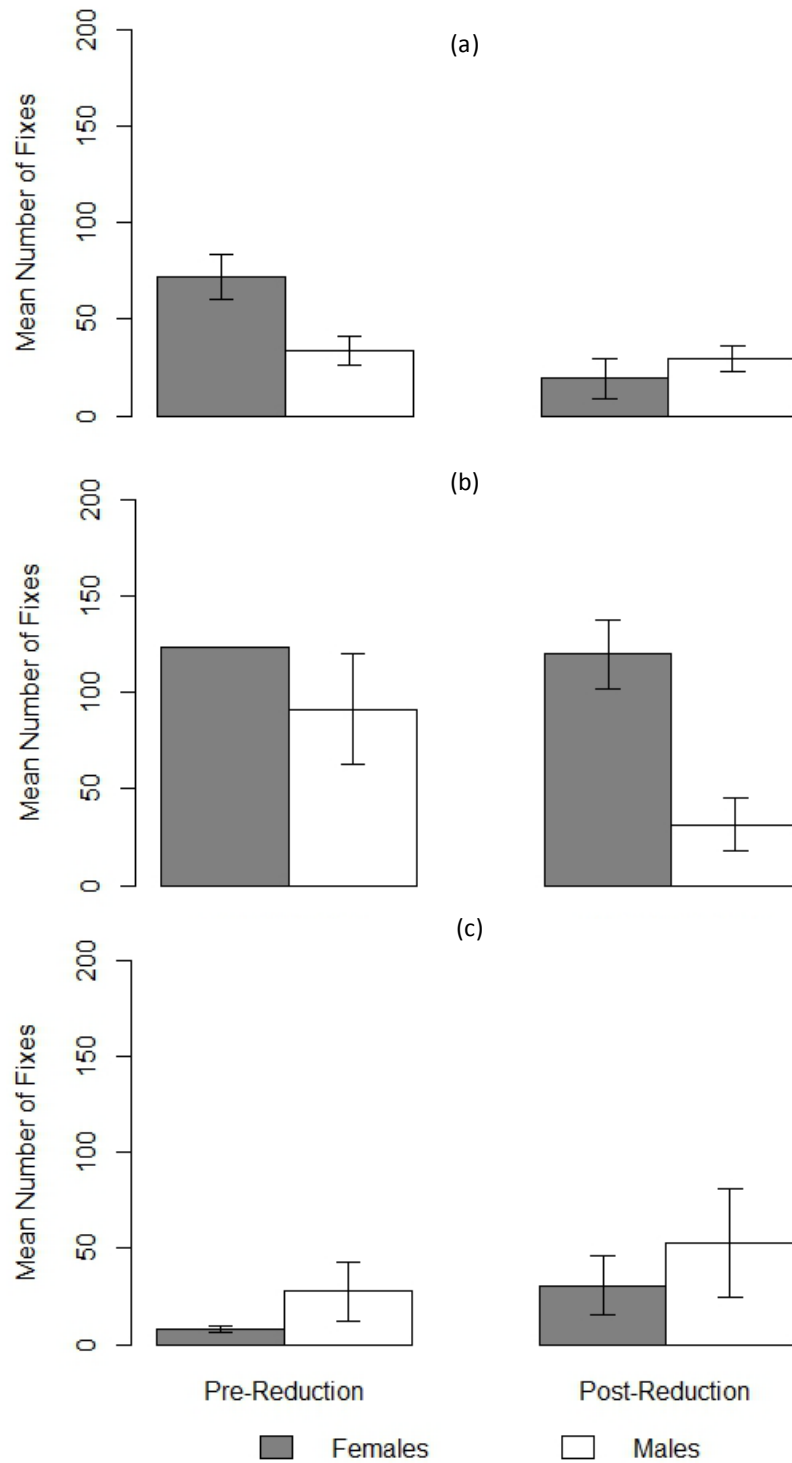


Figure 5.2 Mean number of GPS fixes required for home ranges to be fully revealed, before and after density reduction at (a) Manipulated Site 1, (b) Manipulated Site 2 and (c) Non-Manipulated Site. Error bars are \pm the standard error. The mean without an error bar is due to only one female possum revealing its home range in this monitoring event.

5.4.4 Home range size

All measures of home range size (95% KDE, 50% KDE, 100% MCP and home range length) increased substantially following density reduction at Manipulated Site 1, for both males and females (Table 5.3, Table 5.4 and Plate 5.1). The 95% and 50% KDE sizes for females at Manipulated Site 2 also increased considerably following density reduction; however, there was little variation between monitoring events for the other home range size variables at this site, for both males and females (Table 5.3, Table 5.4 and Plate 5.2). At Non-Manipulated Site, home range size generally did not change substantially between monitoring periods for either sex (Table 5.3, Table 5.4 and Plate 5.3).

The model with the best support for the 95% KDE at Manipulated Site 1 was 'Event' (Akaike Weight of 0.69; Table 5.2). However, the 'Null' model was within two ΔAIC_c of this model, suggesting that there was no difference in this variable due to event, sex or the bodyweight of individuals. 'Event' was also the model with the best fit for the 50% KDE and 100% MCP at this site (Akaike Weights of 0.72 and 0.89, respectively; Table 5.2). This was due to both males and females increasing these variables substantially following density reduction (Table 5.4). The model with the most support for range length at Manipulated Site 1 was the 'Null' model (Akaike Weight of 0.71; Table 5.2). This suggests that event, sex or the bodyweight of individuals did not influence home range length. In contrast to Manipulated Site 1, the best model for all the home range size variables for Manipulated Site 2 and Non-Manipulated Site was the 'Null' model (Table 5.2). This shows that there was no difference in home range size at these sites due to event, sex or the bodyweight of individuals.

Table 5.3 Mean (\pm standard error) home range size and overlap pre-reduction and post-reduction for possums at the three sites. KDE = Kernel Density Estimates and MCP = Minimum Convex Polygons.

Response variable	Manipulated Site 1		Manipulated Site 2		Non-Manipulated Site	
	Pre	Post	Pre	Post	Pre	Post
<i>95% KDE size (ha)</i>						
Males	1.2 (0.4)	2.4 (0.8)	13.8 (2.6)	12.9 (3.0)	4.7 (1.5)	6.1 (3.0)
Females	0.7 (0.2)	1.1 (0.2)	3.8 (2.2)	7.9 (1.7)	5.2 (3.3)	7.1 (4.7)
<i>50% KDE size (ha)</i>						
Males	0.4 (0.5)	0.9 (0.5)	3.9 (1.5)	2.9 (0.8)	1.0 (0.8)	1.4 (1.1)
Females	0.2 (0.3)	0.4 (0.1)	0.9 (0.6)	1.8 (0.8)	1.7 (1.5)	1.7 (1.4)
<i>100% MCP size (ha)</i>						
Males	1.5 (1.0)	5.1 (2.1)	18.9 (2.6)	19.0 (2.7)	16.5 (3.6)	13.6 (4.0)
Females	3.2 (2.0)	5.3 (2.6)	10.0 (2.8)	8.2 (0.5)	18.5 (5.1)	11.0 (3.9)
<i>Length (m)</i>						
Males	208.8 (10.2)	411.3 (15.2)	644.3 (13.4)	597.4 (7.1)	687.4 (19.8)	580.6 (15.6)
Females	326.3 (15.3)	351.2 (15.2)	471.5 (12.7)	453.0 (9.6)	674.5 (23.8)	494.9 (19.5)
<i>95% KDE overlap (ha)</i>						
Males	0.2 (0.0)	0.7 (0.1)	3.2 (0.5)	1.9 (0.3)	0.5 (0.1)	1.6 (1.1)
Females	0.1 (0.0)	0.3 (0.1)	2.2 (1.1)	2.6 (0.4)	0.7 (0.4)	1.1 (0.3)
<i>50% KDE overlap (ha)</i>						
Males	0.1 (0.1)	0.2 (0.0)	0.2 (0.1)	0.4 (0.4)	0.2 (0.1)	0.1 (0.1)
Females	0.0 ⁷ (0.0)	0.0 ⁷ (0.0)	0.0 ⁷ (0.0)	0.7 (0.7)	0.2 (0.2)	0.3 (0.3)
<i>95% KDE Exclusive Area (ha)</i>						
Males	0.6 (0.4)	0.7 (0.4)	7.9 (1.9)	4.7 (0.8)	2.7 (1.4)	3.3 (2.1)
Females	0.6 (0.3)	0.5 (0.2)	0.2 (0.2)	0.3 (0.3)	3.5 (2.8)	3.7 (3.5)
<i>50% KDE Exclusive Area (ha)</i>						
Males	0.3 (0.2)	0.4 (0.1)	3.7 (1.3)	2.4 (0.7)	0.7 (0.3)	1.1 (0.5)
Females	0.2 (0.1)	0.2 (0.1)	0.9 (0.3)	1.1 (1.1)	1.5 (1.1)	1.4 (1.1)

⁷ Only minimal overlap was recorded for these possums

Table 5.4 Mean (\pm standard error) percent change in home range size for possums at the three sites. KDE = Kernel Density Estimates and MCP = Minimum Convex Polygons.

Response variable	Manipulated Site 1	Manipulated Site 2	Non-Manipulated Site
<i>95% KDE size (ha)</i>			
Males	+119 (28)	-5 (13)	+29 (47)
Females	+102 (38)	+240 (240)	+26 (19)
<i>50% KDE size (ha)</i>			
Males	+150 (74)	-8 (10)	+48 (52)
Females	+105 (35)	+120 (103)	+6 (12)
<i>100% MCP size (ha)</i>			
Males	+205 (41)	0 (5)	-5 (22)
Females	+133 (70)	+15 (61)	-32 (12)
<i>Length (m)</i>			
Males	+91 (6)	-3 (4)	-2 (6)
Females	+27 (8)	+6 (7)	-20 (5)

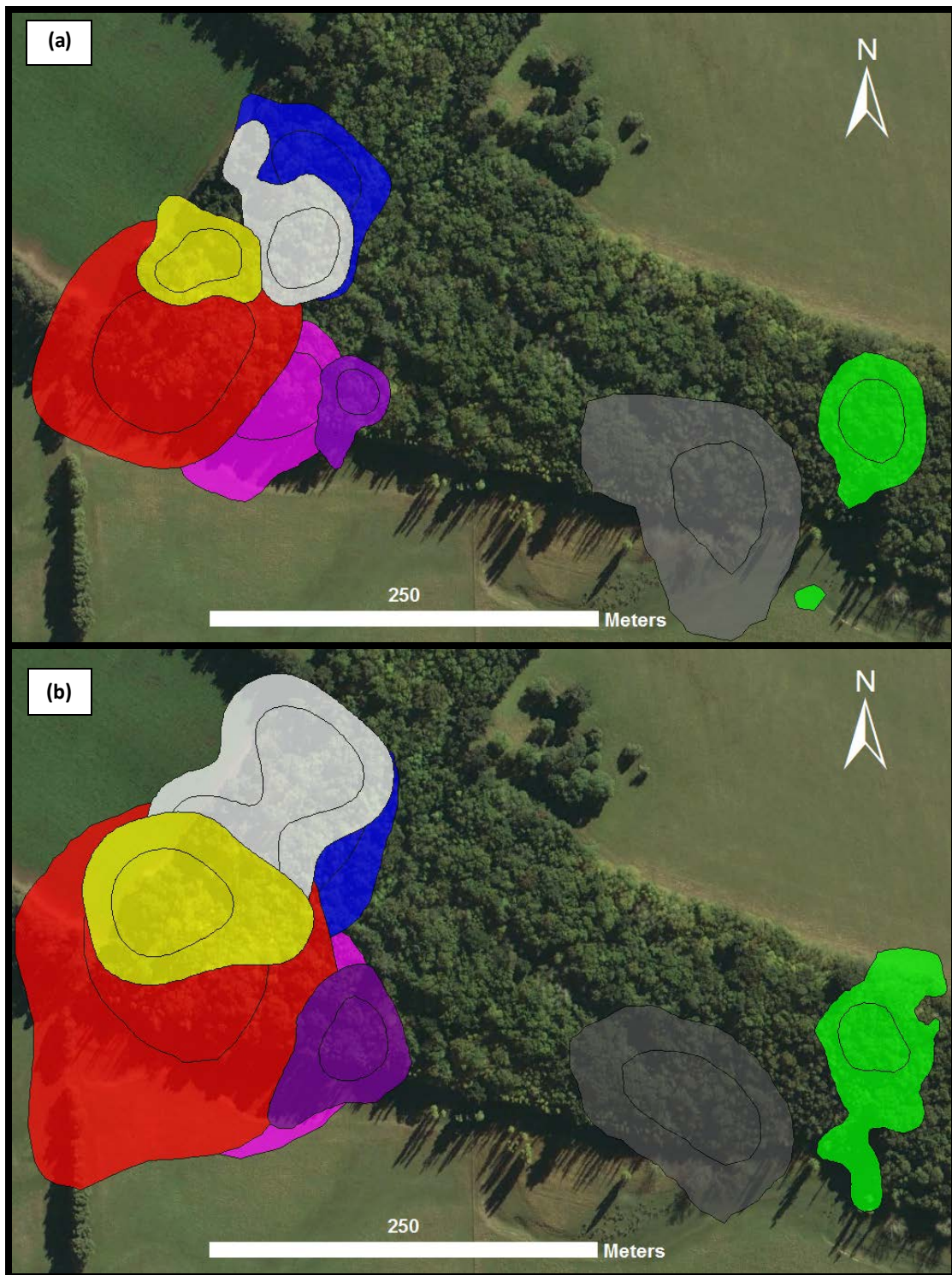


Plate 5.1 95% Kernel Density Estimates (larger polygons) and 50% Kernel Density Estimates (smaller polygons) for the eight possums at Manipulated Site 1 (depicted by different colours) for the (a) pre-reduction and (b) post-reduction monitoring periods.



Plate 5.2 95% Kernel Density Estimates (larger polygons) and 50% Kernel Density Estimates (smaller polygons) for the five possums at Manipulated Site 2 (depicted by different colours) for the (a) pre-reduction and (b) post-reduction monitoring periods. Note that the 'red' possum is concealed in the pre-reduction monitoring period by the home ranges of the other possums.



Plate 5.3 95% Kernel Density Estimates (larger polygons) and 50% Kernel Density Estimates (smaller polygons) for the eight possums at Non-Manipulated Site (depicted by different colours) for the (a) pre-reduction and (b) post-reduction monitoring periods. Two possums and one possum are concealed by the home ranges of other possums in the pre-reduction and post-reduction monitoring periods, respectively.

5.4.5 Timing of movement changes

The weekly home range size for all three variables (95% KDE, 50% KDE and MCP) appeared to be more variable before density reduction, compared to following density reduction (Figure 5.3). However, the model comparisons for all three variables recorded the 'Null' model as having the most support, as this model either had the largest Akaike weighting or was within two $\Delta AICc$ of the best model (Table 5.5). This indicates that there was no influence of monitoring event, sex, the bodyweight of individuals or the week of monitoring (both before and after density reduction) on weekly home range size (Figure 5.3).

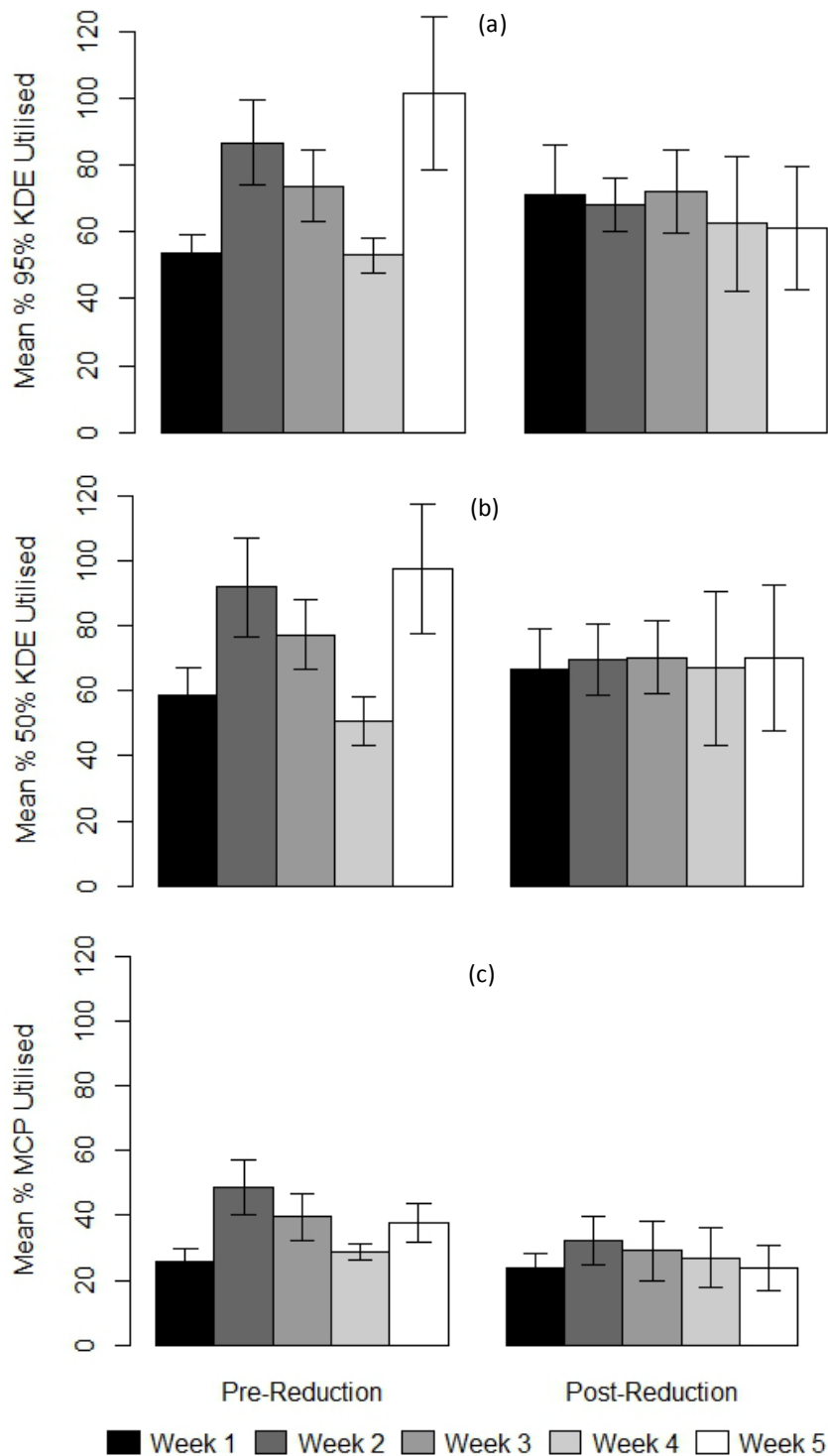


Figure 5.3 Weekly percent home range utilisation by possums of (a) 95% Kernel Density Estimates (KDE), (b) 50% KDE and (c) 100% Minimum Convex Polygons (MCP), for the pre-reduction and post-reduction monitoring periods at Manipulated Site 1. Error bars are \pm the standard error.

Table 5.5 Akaike weights ($\Delta AICc$) from the linear mixed-effects models investigating weekly home range utilisation for possums at Manipulated Site 1. Event is a categorical variable with two categories (pre-reduction and post-reduction), sex is a categorical variable with two categories (male or female), week is a categorical variable with five categories (Weeks 1-5) and bodyweight (BW) is a continuous variable, which was measured in kilograms. Bold numbers indicate models within a set that have a $\Delta AICc$ of less than two. KDE = Kernel Density Estimates and MCP = Minimum Convex Polygons. Level of empirical support for models: substantial = $\Delta AICc$ of 0 – 2, considerably less = $\Delta AICc$ of 4 – 7, essentially none = $\Delta AICc$ of >10.

Response variable	Null	Event	BW	Week	Sex	Week* Event	Week* Event*Sex
95% KDE	0.33 (0.00)	0.23 (0.70)	0.11 (2.29)	0.11 (2.14)	0.10 (2.30)	0.12 (2.10)	0.00 (12.25)
50% KDE	0.33 (0.00)	0.23 (0.69)	0.11 (2.20)	0.12 (2.08)	0.17 (1.32)	0.05 (3.69)	0.00 (12.92)
100% MCP	0.26 (1.11)	0.45 (0.00)	0.08 (3.35)	0.08 (3.47)	0.08 (3.43)	0.04 (4.76)	0.00 (14.54)

5.4.6 Home range shift

The model comparisons for home range shift (the mean distance that home range centroids moved between monitoring periods) recorded the ‘Bodyweight’ model as having the most support (Akaike Weight of 0.68), followed by the ‘Sex’ model (Akaike Weight of 0.19, $\Delta AICc$ of 2.50). There was considerably less support for the null, ‘Site’ and ‘Site*Sex’ models (Akaike Weights of 0.05, 0.04 and 0.04, $\Delta AICc$ of 5.03, 5.59 and 5.89, respectively). These results were due to heavier possums and male possums moving their home range centroids to a greater degree (Figure 5.4). There was little support for differences in home range shift between sites, for either males or females (Figure 5.4). Plate 5.1, Plate 5.2 and Plate 5.3 also show similar locations of home ranges between monitoring periods at three sites.

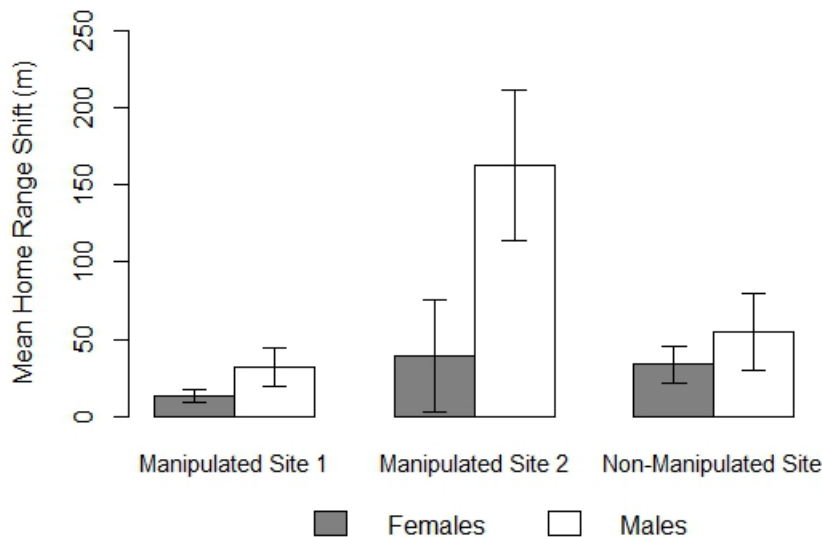


Figure 5.4 Mean home range shift for possums at each of the three sites. Error bars are \pm the standard error.

5.4.7 Home range overlap

For all the home range overlap models at the three sites (95% and 50% area of home range overlap, number of overlaps and exclusive area), the linear mixed effects model with the most support was generally the 'Null' model, as this model either had the strongest Akaike weighting or was within two Δ AICc of the best model (Table 5.6). This indicates that there was no influence of event, sex or the bodyweight of individuals for any of these variables at any of the sites (Table 5.3, Figure 5.5, Figure 5.6, Plate 5.1, Plate 5.2 and Plate 5.3). However, there were two exceptions to this at Manipulated Site 1. The model with the strongest support for the 95% KDE overlap at this site was 'Event' (Akaike Weight of 0.82, Table 5.6). This was due to both males and females increasing this variable following density reduction (Table 5.3). In addition, the model with the most support for the 50% KDE overlap at this site was the 'Sex' model (Akaike Weight of 0.90, Table 5.6). This was owing to males at this site exhibiting greater overlap than females, irrespective of the monitoring event (Table 5.3). This also suggests there was no support for differences in this variable due to event or the bodyweight of individuals.

Table 5.6 Akaike weights ($\Delta AICc$) from the linear mixed-effects models investigating home range overlap for possums at the three sites. Event and sex are categorical variables with two categories (pre-reduction and post-reduction, and male or female), and bodyweight (BW) is a continuous variable, which was measured in kilograms. Bold numbers indicate models within a set that have a $\Delta AICc$ of less than two. KDE = Kernel Density Estimates. Level of empirical support for models: substantial = $\Delta AICc$ of 0–2, considerably less = $\Delta AICc$ of 4–7, essentially none = $\Delta AICc$ of >10.

Response variable	Manipulated Site 1					Manipulated Site 2					Non-Manipulated Site				
	Null	Event	BW	Sex	Sex* Event	Null	Event	BW	Sex	Sex* Event	Null	Event	BW	Sex	Sex* Event
95% KDE overlap	0.15 (3.45)	0.82 (0.00)	0.01 (8.69)	0.01 (8.22)	0.01 (9.28)	1.00 (0.00)	0.00 (13.85)	0.00 (12.37)	0.00 (14.25)	0.00 (130.82)	0.69 (0.00)	0.12 (3.43)	0.13 (3.27)	0.05 (5.27)	0.00 (18.25)
50% KDE overlap	0.04 (6.06)	0.04 (6.18)	0.01 (9.53)	0.90 (0.00)	0.01 (9.34)	0.99 (0.00)	0.00 (13.51)	0.00 (11.93)	0.00 (11.21)	0.00 (129.29)	0.41 (0.47)	0.03 (5.80)	0.52 (0.00)	0.03 (5.49)	0.00 (17.57)
95% KDE number of overlaps	0.51 (0.00)	0.10 (3.21)	0.09 (3.51)	0.30 (1.06)	0.00 (11.70)	0.97 (0.00)	0.01 (8.71)	0.01 (8.95)	0.01 (8.95)	0.00 (53.65)	0.62 (0.00)	0.07 (4.27)	0.22 (2.05)	0.09 (3.84)	0.00 (15.03)
50% KDE number of overlaps	0.32 (0.60)	0.43 (0.00)	0.05 (4.19)	0.18 (1.76)	0.01 (7.67)	0.96 (0.00)	0.01 (8.32)	0.01 (8.66)	0.01 (8.89)	0.00 (52.84)	0.70 (0.00)	0.08 (4.29)	0.11 (3.79)	0.11 (3.69)	0.00 (15.63)
95% exclusive area	0.82 (0.00)	0.06 (5.28)	0.07 (5.05)	0.06 (5.21)	0.00 (19.15)	0.99 (0.00)	0.00 (12.57)	0.00 (15.00)	0.01 (9.55)	0.00 (122.65)	0.80 (0.00)	0.07 (4.78)	0.06 (5.26)	0.07 (4.84)	0.00 (19.38)
50% exclusive area	0.72 (0.00)	0.09 (4.21)	0.08 (4.51)	0.11 (3.68)	0.00 (17.29)	1.00 (0.00)	0.00 (13.99)	0.00 (13.54)	0.00 (13.37)	0.00 (130.69)	0.80 (0.00)	0.07 (4.75)	0.06 (5.07)	0.07 (5.01)	0.00 (17.70)

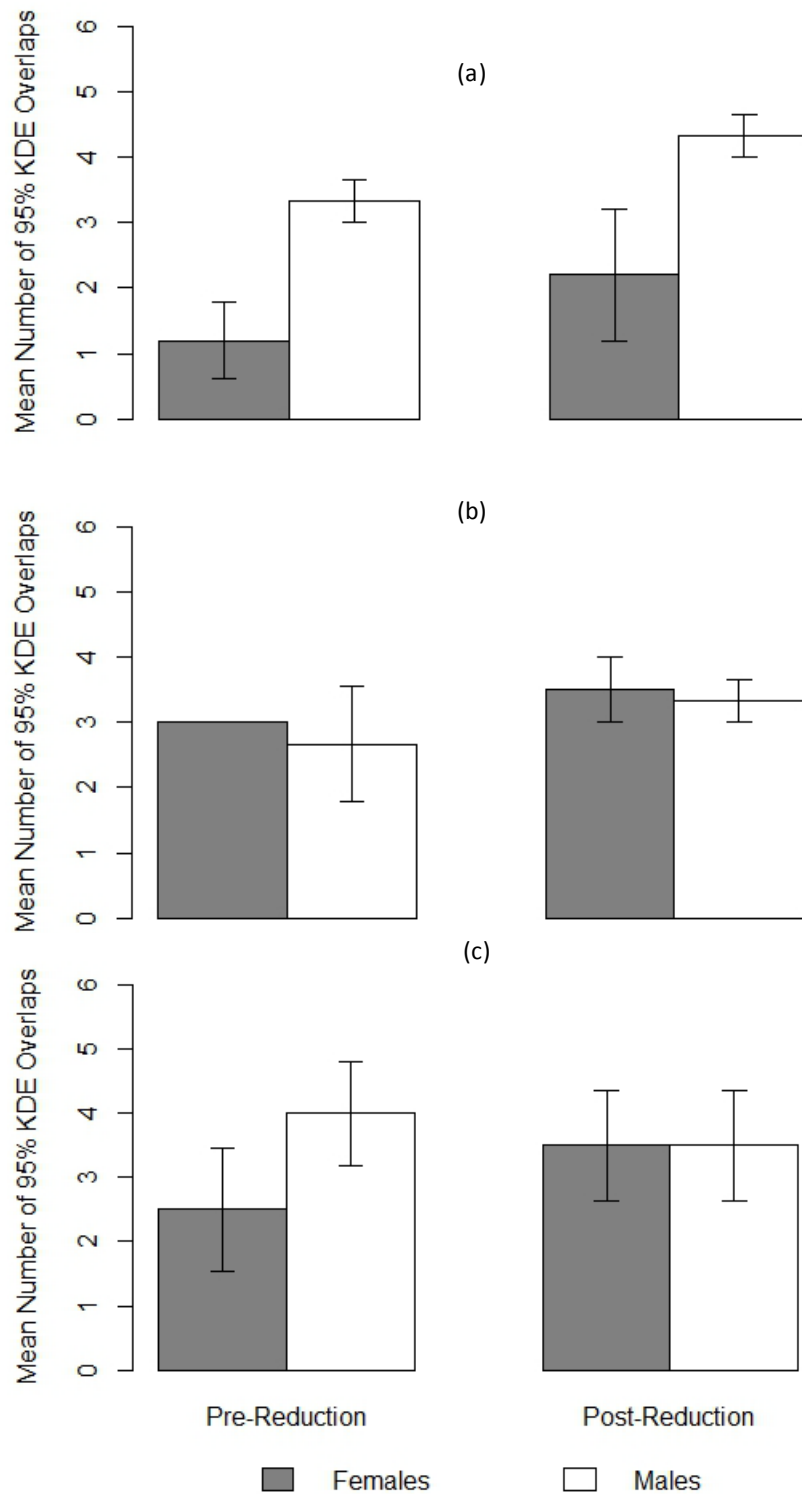


Figure 5.5 Mean number of 95% KDE overlaps per individual before and after density reduction, at (a) Manipulated Site 1, (b) Manipulated Site 2 and (c) Non-Manipulated Site. Error bars are \pm the standard error. The mean with no error bar is due to a lack of variation in the dataset.

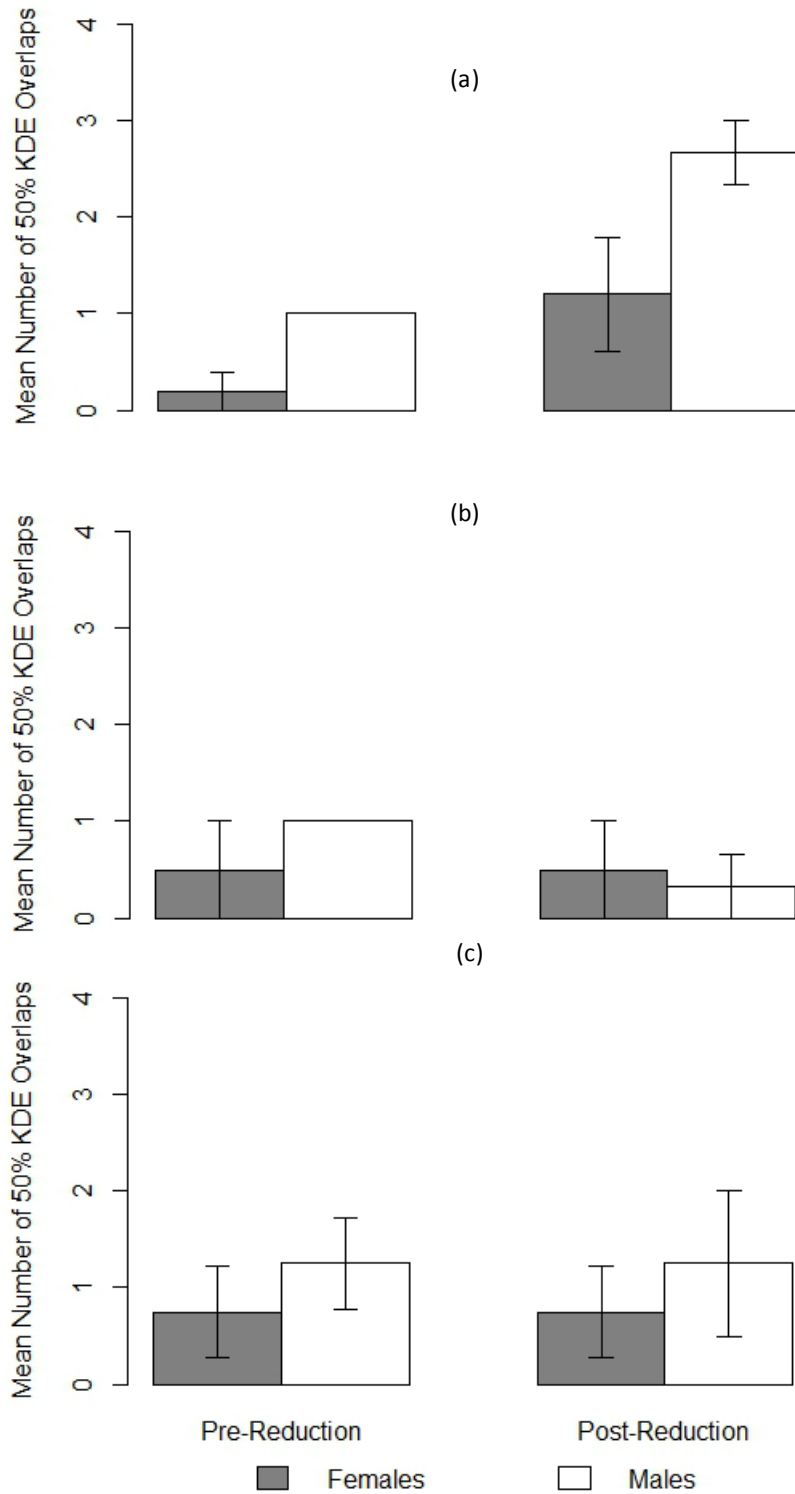


Figure 5.6 Mean number of 50% KDE overlaps per individual before and after density reduction, at (a) Manipulated Site 1, (b) Manipulated Site 2 and (c) Non-Manipulated Site. Error bars are \pm the standard error. The means with no error bars are due to a lack of variation in the dataset.

5.4.8 Pasture use

The modelling for the number of 95% KDE fixes within pasture, recorded the 'Null' model as having the best fit for all sites (Table 5.2). This indicates that there was no influence of monitoring event, sex or the bodyweight of individuals on pasture use by possums, at any of the three sites (Figure 5.7).

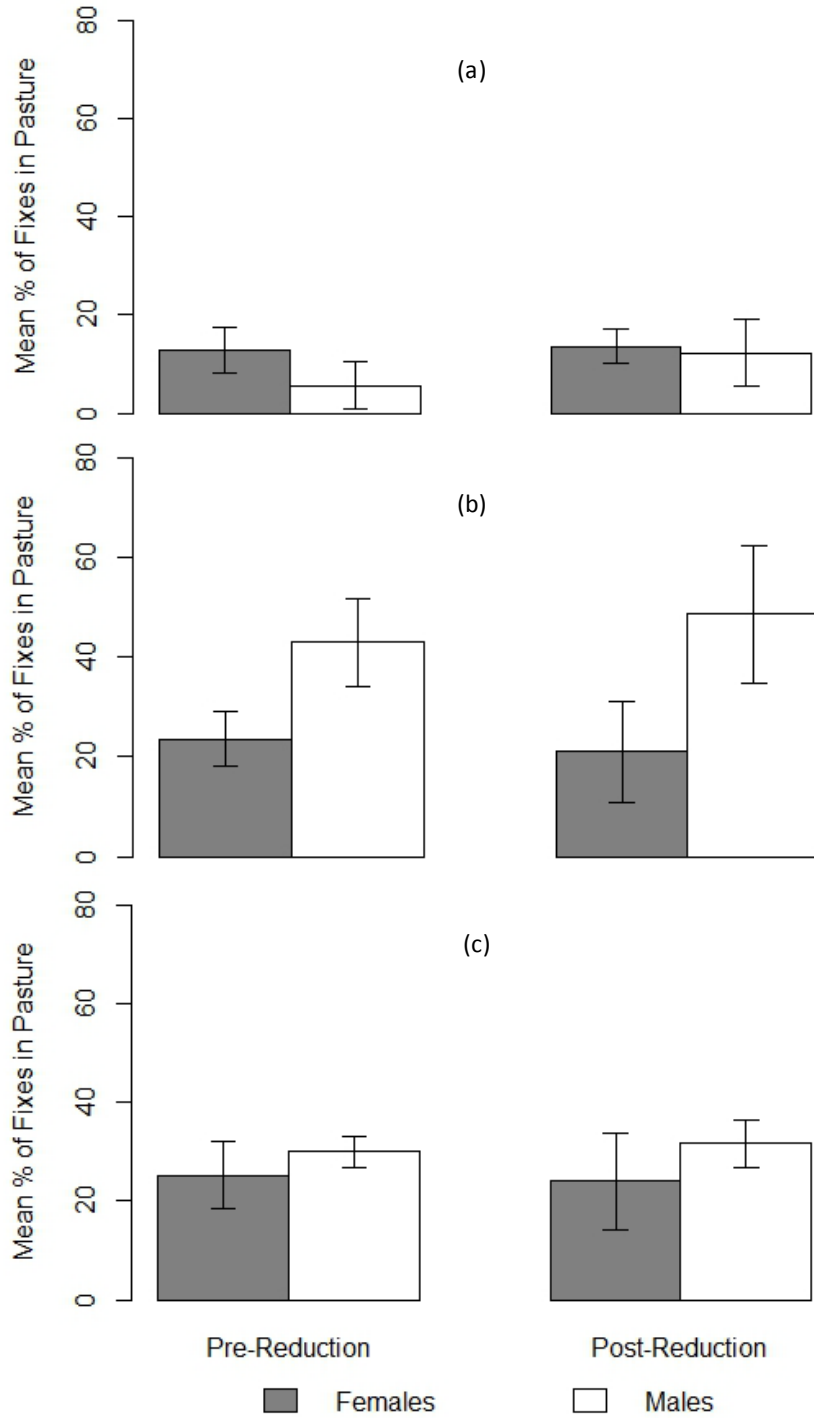


Figure 5.7 Mean percentage of fixes within 95% KDE in pasture habitat before and after density reduction, at (a) Manipulated Site 1, (b) Manipulated Site 2 and (c) Non-Manipulated Site. Error bars are \pm the standard error.

5.5 Discussion

This discussion will firstly highlight the results of the research and then address whether these findings could alternatively be due to habitat, starting possum density, or season and year of monitoring. Male and female possums at the high-density manipulated site (Manipulated Site 1) exhibited spatial perturbation following density reduction, suggesting that the distribution of this possum population was based on available resources (Wiggins et al., 2010). Specifically, possums substantially increased their home range size and degree of home range overlap in response to the removal of their conspecifics. This finding is in line with other studies on a range of species that have recorded spatial perturbation following density reduction, including increases in home range size and overlap (white-tailed deer, Henderson et al., 2000; e.g., red squirrels, Larsen and Boutin, 1995; European badgers, Riordan et al., 2011; Tasmanian pademelon and red-necked wallaby, Wiggins et al., 2010). There was no difference in the magnitude of spatial perturbation between male and female possums at this site. In contrast, home ranges of possums at the non-manipulated site, where density reduction was not carried out, did not vary between the monitoring events for any of the variables. Spatial perturbation also did not occur at the low-density manipulated site (Manipulated Site 2), as a measurable density reduction was unable to be achieved, even though approximately twenty individuals were removed.

It was predicted that possums would take longer to reveal their home ranges following density reduction, due to exhibiting larger home ranges and changing their movement patterns (Hypothesis 1 of Objective 1). However, this was not shown at either of the manipulated sites. This is consistent with other data collected during this project that showed that the time taken for home ranges to be fully revealed does not vary between possums, regardless of differences in home range size (see Chapter 3 of this thesis). This suggests that possums with larger home ranges travel further in the same time period, than those that display smaller home ranges.

Density reduction resulted in an increase in the core area (50% KDE) of possums at the high-density manipulated site. However, although mean 95% KDE also increased, there was limited support for differences between monitoring events in the modelling, indicating that this change was not significant. There is not strong evidence of exclusive territoriality in possums, but it is likely that limited parts of home ranges, such as core areas, are defended (Day et al., 2000a). This partial territoriality might occur due to these core areas containing the most important resources (Powell, 2000). These resources might include dens, as shown in Chapter 3, where female possums were recorded denning in core areas 100% ($\pm 0\%$ SE) of the time at the high-density site (although males were only recorded denning in core areas 37% ($\pm 12\%$ SE) of the time). Therefore, possums may have increased their core range size due to the removal of conspecifics that were constraining movement and the use of preferential resources in these areas, such as dens. In contrast, movements within

95% KDE may not have been constrained, resulting in no change in the ability to use these areas following density reduction. MCP size also increased at this site following density reduction. This home range measurement allows investigation into the exploratory behaviour of individuals, as it calculates the extent of all movements, rather than a given area of utilisation like KDE. This therefore means that possums undertook exploratory movements over a wider area following density reduction. This might be due to possums dispersing and re-aggregating after the removal of conspecifics (Sweetapple and Nugent, 2009). However, home range length, which was measured across the MCP, did not vary between monitoring events. This is likely due to MCP increasing across all boundaries, resulting in only a small increase in home range length. Overall, these results support the hypothesis that possums would increase their home range size following density reduction (Hypothesis 2 of Objective 1).

Assessments of home range utilisation did not indicate any difference between weeks for the post-reduction monitoring period at the high-density site. Therefore, it is not clear when changes in movement patterns occurred and as such, whether possums responded immediately to the physical removal of conspecifics, or the dissipation of their scent. It may have been that possums utilised the same relative home range size each week, but investigated new areas at some point during this monitoring period. This would explain the lack of difference between weeks. However, this assessment was likely strongly limited by the fact that the numbers of fixes per week for some possums were few, potentially resulting in inaccurate assessments of weekly home range utilisation. If individuals did exhibit a delay in movement changes, the home range analyses may have underestimated the magnitude of this change, as analyses were conducted on the entire 5-week post-reduction monitoring period. For example, if a possum did not increase their home range until two weeks into the post-reduction monitoring period, inclusion of the first two weeks of this monitoring period may have resulted in a smaller home range estimate than if the analyses were conducted from the time the possum increased its home range.

The home range centre of possums did not shift at either of the manipulated sites in response to density reduction (Hypothesis 3 of Objective 1). Even though home ranges increased following density reduction, expansion occurred from the same area across all home range boundaries. Possums may have been testing the extent of these boundaries, rather than moving into a particular area. This expansion may be a less costly option than complete relocation, allowing familiar and key resource-rich areas of territories to be retained while still acquiring newly available resources (Larsen and Boutin, 1995). Regardless of the monitoring event or site, heavy male possums were recorded shifting their home ranges to a greater degree than lighter or female possums. Males may be less territorial and therefore have less stable ranges, due to prioritising access to receptive females and not resources required to raise offspring (e.g., food) like females likely do (Coleman & Downs 2010). In addition, heavier individuals are likely more dominant than lighter individuals and

their movement patterns may consequently be less constrained by conspecifics compared to lighter individuals.

Home range overlap between pairs of collared possums was hypothesised to increase following density reduction (Hypothesis 4 of Objective 1), in line with that observed in badgers following culling (e.g., Riordan et al., 2011). This hypothesis was supported at the high-density manipulated site for the 95% KDE area overlap, but not the 50% KDE. Again, this may be due to possums defending core areas regardless of density, preventing overlap between conspecifics, but not the larger 95% KDE areas. The increase in 95% KDE overlap may then be due to increases in the home range size of surviving possums, resulting in a greater chance of home ranges coming in contact with each other. There were also some intersexual differences in home range overlap at this site, with males exhibiting greater 50% KDE overlap than females, irrespective of the monitoring event. This may be due to females being more likely to defend these areas, perhaps due to females (and not males) exhibiting natal philopatry, whereby home ranges are inherited from their mothers (Ji et al., 2001; Stow et al., 2006). This is further accentuated by the fact that all dens of females at this site were located within core areas. With all these home range overlap results, it is important to note that although comparisons between monitoring events were relative, changes in overlap may have been influenced by which animals were tracked, as only a sample of each population were collared and therefore analysed.

There was no difference in the use of pasture between pre-reduction and post-reduction monitoring periods at any of the sites (Hypothesis 5 of Objective 1). This is likely due to pasture not being a limited resource at these sites, regardless of density, and therefore no competition for this habitat occurring. In addition, although percent change in home range size and overlap following density reduction was greater in males at the high-density site, there was not strong statistical support for intersexual differences in the magnitude of perturbation (Objective 2). Moreover, regardless of the monitoring event, there was little statistical support for differences in home range characteristics between males and females at any of the sites.

The changes in home range characteristics observed at the high-density manipulated site may have been due to seasonal changes in behaviour, rather than in response to density reduction. The home ranges of possums do not appear to vary between seasons, and adult possums tend to occupy their home ranges for life, with shifts of more than a few hundred metres highly unusual (Cowan and Clout, 2000; Pech et al., 2010). Furthermore, the resources at this site (i.e., den sites, crops, seeds, flowers and fruit) appeared to be constant throughout the monitoring period. Therefore, the changes observed at this site are unlikely to be due to seasonal changes in habitat or resources.

The movement patterns of possums can also vary during the breeding season (Cowan, 1989; Crawley, 1973; Paterson et al., 1995), which mainly occurs in New Zealand from approximately

March – November (Fletcher and Selwood, 2000), during the monitoring periods of all three sites. However, it is noted that the low-density non-manipulated site was monitored during the same season as the high-density manipulated site and these sites were in close proximity to each other; yet spatial perturbation was not observed at the non-manipulated site. In addition, breeding can occur at any time of the year (Fletcher and Selwood, 2000; J. Bothwell, Lincoln University, personal communication, 2013), and adult females were observed with joeys and backriders during the monitoring period at all three sites, suggesting continuous breeding. Therefore, it is considered unlikely that the changes observed were due to breeding behaviour. As breeding appears to occur all year round, this means that it would be difficult to design a study to account for the effects of breeding.

It is possible that the lack of perturbation at the low-density manipulated site was not due to a lack of measurable density reduction, but due to the habitat and the low population density at this site. As discussed in Chapter 3, this pine site potentially had lower available resources than the high-density site and lower levels of competition due to the lower population density. Density reduction may therefore not have changed the availability of resources (by reducing competitors) or competition between conspecifics, resulting in no need for survivors to change their home range characteristics. On the flipside, possums may also not change their home ranges in habitats where resources are abundant, because density reduction will not increase the availability of resources by removing competitors. The lack of spatial perturbation at the low-density manipulated site compared to the high-density manipulated site may also have been due to differences in the season and year of monitoring. Had the study at the low-density manipulated site been conducted at a different time, differences in resources or population density (and therefore potentially competition levels) may have resulted in survivors responding differently to density reduction.

The lack of a measurable density reduction and therefore spatial perturbation at the low-density manipulated site may have been due to a number of reasons. Possums in this area already had large home ranges even before density reduction was carried out (e.g., approximately 13 hectares for males) and often moved throughout adjacent forest blocks. Consequently, there appeared to be a large number of transients that visited the site, as new individuals were consistently trapped throughout both the pre-reduction and post-reduction monitoring periods. These transients likely increased the overall density estimate. Furthermore, because the density of the population was low to begin with, it became difficult to find non-collared individuals to remove, so the number of individuals removed was low. In addition, there was an increase in home range by at least one individual at this site. Had more of the collared animals been able to be analysed, this may have resulted in a significant increase.

The density of the high-density manipulated site was reduced by approximately 50%. It is possible that a larger reduction would have resulted in more pronounced changes in home range

characteristics. As such, further research where populations are reduced by much higher densities, such as 90% (which is the level commonly achieved in control operations; P. Livingston, Animal Health Board, Wellington, personal communication, 2011), would be beneficial. However, the 50% reduction in this study allowed an assessment of partial density reduction. This can occur in New Zealand due to trapping by fur harvesters, who have been recorded in one study pulling out of operations when trap-catch rates drop to only 26% on average (Jones et al., 2012). Research could also be extended to investigating juveniles, as they are also known to become infected with bTB (Coleman, 1988; Jackson et al., 1995a). Detailed research that investigates whether possums respond to the physical removal of individuals or the dissipation of scent markings would also be a useful. Although this study was un-replicated, it nonetheless allows us to hypothesise that high-density possum populations exhibit spatial perturbation following density reduction. Future research should involve replication in locations with similar densities and habitats, and experimental controls (to account for the above-mentioned potentially confounding factors of habitat, density, and year and season of monitoring). Longer-term studies would also allow an assessment of whether any changes are permanent, or whether home ranges subsequently return to how they were pre-reduction. This would also allow investigation into potential seasonal or annual variations.

If spatial perturbation occurs due to density reduction, this has implications for the management of possums and other pest species. Increases in home range size and overlap (and therefore contact rates) following density reduction have been suggested to be the reason why culling of badgers can in some instances fail to reduce bTB levels in this species or livestock (Macdonald et al., 2006; Riordan et al., 2011; Vicente et al., 2007). The increase in home range size and overlap recorded in this study, also suggests that density reduction may not result in decreases in bTB transmission in possums and livestock in all cases. This does not mean that control strategies should not be undertaken and that density reduction will not result in a decrease in bTB transmission overall. Instead, it highlights the need for extremely efficient initial control that reduces populations to very low densities across entire sites (i.e., to avoid patchiness in control effort) to prevent potential increases in transmission risk. Spatial perturbation in response to density reduction may also substantially affect the ability of managers to control and monitor populations. Increases in home range size may mean that encounter rates with traps and baits increase (Arthur et al., 2002), meaning that post-control monitoring overestimates densities. This potentially explains why the WaxTag[®] survey at the high-density manipulated site gave similar results pre and post-control, even though approximately 50% of the population was removed (almost 80 individuals). Increases in home range size post-control could also mean that less traps or bait could be used at greater spatial scales to achieve the desired outcome, reducing management costs. Furthermore, the Animal Health Board, which is the organisation responsible for managing and controlling bTb, uses a model to simulate bTB transmission amongst possums and the effect of differing control strategies on disease

persistence (Ramsey and Efford, 2010; Ramsey and Efford, 2005). The results from this study and future studies, could potentially be incorporated into this model to help predict likely changes in home range characteristics and therefore transmission risk due to control (in particular, inefficient control).

In summary, possums at the manipulated site likely exhibited density-dependent home range characteristics, with individuals exhibiting spatial perturbation following density reduction. This suggests that possums may distribute themselves predominantly based on resources. However, additional research is required to test definitively the occurrence and magnitude of spatial perturbation following density reduction. This research suggests that efficient pest control should be carried out that removes the large majority of the population, rather than piecemeal control, to prevent potential increases in transmission risk.

Chapter 6:

Synthesis and Conclusions

6.1 Chapter summary

The aim of this PhD was to investigate whether density is a driver of home range characteristics in possums and whether this is consistent between sexes. Consequently, the first objective of the thesis was to observe whether home range characteristics varied between sites of varying habitat and population density (Chapter 3). The second objective was to investigate whether experimental density reduction results in survivors exhibiting spatial perturbation with respect to den site use (Chapter 4) and other home range characteristics (Chapter 5). Both objectives were addressed by monitoring possums at three sites using VHF and GPS-tracking technology. This chapter synthesises the results obtained from this research and discusses these findings in the context of the theoretical underpinnings presented in the General Introduction (density as a driver of home range characteristics and the occurrence of spatial perturbation in response to density reduction). The implications of this research for science and pest management are then discussed. The chapter concludes with a discussion of the limitations of the research and provides recommendations for future research.

6.2 Summary of thesis main findings

The main findings from this research were:

- (1) Home range characteristics of possums differed between the three sites of varying habitat and population density (Objective 1; Chapter 3)
 - The low-density populations within pine habitat had larger home ranges and exhibited greater home range overlap with conspecifics, than the high-density possum population within oak and sycamore habitat
 - The low-density populations within pine habitat used more dens and changed these dens more often; in addition, these possums denned predominantly on the ground, compared to possums at the high-density oak and sycamore site that generally denned aboveground
 - There was no difference in the number of fixes until home ranges were fully revealed between sites, even though possums at the low-density pine sites had substantially larger home ranges
- (2) Possums therefore exhibit behavioural plasticity with respect to home range characteristics, as well as territoriality potentially, due to differences in home range overlap

- (3) Possums surviving density reduction exhibited spatial perturbation, by changing their den use (Objective 2a; Chapter 4) and other home range characteristics (Objective 2b; Chapter 5)
- Following density reduction at the high-density site:
 - Female possums increased their den use (number of dens and number of changes between dens), but males did not change their den use
 - Both male and female possums increased their home range size and overlap; there were no intersexual difference in the magnitude of perturbation
 - Possums did not change the time taken for their home ranges to become fully revealed, the location of their home ranges or their use of pasture
 - Spatial perturbation at the low-density manipulated site did not occur for either den use or the other home range characteristics, as a measurable density reduction was unable to be achieved, even though individuals were removed
 - Spatial perturbation was also not observed at the non-manipulated site for either den use or the other home range characteristics
- (4) Irrespective of population density, home range characteristics of possums generally did not vary substantially between males and females (Chapters 3–5)
- (5) Based on the Perturbation Model (Appendix A), the results of this research suggest that possums distribute themselves predominantly based on resources, exhibiting either an Ideal Free Distribution or an Ideal Dominance Distribution pattern

6.3 Interpretation of these findings – is density a driver of home range characteristics in possums?

The home ranges of possums tend to be larger in low-density populations compared to higher density populations (Cowan & Clout 2000; Arthur et al. 2002). The low-density pine sites in this site also recorded greater home range characteristics (home range size, home range overlap and den use) than the high-density oak and sycamore site (Objective 1). However, it was not known whether these differences were driven by density or habitat, as larger home ranges in low-density populations may also be due to these habitats not providing sufficient resources, thereby requiring individuals to roam further to obtain their energy requirements (Harestad and Bunnell, 1979).

Manipulating population densities whilst resource levels remain constant is therefore a better way to test if density is a driver of home range characteristics. This was the basis of Objective 2 of this thesis. This research suggested that density is a driver of home ranges in possums, as spatial perturbation was observed following density reduction at the manipulated site, but not at the other two sites where density reduction was either not achieved or carried out. This both supports and contradicts previous conflicting research showing both changes and no changes in home ranges following density reduction, using less accurate monitoring techniques, such as live-capture trapping

(e.g., Brockie et al., 1997; Clinchy et al., 2001; Efford et al., 2000; Morgan et al., 2007; Ramsey et al., 2002). However, there are some limitations to this research, as discussed below, and therefore further research is required to confirm whether possums exhibit spatial perturbation following density reduction.

6.4 Implications of research

6.4.1 Science context

This research supports other studies showing that density is a driver of home range characteristics in some mammals and consequently that density reduction results in spatial perturbation (white-tailed deer, *Odocoileus virginianus*, Henderson et al., 2000; e.g., red squirrels, *Tamiasciurus hudsonicus*, Larsen and Boutin, 1995; badgers, *Meles meles*, Tuytens et al., 2000; Tasmanian pademelon, *Thylogale billardierii* and red-necked wallaby, *Thylogale billardierii*, Wiggins et al., 2010). This thesis also provides a useful structure for which spatial perturbation can be tested, using GPS-tracking technology and before-after experimental design techniques (Smith, 2002). Moreover, this work highlights that there are a range of potentially density-dependent home range characteristics that can be monitored concurrently in studies (e.g., home range size, overlap and shift, and den use, pasture use and time until ranges are fully revealed), instead of just the 'standard' home range size analyses. The development of the Perturbation Model presented in Appendix A also provides a novel theoretical framework to predict whether a species is likely to exhibit perturbation, based on the distribution pattern of the population. This PhD research has also resulted in the generation of a number of hypotheses of relevance to behavioural and spatial ecology, as detailed in the recommendations for future research below.

6.4.2 Pest management context

If the home ranges of a pest vary between different density populations, which may occur with possums, this might have implications for the management of these species. For example, populations that exhibit larger home ranges (e.g., low-density populations) could likely be controlled using a lower density of control devices such as bait-stations and traps, compared to populations that exhibit smaller home ranges (e.g., high-density populations), thereby reducing management costs. Density estimates of these populations may also be overinflated when compared to populations that exhibit smaller home ranges, due to individuals coming in contact with more monitoring devices. This should be factored into population size estimates when comparing across different density populations. In addition, if these pests transmit diseases, this might mean that transmission risk is not uniform across sites, with greater risks in areas where home range size and overlap are larger. These areas may therefore need to become a priority for pest control. With respect to possums, it is therefore recommended that control continues to be undertaken in low-density possum populations

that are infected with bTB or that are within bTB vector risk areas. Given the large home ranges and use of many fragments in the landscape shown in this study, it is recommended that control be undertaken at a landscape scale for maximum effectiveness.

Spatial perturbation following density reduction can also affect the ability of managers to monitor and control pests. For example, if the home range size of pests increase following density reduction this may mean that encounter rates with traps and baits increase (Arthur et al., 2002). This should be taken into account when conducting post-control density assessments, as this behaviour will likely result in overestimation of densities when results are compared to pre-control monitoring (as shown in the WaxTag[®] survey conducted in this study). Increases in home range size may also mean that a lower density of control devices, such as bait-stations and traps, could be used in follow-up density reduction operations to target the remaining individuals. In addition, spatial perturbation following density reduction may potentially cause increases in transmission risk. For example, it has been suggested that increases in home range size and contact rates between badgers following density reduction, is the reason why culling sometimes results in increases in the incidence of bTB in badgers (Riordan et al., 2011; Vicente et al., 2007; Woodroffe et al., 2006b) and therefore livestock (Macdonald et al., 2006). This may also explain why 'hotspots' of bTB infected possums and therefore livestock persist in certain areas of New Zealand, regardless of control. It is therefore recommended that in locations where possum populations are infected with bTB or in bTB vector areas, pest control operations should not be piecemeal and should aim to remove the entirety of the population in one hit. This will prevent potential increases in transmission risk due to a number of individuals surviving and exhibiting spatial perturbation. This is particularly important in the future when the Animal Health Board ceases and local communities become responsible for possum control, who may find it difficult to control possums over large areas for long periods of time.

6.4.3 Societal context

Bovine tuberculosis infection of cattle and deer can cause significant production losses, and can potentially harm New Zealand's reputation as a supplier of high-quality and safe products (MAF, 2010). This is particularly concerning considering that venison, beef and dairy exports provide a revenue of approximately NZ\$15 billion to New Zealand (MAF, 2011). Consequently, NZ\$56 million was spent in 2012 on possum control for bTB purposes alone, the revenue for this coming from industry sector funding, crown funding and regional funding (AHB, 2012). New Zealanders also place substantial value on the conservation of their native species, with the Department of Conservation carrying out possum control over an additional 235,000 hectares of New Zealand in an attempt to protect native species (DoC, 2012). Consequently, any research, such as this study, that contributes even in a small way to increasing the effectiveness (including cost effectiveness) of possum control in New Zealand is of benefit to society.

6.5 Limitations of study and recommendations for future research

This study was un-replicated and did not include an experimental control that was monitored concurrently at a site of the same habitat and population density. Therefore, it is possible that the observed spatial perturbation at the high-density manipulated site was not due to density reduction, but some other factor, such as breeding. To more definitively test whether density is a driver of space use in possums, further research should be conducted that includes replication in sites with similar population densities and habitat, and experimental controls. Monitoring should also be long-term, to determine whether spatial perturbation is maintained, or is temporary in nature, and to investigate seasonal or annual variation in responses.

This research could also be extended to investigate the mechanisms of spatial perturbation in possums and other species. As discussed in Chapter 3, there are likely to be thresholds for territoriality. When productivity is low, the cost of defending a territory outweighs the benefits, and when productivity is high, there is enough of the resource that territoriality is not necessary (Carpenter and Macmillen, 1976). It is hypothesised that there is also a threshold for the occurrence of spatial perturbation due to density reduction, related to the scale of density reduction and the starting density of the population. This might explain why density reduction at the second low-density site did not result in spatial perturbation. Furthermore, it is hypothesised that varying levels of density reduction will result in differences in the magnitude of perturbation; this relationship is expected to be non-linear due to the predicted threshold of perturbation. For example, increases in home range size may occur to a greater degree, the greater the level of density reduction. Although studies on badgers have investigated perturbation in populations subjected to various levels of culling (e.g., Woodroffe et al., 2006a), there does not appear to be any published study in any species that has specifically quantified the magnitude of spatial perturbation based on the level of density reduction. Furthermore, research that empirically tests the predictions of the Perturbation Model (Appendix A) would also provide more information on the mechanisms of spatial perturbation and the predictive value of this model. This could be achieved by observing how populations of a range of known distribution patterns respond to various types of disturbance events, including density reduction. The difficulty in this would be that prior research would be required to determine the baseline distribution patterns of the populations being investigated.

Manipulating densities whilst resources levels remain constant is one way to test if density is a driver of home range characteristics and not food availability. Conversely, it is also possible to manipulate food supply whilst keeping density constant, to test if food availability is a driver (as discussed in Chapter 3). Incorporation of these experimental food supplementation studies into density manipulation research would help tease out the drivers of home range characteristics in species. In possums specifically, it is possible that both density and food availability drive home range characteristics (see Chapter 3). Populations that are naturally low in density (i.e., they are not low in

density due to control) are predicted to be due to resource availability in these areas being low. Therefore, it is hypothesised that food supplementation of these populations would result in individuals contracting their home range sizes, due to their energy demands then being met. In contrast, high-density populations are predicted to be due to high levels of resource availability in these areas. It is therefore hypothesised that the home ranges of these possums will not change in response to increases in food availability, due to their energy demands already being met.

Home range overlap is often used to infer direct and indirect contact (through environmental contamination from bTB excretory products, such as urine and faeces) between individuals and therefore disease transmission risk (Hamede et al., 2009), as was the case in this study. However, directly recording contact rates between individuals through the use of proximity collars may be a more robust way of measuring transmission risk (Bohm et al., 2009). Proximity collar studies have been undertaken in a number of species that transmit diseases, such as the Tasmanian devil (*Sarcophilus harrisii*), which are affected by devil facial tumour disease (Hamede et al., 2009). Other studies have also used proximity collars to determine contact rates amongst badgers, and between badgers and livestock, to quantify bTB transmission risk (Bohm et al., 2009; Drewe et al., 2013). It is important to understand whether density reduction results in increases in contact rates and therefore transmission risk, to confirm that the appropriate control strategies are being used. Furthermore, an understanding of changes in contact rates due to density reduction is important for models that predict disease transmission; for example, the possum-bTB model in New Zealand is sensitive to contact rates, for which there are few data (Ramsey et al., 2002). A study by Ramsey et al. (2002) has investigated changes in contact rates following density reduction in possums, but only using VHF radio-tracking techniques that could not definitively determine whether individuals were close enough to make direct contact (no change in contact rates was recorded). Another study has also investigated contact rates between possums using proximity loggers, at three sites of varying density and habitat (Ji et al., 2005). This study recorded no difference in the frequency or duration of contacts between sites, suggesting that contact rates are not density-dependent (Ji et al., 2005). However, these results may have been confounded by differences in behaviour between sites, due to variations in habitat. It appears that no study has definitively quantified changes in contact rates following density reduction in any species, including possums. Although it is noted that the relationship between contact behaviour and disease transmission is unknown (Ji et al., 2005), it would still be beneficial to undertake this research. It is hypothesised that contact rates of possums do not increase following density reduction, based on the lack of density-dependence in contact rates recorded in the Ji et al. (2005) study.

The observed variations in home range size between the low and high-density sites in this study were used to validate one of the parameters of the Animal Health Board Spatial Possum Model (Chapter 3). As a number of additional parameters in this model are estimated or based on limited

field data (Ramsey and Efford, 2010; Ramsey and Efford, 2005), it is possible that the results from this research could also be used to update other key parameters in this model. For example, the results of this study could be used to assess the current assumption that possum home ranges are randomly distributed in space, rather than aggregated or uniformly distributed. Additional research could also be undertaken to field validate other parameters in the model, such as contact rates and therefore transmission rates.



Photos of some of the possums studied during this research

Appendix A: Perturbation Model

A.1 Appendix summary

This appendix presents a 'Perturbation Model' that was developed for this thesis, which synthesises population distribution pattern theories in the literature to predict whether a population will exhibit spatial or socio-spatial perturbation following a disturbance event (see Table A.1 for definitions of the terms used in this Appendix). This model is applied to brushtail possums and is also compared to the actual response of a number of species to density reduction (a disturbance event), to test the predictive value of the model.

Table A.1 Glossary of terms used in Appendix A

Term	Definition
Den Site Distribution	Individuals in a population distribute themselves based on fixed den sites, as these are long-term investments that are difficult to relocate
Disturbance event	A natural or anthropogenic event that results in a loss or reduction of biomass (e.g., loss of vegetation due to fire, or the removal of individuals due to culling)
Dominance hierarchy	Social ranking system of dominant and subordinate individuals, maintained by aggression
Exploitation Competition	Individuals do not interact with one another directly, but compete by depleting available resources
Fixed Home Range Distribution	Individuals in a population distribute themselves based on fixed home ranges, as these are long-term investments that are difficult to relocate
Home range	Area an animal traverses in its normal activities of food gathering, mating and caring for young
Ideal Dominance Distribution	Individuals in a population distribute themselves to maximise their supply of resources, but they are not free to do so due to territoriality
Interference Competition	Individuals fight one another for access to resources
Ideal Free Distribution	Individuals in a population are free (i.e., there is no territoriality or fighting) to distribute themselves to maximise their supply of resources
Natal philopatry	The tendency of an animal to return to or remain near the area they were born
Perturbation	The response of an ecological component or system to disturbance
Philopatry	The tendency of an animal to return to or remain near a particular site
Population	Group of individuals of same species that occupy the same geographical area at the same time
Predation Risk Distribution	Individuals in a population distribute themselves where predation risk is lowest
Resource	A substance or object required by a living organism for growth, maintenance of health and reproduction, e.g., food, nest sites and mates
Rose Petal Distribution	Individuals in a population distribute themselves based on the establishment of natal philopatric home ranges
Spatial perturbation	The disruption of the home range characteristics of individuals within a population due to a disturbance event
Social perturbation	The altering of dominance of individuals within a territorial population due to a disturbance event
Socio-spatial perturbation	The altering of dominance and home range characteristics of individuals within a territorial population due to a disturbance event
Territory	Area an animal defends within its home range

A.2 Mechanisms of perturbation: population distributions

It is likely that the occurrence of perturbation following a disturbance event is dictated by the overriding distribution pattern of a population (Wiggins et al., 2010). This concept will be discussed in detail in 'Section A.3: Perturbation Model', but first this section discusses a number of hypotheses relating to how populations might distribute themselves. It is important to note that these theories may not be mutually exclusive, with populations potentially exhibiting a combination of distribution patterns (Wiggins et al., 2010). There may also be other distribution patterns not presented here that are also relevant to this model.

A.2.1 The Ideal Free Distribution

In the Ideal Free Distribution, individuals in a population distribute themselves to maximise their supply of resources, with individuals choosing a patch based on resource supply, and the distribution and intake rate of competitors' (Fretwell and Lucas, 1969). In this hypothesis, 'ideal' pertains to individuals going to the patch where their rewards are highest (Sutherland, 1996). There is no territoriality or fighting in the population, so each individual is 'free' to exploit the areas with greater resources (Fretwell and Lucas, 1969; Sutherland, 1996). In other words, each competitor is expected to go to the patch where they serve to gain the most resources (Hakoyama, 2003). In essence, the Ideal Free Distribution is competition by exploitation, with all competitors equal (Davies et al., 2012).

Individuals in an Ideal Free Distribution population may consequently respond to shifts in resource levels by adjusting their home range size (Moorcroft, 2008). For example, kangaroos are considered to conform to the Ideal Free Distribution, as they select patches of high-quality areas and change their foraging in response to resource abundance; there is also little difference in competitive ability between individuals (Coulson, 2009). Geographical expansion of populations under an Ideal Free Distribution pattern will therefore occur based on habitat suitability (Fretwell and Lucas, 1969). In reality, however, there is heterogeneity in competitive ability between individuals (Giraldeau, 2008). Furthermore, the Ideal Free Distribution assumes individuals have complete knowledge of available resources and will proceed towards them; but individuals may in fact have partial, biased or false information (Giraldeau, 2008).

A.2.2 The Ideal Dominance Distribution

The Ideal Dominance Distribution (also known as the Ideal Despotism Distribution) is an extension to the Ideal Free Distribution, where competitors are not 'free' to move among all available habitats, due to aggression; consequently competitors are unequal (Fretwell and Lucas, 1969; Krebs, 2009). The first competitors to the area defend their resources by establishing territories, so later arrivals are forced to inhabit poorer habitat than the territory holder does. Competition is therefore interference competition (Davies et al., 2012). For example, in wild chimpanzee (*Pan troglodytes*)

populations in Tanzania, dominant females outcompete subordinates, forcing them to settle elsewhere and range more widely (Murray et al., 2007). Dominant crayfish (*Procambarus clarkii*) have also been shown to gain significantly greater access to resources than subordinate crayfish (Tattersall et al., 2012). As with the Ideal Free Distribution, geographical expansion is based on habitat suitability. Although this hypothesis removes the limitation of the Ideal Free Distribution with respect to heterogeneity of competitive ability, it is still assumed that individuals have complete knowledge of available resources and will proceed towards them.

A.2.3 The Rose Petal Distribution

Philopatry is when individuals breed on the site where they were born (natal philopatry) or have previously bred (Boulinier et al., 2008). The Rose Petal Distribution is formed by the establishment of natal philopatric home ranges that are independent of resources (Porter et al, 1991, as cited in McNulty et al., 1997; Wiggins et al., 2010). Geographical expansion of populations under this hypothesis occurs through the addition of female home ranges that partially overlap their mother's home range, hence forming a nested pattern analogous to rose petals (Porter et al, 1991, as cited in McNulty et al., 1997; Wiggins et al., 2010). Male home range establishment is controlled by the females and therefore they do not contribute to the spatial expansion of the population (Wiggins et al., 2010). The Rose Petal Distribution has been shown in Florida black bears (*Ursus americanus floridanus*), as genetically related individuals establish home ranges close to each other and unrelated females are geographically separated (Moyer et al., 2006). Moreover, female bears with overlapping home ranges were more closely related than female bears whose home ranges did not overlap. This type of population distribution has also been shown in voles in Canada (Lambin, 1994).

A.2.4 The Den Site Distribution

The Den Site Distribution was developed to explain why badgers still occupy den sites (setts), even when these have been highly disturbed (Doncaster and Woodroffe, 1993; Revilla, 2003). It is postulated that den sites are a long-term investment, as they are difficult for an individual to relocate, and therefore territory size and shape is determined by their location (Doncaster and Woodroffe, 1993; Revilla, 2003). This distribution might encompass populations of birds that re-use burrows or cavities. Or colonial bird species that build structures up over time, such as the barn swallow (*Hirundo rustica*), which remains faithful to previously used colonies and nests (Shields, 1984). This Den Site Distribution may in some circumstances deviate into an Ideal Free Distribution or an Ideal Dominance Distribution. For example, some individuals, such as juveniles, may be excluded from preferential dens or nests if they are in limited supply. If an individual occupying a nest or den leaves or dies, these subordinate individuals may consequently obtain these areas. Furthermore, increases in food availability may result in expansions of colony or group sizes. For example, the

group size of caviomorph rodents increases as resource availability, in particular food, increases (Maher and Burger, 2011). These increases in group size may in turn result in subordinate individuals being displaced from dens or nests through interference competition, due to a lack of this resource. There does not appear to be any testing of the Den Site Distribution hypothesis in the literature.

A.2.5 The Fixed Home Range Distribution

Home ranges and territories of animals may remain fixed in both location and size, regardless of fluctuations in resource levels (Sutherland, 1996; Von Schantz, 1984). For example, the rainforest ant *Aphaenogaster araneoides* in Costa Rica does not modify its home range areas in response to poor habitat quality (McGlynn et al., 2002). The home ranges of coral trout (*Plectropomus leopardus*) are also stable year-round (Zeller, 1997). Species may fix their home ranges due to the benefits from being familiar with an area. For example, it has been shown in cliff swallows (*Petrochelidon pyrrhonota*) that familiarity of a site increases the survival probability of birds, possibly due to experienced individuals having knowledge of foraging areas and the habits of local predators (Brown et al., 2008). Ruffed grouse (*Bonasa umbellus*) inhabiting unfamiliar space also have much higher risk of predation than individuals inhabiting familiar space (Yoder et al., 2004). With respect to territorial behaviour, establishment of a territory may be a long-term investment due to the significant costs of defending this area, resulting in the costs of re-location being too high. Changing territory size relative to resource availability may mean that individuals have to fight against conspecifics each time a change occurs; whereas, individuals that maintain their territory regardless of fluctuations in resources will not need to fight and will therefore have more energy in reserve for when resources are low (Von Schantz, 1984). This type of distribution pattern is referred to in this thesis as the Fixed Home Range Distribution hypothesis.

A.2.6 The Predation Risk Distribution

In this distribution, individuals distribute themselves based on a continuum of predation risk, avoiding areas of high predation risk. This is supported by research on Atlantic salmon, where individuals decrease their territory size in response to experimental increases in predation risk (Kim et al., 2011). Wild guinea pigs (*Cavia aperea*) have also been shown to temporarily shift their home ranges to areas of greater cover to decrease predation risk (Asher et al., 2004). Bank voles (*Myodes glareolus*) in Finland decrease their home ranges in summer to most likely protect their nestlings from predation by common shrews (Liesenjohann et al., 2011). This distribution is an extension to the Ideal Free Distribution, as predation risk may vary across habitat patches, just like resource availability and competition can. This type of distribution pattern is referred to in this thesis as the Predation Risk Distribution.

A.3 Perturbation Model

The Perturbation Model predicts whether individuals will exhibit spatial or socio-spatial perturbation based on whether the population has an Ideal Free Distribution, Ideal Dominance Distribution or other type of population distribution (Figure A.1). Central to this model is the assumption that disturbance events will generally affect resource availability, either directly (e.g., fire reducing food availability) or indirectly (e.g., changes in population density subsequently adjusting resource availability). In the Perturbation Model, populations with an Ideal Free Distribution or Ideal Dominance Distribution are predicted to display perturbation following a disturbance event, due to resource levels being affected. If a population follows an Ideal Free Distribution, this perturbation is likely to be spatial only. In contrast, if populations follow an Ideal Dominance Distribution pattern, they are predicted to exhibit socio-spatial perturbation, due to not only changes in resource availability, but potentially also the re-shuffling of dominance hierarchies (e.g., due to the removal of dominant individuals). Localised culling of Ideal Free Distribution and Ideal Dominance Distribution populations will likely create a population sink that is filled as individuals reoccupy patches of reduced competition (Coulson, 2009).

Populations with other types of distributions (Rose Petal Distribution, Den Site Distribution, Fixed Home Range Distribution or Predation Risk Distribution) are not predicted to exhibit immediate perturbation following a disturbance event, as home ranges are not primarily dictated by resource availability. In Rose Petal Distribution populations, home ranges are determined by philopatry; in Den Site Distribution or Fixed Home Range Distribution populations, the cost of relocating a den site or home range/territory is too high for settled individuals; and in the Predation Risk Distribution populations, changes in predation risk primarily determine home ranges. For example, female white-tailed deer (*Odocoileus virginianus*) in Huntington Wildlife Forest in New York are very philopatric to their summer home range and this is postulated to be the reason why female deer do not move into new areas where family groups are removed (McNulty et al., 1997; Oyer and Porter, 2004). Culling of these four populations types will consequently result in gaps in the distribution of a population, which could persist for several generations (Coulson, 2009), or at least until juveniles disperse and repopulate these cleared areas. Populations with these types of distribution patterns are therefore considered to be the most stable to disturbance. However, these populations may still alter their home ranges if the intensity of the disturbance is great enough. For example, if a fire removes all resources from an area, it is likely that these populations will be forced to move to new areas to survive.

The intensity and permanence of the disturbance may in turn influence the intensity and permanence of the perturbation. For example, perturbation may not be long-term if the disturbance is temporary or low in intensity. Seasonality may also influence the occurrence of perturbation. If a disturbance event affects the availability of mates, for example, individuals may only change their

home ranges if the disturbance occurs during the breeding season. Moreover, territorial behaviour is generally more pronounced during the breeding season (Sutherland, 1996), therefore populations following an Ideal Dominance Distribution pattern may respond to a greater degree during this time. The occurrence and magnitude of perturbation may also vary between sexes. Females tend to compete for food and nest sites, as these resources generally limit their reproductive success (Davies et al., 2012). In contrast, mates generally limit reproductive success of males, so they will likely compete against each other for access to females, either directly or by controlling the resources that females require (Davies et al., 2012). This may result in males and females responding to disturbance in varying ways, depending on which resources are affected. Furthermore, if males and females display different distribution patterns, such as females displaying a Rose Petal Distribution and males displaying an Ideal Dominance Distribution, then according to the Perturbation Model this will result in gender-related differences in the occurrence of perturbation. Males also often have larger territories than females, and can be more aggressive and territorial (Carpenter, 1987; Whitworth and Southwick, 1984). In these cases, males may exhibit socio-spatial perturbation to a greater degree than females.

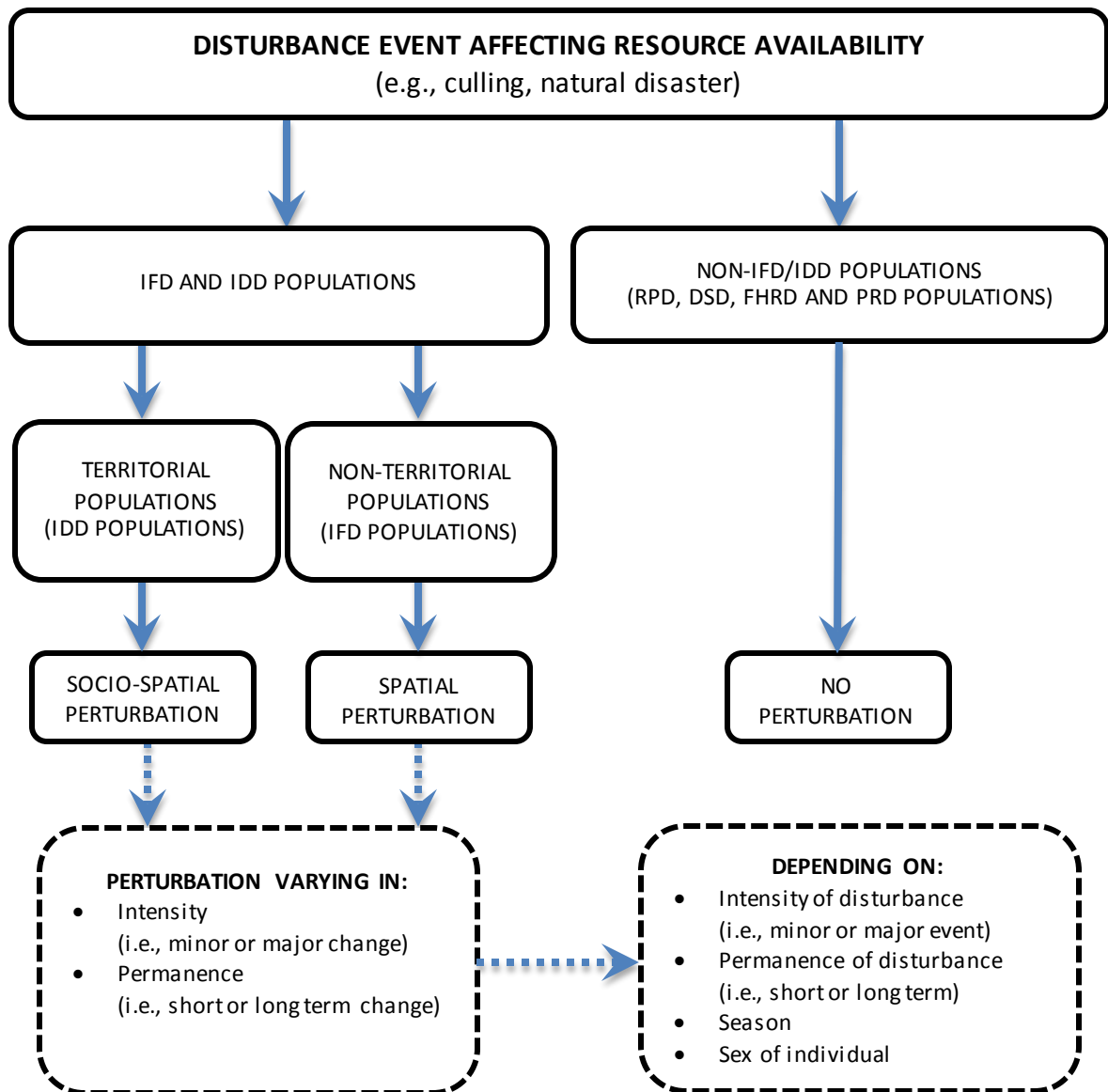


Figure A.1 Perturbation Model predicting whether a disturbance event will result in spatial perturbation, socio-spatial perturbation or no immediate perturbation, depending on the distribution pattern and territoriality of the population. IFD = Ideal Free Distribution, IDD = Ideal Dominance Distribution, RPD = Rose Petal Distribution, DSD = Den Site Distribution, FHRD = Fixed Home Range Distribution and PRD = Predation Risk Distribution.

A.3.1 Application of the Perturbation Model to possums

Possums exhibit a dominance hierarchy (Biggins and Overstreet, 1978; Green, 1984; Jolly and Spurr, 1996; Wehi et al., 2006). Some studies have recorded males as being dominant (e.g., Biggins and Overstreet, 1978) and others, females (e.g., Jolly and Spurr, 1996; Spurr and Jolly, 1999). This social behaviour may regulate possum density, with dominant individuals preventing subordinates from accessing limiting resources, such as food and dens (Green, 1984). In support of this, male and female possums have been recorded defending their dens and feeding sources if challenged by other possums (Biggins and Overstreet, 1978; Day et al., 2000a; Hickling and Sun, unpublished data; Spurr and Jolly, 1999). In addition, although there is not strong evidence of complete territoriality in possums, it is likely that limited parts of home ranges, such as core areas, are defended (Day et al., 2000a). This suggests that both male and female possums might follow an Ideal Dominance Distribution pattern. According to the Perturbation Model, this would mean that both sexes would exhibit socio-spatial perturbation following a disturbance event.

Female possums, however, generally show natal philopatry, inheriting home ranges that overlap with their mothers; in contrast, males disperse from natal areas to establish new home ranges (Clinchy, 1999; Clout and Efford, 1984; Crawley, 1973; Ji et al., 2001; Stow et al., 2006). This may mean that female possums follow a Rose Petal Distribution pattern and males follow an Ideal Dominance Distribution pattern. Under the Perturbation Model, this would mean that females would not exhibit perturbation following a disturbance event, whereas males would exhibit socio-spatial perturbation.

Possums are not expected to follow a Den Site Distribution pattern, as they move freely between dens in the landscape. They use approximately 11 – 15 dens per year and change these every two nights in three on average (Cowan, 1989). It is also predicted that they do not follow a Fixed Home Range Distribution pattern, as individuals likely disperse and re-aggregate after density reduction (Sweetapple and Nugent, 2009). As possums in New Zealand have no known predators, they are also not expected to follow a Predation Risk Distribution pattern.

A.4 Testing of the Perturbation Model

Research investigating the response of a number of species to density reduction was discussed in the General Introduction (Section 1.3.1 'Studies investigating perturbation due to density reduction'). This research provides useful case studies for testing the accuracy of the Perturbation Model. Each of these species was therefore assessed against this model, to predict their likely response to density reduction (Table A.2). These predictions were then compared to observed responses. To allow these comparisons, the distribution patterns of each population were predicted based on the information provided in the literature.

The majority of populations were postulated to have an Ideal Dominance Distribution pattern, due to exhibiting territoriality. The exception to this was female white-tailed deer in the forested habitat in New York, which likely had a Rose Petal Distribution pattern. The literature also suggested that badgers might follow either an Ideal Dominance Distribution pattern, due to being territorial (Tuytens et al., 2000), or a Den Site Distribution pattern, due to occupying setts even if they are disturbed (Doncaster and Woodroffe, 1993; Revilla, 2003). None of the case studies were predicted to follow an Ideal Free Distribution, Fixed Home Range Distribution or Predation Risk Distribution pattern. One potential limitation to this assessment was that definitive information on the population distribution patterns of each species was often not available in the literature. Distribution patterns were on occasion surmised by the researchers *a posteriori*, to explain the observed perturbation.

It was difficult to determine whether social perturbation occurred in the territorial species following density reduction, because generally only spatial perturbation was investigated. Testing of social perturbation would involve assessing whether the dominance hierarchy of a population changed following density reduction. These territorial populations did, however, all exhibit spatial perturbation. In contrast, the population with the Rose Petal Distribution pattern did not exhibit perturbation. The expression of socio-spatial perturbation in badgers suggests that this species follows an Ideal Dominance Distribution, not a Den Site Distribution pattern. These case studies therefore appear to support the predictions of the Perturbation Model. However, this is only a rough-and-ready assessment and further experimental research is required to test this model robustly. In particular, further investigation into populations with non-Ideal Free Distribution or Ideal Dominance Distribution patterns is required.

Table A.2 Predicted response of eight case study species to density reduction, based on the Perturbation Model (PM) and postulated population distribution patterns, compared to their actual response. IFD = Ideal Free Distribution, IDD = Ideal Dominance Distribution, RPD = Rose Petal Distribution and DSD = Den Site Distribution.

Species	Population Distribution	Reasoning for Population Distribution	Response Based on PM	Actual Response	PM Supported?
Bobcat (<i>Lynx rufus</i>)	IDD	Likely territorial, with interactions strongly influencing home ranges (Benson et al., 2006)	Socio-spatial	Spatial (social undetermined) (Benson et al., 2006)	Yes ⁸
European badger (<i>Meles meles</i>)	IDD or DSD	Social groups territorial (Tuytens et al., 2000); badgers occupy disturbed setts (Doncaster and Woodroffe, 1993)	Socio-spatial or none	Socio-spatial (Pope et al., 2007; Riordan et al., 2011; Tuytens et al., 2000; Woodroffe et al., 2006a)	Yes
House mouse (<i>Mus musculus</i>)	IDD	Territorial (Fitzgerald et al., 1981)	Socio-spatial	Spatial (social undetermined) (Fitzgerald et al., 1981)	Yes ⁸
Red-necked wallaby (<i>Macropus rufogriseus rufogriseus</i>)	IDD	Re-distribute to take advantage of increased patch quality, potentially territorial ⁹ (Wiggins et al., 2010)	Socio-spatial	Spatial (social undetermined) (Wiggins et al., 2010)	Yes ⁸
Ship rat (<i>Rattus rattus</i>)	IDD	Territorial (Innes and Skipworth, 1983)	Socio-spatial	Spatial (social undetermined) (Innes and Skipworth, 1983)	Yes ⁸
Tasmanian pademelon (<i>Thylogale billardierii</i>)	IDD or IFD	Territorial (Its Nature, 2012; Riley, 2012), re-distribute to take advantage of increased patch quality ⁹ (Wiggins et al., 2010)	Socio-spatial or spatial	Spatial (social undetermined) (Wiggins et al., 2010)	Yes ⁸
Female white-tailed deer (<i>Odocoileus virginianus</i>) (forest habitat)	RPD	Females philopatric (McNulty et al., 1997; Oyer and Porter, 2004)	None	None (McNulty et al., 1997; Oyer and Porter, 2004)	Yes
Female white-tailed deer (<i>Odocoileus virginianus</i>) (urban habitat)	IDD	Interact socially – may be territorial ⁹ (Henderson et al., 2000)	Socio-spatial	Spatial (social undetermined) (Henderson et al., 2000)	Yes ⁸

⁸ Although social perturbation cannot be confirmed as this was not tested

⁹ This was postulated *a posteriori* when density reduction resulted in perturbation

A.5 Conclusions

The Perturbation Model presented in this appendix provides a theoretical framework to assess whether populations will likely exhibit spatial or social perturbation following a disturbance event. This model shows some promise when compared to real-life case studies. However, further experimental research is required to confirm the accuracy of this model. This research should include testing the response of populations with various distribution patterns to a range of disturbance events and observing whether perturbation is exhibited. With respect to possums, it is predicted that both male and female possums exhibit an Ideal Dominance Distribution pattern. This is due to this species defending resources (Biggins and Overstreet, 1978; Day et al., 2000a; Hickling and Sun, unpublished data; Spurr and Jolly, 1999) and having a dominance hierarchy (Biggins and Overstreet, 1978; Green, 1984; Jolly and Spurr, 1996; Wehi et al., 2006). Therefore, based on the Perturbation Model, it is hypothesised that this species will exhibit socio-spatial perturbation following a disturbance event. Testing of the spatial perturbation component of this hypothesis is the basis of Objective 1 of this thesis (as outlined in the General Introduction, and Chapters 4 and 5).

Appendix B:

Population Size and Density Reduction Estimates

B.1 Appendix summary

This appendix details the population size and density reduction estimates for the three sites, calculated using mark-recapture events pre-reduction and post-reduction¹⁰, and Program MARK. The methodology used in these assessments is presented in Section 2.5.1 (Population size assessments: Mark-recapture operations) of Chapter 2: General Methodology. This work was peer-reviewed by a biometrician, Dr Darryl MacKenzie of Proteus Wildlife Research Consultants.

B.2 Population size models

The models with the most support for the population estimates were the 'changes in the behaviour of possums after initial capture' model (M(b); 3 of the 6 model sets – 50%) and the null model, (M(o); 2 out of the 6 model sets – 33%) (Table B.1). These results suggest that the trapping efficiency of possums is not always affected by the behaviour of individuals. However, some individuals do change their behaviour after initial capture, becoming 'trap-happy' or 'trap-shy' (Lettink and Armstrong, 2003). It was not known in this study whether individuals were predominantly trap-happy or trap-shy, or a mixture of both. Biases due to these behavioural effects were accounted for by the model estimation parameters (Lettink and Armstrong, 2003; White, 2010). From a management perspective, these behavioural variations are unlikely to be relevant as possums are generally killed the first time they are caught.

¹⁰ Although 'post-reduction' mark-recapture events are referred to in this appendix for the non-manipulated site, no density reduction was carried out at this site

Table B.1 Weightings of the AIC models estimating density at the three sites, before ('pre') and after ('post') density reduction. $M(o)$ = null hypothesis model, $M(b)$ = behavioural response after initial capture model, $M(t)$ = time specific variation in trapping probabilities model and $M(tb)$ = time-specific variation and behavioural response after initial capture model. Dashes indicate models that did not run; bold numbers indicate the best models in the set.

Event	AIC Model Weightings			
	$M(o)$	$M(b)$	$M(t)$	$M(tb)$
<i>Manipulated Site 1</i>				
Pre	0.93	0.07	0.00	0.00
Post	0.00	1.0	0.00	-
<i>Manipulated Site 2</i>				
Pre	0.00	1.00	0.00	0.00
Post	0.00	0.00	1.0	0.00
<i>Non-Manipulated Site</i>				
Pre	0.00	1.00	0.00	0.00
Post	0.96	0.02	0.00	0.02

B.3 Population size estimates

Total population sizes at the beginning of the experiments were similar between Manipulated Site 2 and Non-Manipulated Site (Table B.2). However, the population estimate for Manipulated Site 1 was approximately five-times higher than these two sites. Based on these estimates, the density at Manipulated Site 1 was seven possums per hectare, and the densities at Manipulated Site 2 and Non-Manipulated Site were two and one possum per hectare, respectively. The habitat at Manipulated Site 1 consisted of English oak (*Quercus robur*) and sycamore (*Acer pseudoplatanus*), whereas the habitat at Manipulated Site 2 and Non-Manipulated Site consisted of pine (*Pinus radiata*). It is possible that the higher density at Manipulated Site 1 was due to this differing habitat providing a greater supply of resources, such as food and den-sites, compared to the habitat at the other two sites. Differences in density were not due to previous density reductions at these sites, as no control other than incidental trapping had been undertaken at any of these sites for many years.

Generally, a smaller proportion of juveniles were caught compared to adults in both events at all three sites (Table B.2). The sex ratio between males and females at the start of experiments was approximately even at Manipulated Site 1 and Non-Manipulated Site; however, more males than females were recorded at Manipulated Site 2 (Table B.2). Following density reduction, the proportion of females to males was greater at Manipulated Site 1, approximately equal at Manipulated Site 2,

and lower at Non-Manipulated Site (Table B.2). These results suggest that males are initially easier to trap and remove from the population than females. In addition, some of the population estimates at Manipulated Site 2 and Non-Manipulated Site had confidence intervals the same as the estimates (e.g., adults in the Manipulated Site 2 pre-reduction event; Table B.2). This likely reflects the low densities at these sites and subsequently the low sample sizes for analyses, with the majority of the population caught during the mark-recapture operations.

The probabilities of capture show that possums were more likely to be caught during the post-reduction event at Manipulated Site 1 than the pre-reduction event (Table B.3). This is likely due to traps being saturated in the pre-reduction period due to the high densities, preventing some individuals being caught. In contrast, capture probabilities were generally higher during the pre-reduction monitoring period at Manipulated Site 2 and Non-Manipulated Site (Table B.3). This may have been due to the traps no longer being novel in the possums' environment and individuals being less likely to re-enter traps (being 'trap-shy'). This is contrary to other studies that have shown that possums are not intrinsically un-trappable and that previous capture is unlikely to have a long-lasting effect on the trappability of individuals (Morgan et al., 2007). These differences in capture probabilities between monitoring events may have resulted in biases in the population size estimates. However, as trapping methodology was consistent across sites it is considered that these estimates still provided a robust relative measure of changes in density. There did not appear to be any distinct pattern in capture probabilities at the three sites between adults and juveniles, or males and females (Table B.3).

Table B.2 Results of the population estimates for the three study sites before ('pre') and after ('post') density reduction, including the number of individuals caught during the mark-recapture events, the population estimate (with standard errors in parentheses) and 95% Confidence Intervals (CI) for the population estimate. A = Adults, J = Juveniles, M = Males, F = Females and T = Total population.

Event	Number Caught					Population Estimate					95% Confidence Interval				
	A	J	M	F	T	A	J	M	F	T	A	J	M	F	T
<i>Manipulated Site 1</i>															
Pre	51	5	27	29	56	99 (20.64)	6 (1.67)	51 (14.10)	50 (12.01)	103 (19.08)	72 - 158	5 - 16	35 - 97	37 - 89	78 - 157
Post	42	6	16	32	48	46 (3.93)	6 (0.07)	16 (1.46)	35 (3.14)	52 (3.89)	43 - 62	6 - 6	16 - 26	32 - 49	49 - 68
<i>Manipulated Site 2</i>															
Pre	22	1	16	7	23	22 (0.17)	1 (0.00)	16 (0.00)	7 (0.00)	23 (0.00)	22 - 22	1 - 1	16 - 16	7 - 7	23 - 23
Post	14	5	9	10	19	14 (1.24)	5 (0.00)	9 (0.00)	13 (3.79)	20 (1.89)	12 - 17	5 - 5	9 - 9	8 - 23	17 - 25
<i>Non-Manipulated Site</i>															
Pre	16	6	10	12	22	16 (0.01)	6 (0.01)	10 (0.01)	12 (0.01)	22 (0.01)	16 - 16	6 - 6	10 - 10	12 - 12	22 - 22
Post	11	11	14	8	22	13 (2.39)	11 (0.00)	15 (1.99)	8 (0.00)	23 (1.48)	11 - 24	11 - 11	14 - 25	8 - 8	22 - 30

Table B.3 Probability of captures (\hat{p}) at the three study sites before ('pre') and after ('post') density reduction, derived from the AIC model averaging analyses. A = Adults, J = Juveniles, M = Males, F = Females and T = Total population. Standard errors are in parentheses.

Event	Probability of Capture (%)				
	A	J	M	F	T
<i>Manipulated Site 1</i>					
Pre	14 (4)	30 (13)	14 (6)	16 (5)	15 (4)
Post	44 (9)	60 (16)	53 (13)	45 (10)	45 (8)
<i>Manipulated Site 2</i>					
Pre	71 (8)	100 (0)	67 (10)	88 (12)	72 (8)
Post	42 (13)	60 (22)	56 (17)	30 (15)	44 (12)
<i>Non-Manipulated Site</i>					
Pre	76 (9)	46 (14)	67 (12)	63 (11)	65 (8)
Post	35 (10)	64 (8)	40 (9)	66 (9)	50 (6)

B.4 Density reduction estimates

The density of the total population at Manipulated Site 1 halved due to the density reduction (Table B.4). This resulted in a reduction in density from seven to three possums per hectare. Although a number of individuals were removed at Manipulated Site 2, the population did not markedly decrease (11% decrease; Table B.4), with a difference in population size between monitoring events of only three individuals (Table B.2). The density of possums at Non-Manipulated Site also did not change markedly (4% increase; Table B.4), with population estimates differing between monitoring periods by only one individual (Table B.2).

The lack of a measurable density reduction at Manipulated Site 2 may have been due to a couple of reasons. Possums in this area had large home ranges even before density reduction was carried out (e.g., approximately 13 hectares for males) and often moved throughout adjacent forest blocks (refer to Chapter 3: Differences in Possum Home Range Characteristics between Sites of Varying Habitat and Population Density). Consequently, there appeared to be a large number of transients that visited the site, as new individuals were consistently trapped throughout the study. These transients likely increased the overall density estimate. Furthermore, because the density of the population was low to begin with, it became difficult to find non-collared individuals to remove, so the number of individuals removed was low. This may also explain why females increased in the post-reduction monitoring period at this site by six individuals, resulting in an 89% increase in the density of this sex (Table B.2 and Table B.4).

Of particular note is that the population sizes for juveniles increased in the post-reduction monitoring period at all three sites, regardless of the density reduction operations at the two manipulated sites (Table B.4). Female adults were caught frequently with joeys and backriders throughout the experiments, and these individuals were not marked. Therefore, recruitment of juveniles from joeys and backriders likely occurred, resulting in the density increases in this age class.

Table B.4 Density reduction estimates for the three sites calculated from the population estimates (with 95% confidence intervals in parentheses). Density increases are denoted by plus signs. A = Adults, J = Juveniles, M = Males, F = Females and T = Total population.

Site	Density reduction (%)				
	A	J	M	F	T
<i>Manipulated Site 1</i>	53 (33 - 72)	+8 (40 - +94)	68 (48 - 83)	31 (8 - 69)	49 (30 - 68)
<i>Manipulated Site 2</i>	35 (25 - 46)	+400 (+364 - +438)	44 (41 - 46)	+89 (+8 - +231)	11 (2 - 39)
<i>Non-Manipulated Site</i>	20 (4 - 61)	+83 (+83 - +84)	+55 (+20 - +99)	33 (33 - 33)	+4 (8 - +18)

Appendix C:

Lincoln University Standard Operating Procedure:

Anesthesia of Possums using Halothane¹¹

C.1 Background

- This procedure is to allow the safe handling of possums, for such things as the fitting of collars, weighing and tagging. This reduces stress and injury to the possums during handling, and also minimises injury to handlers.
- Short-term anesthesia is achieved by converting pure liquid halothane (fluothane) to gas within an anaesthetising box, which is then inhaled by the possum.
- Halothane is potent and effective, yet is non-irritant and safe at correct concentrations (Flecknell, 2009).
- Induction and recovery after halothane inhalation is rapid in most species, taking approximately 1 – 3 minutes and 3 – 12 minutes, respectively (Flecknell, 2009; Hall et al., 2001). From our experience, this is also the case with possums.
- This procedure can be undertaken in the laboratory or in the field.

C.2 Veterinary approval and training

- This procedure has been approved by Dr Robin McFarlane, a Veterinarian at Lincoln University.
- Training by a proficient handler and/or a veterinarian should be undertaken before attempting this procedure.

C.3 Procedure

- Possums are transferred into an anaesthetising box and halothane gas is then pumped into the box, which causes the individual to lose consciousness. This gas is created by pumping air into a flask containing liquid halothane.
- The set-up works by inserting a bung with two pipes into a flask containing halothane liquid (one of these should finish below the level of the liquid and one above the liquid, to collect the gas). The other end of the liquid pipe is then connected to a pump (this is permanently connected) and the other pipe for the gas needs to be inserted into the anaesthetising box.

¹¹ Prepared by Belinda Whyte, December 2011

- When not in use, the bung should be removed and the normal airtight flask lid used to ensure safe transporting or storage of the halothane.
- The box should have a clear Perspex top and door so that the consciousness of the individual can be observed.
- Anaesthetising equipment is shown in Plate C.1 and Plate C.2.

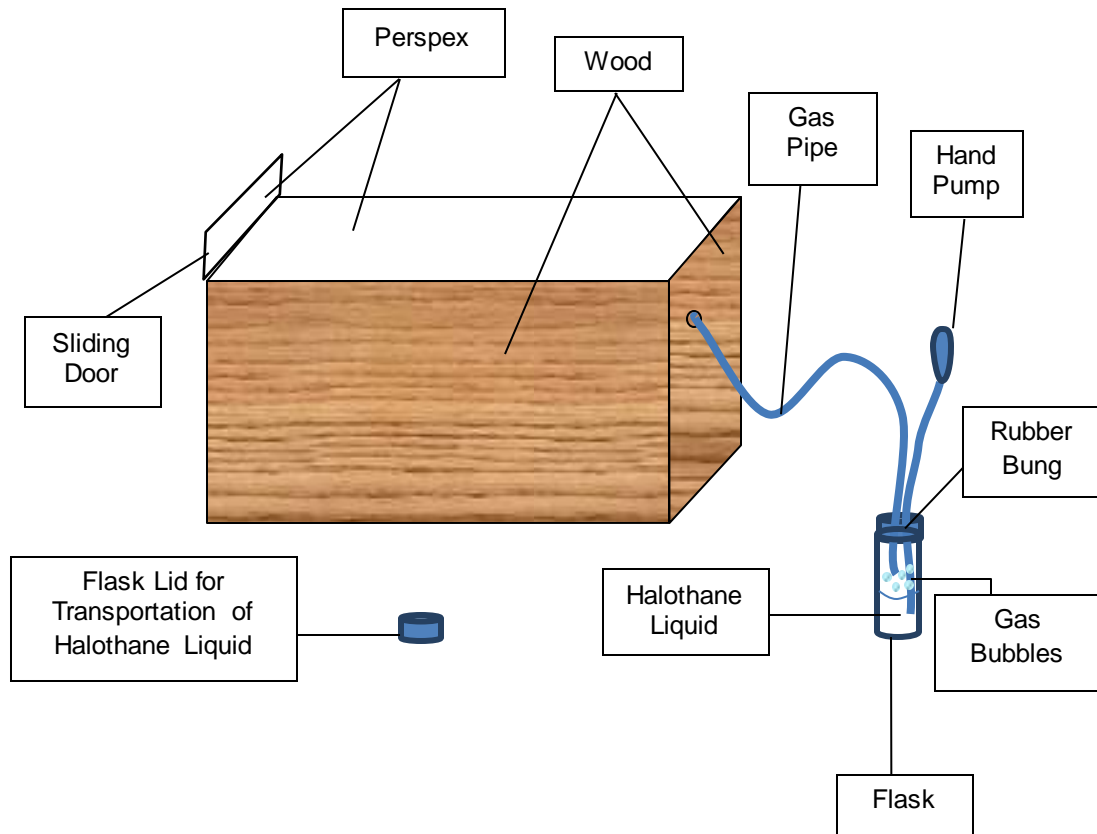


Plate C.1 Equipment used to anaesthetise possums

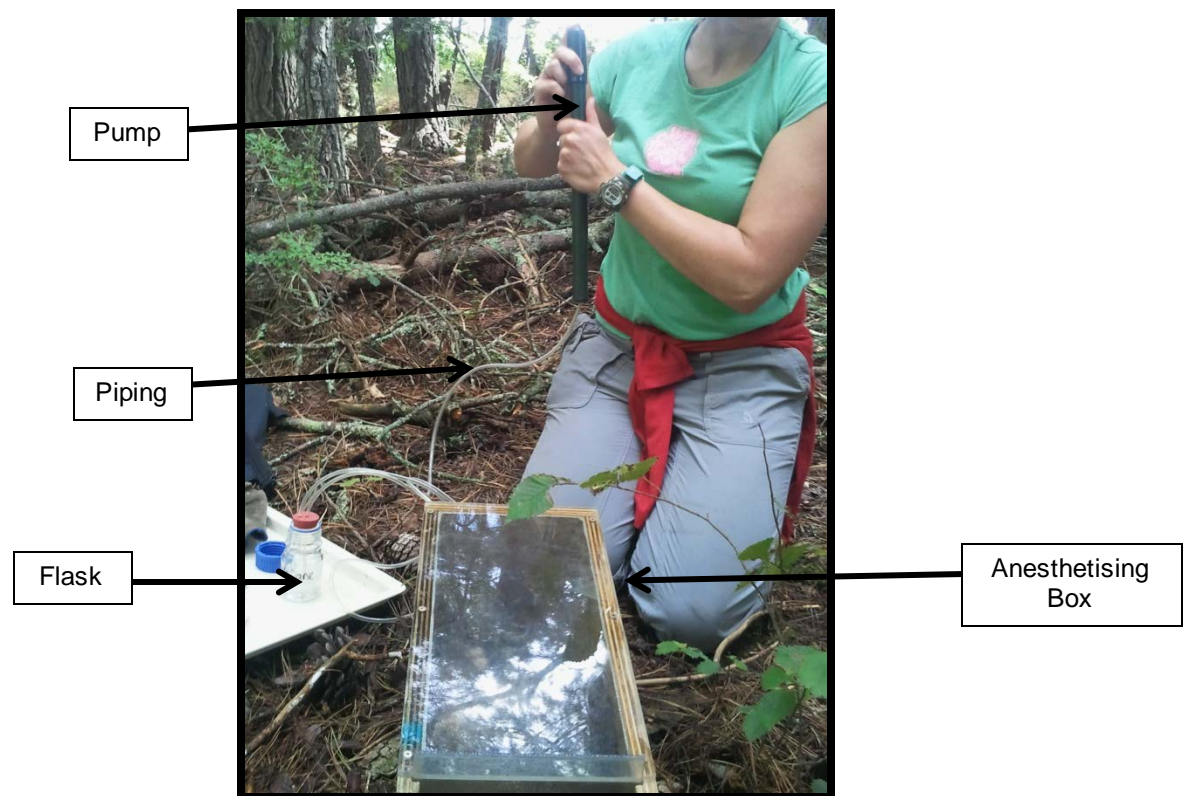


Plate C.2 Possum anaesthetising equipment being used in the field

C.4 Equipment

- Live-capture cage trap.
- Sack (if necessary – see below).
- Anaesthetising box, pipes with bung and pump, and halothane flask with lid (Plate C.1 and Plate C.2).
- Thick gardening gloves for transferring possums safely.
- Nitrile gloves to carry out tagging etc. and prevent exposure to bodily fluids.
- Notebook and pencil.

C.5 Technique

- It is recommended that a minimum of two people are involved in the conduct of this procedure, to ensure minimal risk to both the possums and the handlers.
- The best approach is to transfer the individual possum from a live-capture cage trap into the anaesthetising box. If you are unable to set a trap to catch the individual (e.g., the possum is in

a pen), the best way to get an individual into a live-capture cage trap is to place a sack over top of them that they can grab and then lift them into the cage.

- Coax the individual from the live-capture cage trap into the anaesthetising box, by blowing on their face or rustling a plastic bag.
- Once the animal is in the box, insert the bung with tubing into the flask, insert the tubing into the box and then administer the halothane gas via the pump.
- Once the gas is administered, replace the flask bung with the lid, remove the piping from the box, and cover the piping hole in the box with insulation tape to prevent seepage of gas out of the box.
- The responsiveness of possums to halothane varies and caution is advised, as too much halothane will euthanize the animal. Approximately 20 pumps is usually a good starting point.
- Once the halothane has been administered, watch the consciousness of the individual – the animal should not be removed from the box until their eyes are closed and they are completely limp (i.e., not gripping the box); this must be tested by rolling them around the box to see if they react. If they do react, leave them for a couple more minutes. If they are still awake after this time, add another few pumps of halothane.
- The animals will only remain lightly anaesthetised for a few minutes, so ensure you carry out the required work as quickly as possible. The animal may be placed back in the box for further anaesthetising if required – be aware that they will already have some halothane in their system, so administer the ‘top-up’ with caution.
- The best way to manipulate a possum (e.g., collaring or tagging) is to leave its head in the box, tuck its legs underneath it and pin the animal between your knees.
- When collaring animals, check that you can place three fingers between the possum and the collar to ensure it is not too tight.

C.6 Paperwork

- The following details should be recorded for every possum anaesthetised:
 - Location and date of capture
 - Maturity (adult or juvenile)
 - Sex
 - Weight (if time allows)
 - Any visible injuries
 - Any unusual reactions to the anaesthesia
- A record of halothane use should also be kept, as the use of this substance is restricted.

Appendix D:

Possum Den Site Descriptions

D.1 Appendix summary

This appendix presents the field descriptions of the den sites used by each possum at the three sites. Dens used during the pre-reduction and post-reduction monitoring periods are depicted by bold font and italic font, respectively. Dens used during both periods are depicted by bold and italic font. All data for all possums is presented, regardless of whether individuals could be analysed or not (i.e., regardless of whether dens could be tracked for the entire monitoring period).

D.2 Site 1

Table D.1 Description of the den sites of possums at Site 1

POSSUM	DEN 1	DEN 2	DEN 3
1	Tree	Tree - overhanging branch	Under log on ground by fenceline
2	Tree	<i>Big tree up high, close to Den 1 - better den?</i>	<i>Big macrocarpa - GPSR4's old Den 1</i>
3	Tree hollow (seen)	<i>Tree up high, next to VHF2 Den 2 - less exposed den to Den 1</i>	
4	Tree - hanging branch		
5	Roots of fallen tree by fenceline		
6	Tree	Tree	Tree
7	Tree by fenceline	Tree by fenceline, ~10m from Den 1	
8	Tree		
9	Tree	<i>Tree up high, less exposed than Den 1</i>	
10	Tree	Tree ~10m from Den 1	
11	Tree by fenceline	<i>Big tree by fenceline and Den 1, up high</i>	
12	Fallen tree by fenceline - underground	Big tree by fenceline opposite holly bush	On ground in big holly bush
13	Tree, up high, same as VHF6		
14	Poplar in pasture	Hollow tree stump - seen	In poplar tree next to Den 1, in trunk about eye level
15	Tree	Tree by fenceline	In south kale crop - seen sleeping
16	Dead tree		
17	Tree by fenceline	Tree	Tree near fallen tree by fenceline and VHF5 Den 1
18	Tree	<i>Tall tree</i>	<i>In VHF8 Den 1 with VHF8 but at lower height in tree</i>
19	Tree	Tree	<i>Big macrocarpa by fenceline</i>
20	Tree	High tree stump by fence	Gum tree in adjacent shelter belt/pasture
21	Tree		<i>Tall macrocarpa by fence</i>
22	Tree	Tree - overhanging branch	
23	Tree by fenceline - eye level	<i>Big macrocarpa by fenceline - better than Den 1?</i>	
24	Tree - likely hanging branch		
25	Roots of fallen tree by fenceline	Tree	
26	Tree		
27	Tree - hanging branch		

POSSUM	DEN 4	DEN 5	DEN 6
1	Tree, overhanging branch	<i>In hollow up high in dead tree - VHF aerial seen</i>	
2	<i>GPS4's old Den 3 - big macrocarpa by fenceline</i>	<i>GPSR4's old Den 4 - tall tree further into interior</i>	<i>In top of hollow tree (seen) - also GPSR2 Den 2</i>
3			
4			
5			
6	Fallen tree by fenceline, same as VHF5 Den 1	<i>Tree behind Den 2, up high</i>	
7			
8			
9			
10			
11			
12	Dead tree roots on ground by fenceline - old GPSN5 Den 6		
13			
14	In southwest kale crop - seen and saw den with eaten plants	Tree by fenceline	Dead tree roots on ground by fenceline
15	In kale - same crop as previous	<i>In kale - same crop as previous</i>	In tree hollow near kale fenceline - seen
16			
17	In south kale crop - seen	In same kale crop as previous - seen	In kale - same crop as previous
18	<i>Big macrocarpa adjacent to Den 1</i>		
19	<i>GPSR4's old Den 1 and VHF2's old Den 3</i>		
20	Tree, off overhanging branch	Tree close to other dens	<i>Massive macrocarpa next to Den 2</i>
21	<i>Tall tree further into interior</i>		
22			
23			
24			
25			
26			
27			

POSSUM	DEN 7	DEN 8
1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14	<i>Dead tree branch leaning against tall tree - old VHF10 Den 1</i>	
15	<i>In hollow of tree by kale fenceline - seen</i>	Tree up high
16		
17	In kale - same crop as previous	In massive shelterbelt woodpile at end of kale paddock
18		
19		
20	<i>Tall tree stump with open top by fenceline</i>	
21		
22		
23		
24		
25		
26		
27		

D.3 Site 2

Table D.2 Description of the den sites of possums at Site 2

POSSUM	DEN 1	DEN 2	DEN 3
1	On ground in gorse/blackberry gully - seen	On ground/underground in gorse gully close to Den 1	<i>On ground in gorse gully close to other dens</i>
2	On ground in gorse/blackberry slope by road		
3	On ground in gully	On ground/underground in gully adj. to Den 1 - heard	
4	On ground under fallen trees on gully slope		
5	On ground in gorse in gully		
6	On Ground under broken trees/blackberry in gully by tree		
7	On ground in gorse/blackberry gully slope	On ground in gorse/blackberry gully slope	
8	On ground in gorse/blackberry gully - heard		
9	On ground in gully in paddock	<i>On ground under broken trees & blackberry in gully</i>	
10	On ground in gorse/blackberry gully	On ground in gorse/blackberry gully	
11	On ground in gorse/blackberry gully	On ground under broken trees & blackberry in gully	
12	On ground in gorse/blackberry gully by stream		
13	On ground in dead trees on side of gully	On ground in gorse/blackberry gully	
14	Underground or under branches in gorse gully	<i>On ground in gorse/blackberry gully</i>	
15	Underground/under branches in gorse gully - heard		
16	On ground in gorse/blackberry gully		

D.4 Site 3

Table D.3 Description of the den sites of possums at Site 3

POSSUM	DEN 1	DEN 2	DEN 3
1	<i>In crook of large pine tree - seen</i>	<i>Inside hollow tree above ground</i>	On ground in holly/fern/vegetation gully
2	<i>In hole of hollow tree on forest edge - seen</i>	<i>In hole in ground under tree</i>	<i>In hole in ground under tree</i>
3	<i>On ground in vegetated gully in rocks</i>	<i>On ground in vegetated gully</i>	On ground in vegetation patch
4	<i>On ground in gorse at forest edge</i>	<i>On ground in gorse at forest edge</i>	On ground in debris pile in adjacent paddock
5	<i>On ground in gorse at forest edge</i>	On ground in gorse at forest edge	
6	<i>On ground in vegetated gully at forest edge</i>	<i>On ground in gorse at forest edge</i>	Underground in hole by gully
7	<i>On ground in vegetated gully</i>	On ground in gorse at forest edge	<i>On ground in gorse at forest edge</i>
8	<i>On ground in vegetated gully</i>	<i>On ground in vegetated gully</i>	On ground in vegetation in gully
9	On ground in gorse shelter belt	On ground in gorse shelter belt in paddock	In adjacent property - exact location not found
10	<i>On ground in vegetated gully</i>	On ground in gully vegetation near forest edge	In hole vegetation
11	On ground in shrubs	On ground in hole under tree in gully	<i>On ground in vegetated gully</i>
12	<i>On ground in gorse at forest edge</i>	<i>On ground in wood debris pile in adjacent paddock</i>	On ground in gorse at forest edge
13	On ground in gorse gully	<i>Deep underground in hole in bank</i>	
14	<i>On ground in gorse at forest edge</i>	<i>On ground in gorse at forest edge</i>	
15	On ground in vegetated gully	On ground in vegetated gully	On ground in tall vegetation
16	<i>On ground in vegetated gully</i>	On ground in gorse on forest edge	<i>On ground in tall vegetation</i>

POSSUM	DEN 4	DEN 5	DEN 6
1	<i>On ground in vegetated gully</i>		
2	<i>Underground in hole in gully under trees</i>	<i>Underground in hole under tree in gully</i>	In hole in ground under tree (same as GPS22 Den 2)
3	<i>In hole in ground under tree - seen</i>	<i>On ground in vegetated gully</i>	<i>On ground in tall vegetation</i>
4	<i>On ground in vegetated gully</i>	<i>In gorse at edge of forest</i>	
5			
6	<i>On ground in gorse at forest edge</i>		
7	<i>In crook of tree</i>	<i>On ground in gully in tall vegetation</i>	<i>In hole in ground under vegetation</i>
8	<i>On ground in vegetated gully at forest edge</i>	<i>On ground in vegetated gully</i>	<i>On ground in vegetation by fallen tree</i>
9	<i>In adjacent property - exact location not found</i>	<i>On ground in grass/thistles in adjacent paddock</i>	<i>On ground in gorse hedge next to site</i>
10	<i>In hole under bank - same as GPS24 Den 2</i>	<i>In large tree at edge of shelter belt</i>	<i>On ground in gorse at edge of forest</i>
11	<i>In hole in bank - seen</i>	<i>On ground in vegetation</i>	<i>On ground in vegetated gully</i>
12	<i>On ground in gorse at forest edge</i>	<i>On ground in gorse on forest edge</i>	<i>On ground in tall vegetation</i>
13			
14			
15			
16	<i>On ground in vegetation next to gully</i>	<i>On ground in tall vegetation</i>	<i>On ground in vegetated gully</i>

POSSUM	DEN 7	DEN 8	DEN 9	DEN 10
1				
2				
3	<i>In hole in tall vegetation</i>			
4				
5				
6				
7				
8				
9	<i>In pine tree in shelter belt south of site</i>	<i>On ground in gorse in shelter belt adjacent to site</i>	Up pine tree in shelter belt south of site	Up tree in shelter belt south of site
10	<i>South of Den 5, exact location unknown</i>	In gorse at edge of forest	In gorse at edge of forest	
11	On ground in vegetation at forest edge	<i>On ground in vegetated gully</i>	<i>On ground in vegetated gully</i>	On ground in vegetated gully
12				
13				
14				
15				
16	Up large pine tree in crook - seen			

POSSUM	DEN 11	DEN 12	DEN 13	DEN 14
1				
2				
3				
4				
5				
6				
7				
8				
9	<i>On ground in gorse at edge of shelter belt</i>	<i>In large pine tree at edge of shelter belt</i>	<i>In epiphyte in eucalyptus tree above ground</i>	<i>In pine tree at edge of shelter belt</i>
10				
11				
12				
13				
14				
15				
16				

POSSUM	DEN 15	DEN 16	DEN 17
1			
2			
3			
4			
5			
6			
7			
8			
9	<i>In large pine tree at edge of shelter belt</i>	<i>In large pine at edge of shelter belt</i>	<i>Up tall pine tree at edge of shelterbelt</i>
10			
11			
12			
13			
14			
15			
16			

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