The ecology of feral cats (*Felis catus*) on a New Zealand offshore island: Considerations for management

A thesis presented in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

in

Zoology

at Massey University, Manawatu,

New Zealand.

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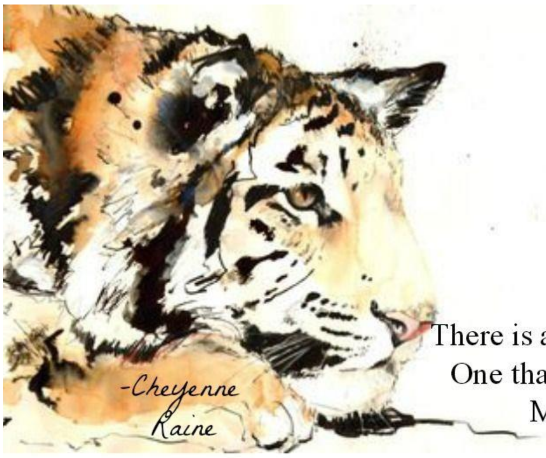
2018



There is a predator within me
One that craves to stalk you
My neverending prey
For with you I have
The thrill of the hunt
In the night and in the jungle
Feel my roar vibrate through your bones
And know me to be a beast
Aggressively marking you as my territory
Claws that dig into your fur
Canines that linger in your warmth
And this is the beginning
Of our wild hunt

Poem by Cheyenne Raine (www.rainepoetry.com) and artwork by Lucy Newton.

Abstract

Invasive species have contributed to the global biodiversity crisis, with the majority of recent-day terrestrial vertebrate extinctions implicating invasive predators. Domestic cats (*Felis catus*), particularly feral cats, are among the main culprits. In New Zealand, the continued decline of native species is largely due to invasive predators, which has led conservation efforts to focus on pest management. Feral cats are often a secondary focus for pest control, and their impacts within an ecosystem are not well understood. The main objective of this study was to produce a comprehensive study of feral cat ecology using a population of feral cats on Ponui Island, New Zealand, and highlight factors that should be considered for efficient control operations.

Predators distribute themselves and move within their environment in relation to prey availability and habitat type. These factors vary between locations, leading to differences in home range sizes that are difficult to predict. A relationship between home range size and population density was identified in the literature, which I used to predict changes in home range size with changing population density. I mapped the home ranges of eight cats for one year using location points from Very High Frequency (VHF) radio-telemetry and camera traps, then two males were removed from the population, seven months apart. The first removal resulted in an increase in the home range sizes of the remaining cats, whereas the second removal saw an invasion of four unmarked male cats. These results show that feral cats change their home ranges accordingly with changes in density, and removals (such as control operations) result in a change in feral cat ranging behaviour.

Feral cats are often live-trapped during control programmes to reduce capturing non-target animals. This technique is labour intensive because traps need to be checked frequently for welfare purposes. Describing feral cat activity patterns can dictate when live-traps should be set and checked. Camera traps have recently been used to estimate activity patterns, but have yet to be validated against accelerometry devices. Therefore, I compared the activity patterns obtained through camera trap data to that from collar-mounted accelerometry devices, and found a high correlation ($R^2 > 0.9$) between the two methods. The highest correlation was when activity from 600 or more videos was used. Feral cats were most active between sunset and sunrise, and live-traps should be set during these times to increase trapping efficiency and reduce bycatch.

The reproductive biology of invasive predators can be used to predict the recovery of populations following control operations, however there is very little information available for feral cats. Therefore, I investigated the reproduction of feral cats in a stable, insular population. Using camera trap data, I found that females had high reproductive output, averaging three kittens per litter and two litters per year. However, the recruitment rate was low in this population; only 3-4% of kittens survived to one-year-old. There were two infanticide events observed; the first reported for solitary-living feral cats. Females moved shorter distances when they had young kittens (less than seven-weeks-old). These results show that feral cats can rapidly recover from control operations. Females are less likely to encounter traps when they have young kittens, suggesting there are optimal seasons to capture cats.

Population genetics is used in invasive biology to identify populations that are isolated and have limited immigration. Eradication of isolated populations will be easier and more cost-efficient, with low chances of reinvasion. Although offshore islands are geographically isolated, there is the chance of reinvasion that is assisted by humans. I investigated the population genetics of the feral cats on Ponui Island using genetic samples collected from adults and kittens, and also opportunistically studied parentage. Most of the fathers of the litters were the heaviest males, and the males that had the most home range overlap with queens. Population genetics showed that the cats have most likely been isolated with no recent introductions, suggesting the removal of cats from this island would be successful with low chances of reinvasion.

Feral cats can have large impacts on native species, but prey on rats that also have detrimental effects on wildlife. This led me to investigate the diet of feral cats using scat analysis on an island with native birdlife, and rodents at high densities. I examined season and sex differences on diet and the impacts of cats on native species. Feral cats consumed prey based on seasonal availability, with cats eating rats when rats were at their highest density. Females ate smaller prey more frequently than males, such as passerines. The cats on this island are not reliant on the rat population, and were found to eat many native species such as brown kiwi, morepork, and fantails.

The findings from this thesis can be applied to feral cat management to develop efficient control operations. The decision to control a population should be based on both dietary and genetic data to reduce possible cascading ecological effects from the predator removal and identify genetically isolated populations. Home range, activity, and diet data can be used to determine the control protocol, such as; trap spacing, the time traps should be set and checked, and if secondary or primary poisoning should be used and the seasons that cats would uptake the baits. Finally, knowledge of feral cat reproduction can be used to predict the recovery of the population.

Acknowledgements

My supervisors, Isabel Castro, Murray Potter, and Nick Cave. Isabel, I guess this journey started because of you. I had been applying for PhDs overseas when you invited me on a trip to Ponui, got me talking to the Chamberlins about the feral cats, and convinced me to apply for funding at Massey. I see what you did there… I appreciate you encouraging me to take every opportunity that came my way, not only for my PhD. Often, I felt like it would have been easier to herd cats than what it was to get all of you in one room at the same time, but the great ideas talked about in these meetings was worth it. I appreciate you all taking on this project and I feel like everyone had a different expertise to offer that moulded this thesis into what it is.

Kristene Gedye, you were basically my genetics supervisor. Thank you for holding my hand throughout all of my lab work. For teaching me so much about genetics, coming up with new ways that we could extract DNA (in a simple and cheap way), and boosting my spirits when the PCR gods really didn't like me. I learnt a lot of things from you, and I really appreciate all of the new skills I have.

Steve Trewick, thank you for giving me a very quick crash course on population genetics. Chapter 5 would not have been the same without your input. Thank you for reading through the drafts to make sure I knew what I was talking about!

My sincere thanks goes to all of the volunteers and interns who helped me in the field. Aden and Sarah, thank you so much for all of your hard work. Your company out on Ponui was amazing, as well as binge watching Friends and Game of Thrones at night. I appreciate the many sleepless nights trapping, walking endless kilometres to find cats, sorting through the massive dataset that was our camera trap data, and sorting through cat scats and pitfalls in the lab. Cecilia, thank you for coming out and helping me re-bait traps and keeping me company in the field. Warren, thank you for sorting through cat scats. It really helped me with being able to finally sort through the mountain of scats that awaited me after finishing field work.

To the Rawhiti guys, Inge and John, Tom Dixon, Alex Wilson, and Alex Brighton; I have loved your company every catch week. I appreciated you all coming out to help me check traps during my first week trapping. Rana, thank you for lending me traps, running around the island after the pit tag reader, and for your quick hands when Tigger refused to go into the crush cage. Inge, you taught me so much during that first week of trapping. I never would have gained the confidence to anaesthetise feral cats without you being there that first time. John, you also ran around for me checking traps, and even brought us hot chocolate all the way up to Road trap on a long, miserable night trapping. Maria, I owe you a lot. You enthusiastically took over the position from Inge of accompanying me out on trapping nights. Your vet knowledge is incredible, and I will forever appreciate you being on call for me, and for looking after Shadow.

To the Chamberlins, words cannot express my gratitude. None of this would have been possible without you guys. Thank you for welcoming me and sharing your amazing island and farm with me. Ponui is absolutely one of my favourite places in the world. Thank you for letting me borrow vehicles when I was trapping, for the many barge and boats trips, the impromptu trips to Rotoroa Island, teaching me about sheep farming, all the fruit from the orchard (especially the wheeny grapefruit!), collecting dead cats for me whenever you came across them on the farm, and most of all, your company.

Maurice Alley, thank you for teaching me so much about post-mortems, and for not laughing at me when I brought you bones and asked you what it died from. You are quite the investigator, and I enjoyed piecing together the puzzle with you for both the kiwi and cat post-mortems.

To all those people who helped in what may seem like small but were very important ways. Ellen Schoener, Kim Singleton and the Wilson family, thank you for honouring my unusual request to be sent some of your cat's hairs for the genetic sampling. Paul, Tracy, Shaun, Cleland, Sharon, and Sandra, thank you for making it easier to get things done for this PhD. For mending equipment, building antennas, and ordering endless amounts of batteries. The Ecology Group would be lost without you. To the Waikato DOC office in Rotorua and the Palmerston North City Council, thank you for lending me traps. Thanks goes to Phil and Katie for helping me identify the munched up feathers that I found in cat scats. Keren Dittmer, for letting me use your lab for all of my genetic work, and checking up on me when I was working late nights in the lab. Anastasia, for helping Kristene and I grind up the bone samples for the genetic work. Lee Shapiro, thank you for the initial advice on setting up the trapping programme for the feral cats on the island and for all of the advice on baiting and also collaring the cats. To the girls at the Feline Unit; thanks for the many coffees, the kitten cuddles, for lending me data, and letting me store my anaesthetic.

To the Ponui team, enjoy! Good luck for your postgrad studies, and thank you for all of the trips that we shared together on Ponui. Thanks especially to Tom and Alex who taught me so much about the island when I was just a newbie.

To my friends, my office mates, and the Ecology Group, I could not think of better people to go through this with. Thank you for all of the support, the lunches at 12pm on the dot, the movie and Game of Thrones nights, and the parties when we really needed them. Nina, the weekly pints before pilates really saved me (for both my PhD and pilates)! Yvonne, the endless coffees at uni and de-briefs, and just lending an ear when it was a bad health week. Nicki, Katie, and Emily, you know everything that you have done for me; the surprise trips, Mean Girl movie nights, and the very weird but so much fun Spice Girl night, to name a few. Thank you for it all.

My family, thank you for all of the support. Thank you Mum and Dad for instilling hard-working values into me throughout my life, it certainly helped prepare me for the long days in the field, lab and office. Thanks for the petrol and food top-ups on my way through to either Ponui or back down to Palmy. And most of all, thanks for taking an interest in the feral cats on Ponui every time I called in.

My thanks goes to those who saw the value in my research on an underestimated invasive predator: Massey University Doctoral Scholarship, Julie Alley Bursary, JP Skipworth (Ecology) Scholarship, Ecology Bursary, NZVA Wildlife Society Marion Cunningham Memorial Fund, Freemasons Postgraduate Scholarship, Australasian Wildlife Management Society Postgraduate Student Award, Lovell & Berys Clark Scholarship, and Massey University Doctoral Completion Grant.

This thesis was not possible without the help of so many people, and a huge amount of effort went into this (summarised in the table below). Cats are not always easy to track, and unorthodox methods were used at times, such as the top of the barge. Results from this thesis have been presented at numerous conferences, which is summarised in Appendix A.

Days spent on Ponui from 2014-2018	375
No. of boat trips to Ponui	43
Kilometres driven between Palmerston North and Kawakawa Bay	42570 (559 hours)
Kilometres of transect walked	924
Sleepless nights trapping	24
No. of camera trap videos	174571
Hours of camera trap footage	1454 (60 days)
Hours spent sifting and IDing cat scats	325
PCRs run	2589
PCRs rerun (because the PCR gods failed me)	975
No. coffees drunk during PhD	~5200
No. muesli bars eaten in the field (they are a lifeline)	~774

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Plate 1: Still from a camera trap video of one of the study cats (Midnight) with a rat he had caught.

The contribution of invasive species to the global biodiversity crisis

Habitats and whole ecosystems have been modified drastically by humans, resulting in the loss of many native species and global biodiversity (Wilson, 1989). Invasive predator species have caused many extinctions of native vertebrates, and continue to pose a major threat (Gurevitch & Padilla, 2004; Clavero et al., 2009; Kingsford et al., 2009; McGeoch et al., 2010). Doherty et al. (2016) found that the majority of recent bird, mammal, and reptile species extinctions throughout the world were either caused directly by invasive predators, or that they contributed in some way to their demise. Domestic cats (*Felis catus*) and rodents (particularly ship rats (*Rattus rattus*)) were the main culprits, contributing to 44% of these extinctions (Doherty et al., 2016). Native species most at risk from invasive predators were those that inhabited insular environments, were genetically distinct, and came from unique evolutionary lineages (Doherty et al., 2016).

Invasive predators can impose negative pressures on native species through competition and depredation (Gurevitch & Padilla, 2004), and can have vastly different effects on naïve fauna than on the prey species that they have co-evolved with (Salo et al., 2007). The predator's natural prey has evolved anti-predator behaviours that allow them to coexist with their predator (Dawkins & Krebs, 1979). Species that have evolved in isolation from particular predators can be extremely vulnerable to them, because they display ineffective anti-predator behaviours (Duncan & Blackburn, 2004; Sih et al., 2010). The naivety of native species towards invasive predators has contributed to the unsustainable depredation rates imposed on those species, particularly in insular environments (Sih et al., 2010; Doherty et al., 2016).

Invasive predators in New Zealand

New Zealand is classed as a biodiversity hotspot (Myers et al., 2000) and a global conservation priority area (Brooks et al., 2006), partly due to its highly unique avifauna (Driskell et al., 2007). A large number of New Zealand faunal species are under threat by continued depredation or competition from invasive species (Towns & Daugherty, 1994; Duncan & Blackburn, 2004). Vitousek et al. (1997) and McGeoch et al. (2010) identified New Zealand as one of the countries with the highest number of invasive species for its area; the latter reported that New Zealand had the highest number of invasive species out of the 57 countries they assessed.

Rabbits (*Oryctolagus cuniculus*) were introduced into New Zealand in 1777 and their rapid range expansion and population growth caused widespread damage to pastoral systems (Veitch & Clout, 2001; Norbury & Reddiex, 2005; King, 2017). This led to attempted biocontrol measures

(King, 2017) including the intentional introduction of mustelids (*Mustela* spp.) in the late 1800s (King & Murphy, 2005). Cats were first introduced to New Zealand by Europeans in 1769, when cats were taken on ships to control rats (Fitzgerald, 1990). Farmers also contributed to the introduction and dispersal of cats throughout the mainland by sourcing cats from cities and releasing them into rural areas for rabbit and rodent control (Gillies & Fitzgerald, 2005). However, the introduced mammalian predators preyed on naïve native fauna because they were easy to detect and catch, contributing to the decline in native biodiversity after human arrival (Holdaway, 1989; Wilson, 2004). Thus today, invasive pest control is a major component of conservation efforts in New Zealand.

Predator-prey dynamics

Many of the introductions of mammalian species into New Zealand have resulted in both the predator and their natural prey being introduced (such as cats and rats; weasels and mice), which has led to multiple invasive species that fill multiple guilds within ecosystems. Invasive prey species also have detrimental effects on native fauna and flora, which has led to debates on whether the introduced mammalian predator suppresses the invasive prey population. Therefore, there is a need for research on introduced predator species to inform control or eradication programmes (Doherty & Ritchie, 2017), because the removal of a predator from ecosystems can have cascading effects on other species, both native and introduced (Zavaleta et al., 2001). In order to minimise potential negative effects, the ecology of a predator needs to be understood in an ecosystem before management operations are applied.

Understanding predator-prey relationships can help predict how prey populations will respond to the decline of native top predators, or removal of invasive predators. Predator-prey systems are regulated by either top-down (predator controlling prey numbers) or bottom-up (food resources controlling prey numbers) processes (Sinclair, 2003). In top-down systems, the mesopredator (medium-sized predators in the middle of a trophic level) is not limited by food, instead the predator regulates the prey numbers (Russell et al., 2009). In bottom-up systems, mesopredator numbers are controlled by food abundance as food is a limiting resource (Russell et al., 2009). Predators can regulate a prey species if they are the main or primary prey, but cannot cause the extinction of this species because the predator numbers decline as the prey numbers decline (Sinclair, 2003). An example of this is the snowshoe hare (*Lepus americanus*) and its predator, the Canada lynx (*Lynx canadensis*) (O'Donoghue et al., 2010). When the snowshoe hare density increased rapidly from high food abundance, it was followed a year later by an increase in the density of the lynx (Krebs et al., 1995; Krebs et al., 2001; O'Donoghue et al., 2010). When the snowshoe hare population decreased due to the high depredation pressure, the lynx population did likewise (Krebs et al., 1995; Krebs et al., 2001; O'Donoghue et al., 2010).

Coupled responses between predator and primary prey densities mean that an increase in prey density leads to an increase in predator density, which also occurs between invasive predators and invasive prey (Sinclair, 2003). However, a decline in the invasive prey due to density-dependent population growth does not always lead to a reduction in the predator's density if there are alternative prey available. Instead, the invasive predator may prey switch to native species, leading to increased depredation pressure on native species which can cause a decline in their population (Sinclair, 2003). Extinction of a prey species by depredation can occur when it is the secondary prey (Sinclair, 2003). A decline in the density of the secondary prey does not necessarily cause a collapse in the predator density, because the predators do not depend on this prey species (Sinclair, 2003). This is how the fox (*Vulpes vulpes*), that preys primarily on rabbits, drove a black-footed rock-wallaby (*Petrogale lateralis*) population to extinction in Australia (Kinnear et al., 1998; Sinclair, 2003), and why invasive species pose a major threat to native fauna.

Top predators play an important role in ecosystems by regulating mesopredators and herbivores, which affect the vegetation and habitat (Sergio et al., 2008). The decline in a top predator population can have drastic effects throughout the whole ecosystem (trophic cascades). Examples include removal of Eurasian lynx (*Lynx lynx*) from Britain and other parts of Europe that resulted in an increase in the number of roe deer (*Capreolus capreolus*), which competed with other wild ungulates (Melis et al., 2009). The increased browsing pressure changed the species composition of the woodland (Gill, 2000). This affected many species because a reduction in plant richness led to a reduction in insect diversity, decreasing the food available to insectivores (Gill, 2000). There have been recent discussions on whether lynx should be reintroduced to suitable habitat in Scotland to control deer populations, which might aid in the regeneration of the forests (Gill, 2000; Hetherington et al., 2008; Johnston, 2015). Another well-known example of a trophic cascade occurred in Yellowstone National Park when the extirpation of wolves (*Canis lupus*) led to increased foraging by elk (*Cervus elephus*) on deciduous woody tree species, particularly aspen (*Populus tremuloides*) (Ripple et al., 2001; Ripple & Beschta, 2004, 2012). The change in vegetation also drove declines in the numbers of beavers (*Castor canadensis*), through reduction in food and availability of material for dam construction, and bison (*Bison bison*) from increased levels of interspecific competition (Ripple & Beschta, 2004, 2012). The reintroduction of wolves back into Yellowstone National Park not only reduced the elk numbers through depredation, but also changed elk foraging behaviours causing increased avoidance of areas with a higher risk of wolf depredation (Ripple et al., 2001; Ripple & Beschta, 2004; Fortin et al., 2005). The decreased foraging pressure by elk led to a change in vegetation, resulting in an increase in beaver and bison numbers (Ripple & Beschta, 2012). These flow-on effects have led to the view that top predators could be used for ecosystem restoration (Ritchie et al., 2012).

The removal of top predators from ecosystems can affect mesopredators. The mesopredator release hypothesis, whereby the removal of a top predator leads to an increase in the abundance of mesopredators and thus causing increased depredation pressures on the prey species of the mesopredator (Allen et al., 2011), has become an important concept in terms of ecosystem conservation (Crooks & Soulé, 1999). An examination of North American carnivores showed that while mesopredator ranges have expanded, top predator ranges have contracted (Prugh et al., 2009). These interactions become more complicated when viewing an ecosystem with both invasive prey and predator species. The removal of the invasive predator that is consuming the invasive prey species could lead to an increase in the prey population (Zavaleta et al., 2001). If the invasive prey has a negative impact on native species by either depredation or competition, then the increase in numbers of the invasive prey could lead to a reduction in the native species (Zavaleta et al., 2001). Mesopredator release can only occur in systems that are top-down regulated rather than bottom-up (Sinclair, 2003; Russell et al., 2009). In New Zealand, feral cats were found to be preying on the critically endangered kakapo (*Strigops habroptilus*) on Stewart Island although the majority of their diet comprised of rats (*Rattus* spp.) (Karl & Best, 1982). Courchamp et al. (1999) predicted that the removal of cats from the island could result in mesopredator release of rats, and increased depredation pressures on kakapo by rats. It transpired that cats were not removed; rather, the kakapo were translocated to predator-free islands (Lloyd & Powlesland, 1994; Clout & Merton, 1998). Invasive predators may be able to regulate the abundance of invasive herbivorous species that also have detrimental effects on native fauna. On Macquarie Island, the eradication of feral cats caused an increase in the population of rabbits which, in turn, caused substantial damage to the vegetation and secondary effects on burrowing seabirds (Bergstrom et al., 2009).

Invasive predators could fill the niche of an extinct native top predator and suppress the activity and abundance of mesopredators that also have detrimental effects on native fauna. For example, in Australia, the now-extinct thylacine (*Thylacinus cynocephalus*) was the top mammalian predator (Paddle, 2002; Letnic et al., 2012), and dingoes (*Canis lupus dingo*), an introduced species, are now the top predator in many areas and have been shown to suppress invasive mesopredators (Colman et al., 2014; Gordon et al., 2015; Hunter et al., 2015). This relationship between dingoes, mesopredators, and native prey, although weak and needing further exploration (Allen et al., 2011; Allen et al., 2015), does pose the question of whether invasive top predators could be used to regulate invasive mesopredators (Ritchie & Johnson, 2009).

Animals face a food acquisition trade-off between the energy obtained from food, and the energy expended acquiring the food (Oksanen et al., 2001). For predators, this translates to the availability of the prey, which is a combination of prey abundance and their ease of capture (Ewer, 1998). Seasonal declines in main prey availability can lead to higher depredation rates on secondary prey species. For example, Latham et al. (2013) studied the movements of wolves during seasonal fluctuations in their main prey. The wolves mainly consumed deer in the winter and beavers in the summer (Latham et al., 2013). During summer, wolves used habitats that were more frequented by beavers, and also caribou (*Rangifer tarandus caribou*). Depredation of caribou by wolves increased and the population of caribou declined (Latham et al., 2013). A similar situation occurs within New Zealand, between an invasive predator, and invasive and native prey. House mice (*Mus musculus*) and ship rats have an eruptive system in beech forests (*Nothofagus* spp.), where there is a rapid increase in rodent numbers in response to an increased food supply during a beech mast season (King, 1983). In turn, this leads to stoats preying on more rodents and an increase in stoat density (King, 1983; Blackwell et al., 2003; White & King, 2006). Density-dependent effects, as well as the increased depredation by stoats, cause the rodent populations to decrease (Choquenot & Ruscoe, 2000; Blackwell et al., 2001). The reduction in availability of their main prey leads to prey switching, where stoats switch to consuming native bird species. King (1983) found an inverse relationship between the occurrence of mice and birds in the diet of stoats, and O'Donnell & Phillipson (1996) found increased depredation on the endangered passerine bird mohua (*Mohoua ochrocephala*) following a beech mast season that increased invasive prey, and subsequently predator, numbers. This is an example of how fluctuations in prey species can lead to prey switching by the predator, or increased depredation pressure on native species.

Hyper-predation is a process whereby the high availability of introduced prey can cause an increase in the population size of an invasive predator, leading to higher depredation pressures on native species (Courchamp et al., 2000). Courchamp et al. (2000) found that native prey populations needed a high intrinsic growth rate or high carrying capacity, and show effective anti-predator behaviours, to overcome hyper-predation. The chances of native species in New

Zealand having these characteristics are low, considering many show predator naivety and ineffective anti-predator behaviours (Sih et al., 2010). The hyper-predation process was likely the cause of extinction of the endemic parakeet (*Cyanoramphus novaezelandiae erythrotis*) on Macquarie Island (Taylor, 1979). The parakeet persisted on the island despite the introduction of cats, but the number of parakeets decreased rapidly following the introduction of rabbits (Taylor, 1979). This introduction of rabbits led to an increase in the number of cats, resulting in higher depredation rates on parakeets by cats (Taylor, 1979) and possibly the extinction of the parakeets.

Predator-prey dynamics are incredibly complex, particularly when there are invasive species filling multiple guilds in an ecosystem. It is important to understand these dynamics in an ecosystem before removing an invasive species, to be able to predict and minimise potential negative effects from removing a top predator.

Feral cats: A global issue

Definitions

There are many terms that are used throughout the literature describing different living situations for the domestic cat. Here I have provided definitions of the terms used in this thesis. The domestic cat is morphologically similar to wildcats (Daniels et al., 2001) and descended from the *Felis silvestris* lineage that was a mix of the Near Eastern and Egyptian lineages (Driscoll et al., 2007; Ottoni et al., 2017). Due to the similarities between many of the species in the Felidae family, in this thesis I have used examples from other felid species where there are no previous studies on feral cats. There are some discrepancies between the classification of terms listed here and studies from other countries that list “stray” cats as “feral” cats (Page et al., 1992). They are the same species, but they differ in the habitat they use, population densities, and social behaviours. Where possible, I have reclassified these discrepancies to align with the definitions stated here.

- **Domestic cat** - This term is used for the *Felis catus* species, and encompasses feral, stray, house, colony/lab, and free-roaming/free-ranging cats.
- **Feral cat** – This is a term used for domestic cats that have no association with people (Farnworth et al., 2010; Spotte, 2014). Feral cats avoid contact with people, obtain food through hunting prey species, and reproduce in the wild.
- **Stray cat** - These are domestic cats typically found in urban areas (Farnworth et al., 2010) and are semi-dependent on human resources. This term encompasses domestic

cats that have been abandoned by people or are ownerless. Stray cats tend to live at higher densities than feral cats and form colonies. They are sometimes fed by people, scavenge for food, exploit rubbish dump sites, and supplement their diet through hunting.

- **House/pet cat** - These are domestic cats that are owned and live in close proximity to people (Farnworth et al., 2010). House cats are dependent on people for food and shelter, and may be either living indoors or outdoors. They are also referred to as companion cats in the literature (Farnworth et al., 2010).
- **Farm cat** – These are domestic cats that not only live in rural areas and are on farms, but also tend to live in close proximity to people. Farm cats are fed by farmers and use farm buildings as shelter, so are not completely independent of people (Macdonald et al., 1987). These cats have higher population densities than feral cats, can live in colonies, and sometimes form nursing coalitions (Macdonald et al., 1987).
- **Free-roaming/free-ranging cat** – This term is used in the literature to describe house cats that are allowed to roam outside, stray cats, and sometimes feral cats. This term will only be used in this thesis when the study has not defined between stray, house, or feral cats.
- **Colony cat** – These are cats that typically live in a captive situation, such as a research facility. They live in controlled settings and do not roam outside.
- **Wildcat** - A wildcat is a species belonging to the *Felis* genus, not including the domestic cat.
- **Felid** - The term felid in this thesis is used for any species belonging to the family Felidae, whereas “non-domestic felid” is used for all Felidae species except *Felis catus*. The term is used when talking about features that are similar between members of the Felidae family, and when examples are given from different felid species.

The domestic cat has a widespread distribution that is highly correlated with human colonisation (Long, 2003; Koch et al., 2016), including their introduction to many islands worldwide (Long, 2003). Their introduction to every continent, except Antarctica, has led to this species being listed as one of the 100 worst invasive species in the world, due to the negative impacts they have on native fauna (Lowe et al., 2000). An estimated 30-80 million stray and feral cats in the United States prey on 1.4-3.7 billion birds and 6.9-20.7 billion mammals every year, with over 66% of these being native species (Loss et al., 2013). Loss et al. (2013) also estimated that between 95-299 million amphibians and 258-822 million reptiles in the United States were being eaten by these cats annually. In Australia, previous predator control targeted foxes, and recently there has been a population explosion of feral cats which have devastated small native mammal populations (Glen & Dickman, 2005). On islands, feral cats have caused the extinction of at least 14% of bird, reptile and mammal species worldwide (Medina et al., 2011), and pose a continued threat to native species (Nogales et al., 2013).

Feral cats in New Zealand

Although the domestic cat was introduced to New Zealand in 1769, feral populations did not become established until the 1830s (Fitzgerald, 1990). Cats then became progressively widespread (Fitzgerald, 1990) and are now distributed throughout all three mainland islands, and have been present on at least 31 offshore islands (Gillies & Fitzgerald, 2005).

Feral cats prey mainly on the introduced ship rat (Gillies & Fitzgerald, 2005) which is the most common rat in New Zealand forests (Innes, 2005). Ship rats compete with many native fauna for food and are the biggest threat to native passerines by preying on eggs, chicks, and adults (Atkinson, 1978; Brown, 1997). With the removal of cats from some islands, there is the potential for mesopredator release of rats that could lead to reduced food resources and increased depredation on native birds (Zavaleta et al., 2001).

Many vulnerable native species have been affected by feral cat depredation in New Zealand. Karl & Best (1982) found evidence of kakapo depredation by feral cats on Stewart Island. Habitat destruction contributed to the decline of the Stephens Island wren (*Traversia lyalli*), a flightless passerine, however, their extinction was mainly attributed to depredation by feral cats (Galbreath & Brown, 2004; Medway, 2004). Records also show that the wren was not the only native bird population to decline under the depredation pressure imposed by cats; saddleback (*Philesturnus carunculatus*) and piopio (*Turnagra capensis*) (a native passerine similar to a thrush) populations also declined (Medway, 2004). Ultimately, cat depredation was also responsible for the extinction of the piopio on Stephens Island (Medway, 2004; Tennyson & Martinson, 2006).

Birds are not the only native fauna being preyed on by feral cats in New Zealand. Middlemiss (1995) found that approximately half of the digestive tracts and scats from feral cats in Otago contained skink remains. Some of the lizards may have been the nationally endangered *Oligosoma otagense* and *O. grande* (Hitchmough et al., 2016) although this species-level identification was not confirmed (Middlemiss, 1995). Nevertheless, this finding shows that feral cats have a negative impact on native reptile species. Endemic invertebrates are also a prey of cats; for example weta (Orthoptera; Anostostomatidae and Raphidophoroidea), were the most frequently occurring invertebrates eaten by feral cats in Orongorongo Valley, Wellington (Fitzgerald & Karl, 1979).

Continued depredation on native species by feral cats has led to the need to understand their ecology. Usher (1953) was one of the first to recognise the negative impacts of feral cats in New Zealand. During the 1980-90s there was a research focus on feral cat ecology, with studies looking at cat populations throughout the mainland of New Zealand, as well as offshore islands. The majority of these studies focused on describing the diet of feral cats to enable the identification of vulnerable species (Karl & Best, 1982; Fitzgerald & Veitch, 1985; Baker, 1989; Alterio & Moller, 1997a). From 2000-12 there was a substantial increase in the number of publications on feral cats in New Zealand, with a switch in research themes in the last decade from diet studies towards management (Farnworth et al., 2013).

Studies focusing on quantifying home range sizes and describing habitat use of feral cats emerged following the development of Very High Frequency (VHF) collars (Fitzgerald & Karl, 1986; Norbury et al., 1998a). The creation of Global Positioning Systems (GPS) collars allowed the movements of feral cats to be studied further, providing more information on fine-scale habitat use (Recio et al., 2010; Recio et al., 2014). Feral cat home ranges are influenced by food abundance and availability, with previous studies on New Zealand populations relating large home ranges sizes to low prey availability (Harper, 2007). Norbury et al. (1998b) also recorded an increase in feral cat home range in response to a reduction in the density of their main prey (rabbits) in a South Island site. Prey availability affects population density, and Liberg et al. (2000) found a strong relationship between the population densities of feral cats and the size of their home ranges when examining data from feral cat populations worldwide. As feral cats are controlled in New Zealand by removing a few individuals over time, the home range versus density relationship needs to be investigated to determine how these changes in density affect the movements of the remaining feral cats.

Invasive predator control and public perceptions

In New Zealand, control efforts are focused on possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*), and rodents (Parkes & Murphy, 2003). Emphasis on possum control is not only due to the threat they pose to native fauna and flora, but also because they are vectors for the spread of bovine tuberculosis (caused by the bacterium *Mycobacterium bovis*) throughout New Zealand

(Pfeiffer, 1994; Parkes & Murphy, 2003). This disease can be transmitted to domestic animals and humans, having economic costs and human health implications (Pfeiffer, 1994).

Stoats are also heavily targeted for pest control and eradication due to their prevalent negative impacts on native birds through depredation (Parkes & Murphy, 2003). Stoats are a particular threat to kiwi (*Apteryx* spp.), with McLennan et al. (1996) observing depredation rates of up to 60% on juvenile kiwi. More money is also directed at research on stoats, possums, and rats than on any other wild or feral introduced mammal species (Parkes & Murphy, 2003). While stoats have large and far-reaching impacts on native species (King & Murphy, 2005), so, too, do feral cats, but less funding is available for feral cat research. Parkes & Murphy (2003) found that in 2000-01 $1.3 million was spent on research on stoats compared with just $40,000 spent on feral cat research (ecology and optimising conventional control methods).

Feral cats not only pose a threat to native species, but also to human health (Dabritz & Conrad, 2009). Toxoplasmosis is caused by the protozoan *Toxoplasma gondii* and felids are the definitive hosts (Conrad et al., 2005). Oocysts can be transmitted through contaminated water and soil, leading to many mammals (including humans) and birds ingesting the oocysts and becoming the intermediate host (Conrad et al., 2005). Toxoplasmosis can be transmitted to humans through uncooked meat and ingesting oocysts from the environment (Dabritz & Conrad, 2009). The disease in humans generally has symptoms of malaise and fevers but can become severe and even fatal in rare cases (Dubey & Jones, 2008). *T. gondii* is easily spread throughout the environment through infected cat scats, affecting many different native species. Conrad et al. (2005) traced toxoplasmosis infections in threatened sea otters (*Enhydra lutris nereis*) to infected felid scats that were transported to sea via freshwater runoff. Toxoplasmosis-caused mortality has contributed to the population decline and slow recovery of sea otters in California (Conrad et al., 2005). Toxoplasmosis also infects native species in New Zealand, such as birds and marine mammals (Hartley & Dubey, 1991; Howe et al., 2013; Roe et al., 2013; van Zyl, 2014). Therefore, the management of feral cat populations is important for not only conservation reasons, but also disease transmission and human health.

Feral cat control is often hindered by public perception. In 2008, Farnworth et al. (2011) found that people in New Zealand were more accepting of contraception and trap-neuter-rehome methods than lethal methods of feral cat control such as poisoning and shooting. Trapping was ranked the most acceptable lethal control method by people in 2008 (Farnworth et al., 2011). These were opposite to Fraser's (2001) results from 1994 when New Zealand's general public showed more support for poisoning, followed by shooting, than for lethal trapping. This suggests that there may have been a shift in the public's preference of feral cat control from lethal to non-lethal methods over the 14 years between surveys. Public favour towards non-lethal feral cat control is not limited to New Zealand. A study in the United States also found that people preferred non-lethal approaches to feral cat control (Loyd & Hernandez, 2012).

Surveys have not only revealed that the public generally prefers non-lethal control of feral cats, but that the public is sometimes opposed to any cat control. Ash and Adams (2003) conducted a survey of employees at Texas A&M University in the United States, and found that although people acknowledged the negative effects of free-ranging cats on wildlife, it was not considered to be a "legitimate reason" for cat control. Human intervention and the public's opposition to feral cat control also caused the failure of the attempted eradication of cats from South Molle Island (Australia) because the staff at the resort hid cats in their rooms (Campbell et al., 2011). The push for wildlife managers to integrate societal values into management decisions (Fraser, 2001), coupled with the negative public attitude towards feral cat control, has led to pest control focusing on less publically favourable species in New Zealand.

New Zealanders are fond of domestic cats, with just over 40% of New Zealand households owning a cat (MacKay, 2011; New Zealand Companion Animal Council Inc., 2016). This is likely to exacerbate negative public attitudes to feral cat control. Predator control of animals that people relate to and have an emotional connection with can lead to resistance to control for that pest (Robertson, 2008). The threat of accidental poisoning or shooting of pet cats may also lend public support for non-lethal control methods for stray and feral cats. Farnworth et al. (2011) found that cat owners were typically more supportive of non-lethal controls than non-cat owners. Feral cats are often live-trapped, identified, and euthanised to reduce the risk of euthanising a pet cat, whereas poisoning and shooting are indiscriminate. These public attitude shifts regarding lethal control methods reflect these perceived threats to pet cats.

Research priorities to inform feral cat management

In New Zealand, the importance of cats as predators on native species have generally been considered secondary to depredation by mustelids. For example, there were 19 operations targeting mustelids in 2008-09 compared to nine operations targeting feral cats (Clayton & Cowan, 2010). The ambitious Predator Free 2050 project aims to eradicate the "big three" mammalian pests; possums, mustelids, and rats (New Zealand Government, 2016). Therefore, it is not surprising that while there are some studies on the diet and home ranges of feral cats in New Zealand (as mentioned above), there have been few studies on other ecological aspects, particularly activity patterns, reproduction, and genetics. However, this information is vital to inform successful control and eradication programmes. Next, I will outline the aspects of feral cat ecology that I believe to be important for understanding the effect feral cats have in an ecosystem, and knowledge that could be used to develop efficient control programmes.

Home range

Feral cats are often secondarily targeted for control programmes and this leads to fluctuations in their density since only a few individuals are removed over extended periods of time (van Rensburg & Bester, 1988; Parkes & Murphy, 2003). It is not known how these fluctuations in density affect the remaining resident feral cats, particularly in terms of their home ranges. Liberg et al. (2000) identified a strong relationship between the home range size of resident feral cats and their population density, and showed that as population density decreases, the home range size increases. This relationship between home range size and population density was based on different feral cat populations, and it is unknown whether feral cats within a population will behave in a similar manner to changes in population density. It is important to understand whether there are changes in movements and the home ranges of the resident cats following a change in density as the cats may range further to find newly unoccupied areas into which they could expand their home range. If this is the case, then control operations may need to be adapted to ensure success.

Activity

The activity of feral cats is often influenced by the availability and activity of their main prey species (Garvey, 2016). Feral cats are mainly nocturnal, though this can vary based on other predators being present and the main prey that they are hunting. This flexibility in the timing of activity may increase the vulnerability of depredation for native species that are active at the same time as cats. In New Zealand, this is of major concern because many of our native species are nocturnal (Holdaway, 1989). Describing the activity of feral cats is also important because control operations often use live-traps to capture and remove feral cats while reducing the risk of euthanising pet cats. Other control methods, such as poison baits or disease, are indiscriminate between feral and house cats so are often not used in human-inhabited areas. It is not known when feral cats are most likely to visit live-traps, and whether they visit traps more when they are the most active. Feral cat activity can be used to determine when live-traps should be set and checked to reduce catching non-target species and increase catching efficiency.

In previous studies, feral cat activity in New Zealand has been estimated using differences in diurnal and nocturnal home range size (Langham & Porter, 1991), and using active and inactive radio-transmitter signals (Alterio & Moller, 1997b). There is opportunity to investigate new methods such as camera traps, which are used widely overseas (Burton et al., 2015; Caravaggi et al., 2017). Camera traps can target many individuals at the same time, are non-invasive, and can collect data for prolonged periods. However, camera traps are sampling fixed points and they can only detect an animal if it walks in front of the camera. There have been no published studies on whether the activity patterns as determined by camera traps reflect activity as determined using other methods. So, there is a need to investigate whether the activity of feral cats determined from camera trap data reflects other indices of activity.

Reproduction

Feral cat populations are often reduced through control operations but are often not eradicated. This means that the population can recover and increase to their original size following control operations (Campbell et al., 2011). The initial reduction in population size and reproductive and recruitment rates of an invasive species determine the speed at which a population can recover from control (Veltman & Pinder, 2001; Melero et al., 2015). For example, following the control of mink (*Neovison vison*) in the Cairngorms National Park (Scotland), Melero et al. (2015) predicted higher fecundity in reinvading females and in those occupying a newly eradicated area. This was due to an inverse relationship between the density of mink and litter size (Melero et al., 2015). House and colony cats can have large litters and multiple litters a year, therefore feral cats could have high reproductive and recruitment rates (Robinson & Cox, 1970; Ogan & Jurek, 1997). There is very little information available describing the reproductive potential of feral cat populations. This information could be used to determine how many individuals could be replaced through reproduction and, therefore, the minimum number of individuals that need to be removed from a population in order to see a noticeable decline in population size. Information on the reproduction of feral cats could also be used to estimate the recovery of feral cat populations to control.

The use of dens by female feral cats and kittens has also been described in little detail in previous studies (Langham, 1992). Females are unlikely to move far from dens when kittens are young (as seen in lynx (Jędrzejewski et al., 2002)), and are most likely to hunt prey species in areas close to their dens. Identifying the habitat types that females use for dens may help identify areas in which prey species may be more vulnerable to feral cat depredation. Monitoring feral cat movements during different reproductive phases will also provide information on whether female cats have reduced movements when they have young kittens. If this is the case, then this information can be used to determine the timing of control programmes so that females are also targeted.

Kittens are difficult to monitor as they are kept in dens, and tracking them requires specialised devices attached to collars or harnesses that expand as the kittens grow (Kitchener, 1991; Clark et al., 2015). Due to these difficulties, only one published study has reported causes of mortality in feral kittens (Apps, 1983). In that study, six kittens were found that had died from natural causes including starvation and upper respiratory tract infections (Apps, 1983), and there have been no studies that have measured feral kitten growth. Identifying causes of mortality could provide information on what naturally limits population growth of feral cats.

Genetics

Feral cats can have varied mating systems, from polygynous to promiscuous, dependent on population density (Say et al., 1999; Say et al., 2002). There has been evidence of multiple paternity within feral cat litters (Say et al., 1999), and multiple paternity is often used by female mammals as a strategy to reduce infanticidal behaviour from males (Wolff & Macdonald, 2004). Few studies have combined parentage analyses with ecological data such as home range overlap between potential fathers and the females (Say & Pontier, 2004). Trapping and control are often male-biased (see Chapter 7 and Appendix B), and the removal of males could reduce the competition between males for access to females.

Eradication and control of pests is a difficult and ongoing process, mainly due to the threat of reinvasion of animals into a newly eradicated area, and continuous immigration from connecting populations (Parkes & Murphy, 2003). Study of the genetic structure of a population can help identify whether there have been any new introductions into an area and whether there is gene-flow with peripheral populations (Ficetola et al., 2008). Identifying isolated populations of pests, such as those in island ecosystems, increases the likely success of eradication attempts (Parkes et al., 2017). Feral cat dispersal is largely human-mediated, and their establishment on offshore islands was due to introductions by people (Koch et al., 2016). Despite the release of cats or pest species on to islands being illegal (New Zealand Government, 1999) people may still release unwanted cats, or pet cats may escape on inhabited islands potentially leading to the establishment of a feral population (Atkinson, 1973). There has been only one study that has looked at the genetic structure of feral cats in a mainland population (in Southland) (Cross, 2016) and no studies that have assessed this in offshore island populations in New Zealand.

Diet

Feral cats have had devastating effects on native fauna since their introduction to New Zealand. The recent New Zealand Government (2016) announcement of a plan to eradicate possums, mustelids, and rats whilst leaving feral cats uncontrolled in many areas has led to a need to better understand the impact that feral cats have on native fauna. Feral cats compete with mustelids for access to small mammal species and birds (Gillies & Fitzgerald, 2005; King & Murphy, 2005). There have been a few studies that have assessed feral cat diet where there are no mustelids, and where cats are the top predator (Karl & Best, 1982; Fitzgerald & Veitch, 1985; Fitzgerald et al., 1991; Harper, 2005). Dietary resource partitioning, where coexisting predators have some degree of separation in their diet to reduce interspecific competition, can occur in species with similar niches (Schoener, 1974; Kitchen et al., 1999). Feral cats may have a different diet in areas where stoats are absent than in areas where stoats are present.

Rats are the main prey for feral cats in many areas, with evidence of their ingestion in 90% of scats or gut contents analysed in some studies throughout New Zealand (Dilks, 1979; Karl & Best, 1982; Gillies & Fitzgerald, 2005). The high consumption of rats in some areas means that removal of rats could lead to reduced feral cat densities through coupled predator-prey responses as described previously (Sinclair, 2003). The removal of rats may not reduce feral cat populations in areas where; rats are a smaller part of the diet of feral cats, cats consume rats based on their seasonal availability, or when alternative prey is available. This is because feral cats show flexibility in their diet, often consuming prey species that are seasonally available (Borkin, 1999; Bonnaud et al., 2011), and the removal of rats may lead to increased depredation pressures on native fauna.

Stoats are targeted for control in areas where kiwi are present, due to their high rates of depredation on kiwi chicks (McLennan et al., 1996). Wilson (2013) found that on Ponui Island, where stoats are absent, 29% of kiwi chicks monitored died from cat depredation. The removal of stoats, but not feral cats, from areas with kiwi may reduce overall depredation pressure but may incidentally increase depredation from feral cats.

Feral cats are sexually dimorphic in body size (Gillies & Fitzgerald, 2005), and this could lead to the smaller female consuming smaller prey than the larger male. Two studies have identified sex differences in diet in feral cat populations (Middlemiss, 1995; Pascoe, 1995). Both had small sample sizes and were based on gut content analysis (Middlemiss, 1995; Pascoe, 1995). Felid-specific sex primers (Pilgrim et al., 2005) could be used to identify the sex of the cat that deposited a particular scat, potentially allowing for larger sample sizes to be obtained and greater analysis on dietary differences between male and female cats. Identifying dietary differences between males and females is important for management programmes considering there is a bias in the sex ratio of feral cats live-trapped; more males are captured than females. The removal of mainly male cats from a population may reduce the depredation pressure on some prey species, but other species may still be threatened by the remaining female cats.

Integrating knowledge on feral cat ecology for control operations

Knowledge on home range size, activity, reproduction, genetics, and diet of feral cats can be used in a decision as to whether a feral cat population should be eradicated or controlled, and how the population could be controlled. There have been at least 146 eradication attempts for feral cats globally on 129 islands, of which 102 were successful (DIISE, 2015). One of the main reasons for eradication failure has been the use of removal techniques that were inappropriate for the targeted population, such as hunting feral cats in habitat consisting of long-grass (Campbell et al., 2011). An eradication method might be successful for one population, but it might not be an appropriate method on another population due to factors such as habitat differences, feral cat population size, or the presence of vulnerable species. The most successful eradications, where populations were eradicated in less than a month, were those that used several removal techniques, and where the ecology of the feral cats was studied first and this information was used to develop an eradication protocol (Algar et al., 2010; Campbell et al., 2011; Robinson et al., 2015).

Doherty and Ritchie (2017) suggested that the first step to controlling or eradicating a pest population is to study their interactions with native and introduced species, and then to control the pest. The interactions between the pest and other species need to be understood so any cascading effects in the ecosystem can be mitigated. Understanding the ecology of the pest also allows the development of specific control plans that would be the most efficient for removing that population. This would reduce the overall cost whilst increasing the chances of success.

Thesis structure

The central aim of this thesis was to study and understand different aspects of feral cat ecology in an area where it is a top predator in the presence of a threatened New Zealand species (North Island brown kiwi), and to use this knowledge to inform management strategies for feral cat control. This study is unique in that multiple aspects of feral cat ecology were studied concurrently, with the objective in mind of understanding the impact these predators have on native species, and to use knowledge of feral cat ecology to develop more efficient feral cat control. This thesis has been divided into six main research questions that formed the basis for each chapter.

Population density is dependent on resources such as food and shelter, and while home range is also influenced by these resources, cats also distribute themselves according to access to mates. It is known that there is a relationship between the density of feral cat populations and the home range size of the resident cats, however, this relationship has not been tested within a population. In Chapter 2, I addressed the following question: does a change in feral cat density lead to a change in home range size of the remaining resident cats? I hypothesised that after the removal of male cats from the population, the remaining cats would increase their home range size. I used and compared two methods for estimating home range: radio-telemetry and camera trapping.

Feral cats are often live-trapped during control operations to reduce the chances of pet cats being accidentally euthanised, and it is currently unknown whether feral cats visit traps when they are the most active. Camera traps have become a more common technique used to describe the activity of wild animals, due partly to its non-invasive nature to monitor animals. However, it is unknown whether the activity detected by camera traps reflects the activity of the species using other techniques. This led me to my main research question in Chapter 3: do feral cats visit traps when they are the most active, and does the activity detected by camera traps reflect the activity detected by accelerometers? I hypothesised that feral cats would visit traps when they are the most active (between dusk and dawn), and that the activity detected by camera traps would be similar to the activity detected using collar-mounted accelerometers.

Very little is known about the reproductive biology of feral cats, and there were three main aspects that I identified as being important to management protocols. While it is known that domestic cats can have large litters, and multiple litters per year, it is not known whether these reproductive parameters are maintained in the wild, how many juveniles survive, and the cause of juvenile mortality. The recruitment rate has been measured in two feral cat populations, however, the populations had undergone a recent reduction in density, and population size was increasing. Females can have restricted movements when they have dependent young, and there have been no studies that have investigated the ranging behaviour of feral queens during different reproductive phases. This led to the following research question, addressed in Chapter 4: what are the causes of mortality in feral kittens, what is the recruitment rate for a stable island feral cat population, and do queens change their ranging behaviours during different reproductive phases? I hypothesised that causes of juvenile mortality would mainly be from natural causes, such as disease and starvation, and that the recruitment rate for the stable Ponui Island population would be low. I also hypothesised that feral queens would have restricted ranging movements when they had young kittens. I used radio-telemetry, camera trap data, and post-mortems to answer this research question.

Population genetics allows conservation scientists to identify genetically isolated populations, and is also used by managers to identify populations of pests that have a high chance of successful eradication. Although island populations are geographically isolated, there is the potential for human-mediated introductions of new cats. I investigated whether an island population that was established over 100 years ago and is located close to a major city, was genetically isolated. My research question for Chapter 5 was: is the Ponui Island feral cat population genetically isolated? I hypothesised that the population would be clustered separately to mainland populations, indicating genetic isolation. I extracted DNA from hair, blood, tissue, and bone, genotyped the samples, and used population genetic software to answer the research question.

Feral cats have varied diets across New Zealand, dependent on the prey species available. Rats have been identified as the main prey eaten by feral cats in many populations throughout the country, and it is thought that high availability of rats may reduce the depredation rates on native fauna. I addressed the following research question in Chapter 6: are feral cats depredating native species when there are high densities of rats available? I hypothesised that feral cats would be depredating native species throughout the year, and that depredation on native fauna would increase during seasons of low rat density. I collected scat samples year-round and analysed their contents to address this question.

Knowledge of the ecology of feral cats could be used to design control protocols that are tailored to feral cat populations, and are more efficient at eradicating the population. In Chapter 7, I used the knowledge gained from this thesis on feral cat ecology to aid the development of effective control programmes targeting feral cats.

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Chapter 2 – Changes in feral cat home range in response to an experimental removal of males: Considerations for control operations.

Plate 2: Photo showing part of the study site taken from the Eastern ridge transect (taken by author).

Introduction

While knowledge of the predator-prey dynamics (Chapter 1) of feral cats is essential to understand their impacts on prey species, it is important to study their movements and ranging behaviours to be able to manage feral cats effectively. This knowledge can help managers to estimate optimal trap spacing, informed by how far the targeted animals move (Smith et al., 2015). The degree of home range overlap between cats in the population would also help estimate the number of traps required within a specific area (Bengsen et al., 2012; Smith et al., 2015).

The home range is an area that an animal frequents and uses for obtaining resources, such as food (Burt, 1943). Prey availability is, therefore, a key driver in determining the home range size for most animals, including feral cats (Burt, 1943; Liberg et al., 2000). Cats studied on Stewart Island had large home range sizes (mean ± SE (ha); males = 2083 ± 457, females = 1109 ± 53), which Harper (2007) suggested may be the result of low prey availability. Norbury et al. (1998a) estimated home range size of feral cats and ferrets (*Mustela furo*) before and after poisoning rabbits (*Oryctolagus cuniculus*) in Central Otago and the Mackenzie Basin. A 99% reduction in rabbit population size caused an increase in the home range size for both species, though a small sample size of cats made this relationship less clear (mean ± SE (ha); ferrets, before = 85 ± 12, after = 230 ± 48; feral cats, before = 155 ± 53, after = 499 ± 319) (Norbury et al., 1998a). These studies support the idea that food abundance may be an important factor for determining home range size in feral cats.

Habitat type can also influence the home range size of feral cats, though this may be confounded with prey availability, because prey may be more abundant in certain habitat types. McGregor et al. (2015a) found that the feral cat home ranges in semi-arid areas in Australia containing 40% riparian vegetation were approximately 500 ha in size. Cats that had home ranges containing no riparian vegetation were estimated to be twice the size (1000 ha) (McGregor et al., 2015a). This was most likely related to the higher small mammal abundance found in riparian vegetation (Legge et al., 2011; McGregor et al., 2015a). In braided river systems in New Zealand, feral cats were distributed based on habitat type and landscape features that sustained higher rabbit densities (Recio & Seddon, 2013). Although prey may be more abundant in particular habitats, they may not be as easy for the cats to hunt. Collar-mounted cameras in north Australian tropical savannah showed that feral cats were more successful in capturing prey at open areas than dense grass or rocky areas (McGregor et al., 2015b).

There are sex differences in home range size in feral cats. Typically, male cats have a larger home range than female cats (Table 1). Although the male is both heavier (weight) and larger (head-body length) than the female (Gillies & Fitzgerald, 2005), and has higher activity levels (Chapter 3), differences in the home range size between the sexes are not explained by differences in weight or energy requirements, suggesting that home range size is influenced by factors other than prey abundance exclusively (Liberg et al., 2000). Males may distribute themselves to increase their access to females. Intact males have been found to have larger home ranges than neutered male cats (Turner & Mertens, 1986; Barratt, 1997), and Mirmovitch (1995) and Corbett (1979) both reported increases in the home range size of intact males during the breeding season.

The previous studies mentioned above suggest that home range size is influenced by many different factors, making it difficult to predict the spatial distributions of feral cats. However, Liberg et al. (2000) has shown that there is a strong positive correlation ($R^2 > 0.83$) between the density of cats and home range size in both mainland and island studies. At higher densities, both male and female cats had smaller home ranges (Figure 1). Females appear to follow the relationship more closely than males (females, $R^2 = 0.841$; males $R^2 = 0.791$) (Jones & Coman, 1982; Apps, 1983, 1986; Fitzgerald & Karl, 1986; Page et al., 1992; Norbury et al., 1998a; Edwards et al., 2001; Harper, 2007; Bengsen et al., 2011, 2012) (Figure 1). There appears to be a strong relationship between the home range and the population density, suggesting that density is likely to be influenced by similar factors as home range, such as prey availability, habitat type, and sex.

The home range versus density relationship has been identified by assessing the home range sizes and densities of different feral cat populations. In this thesis, studies were selected based on those that reported both home range size and density for feral cat populations, and that used robust and similar methods for estimating population density (such as mark-recapture techniques) and home range analysis. Home range estimates using 100% Minimum Convex Polygon (MCP) methods were used for consistency. Care must be taken interpreting the results because some of the study sites were islands with natural boundaries to feral cat movement, whereas other study sites were on the mainland.

The strong relationship between population density and home range size of feral cats identified by Liberg et al. (2000) has only been assessed using different populations of feral cats, and it is not known how a change in population density affects the home range sizes of the remaining resident cats. At present, feral cat control in New Zealand is less of a conservation focus than mustelid, rodent and possum (*Trichosurus vulpecula*) control (Parkes & Murphy, 2003). When cats are controlled, often only a few cats are removed over long periods of time. Their populations, therefore, experience continuous density fluctuations (van Rensburg & Bester, 1988), and there is very little information on how surviving feral cats respond to these changes in density caused by the death or removal of some cats. The home range versus density relationship suggests that the reduction in density would lead to an increase in home range size of the remaining cats. It is also possible that feral cats respond to these density fluctuations by filling unoccupied areas through immigration, or extending their territory after control operations (Liberg et al., 2000; Oliver et al., 2016), which could make opportunistic culling of feral cats an ineffective population control method.

Despite feral cats often being targeted for removal on offshore islands (Campbell et al., 2011), there is a lack of information on the size of home ranges of feral cats in insular environments. There have been several studies on the home ranges of feral cats on mainland New Zealand (Fitzgerald & Karl, 1986; Norbury et al., 1998b; Moller & Alterio, 1999; Gillies et al., 2007; Harper, 2007; Recio et al., 2010; Recio & Seddon, 2013) (Supplementary material; Table S1), but only one study has been conducted on an offshore island (Motuihe Island) (Dowding, 1998). These studies have looked at feral cat movements in various habitats, including around braided rivers (Recio & Seddon, 2013), native forest (Gillies et al., 2007), and farmland (Langham & Porter, 1991), and the home ranges of the cats varied greatly depending on the habitat they inhabited. The cats on Motuihe Island were at a higher density (16.8 cats/km^2) than those on the mainland (Fitzgerald & Karl, 1986; Harper, 2007) and had small home ranges (47 ha) (Dowding, 1998) (Supplementary material: Table S1). The home range size of feral cats on Motuihe Island was restricted because the island has a total area of 179 ha (Dowding, 1998).

Home range size and movements of feral cats have been monitored using Very High Frequency (VHF) radio-telemetry, and more recently Global Positioning System (GPS) collars (Kie et al., 2010). Radio-telemetry is a well-established technique and is often the standard that other monitoring methods are compared to. While GPS technology allows finer-detail on habitat use and movements of individuals (McGregor et al., 2016), and is less labour intensive because the animals do not need to be manually tracked (as with VHF technology), the GPS units are relatively expensive, often requires recapturing the study animals to obtain the data, and can have low GPS fix rates in dense forest (Recio et al., 2011). There has been a recent move towards using camera traps to monitor wild animals, particularly carnivores (Burton et al., 2015; Caravaggi et al., 2017). Camera traps are often used to obtain other information on animals, such as density, behaviour, and daily activity (Burton et al., 2015; Caravaggi et al., 2017). No published studies have estimated home range sizes from camera trap data, but this is a real possibility, provided the animals can be individually recognised.

In this study I investigated the home range of a population of feral cats on a New Zealand offshore island using camera traps and radio-telemetry. I used removals of males (either natural deaths or culls) to test the hypothesis that other cats in the area would increase their home range as a result. I hypothesised that a reduction in feral cat density would lead to an increase in home range of the remaining feral cats, following the home range versus density relationship that has been identified in the literature (Liberg et al., 2000). A secondary aim was to assess camera traps as a method to measure cat home range sizes.

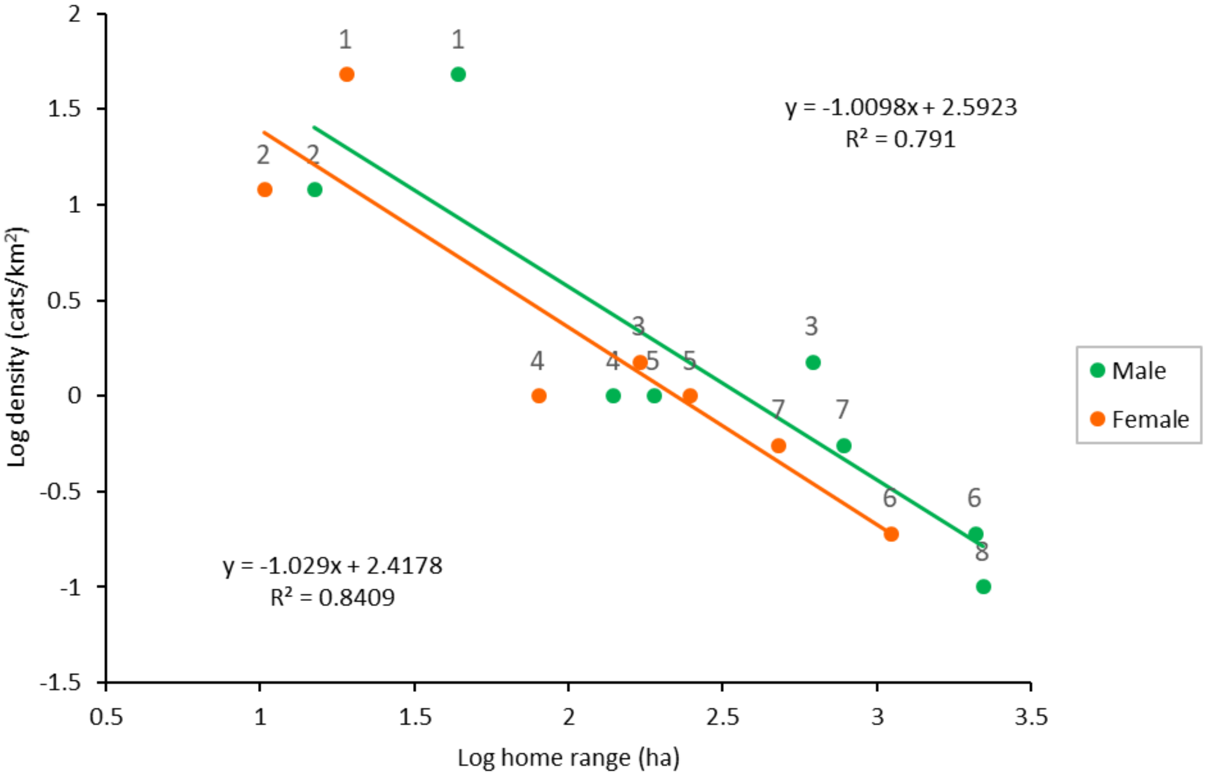

Figure 1: Relationship between home range size and population density of female and male feral cats in eight different populations. Values are presented as the logarithms of data presented in Table 1. Regression trend-lines and equations are shown; males at the top right, females at the bottom left in the graph. Numbers next to points are the study numbers from Table 1.

Table 1: Modified table from Liberg et al. (2000) showing a summary of the home range sizes and population densities of feral cats. The table includes data for a range of factors that may affect the home range size or density of feral cats, such as habitat type and prey abundance (when available). – indicates where data were not presented in the studies. Home range sizes are presented as averages ± SE.

Study No.	Reference	Location	Study area (km^2)	Habitat	Method	Food type	Prey Abundance	Population density ($cats/km^2$)	Female home range (ha)	Male home range (ha)
1	Apps (1983, 1986)	Dassen Island, South Africa	2.24	Subtropical scrub	Radio-telemetry and sightings	Prey	4.46-8.93 rabbits/ha	16.5-48	19 (11-32)	44 ± 3
2	Page et al. (1992)	Avonmouth, England	1.8	Docks	Radio-telemetry and sightings	Supplementary feeding and prey	-	9-15	10 (3-18)	15 ± 4
3	Jones & Coman (1982)	Victoria, Australia	190	Grassland	Radio-telemetry	Prey	12-30 rabbits/km	1.5	170 (70-270)	620 ± 156
4	Norbury et al. (1998a)	Otago District and MacKenzie Basin, New Zealand	10-60	Tussock grassland	Radio-telemetry	Prey	83-155 rabbits/km	0.6-1.4	249 (79-840)	189 ± 73
5	Fitzgerald & Karl (1986)	Orongorongo Valley, New Zealand	15	Grassland, bush	Radio-telemetry	Prey	0.7-9 rats/ha	1	80 (20-170)	140 ± 56
6	Bengsen et al. (2011, 2012)	Kangaroo Island, South Australia	15-30	Grassland, bush	GPS	Prey	-	0.4-0.7	480 (287-818)	780 ± 182
7	Harper (2007)	Stewart Island, New Zealand	36	Bush, shrubland	Radio-telemetry	Prey	2.94 rats/100 trap nights	0.19	1109 ± 53	2083 ± 457
8	Edwards et al. (2001)	Northern Territory, Central Australia	550	Grassland, bush, shrubland	Radio-telemetry	Prey	-	0.1	-	2210 ± 234

Methods

Study site

This research was carried out on Ponui Island (latitude 36° 55'S, longitude 175° 11'E); most of the work was concentrated at the southern end (approximately 600 ha). The island is in the Hauraki Gulf, 30 kilometres off the eastern side of Auckland, New Zealand (Brown, 1979) (Figure 2A). This study site was selected due to the well-established feral cat population that was introduced in the 1850s (Gillies & Fitzgerald, 2005). There has been limited control of the feral cats on the island over time, and this has been through occasional shooting of cats by the farmers. The long period of establishment and low levels of control suggests that the feral cat population is likely to be at carrying capacity.

The island is 1770 ha, characterised by a series of large ridges, separated by deep gullies, plus areas of swamp (Bellingham, 1979; Brown, 1979; Colbourne, 2005) (Figure 2B). The island is divided into, and managed, as three roughly similar sized farms. John Spencer owns the northern farm (Northern Ponui), Richard Chamberlin the central farm (Central Ponui), and Peter and David Chamberlin the southern farm (Southern Ponui) (Figure 2B) (Miles & Castro, 2000). Ponui Island has a highly modified landscape; the northern half of the island consists mainly of farmland and pasture while the southern half has remnant primary forest consisting of kauri (*Agathis australis*) and broadleaf trees, with one large fragment (250 ha) of forest in the middle of the island (Brown, 1979). The island has been farmed since the 1850s. The kauri forest has been left to regenerate, particularly in Central Ponui farm where it is fenced. In Southern Ponui the forest is generally undisturbed, except for the occasional grazing by sheep and cattle.

Ponui Island has low mammalian diversity compared to other places in New Zealand because rabbits, possums, and hares (*Lepus europaeus*) never established on the island (Miles & Castro, 2000). The only mammalian prey available to feral cats are ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), and mice (*Mus musculus*). Ship rats reach high densities peaking at 22 rats/ha in winter (Shapiro, 2005; Latham, 2006). No other mammalian predators are present on Ponui Island; stoats (*Mustela erminea*) have not been resident on the island for twenty years although the presence of visiting stoats has been detected occasionally. There are six farm dogs living on the island, but they are in kennels at night and working with the farmers during the day, so they do not roam very far from the houses.

The island also has diverse native bird species, including brown kiwi (*Apteryx mantelli*). In 1964, at the request of Peter Chamberlin, six North Island brown kiwi from Little Barrier Island and eight from Waipoua Forest were translocated to Ponui Island (Brown, 1979; Miles & Castro, 2000; Colbourne, 2005). The latest estimation of the kiwi population density is 1 kiwi/ha (Cunningham et al., 2007), making this population one of the highest densities in New Zealand. Kaka (*Nestor meridionalis*), kereru (*Hemiphaga novaeseelandiae*), New Zealand dotterels (*Charadrius obscurus*), small passerines, and other native bird species inhabit the island. There are also many introduced birds, particularly Indian mynas (*Acridotheres tristis*), magpies (*Cracticus tibicen*), and a small population of galahs (*Eolophus roseicapilla*). Reptiles are rarely seen on the island but shore and copper skinks (*Oilgosoma smithi* and *O. aeneum*) have been seen on the island.

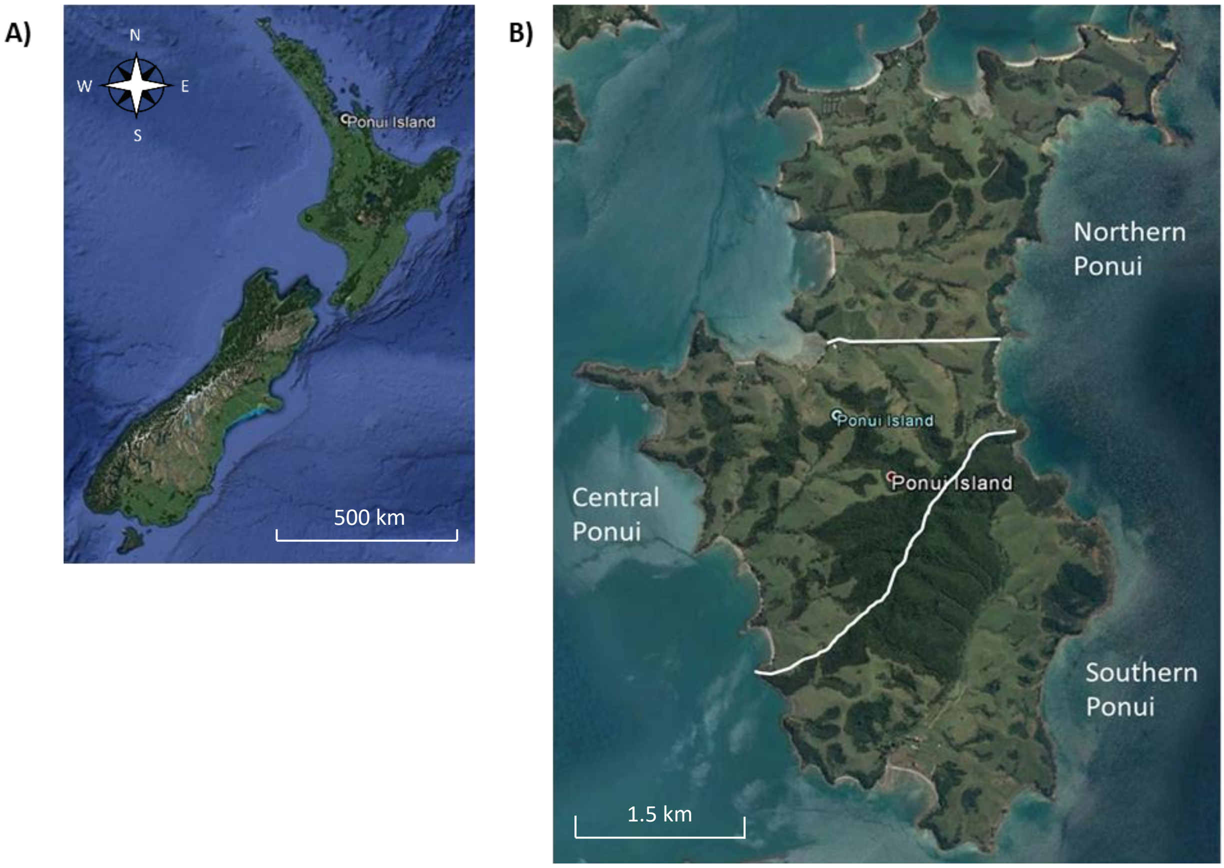

Figure 2: A) Satellite photo of New Zealand showing the location of Ponui Island in the North Island. **B)** Satellite photo of Ponui Island showing the division into three privately-owned farms (Google Earth, 2017). Most of the work in this study was carried out in Southern Ponui.

Baiting phase to attract cats to live-traps

Baiting and trapping methods were based on previous live-trapping studies (Supplementary material: Table S1) and advice from Lee Shapiro at Connovation Ltd.

To capture feral cats three different live-traps were used: two Havahart® large collapsible traps (length x width x height) (82 x 26 x 31 cm high), six possum traps (71 x 31 x 31 cm), and three wooden box cat traps (60 x 31 x 32 cm). I used different live-trap designs because they could be borrowed from the Department of Conservation, City Council offices, and local trappers. To ensure all cats in the area were targeted, I selected the live-trap locations using the number and identity of cats detected in videos captured by camera traps set up and moved around Southern Ponui from January 2014 - January 2015 (Figure 3A).

Eleven live-traps were set up in January 2015 on trails regularly used by cats in preparation for live-trapping in April 2015 (Figure 3B). Two other live-traps were used after the first trapping period because new uncaptured cats were seen at these camera trap locations (Figure 3B). For the first trapping period, live-traps were baited for 54 days starting from January 2015 until the first live-trapping period in April 2015, equating to a total of 594 baiting nights. Live-traps were weighed when they were placed out. During the baiting phase, the door of the cage was wired open so that the cat could freely enter and exit the cage. Live-traps were baited for this length of time to increase the chances of recapturing cats throughout the study, and to increase the chance of live-trapping all the cats in a short time (within a week). The main bait used was a mixture of commercial cat biscuits, chicken necks, and fish oil. Tinned fish, rabbit meat, strips of beef, and commercial canned wet food were used occasionally for bait. I switched the bait type to keep the cats interested in returning to the live-traps.

Before all other trapping periods, the live-traps to be used were baited every day for at least two days prior to being set. Again, this was to encourage the cats to return to the live-traps each night. At the end of a live-trapping period, the trap doors were wired open and live-traps remained in the field for the entire project from January 2015 - January 2017.

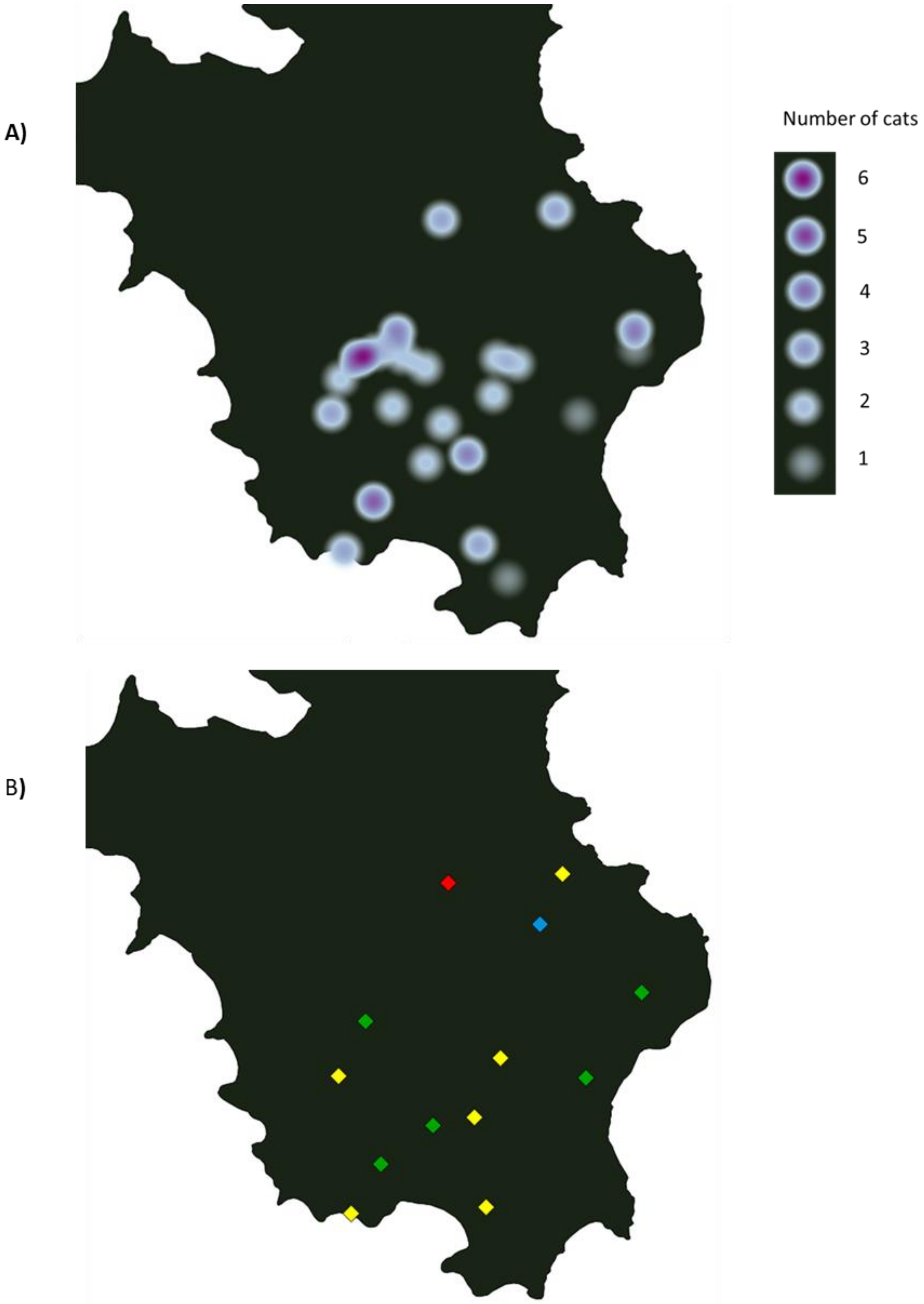

Figure 3: A) Heatmap showing the number of individual cats detected at camera trap locations from January 2014 - January 2015 around Southern Ponui Island. **B)** Map of the study site showing the set-up of live-capture traps during the study. Yellow and green diamonds represent the live-traps used in the April 2015 trapping period. The green diamonds (as well as the red diamonds) also represent the live-traps used from April 2015 - January 2017. The live-trap represented by the blue diamond was used from December 2015 - April 2016; the camera was set up in this location from September 2015 - March 2017 so is not present in the heatmap above. Both maps were created in QGIS.

Live-trapping

Feral cats were captured during eight trapping periods, totalling 143 trap nights. Live-traps were set for two to five nights in two months of 2014, five months of 2016, and one month in 2017 (Table 2). A total of 12 individual cats were captured, with 13 recaptures. The number of live-traps set during a trapping period varied (Table 2). Once all of the known cats were caught in an area, that live-trap was closed for the rest of the trapping period. This was to reduce the chances of recapturing a cat that had just been caught, reduce the amount of stress caused by capture, and reduce trap shyness. Live-traps were not set if the weather forecast indicated imminent rain or high wind, to reduce the cats' exposure to the elements.

Live capture started once the wire was removed from the trap doors. A camera trap was set up outside each trap to see which cats entered the live-traps, the time of day they visited, and how long they stayed at the live-traps during the baiting phase. This information was used to determine time of capture. During the first live-trapping period (April 2015) live-traps were set throughout the entire day and night and were checked at 17:00, 22:00, and 06:00 h. Live-traps were not checked during the day because this was when the cats visited the live-traps least often. During the rest of the trapping periods, the live-traps were set between 16:30-06:00 h because cats mainly visited the traps at night (see Chapter 3 for more detail). The traps were checked twice a night while they were set, at 23:00 and 05:00 h. This change in protocol between the first and successive trapping periods was due to more people being available in the first trapping period to check traps. Live-traps were set for 14 hours a day (set at 16:00 h and closed at 06:00 h the following day) during the other live-trapping periods to reduce the chances of cats being stressed by farm animals while in the live-trap.

Live-traps were approached with red lights to reduce the stress caused to the cat from white light. If a cat was caught then the live-trap was covered with a blanket, and the live-trap was left until all of the other live-traps had been checked. Once all the set live-traps were checked, I returned to the traps that had cats. The reason the trap check was carried out this way was to give some cats priority for processing; specifically, pregnant females, those known to have kittens, sub-adults, and cats that were visibly stressed.

The rest of the trapping gear (scales, fluids, anaesthetic) was set up before approaching the live-trap to handle the cat. A crush cage, previously weighed, was attached to the door of the live-trap and both the door to the crush cage and the live-trap door were opened. The blanket was moved from the live-trap to the crush cage to encourage the cat to go into the crush cage. Once the cat was inside the crush cage the door was closed, the blanket was removed, and the cage was weighed. The weight of the cat was calculated from this by subtracting the known weight of the crush cage, and this was used to calculate the mass-dependent anaesthetic dose to be administered. The cat was restrained against the side of the crush cage so that it could not move, and the anaesthetic was administered by injecting the cat through the cage bars (Figure 4A, B). Tiletamine and zolazepam (Zoletil®, Virbac, France) powder had been reconstituted with medetomidine (Domitor®, Vetoquinol, Towchester, UK) prior to live-trapping, and was given at a combined dose rate of 10-15 mg/kg into the cat's quadriceps muscle. Once the anaesthetic was administered, the restraint was released, and the cage was covered with a blanket to reduce stress during induction of anaesthesia.

Table 2: Total number of nights live-trapping feral cats from April 2015 - January 2017 to radio-collar cats or download accelerometry data. The number of live-traps set varied each night as traps were not set if the resident cats in the area had already been trapped in that month. The number of trap nights is a calculation of the number of nights that traps were set and the number of live-traps set each night. The number of new cats caught were cats that had not been live-trapped before, and the number of cat recaptures was the number of cats live-trapped that had been caught previous during a trapping period.

Trapping period	Year	Month	No. traps set	No. nights	No. trap nights	No. new cats caught	No. cat recaptures
1	2015	April	3-11	5	32	7	2
2		December	6-7	3	20	1	4
3	2016	January	3-7	3	15	0	2
4		March	7	2	14	1	1
5		April	7	3	21	0	2
6		June	6	2	12	1	0
7		July	4-6	3	16	1	1
8	2017	January	2-6	3	13	1	1

The possum traps had only one door to the cage and it opened outwards, meaning the crush cage could not be attached to the door without risking the cat escaping. For cats trapped in these cages, the cage was weighed with the cat in it to calculate the cat's weight using the known weight of the cage. The cage was then stood upright, and someone wearing welding gloves loaded towels into the cage to cover the cat. The person with the gloves then restrained the cat in the possum trap using the towels and the cat was anaesthetised through the cage bars. The towels were lifted to ensure the cat had enough room. The cage was then covered with blankets.

Regardless of the live-trap used, the cat was checked for consciousness five minutes after the anaesthetic was administered. The blanket was lifted to see if the cat was still awake. If the cat was conscious after five minutes, it was checked again at ten minutes after being anaesthetised. If the cat was still awake 15 minutes after anaesthesia was administered then the cat was anaesthetised again with Domitor® only, administered at a dose rate of 10 mg/kg, and left for ten minutes. If the cat appeared to be unconscious, the cat was checked more thoroughly, which included gently tapping the eye to check for a palpebral blink reflex.

Once unconscious, the cat was taken out of the cage and laid on a blanket set up with hot water bottles underneath. A corneal lubricant (Lacrilube®, Allergan, Dublin, Ireland) was placed into the eyes of the cat to prevent corneal drying. The eyes were also covered with a blanket for extra protection from light. The heart rate and breathing rate were monitored every five minutes while the cat was anaesthetised. Coat colour and any distinguishing marks were noted and photos were taken. Cats were ear-notched in different patterns based on their sex and coat colour for individual identification on camera traps. Males had their left ear-notched and females their right ear. Ear-notch patterns were repeated for cats with different coat colours. For example, Socks and Cleo both had their inner right ear-notched, but were still individually recognisable because Cleo was black and Socks was a tortoiseshell. Ear-notching involved gently clamping the part of the ear using haemostats to reduce haemorrhage, and cutting off a triangle of tissue (measuring 5 mm each side) with a pair of scissors (Figure 4C). Ethyl cyanoacrylate glue was applied to the wound to facilitate wound closure.

Hair was clipped from the ventral part of the cat's neck and the area wiped with an ethanol swab in preparation for blood sampling and to expose the jugular vein (Figure 4D). A sample of 3 mL of blood was taken from the jugular vein of the cat and placed in an EDTA (Ethylenediamine tetraacetic acid) anticoagulant tube. Blood samples could not be taken from every live-trapped cat, possibly due to low venous blood flow under anaesthesia.

Each cat was sexed; females were examined for signs of pregnancy or lactation, and males were checked for cryptorchidism which could affect their reproduction potential. Cats were given a body condition score (scale from 1-5 where 1 is severely underweight and 5 is morbidly obese (Lund et al., 1999)), and were microchipped under their skin at the back of the neck. The dentition was examined for deciduous teeth, plaque build-up, and dental fractures, and the cat was flea-combed to check for ectoparasites. The head-to-body length was measured from the tip of the nose to the base of the tail. The tail length and distance between upper canine teeth were also measured.

VHF collars (Kiwi Track Ltd., Havelock North, New Zealand) with a 220 mm whip aerial were placed on the adult cats, with each cat having a different radio-frequency for individual identification (Figure 4E, F). The transmitter was turned on using a magnet, and a receiver was used to check it was working before being placed on the cat. A pattern of reflective tape was placed around the collar prior to attachment for identification on the infra-red camera traps. Transmitters had an in-built mortality function, where the signal output was 80 beeps per minute (normal output = 60 bpm) if the transmitter had not moved for 48 hours. Accelerometry devices (Heyrex™, Say Systems, Wellington, New Zealand) were also attached to radio-collars when feral cats were trapped between December 2015 - July 2016 (Chapter 3). The feral cats that were trapped from January 2016 - January 2017 had the data remotely downloaded from the accelerometry devices (for more details see Chapter 3).

When all of the samples and measurements were taken the cat was wrapped in extra towels and blankets. The cat was given 10-20 mL of warmed fluids subcutaneously. Atipamezole (Antisedan®, Vetoquinol, Towcester, UK) was used as a medetomidine antagonist if the cat did not show sign of recovery from the anaesthetic from one hour after it had been anaesthetised. The cat was placed on blankets and hot water bottles in a scrub-covered area. Once the cat started to move its head it was covered by an upside-down box with an opening cut out (Figure 4G, H). This was so that the cat could recover quietly and move away when it was ready. The box also gave the cat some protection from particularly curious farm animals (cattle and donkeys). The cats were left to recover under the box as opposed to inside the live-trap to reduce the association with the live-trap and capture, and potentially reduce trap avoidance. A camera trap was set up to film the cat leaving the box to see that the cats had recovered from the anaesthesia after we had left the area. Later that day, the receiver was used to check if the cat was in the live-trap area and had recovered from the anaesthetic, and the box and equipment were recovered.

All live-trapping and handling protocols were approved by Massey University Animal Ethics Committee 14/122.

Figure 4: Methods used for processing live-trapped cats. **A, B** – Restraining the cat and anaesthetising it in the crush cage. **C** – Clamping the ear and applying glue during ear-notching. **D** – Socks with her right inner ear-notch and prepared for blood sampling. **E** – Collar about to be placed on Tui showing his unique pattern of reflective tape. **F** – Camera trap footage of Midnight showing collar and ear-notch (left inner ear). **G** – Midnight being released under a box to recover. **H** – Camera trap footage of Midnight coming out of the box.

Tracking through radio-telemetry

Cats with radio-transmitters were tracked using an Osprey receiver (H.A.B.I.T Research Ltd., Victoria, Canada) and a Yagi three element antenna (Sirtrack®, Hawke's Bay, New Zealand). Locations of cats were determined through triangulation. Twenty-five triangulation sampling locations were placed at uneven spacing on two, 5-5.5 km long transects along the two main ridges (eastern and western) in the study site (Figure 5). Triangulation points were selected on high ground overlooking gullies to minimise the number of signal blind spots. Transects were walked during the day between 08:00-16:00 h for at least five days every month. These hours were chosen to ensure the cats were least active and reduce inaccuracies in triangulation (Jones & Coman, 1982; Recio et al., 2010; Garvey, 2016).

Two people worked together with one person walking the eastern transect and another person the western transect. At each triangulation point, each person would stop and search for every cat and record the time, the triangulation point, and whether they detected a signal from any of the cats. If a cat's signal was heard, the direction of the strongest signal was found, and a compass was used to find the bearing which was recorded. If the cat was close, the gain (signal strength) on the Osprey receiver was turned down until the signal could only just be heard, and this number was recorded. If a cat had only been heard from two different transect points then all effort was made to obtain an additional bearing on the cat from a third location, not necessarily one of the established triangulation sampling points. This was treated the same as any other transect point (with information noted), but the coordinates of the point from which the signal was heard were also recorded.

Opportunistic tracking with the receiver and antenna was also carried out when there was the chance to join barge trips around the island that were organised by the owners of South Ponui. All cats were searched for around the entirety of the island. The island's terrain necessitated that every bay was investigated to ensure that each coastal gully was searched. If a cat's signal was heard, then an attempt was made to obtain bearings from three different points (with the coordinates of search points taken) in the bay from the barge to be able to triangulate the position. Three barge trips with searches were done throughout the study.

Bearings collected each day from an individual cat were entered into Google Earth Pro. This was in the form of lines from the transect points going in the direction of the cat's position. The cat's position was labelled where the lines intersected (Figure 6). Bearings that were clearly from bouncing signals were discarded (e.g. when one bearing was in the opposite direction to the other bearings taken). The coordinate for the cat's position was entered into an Excel spreadsheet. At times cats were seen or located by honing in on their position using radio-telemetry. Once found, the GPS coordinate was recorded using a Garmin GPS unit, and a photo was taken of the area. All location coordinates from radio-telemetry and camera trapping were entered into Ranges Software version 9, QGIS and R (R Development Core Team, 2008) to determine Minimum Convex Polygons (MCP) and Kernel Density Estimation (KDE).

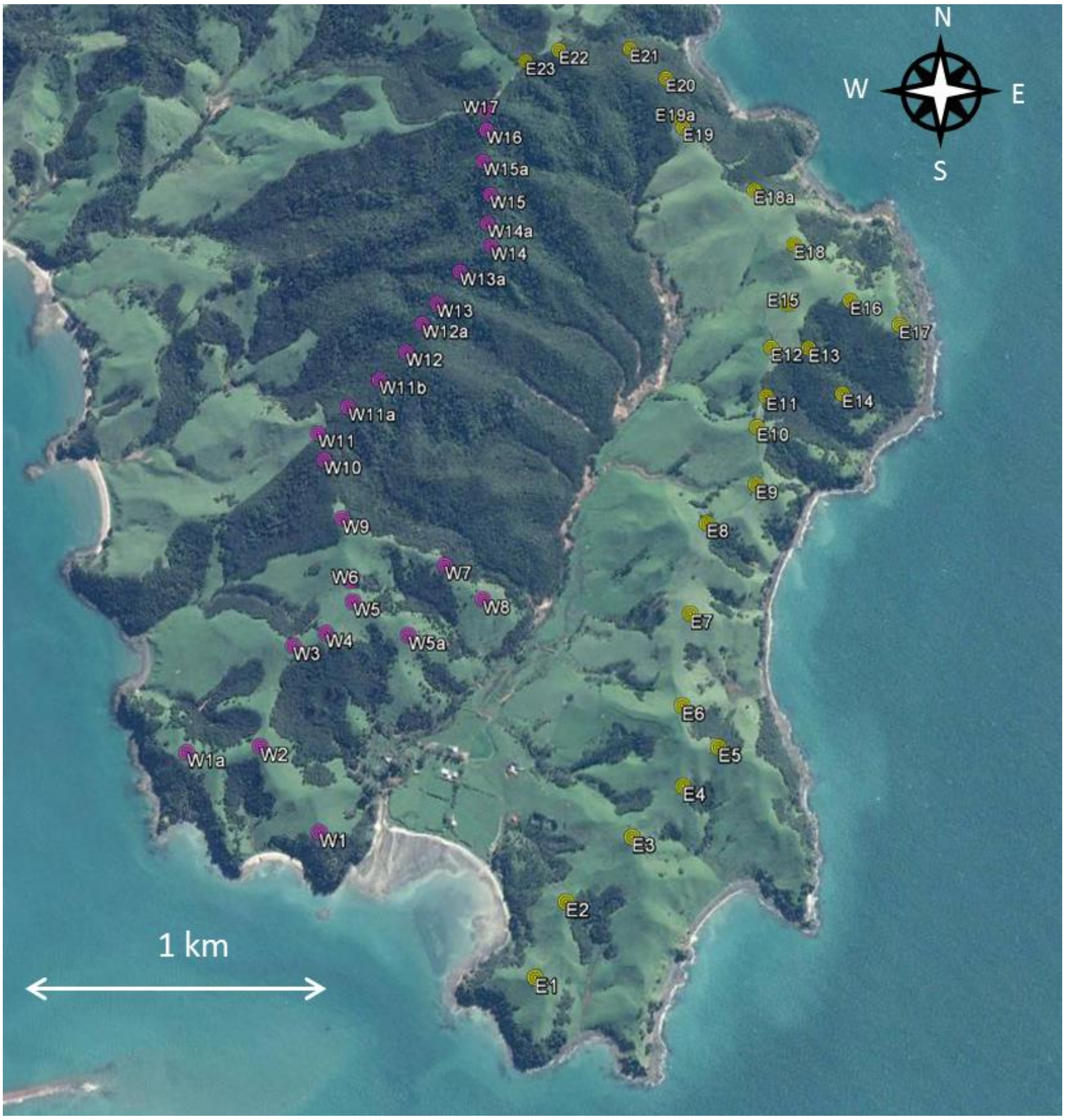

Figure 5: Satellite photo of South Ponui Island showing the two transects and the triangulation sampling locations for each transect. The triangulation points were where each radio-collared cat was searched for using radio-telemetry, and a bearing was taken from the point if the cat's signal was heard. E = eastern ridge/transect, W = western ridge/transect. The numbers represent the order in which the points were searched. Image from Google Earth Pro (2017).

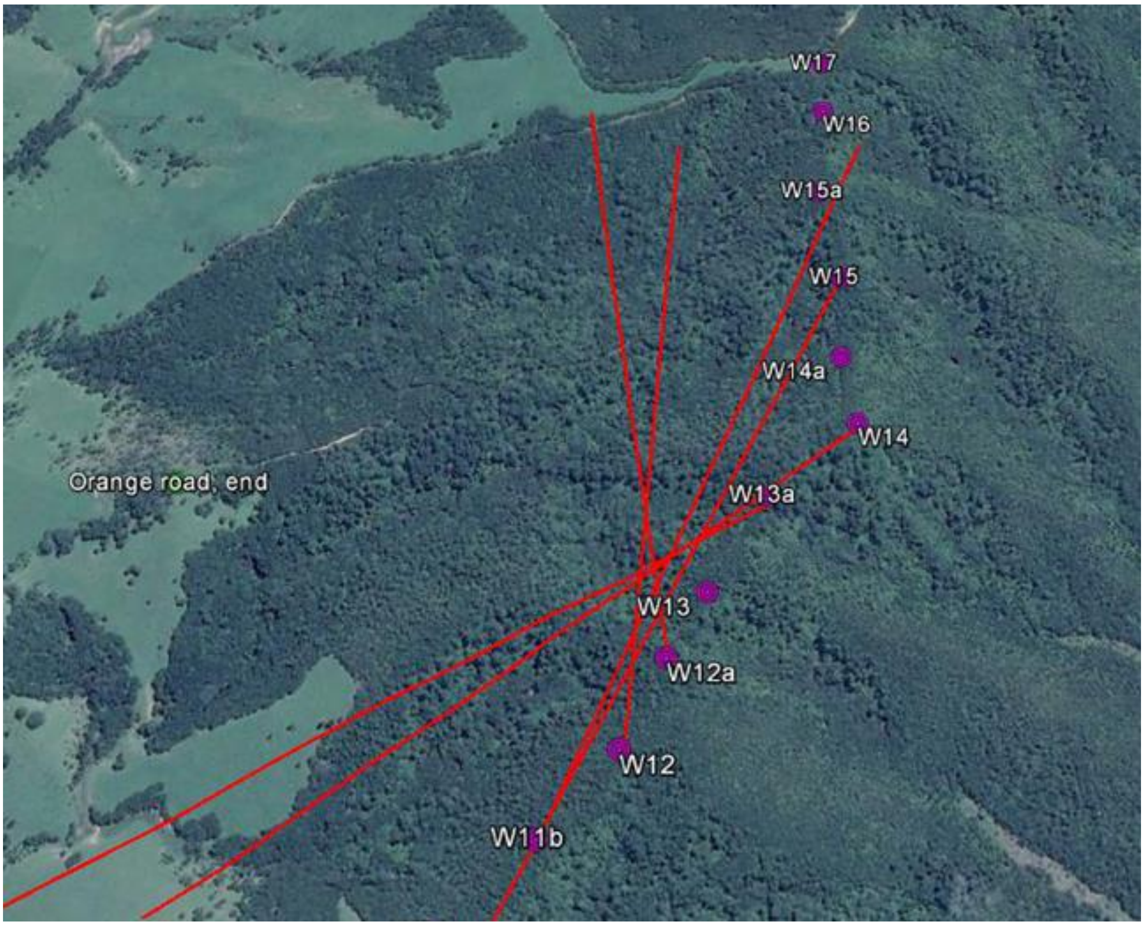

Figure 6: Satellite photo from Google Earth (2017) showing an example of the triangulation of bearings taken from transect points (in this case for the cat "Socks"). The pink points are part of the Western transect. The red lines mark from the point where Socks' signal was heard from and go in a straight line in the direction (from the bearing taken) that the signal strength was the loudest. The converging lines produce a polygon representing the approximate location of Socks. A point was taken from the middle of the polygon and used as Socks' location.

Radio-telemetry error

To determine the error from triangulation, a blind test was conducted once with a VHF-collar being hidden within the study site. The established western and eastern transects were then used to triangulate the position of the test collar as outlined above. The location bearings were entered into Google Earth Pro and the triangulated location was found. This location was then compared to the true location of the cat collar, and the error was found to be less than 50 m (43 m).

Twenty-one location points were also ground truthed, where the signals of different cats were triangulated (as above) and then the cats were located by honing in to their postion. The error for the triangulation of the siganls was also found to be less than 50 m.

The error was incorporated into the 100% MCP home range estimates for each cat. A 50 m radius buffer was drawn around each telemetry location point in QGIS, and the convex polygon encompassed these buffers in the area calculation.

Bearings were taken from a total of 2438 points during the tracking studies. A total of 557 (23%) of the points were discarded, with 78 (3%) of them being inaccurate, where the signal was bouncing in the opposite direction to the other bearings, or because they were taken from transect points too far away and more accurate bearings were taken closer to the position of the cat (479 points, 20%).

Camera trapping

Camera trap footage was collected for 39 months from 2014-2017 giving a total of 12,853 camera trap nights. From January 2014 - August 2015, 6-12 cameras (Bushnell® Trophy Cam) were set up and moved monthly, covering 27 different locations. From September 2015 - March 2017 I set up 28 Bushnell trail cameras (12 Bushnell® Trophy Cam and 16 Bushnell® Aggressor) in fixed locations in a 500 x 500 m grid (Figure 7). One camera was placed in each 25 ha grid square. Grid size was decided using the average minimum home range size of cats studied in New Zealand and on offshore islands (Fitzgerald & Karl, 1986; Konecny, 1987; Moller & Alterio, 1999; Gillies et al., 2007; Recio et al., 2010; Bengsen et al., 2011, 2012). GPS locations of the camera sites were taken using a Garmin eTrex® 20x GPS unit.

Cameras were mainly placed on trails and were attached to trees at a height of approximately 30 cm above the ground. Grass, branches, and other material was cleared away from the front of the camera. The cameras were set to record 30 seconds of footage, with an interval (delay between recordings) of one second. Batteries and SD cards were checked and replaced every month. In general, camera sites were not baited, although seven cameras were baited for a total of 798 camera trap nights (from January 2015 - January 2017) as live-traps were set up in those locations (see Baiting section).

Videos were watched using VLC media player version 2.2.2. Videos that featured a cat were included in the data set. Data were entered into an Excel spreadsheet, and consisted of the camera trap location, date, time, behaviour (e.g. walking, hunting), and sex of the cat. For video sequences where the cat stayed in the frame of the camera for consecutive videos or returned to the camera within 10 minutes of the first video, only details of the first video were used. Each included video was classed as independent.

Figure 7: Satellite image showing the 28 camera traps placed across South Ponui Island from September 2015 - March 2017. Each square represents a camera trap. The spacing of the camera traps was based on a 500 x 500 m grid that had been superimposed on a map prior to placing the cameras in the fixed locations. Image from Google Earth Pro (2017).

Home range calculation from telemetry and camera trap data

The average home range sizes for both sexes (100% MCP, 95% KDE, 50% MCP, 50% KDE) are expressed as median ± interquartile range (IQR) and were calculated from the radio-telemetry and camera trap location points. For the camera trap location data, only the first time that the cat was seen on that camera trap location during the study was used. This was to reduce biasing the movements and home range estimations of the cats to the camera trap locations, which were fixed sampling points.

Calculation of home range from camera trap data was for 100% MCP home range size, unless otherwise stated. All shapefiles produced were clipped to the shape of the island and the area calculated through R (R Development Core Team, 2008). Home range calculation using camera trap data required the use of several methods:

- **1/2 Average distance (AD) –** For each individual cat, the average distance between consecutive camera captures was estimated using Google Earth Pro, with consecutive captures at one camera removed from analysis. This average distance moved between cameras was halved and became the radius of the buffer size around each camera the individual was seen on. A convex hull was produced encompassing this buffer using QGIS.

- **Average distance (AD) –** For each individual cat, the average distance between camera captures was estimated as above. The home range was treated as though circular, and the average distance moved was used as the radius of the home range to estimate the area.

- **1/2 Max –** For each individual cat, the maximum distance moved between consecutive camera captures was estimated using Google Earth Pro. This number was halved, the home range was treated as being circular, and half of the maximum distance moved between cameras was used as the radius to calculate the area.

- **Grid –** Each square for the camera trap grid was 500 m x 500 m, equating to 25 ha in area. The number of cameras an individual cat was captured on was recorded. It was assumed that if a cat was captured on a camera trap, then the cat used the whole grid square as part of its home range. The number of cameras the individual was captured on was then multiplied by 25 ha to estimate home range size.

- **100 m –** A buffer of 100 m was created around each camera trap the individual cat was captured on. A convex hull was produced encompassing this buffer using QGIS.

- **2.45 Sigma –** Each camera capture for an individual cat was entered into DENSITY5 (Efford, 2012). This gave a sigma value (σ), the spatial scale of detection, for each individual cat. The radius of the home range (assuming a circular home range) is estimated to be 2.45x sigma value (Efford et al., 2016). The area of the home range was calculated using the radius, and this area was estimated to be 95% KDE. The home range calculated through this technique was compared to the 95% KDE calculated using the Combined Range Estimate (CRE).

Each method was compared to the CRE and the home range size estimated through the radio-telemetry points only. The CRE is the home range size (100% MCP unless otherwise stated) estimated by combining radio-telemetry and camera trap location points. The home range size estimated for each cat through the CRE or radio-telemetry points only were used as the "true" home range for comparisons with the camera trap methods. Both the correlation in home range sizes estimated from the CRE and the camera trap method, and the correlation between the radio-telemetry points only and the camera trap method, were calculated and graphed. The camera trap method that was deemed the most accurate was the one with the highest correlation to the home ranges estimated with the CRE and the radio-telemetry points, and also that matched the line of equality on the graph. This meant that the camera trap method estimated similar home range sizes to the CRE and radio-telemetry points.

Home ranges were estimated from radio-telemetry points only because it was an independent measure; the CRE included home ranges that were calculated with the inclusion of camera trap location data. Two cats were removed from this analysis due to one having only radio-telemetry locations taken when it was a sub-adult (Shadow), and the other cat (Sylvester) because he spent most of his time outside of the camera trap area, resulting in lower capture rates on cameras.

Estimation of habitat type in home range

The percentage of forest and scrub in the home range of an individual cat was estimated using Google Earth Pro. The 100% MCP of the cat was imported into Google Earth Pro, and polygons were drawn around the forest and scrub areas to estimate the area of the fragment. Fragment areas were summed to give an estimate of the percentage of home range for an individual that contained forest/scrub habitat.

Calculation of home range overlap

Overlap between individual cats was calculated using their 100% MCP home ranges that included using both radio-telemetry and camera trapping location points. Polygons were created in QGIS of the overlap between each cat. The total non-overlapped home range was calculated by forming polygons of the individual cat's home range that excluded any other cat's home range that overlapped it. Polygons were exported to R and the area of the polygon calculated using the packages raster, rgeos, and cleangeo (R Development Core Team, 2008). Average overlap for sexes are stated as mean ± SD.

Removal of male cats

I tested the relationship between density and home range size in two ways; I took advantage of the death of a male cat (Midnight that died from natural causes on 14 February 2016), and I removed another male (Mittens – see below) purposely on 2 September 2016. I continued to follow the remaining resident cats and recorded changes in their home ranges after each of the males were taken out of the population.

Mittens was tracked using radio-telemetry and shot in the head with a 0.22 gauge bullet. The shooter had a firearms license and took the shot when the cat was in full view. The safety protocols for euthanasia by shooting followed those set by the National Pest Control Agencies (Warburton, 2015). This procedure was approved by Massey University Animal Ethics Committee (MUAEC 16/52).

Statistical analysis

Mann-Whitney U-tests were performed in R to test for differences in weight, head-body length, canine distance, and tail length between the sexes. An incremental increase analysis to calculate the increase in home range size with subsequent locations was performed in Ranges v9 for all cats studied (Supplementary material; Figure S5-S8). Generally, a plateau in home range size with increasing location points for an individual cat suggested that the full home range had been estimated. Radio-telemetry and camera points were used for this. Because cameras are a fixed point sampling method, the first time a cat was seen on that camera was used for the incremental increase analysis, and subsequent captures on the same camera were not used here. For home range size analysis, cats which had reached a plateau for their home range size were used. Although one of the cats' (Sylvester) home range had increased with his last two locations, he was still included in the analysis because he had a large home range. Mann-Whitney U-tests were used to test the significance of sex differences in home range size (100% MCP, 95% KDE, 50% MCP and 50% KDE), as well as differences in percentage of forest/scrub in home ranges. Linear regressions were performed to test the linearity between home ranges calculated using the CRE/radio-telemetry methods and different camera trap methods, as well as determining the significance of the home range versus density relationships.

Results

Home range

Differences in home range size between the sexes

The median 100% MCP home range size of males was 428 ± 154 ha which was significantly larger than that of females (203 ± 75 ha) (Mann-Whitney U-test, n = 8, df = 1, W = 0, p-value = 0.036) (Table 3). The mean 95% Kernel Density Estimation (KDE) for males (424 ± 109 ha) and for females (141 ± 157 ha) was not significantly different (Mann-Whitney U-test, n = 8, df = 1, W = 2, p-value = 0.143) (Figure 8). There were no significant differences between sexes in the core home range size using either the 50% MCP technique (Mann-Whitney U-test, n = 8, df =1, W = 3, p-value = 0.250) or the 50% KDE technique (Mann-Whitney U-test, n = 8, df = 1, W = 2, p-value = 0.143).

Home ranges of both sexes encompassed a mixture of forest/scrub and pasture habitat types (Table 4). There were no significant differences in the percentage of forest/pasture in the home range of males versus females (Mann-Whitney U-test, n = 8, df = 1, W = 3, p-value = 0.25).

Table 3: Home range size (ha) estimates for each radio-collared cat using five different levels of measurement. MCP = Minimum Convex Polygon and KDE = Kernel Density Estimation. Locations from both radio-telemetry (from April 2015 – March 2017) and camera trapping (September 2015 – March 2017) techniques were used for the home range estimation. Only the first 'capture' of a cat at a camera site was used, and subsequent captures at the same camera trap location were ignored. 100% MCP measurements include the home range estimate ± the estimated error (in ha) – see methods for further explanation.

Cat	Sex	100% MCP	95% MCP	50% MCP	95% KDE	50% KDE
Cleo	Female	183 ± 17	126	8	85	16
Patches	Female	333 ± 33	299	85	400	106
Socks	Female	203 ± 15	133	26	141	35
Midnight	Male	392 ± 11	368	63	320	64
Tigger	Male	814 ± 39	491	123	610	130
Mittens	Male	396 ± 17	340	77	371	112
Salem	Male	428 ± 25	394	158	480	151
Sylvester	Male	550 ± 38	378	43	424	65

Table 4: Percentage of home range (100% MCP) for each individual cat that encompassed forest/scrub habitat as opposed to pasture. F = female, M = male.

	Cleo	Patches	Socks	Midnight	Tigger	Mittens	Salem	Sylvester
Sex	F	F	F	M	M	M	M	M
% of home range	36	67	41	46	46	33	66	57

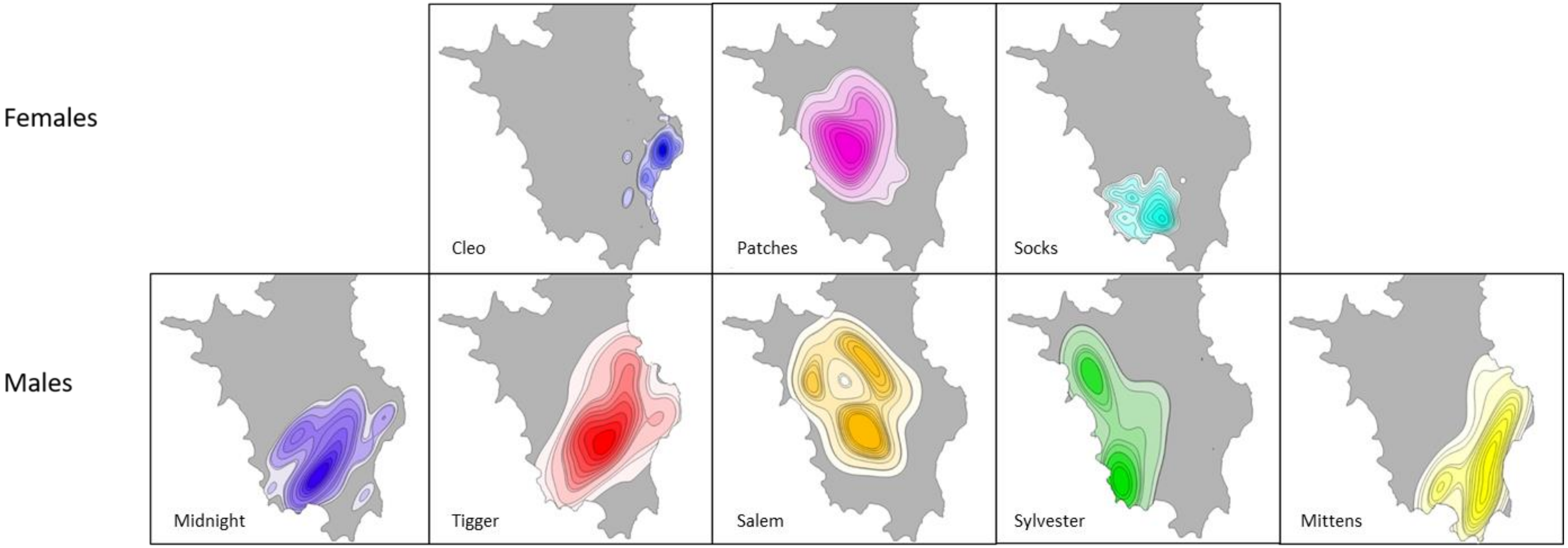

Figure 8: Kernel density estimations (KDE) for the three female and five male cats monitored on South Ponui Island. Contour lines represent 10% KDEs, except the outer two contour plots are the 95% and 99% KDEs. Darker colours represent a higher density of location points for the cat. Locations are based on radio-telemetry (April 2015 – March 2017) and camera trapping (September 2015 – March 2017).

Overlap

The overlap between feral cat home ranges varied between and within sexes (Figure 9). The mean (± SD) overlap between female home ranges was 10.95 ± 7.2%, which was lower than the mean overlap between males (48.77 ± 4.4%) (Table 5). Between males and females there was 39.33 ± 4.2% overlap in 100% MCP home range. Males overlapped in home range with all other cats in the area, whereas two females did not. Two cats did not have any exclusive home range (Patches-female and Mittens-male), meaning that every part of their home ranges overlapped with at least one other cat.

Table 5: Percentage of overlap in home range (100% MCP) between each paired combination of cats. Blue are female-female overlap, green male-male overlap, and yellow female-male overlap. The overlap in home range was calculated through mapping the two cats' home ranges and calculating the size of the overlapping area. The overlap is shown as a percentage of the home range for the cat on the left, and the percentage of its home range that overlaps with the cat in the top row.

		Overlap in home range with cat (%)							
		Cleo	Socks	Patches	Midnight	Tigger	Mittens	Salem	Sylvester
Cats' home range (%)	Cleo	-	0	0	57	39	83	2	26
	Socks	0	-	41	81	77	59	36	80
	Patches	0	25	-	50	47	36	22	49
	Midnight	27	42	27	-	55	86	27	62
	Tigger	11	25	33	34	-	31	42	49
	Mittens	38	30	19	85	49	-	23	53
	Salem	1	17	71	25	62	21	-	76
	Sylvester	9	30	58	44	56	38	59	-

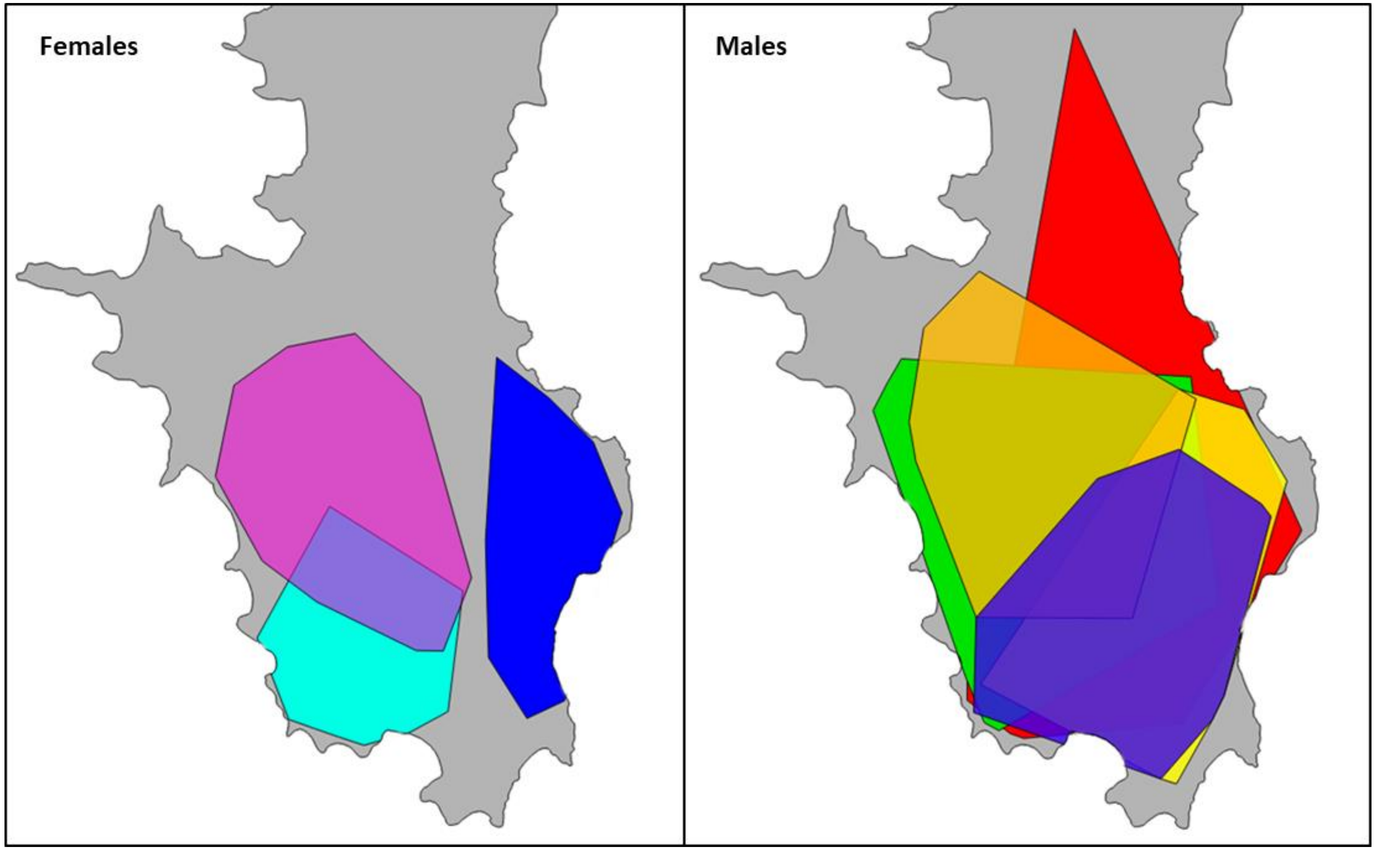

Figure 9: Map showing the 100% MCP home ranges and overlap of the feral cats radio-collared and studied from April 2015 – March 2017 on Ponui Island. Location points are from radio-telemetry and camera trapping data. **Females;** pink = Patches, light blue = Socks, dark blue = Cleo. **Males;** red = Tigger, yellow = Mittens, green = Sylvester, orange = Salem, purple = Midnight.

Morphometrics

Male cats (median = 3662 ± 847 g (IQR)) weighed significantly more than females (median = 2341 ± 246 g) (Mann-Whitney U-test, n = 12, df = 1, W = 0, p-value = 0.004) (Table 6). Males also had longer head-body length (HBL) (median = 552 ± 17 mm) and larger canine distance (median = 20 ± 1.5 mm) than females (median HBL = 483 ± 31 mm; median canine distance = 18 ± 0.75 mm) (HBL: Mann-Whitney U-test, n = 12, df = 1, W = 2, p-value = 0.022; canine distance: Mann-Whitney U-test, n = 11, df = 1, W = 1, p-value = 0.022). There was a linear relationship between the head-body length and the body weight of the feral cats (Figure 10). Males had on average longer tail length (TL) than females (median male = 292 ± 20 mm; female = 265 ± 35 mm) but this difference was not significant (Mann-Whitney U-test, n = 12, df = 1, W = 4.5, p-value = 0.061).

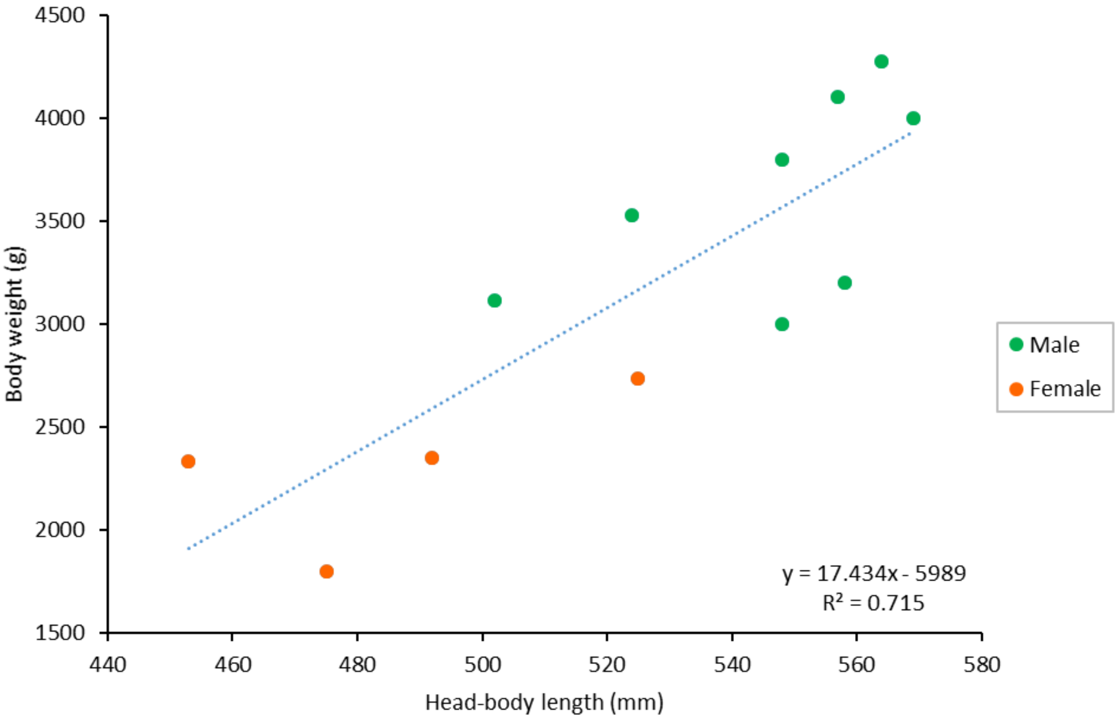

Figure 10: Relationship between head-body length and body weight of the feral cats live-trapped in South Ponui Island. Points are split into male (n = 8) and female (n = 3). The blue line shows the linearity between the body weight and head-body length for all cats, and the equation and R^2 value are shown. Note that the x and y axes do not start at zero.

Table 6: Morphometrics, location data, and general information for each feral cat in the study. Location data were obtained using both the radio-telemetry and camera trap methods. Snowball II and Milo were only used for morphometric analysis and not the home range or movement data, and Simba was not used for either due to a low rate of detection on cameras. – represents data not collected in this study.

ID	Sex	Coat colour	Weight (g)	Head-body length (mm)	Tail length (mm)	Radio-telemetry monitoring		No. radio-telemetry locations	No. camera locations
						Start	Finish		
Cleo	Female	Black	2733	550	306	11/04/2015	17/01/2017	79	222
Patches	Female	Tortoiseshell	2350	500	280	10/04/2015	4/09/2016	59	19
Socks	Female	Tortoiseshell	2333	473	240	12/04/2015	23/03/2017	109	172
Midnight	Male	Black	4273	562	310	15/04/2015	14/02/2016	41	162
Tigger	Male	Ginger	4100	558	298	12/04/2015	22/10/2016	85	167
Mittens	Male	Black/white	3525	524	265	13/07/2016	2/09/2016	11	97
Salem	Male	Black	4000	569	313	19/03/2016	12/01/2017	29	101
Sylvester	Male	Black	3200	558	262	21/06/2016	23/03/2017	20	2
Shadow	Female	Black	1800	475	249	14/12/2015	23/01/2016	7	47
Tui	Male	Black	3800	548	303	9/04/2015	26/07/2015	1	16
Snowball II	Male	Black	3000	548	289	-	-	-	5
Milo	Male	Black	3113	502	291	-	-	-	-
Simba	Male	Ginger	-	-	-	-	-	-	6

Removal of males

The density of feral cats in the study site was estimated to be 1.17 cats/km^2. The Ponui Island data fits into the overall relationship between home range and population density in feral cats from past studies (Figure 11).

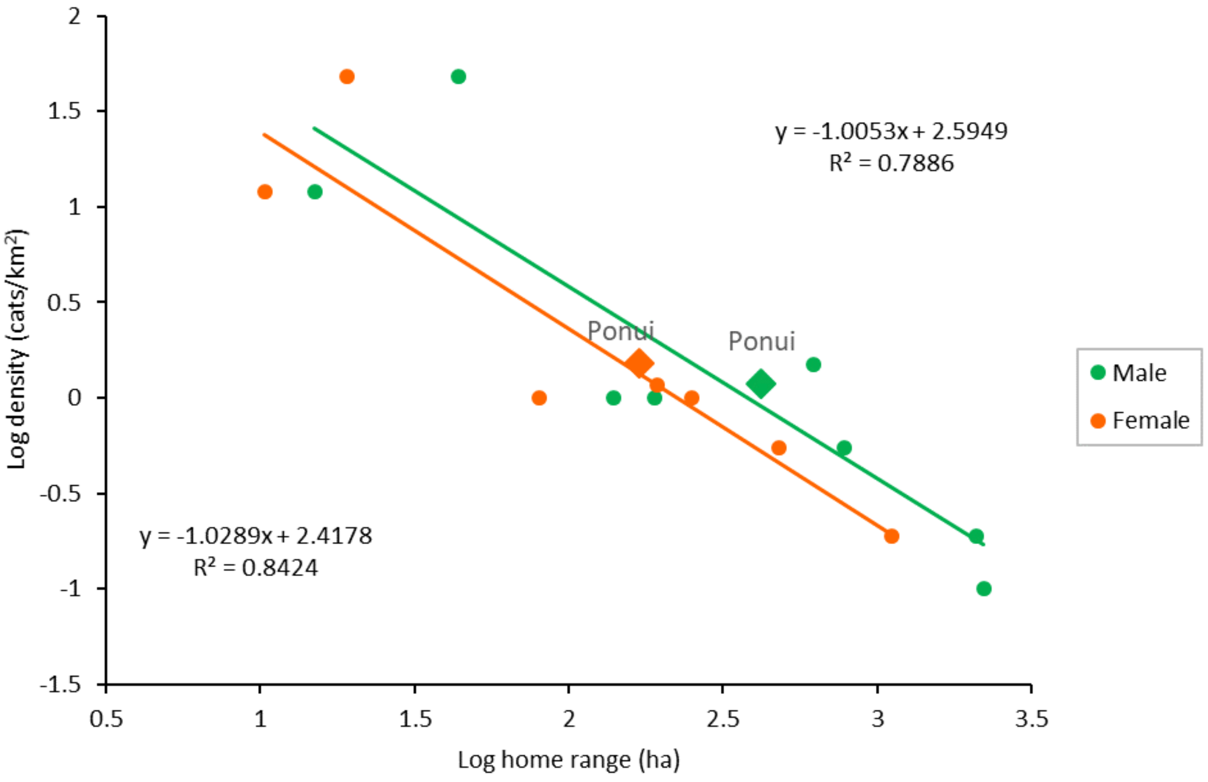

Figure 11: Relationship between home range and density in all feral cat studies from Table 1, as well as information on the Ponui Island cat population from this study. The green line represents the regression line for male feral cats, and the orange line represents the regression line for the female cats. The Ponui Island points for both sexes are labelled and represented by the diamond points. The top regression equation and R^2 values are for the males, and the bottom values are for the females.

The death of the largest male, Midnight (4.3 kg), resulted in the second largest male (Tigger, weighing 4.1 kg) increasing his home range size in the following seven months (Table 7). Tigger's home range (100% MCP) expanded by 183 ha and the areas that he used also changed (99% KDE) (Figure 11). Following the death of Midnight, Tigger was captured on more cameras located in the southern parts of the island which were previously occupied by Midnight (Figure 12).

Table 7: Home range changes of Tigger for Removal 1. The changes in three levels of home range estimation are shown. The number of locations used for the home range calculation are shown. Location points are from both radio-telemetry and camera trap data.

Home range calculation	Home range before Midnight died (ha)	Home range after Midnight died (ha)
No. location points	50	50
50% KDE	71.8	121.6
95% KDE	400.0	405.8
100% MCP	621.8	805.0

The effects of Removal 2 were different to the first removal. There was a temporary reduction in density due to the removal of Mittens, where density decreased from 1.17 cats/km^2 to 1 cat/km^2, and the size of all of the remaining cats' home ranges remained similar. However, in the six months following the removal, four new male cats were seen on nine cameras that overlapped with Mittens' home range (Figure 13), with density increasing to 1.67 cats/km^2. While one of these cats had been seen in the study site before, three of them had not been seen before. There were more captures of unmarked new cats in the area 2-3 months than 5-6 months following the removal of Mittens (Figure 13B & C).

The results from the first removal followed the prediction from the home range versus density relationship; i.e., a reduction in density led to an increase in home range size. Removal 1 (R1) fit into the relationship between density and home range and did not notably change the R^2 values (males before R1, $R^2 = 0.789$; males after R1, $R^2 = 0.785$; females before R1, $R^2 = 0.842$; females after R1, $R^2 = 0.844$) (Figure 14A). The second removal led to a decrease in the strength in the relationship (R^2 value) for both males and females (Figure 14B).

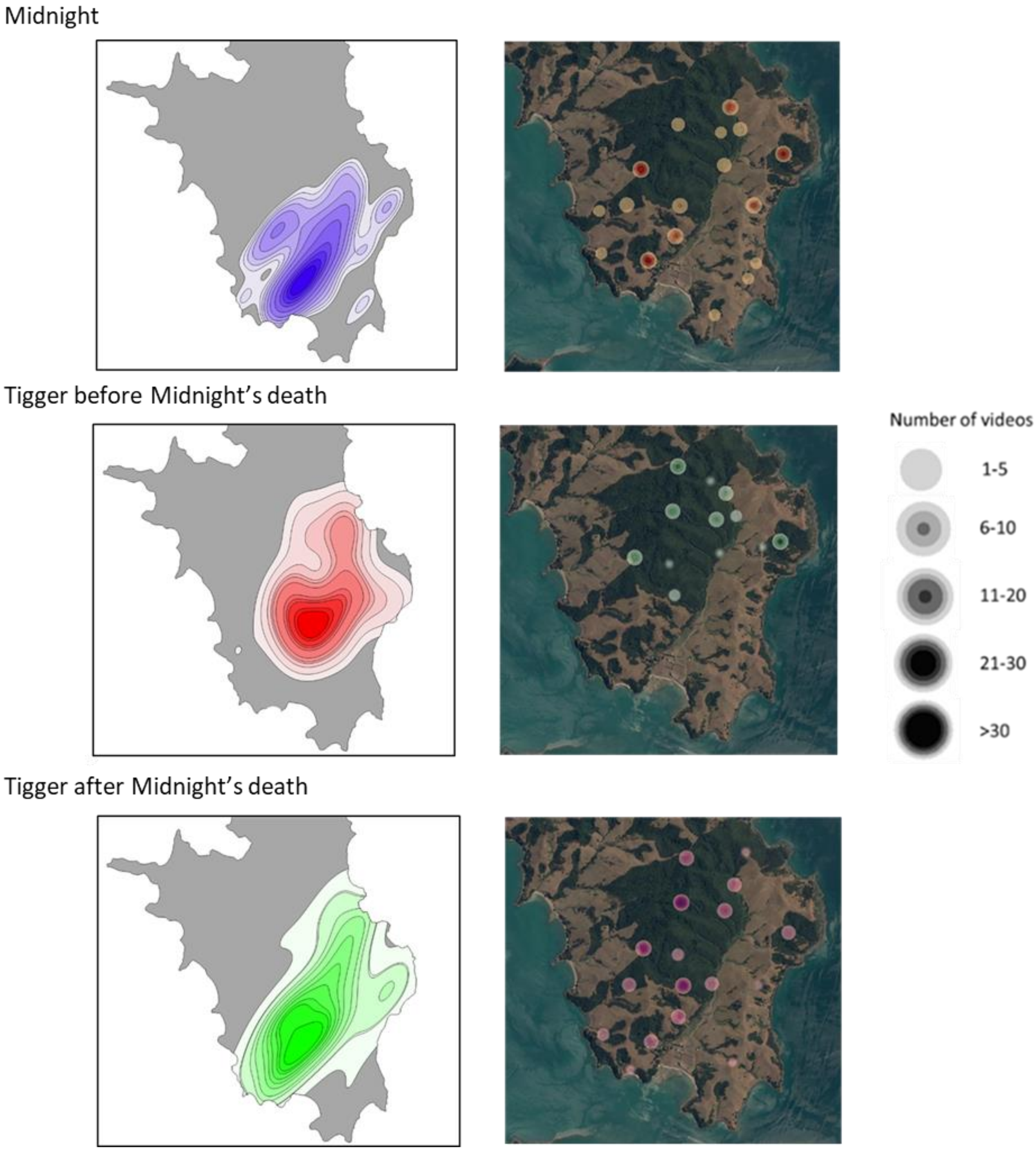

Figure 12: Movements of Midnight, and of Tigger before and after Midnight's death (Removal 1). **Left** = 99% KDE plots of Removal 1. The darker colour represents higher density of location points. Contour lines are in 10% KDE, except the last two are 95% and 99% KDE. **Right** = Number of captures on each camera trap location for each cat.

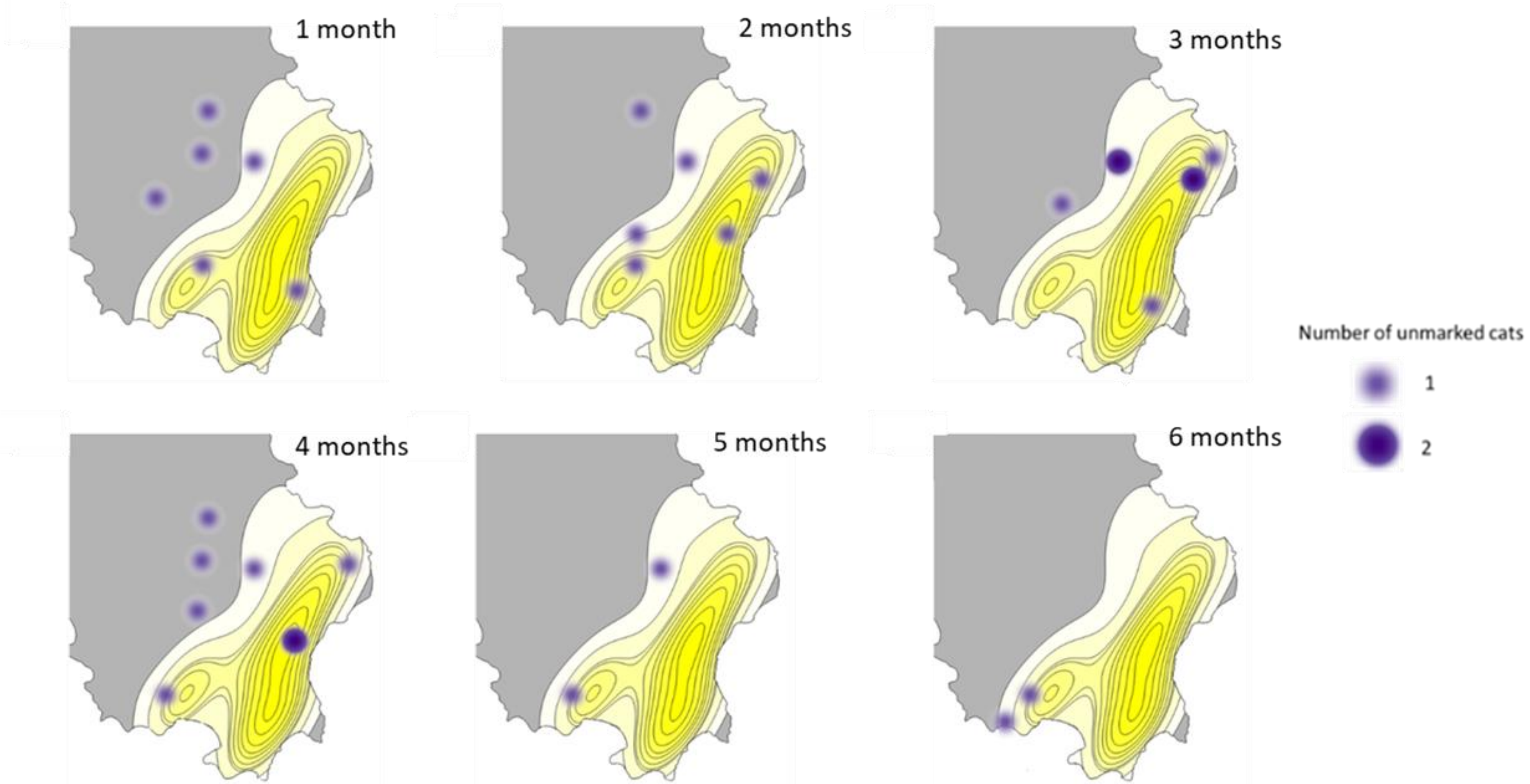

Figure 13: Number of unmarked cats captured on cameras from month 1 to 6 following Removal 2 on South Ponui Island. Yellow filled contour lines show Mittens home range (the male that was removed), from 10% KDE (dark yellow areas) to 99% (light yellow areas). The purple heat map shows the number of captures of unmarked cats. Some cats were captured at multiple locations.

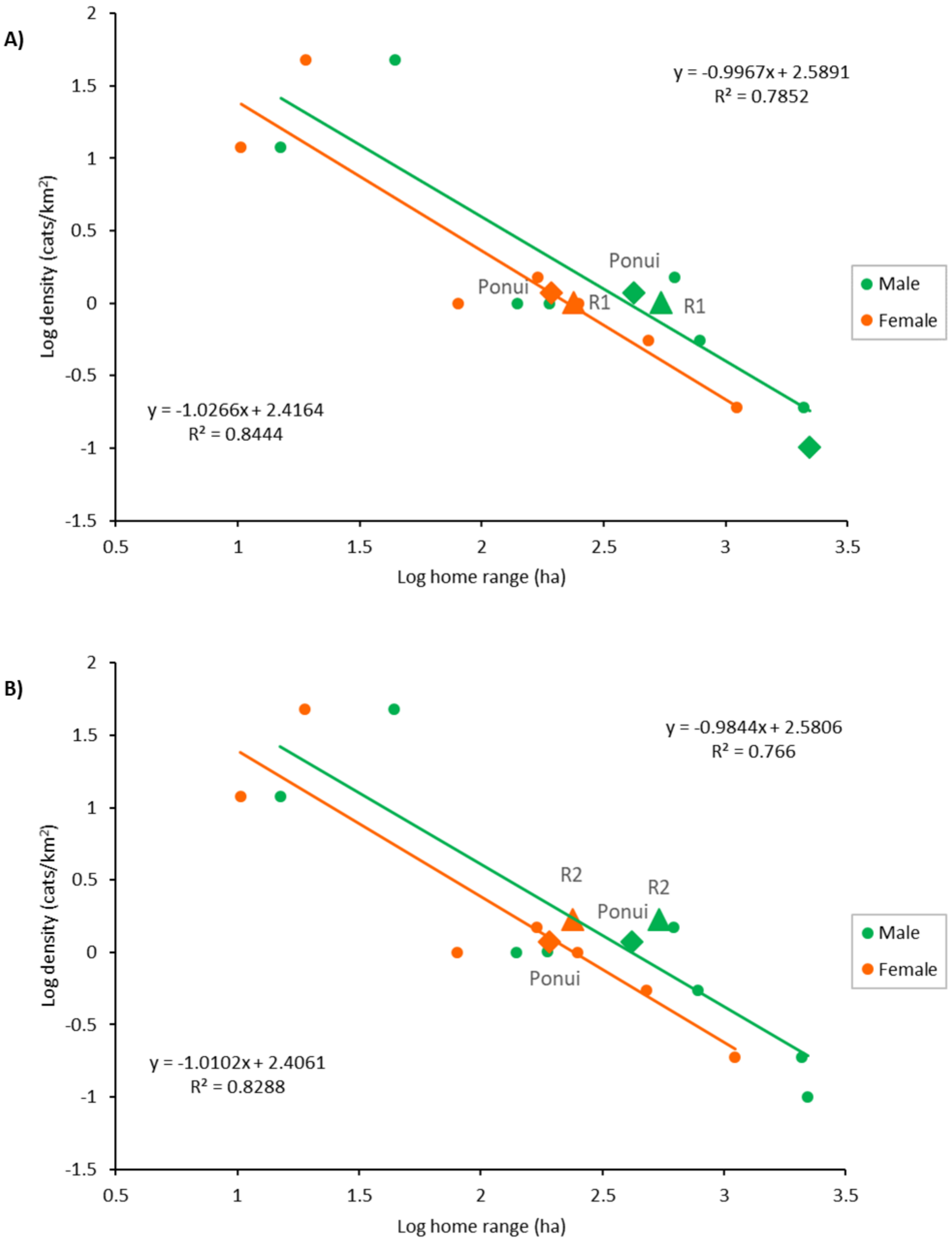

Figure 14: Relationship between home range and population density in all feral cat studies from Table 1, as well as the cats from this study. The green line represents the regression line for male feral cats, and the orange line represents the regression line for the female cats. The top regression equation and R^2 values are for the males and the bottom values are for the females. The Ponui Island results (before removals), Removal 1 (R1), and Removal 2 (R2) points are labelled and represented by the diamond points (Ponui – before removals) and triangles (R1 & R2). Results, regression values, and equations are shown for **A)** Removal 1, and **B)** Removal 2.

Home range estimation using two techniques

The home range size estimated from camera trap data only were compared to that calculated using the CRE (Combined Range Estimate, from camera trap and radio-telemetry locations (100% MCP)) and radio-telemetry only home range estimate (100% MCP). The home ranges estimated by the CRE and radio-telemetry were used as the true home range size of the individual cats. From the six methods tested for estimating home range from camera trap data (Supplementary material; Figure S2 & S3, Table S4), the two methods with the highest correlation (R^2 = 0.34-0.68) with the CRE and radio-telemetry only estimates were the grid and the ½ AD methods. Both methods had higher correlations with the CRE (grid: R^2 = 0.68, ½ AD: R^2 = 0.60) than the home range size estimates with radio-telemetry location points only (grid: R^2 = 0.48, ½ AD: R^2 = 0.34) (Figure 15). The grid technique generally underestimated larger home range sizes, whereas the ½ AD technique overestimated home range size at the larger home range sizes calculated from the CRE.

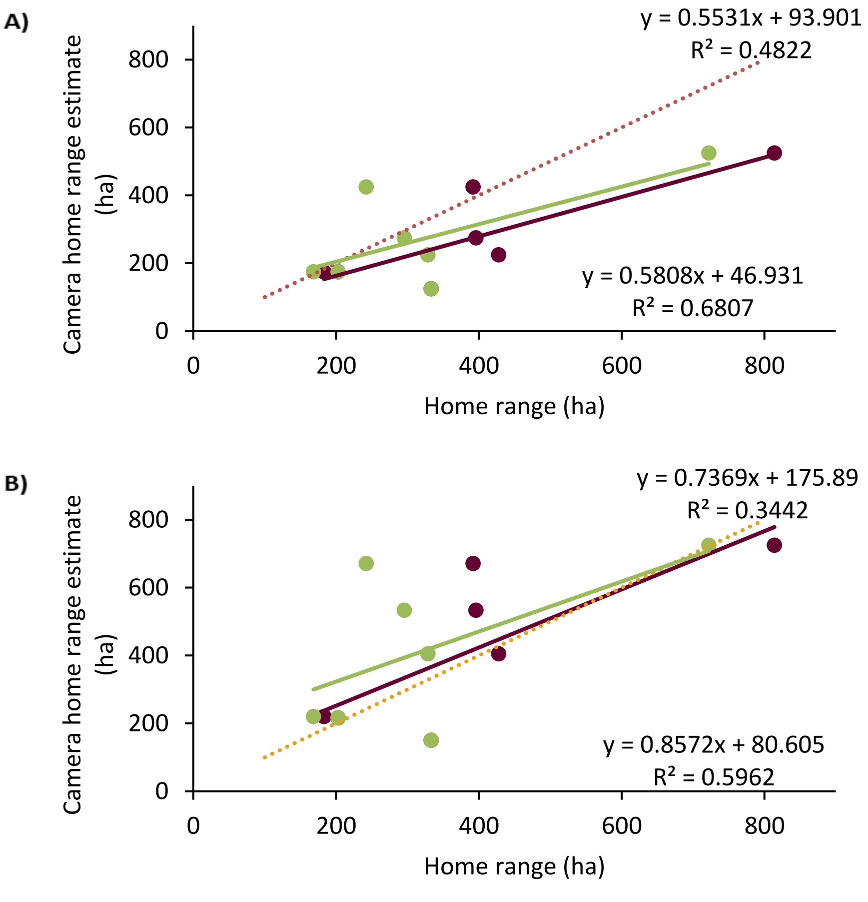

Figure 15: Correlation in home range size (ha) between **A)** grid, and **B)** ½ average distance (AD) camera trap techniques (see methods section). Home range estimation from camera traps based on the camera trap technique compared to the combined range estimate (CRE) (maroon), and radio-telemetry (green) (100% MCP), which are taken to be the "true" home range size. The equation and R^2 value are shown for the radio-telemetry data (top) and CRE (bottom). The orange line represents the line of equality.

Discussion

Home range versus density relationship

The main objective of this study was to determine what happened to a population of feral cats when adult males were removed, resulting in a reduction in the cat density in the area. This replicates the density fluctuations during opportunistic culling programmes that occur throughout most of New Zealand. Ponui Island cats followed the home range versus density relationship identified by Liberg et al. (2000). I found that when the first male (the heaviest) was removed the next heaviest male cat increased his home range size. However, when a second cat was removed, new male cats immigrated into the study site, thereby increasing the density in the area. The findings from the second removal were unexpected because I had predicted that the second removal of a male cat would lead to an increase in home range size for the remaining cats, in accordance with the home range versus density relationship. There was also little change in the home range size of females following the removals.

There are two possibilities that may explain why Tigger's home range expanded further south following the death of Midnight. One may be that Midnight's home range contained better quality habitat. The southern end of the farm, in Midnight's home range, contains the houses on South Ponui farm, so there are higher densities of Norway rats (*Rattus norvegicus*) (I. Castro, 2018, pers. comm.). Norway rats are larger than ship rats (*Rattus rattus*), so may be a more substantial meal (Innes, 2005a, 2005b). However, Childs (1986) found that house cats selected juvenile and smaller rats in preference to large adult rats, with the size of depredated Norway rats being similar to or smaller than the depredated ship rats. Therefore, the presence of Norway rats in the southern area is unlikely to be the reason Tigger expanded his home range.

The most likely reason why this male moved further south may have been so that his home range had greater overlap with the female cats in that part of the island (Liberg et al., 2000; Say & Pontier, 2004), particularly with the female (Socks) in the southern end of the island. Before Removal 1, Tigger and Socks had very little home range overlap. Following Removal 1, their home range overlap increased. Tigger was also the most likely father of one kitten from Socks' November 2015 litter (Chapter 5), also lending support for this. This supports the idea that males may distribute themselves according to female distributions, and not just with respect to other resources such as food and shelter (Liberg et al., 2000).

The second removal manipulation showed a different result to the first; the temporary reduction in density had no effect on the resident cats' home range sizes in the study site. Instead, Ithere was a temporary increase in local density of feral cats, where four new males were seen in the study area. This has been described as the ecological vacuum phenomenon, which is where an animal may move into a newly unoccupied area (Pianka, 1972; Gibson et al., 2002), or simply termed recolonization. This term may need to be used loosely for this result, since the area was not completely unoccupied with the removal of Mittens due to the overlapping home ranges of the feral cats in this study.

Although one of the new males was seen sporadically on camera traps, the other three males had never been seen before. This may suggest that males are often surveying for unoccupied areas. Non-resident males, presumably from the northern end of the island, were often seen throughout the study site in the months following the removal. Most of these new males appeared on the cameras within the first four months following the removal of Mittens, where they would be seen for several days in the study site. These males were seen more on cameras within Mittens' home range, suggesting that they may have used the lack of scent marks as a cue to the area being unoccupied (Rabinowitz & Nottingham, 1986; Feldman, 1994).

In this experiment male cats were removed instead of females. This was because I thought that the sex of the animal removed may affect the response by other members of the population; males had a higher correlation between home range and density in island studies than females (Figure 1). Unfortunately, I was unable to test how the removal of a female would affect the movements of the remaining cats, but this would be interesting to do. Males move over larger areas and overlap greatly with other cats in their home range. Females, on the other hand, have what seems more stable home ranges. The removal of a female may open new areas for other females to occupy. It would also be interesting to see whether the removal of females changes the behaviour and movements of males. Such a finding would provide further support that males distribute themselves not just according to prey availability or habitat, but in relation to females also.

Sex differences between home range size and overlap

I found that males had significantly larger home ranges than female feral cats, consistent with what has been reported in previous studies (Konecny, 1987; Moller & Alterio, 1999; Biró et al., 2004; Recio & Seddon, 2013). Females may distribute themselves based on resource availability, such as prey and shelter, but these factors are unlikely to be the only influence for the home ranges of male feral cats. As mentioned previously, male feral cats may instead distribute themselves according to access to female feral cats (Liberg et al., 2000). Feral cats generally have promiscuous or polygynous mating systems, and males may try to mate with as many females in oestrus as possible (Say et al., 2002). The low overlap in home ranges between neighbouring females may mean the males in this study need large home ranges in order to overlap with several females. This will allow the male to have as many mating opportunities as possible. The two removals in this study also had little effect on the home range size of females compared to that of the males. This may lend some support to the idea that the home ranges of males are influenced by the distribution of females.

Males overlapped in home range with multiple other males, whereas only two out of three females overlapped in home range. These are similar to findings from other home range studies (Turner & Mertens, 1986; Biró et al., 2004), though opposite to results reported by Smucker et al. (2000). Smucker et al. (2000) reported that food resources at their site were quite dispersed. Dispersed food resources can lead to higher territoriality in male cats (Konecny, 1987), so this may explain the low levels of male home range overlap reported by Smucker et al. (2000). There was also a high percentage of overlap in home range between male and female cats, and our results are in agreement with the findings of McGregor et al. (2015a). The large overlap in home range between sexes is likely due to males trying to increase their access to mating opportunities.

Comparison of home range size between Ponui Island and mainland/offshore studies

Home range size and the population density of feral cats is likely to be influenced by a combination of several factors such as resource availability and habitat type, making comparisons between populations difficult. However, information about home ranges at various locations, coupled with environmental data, may help clarify the relationships between these factors, home range, and resulting population densities. The average home range sizes for feral cats in this study were similar to or slightly larger than those reported for mainland cat populations in New Zealand, despite those studies also having mixed habitat sites (Fitzgerald & Karl, 1986; Norbury et al., 1998b; Moller & Alterio, 1999; Gillies et al., 2007). Comparison to other offshore island studies is difficult due to the small number of studies and different climates of the islands. The Ponui Island cats had much larger home ranges than the cats studied on Motuihe Island, perhaps due to the small size of Motuihe Island which, in turn, restricts cat movements (Dowding, 1998).

The Ponui Island cats had much smaller average home range sizes than those in Rakeahua Valley on Stewart Island (Harper, 2007). Though that site is also a mixture of scrub and forest, the feral cats studied there had large average home range sizes (1109 ha females; 2083 ha males) (Harper, 2007) compared to this study. There is also a lower density of feral cats in Rakeahua Valley (0.19 cats/km^2) which may be due to lower rat densities on Stewart Island (Harper, 2007) compared to Ponui island. The number of rats caught over 100 trapping nights (rats/100CTN) is often used as an index of abundance in New Zealand (Cunningham & Moors, 1996), and on Ponui Island in 2004-05 Shapiro (2005) had 9.56 rats/100CTN, and Harper et al. (2005) had 3.26 rats/100CTN. Both islands experience large seasonal fluctuations in rat density (Harper et al., 2005; Shapiro, 2005; Latham, 2006), and Harper (2005) found that feral cats had higher emigration and mortality during seasons when rats were at their lowest density on Stewart Island. During these times of low primary prey availability, the Ponui Island feral cats had higher intakes of other alternative prey (Chapter 6). Whilst Stewart Island has some similar bird species to Ponui Island (native and introduced passerines, and kiwi), the subalpine and forest habitat may make it harder to hunt some of these species. This suggests that habitat type and prey availability are influencing the population density of feral cats, in turn, influencing their home range size.

Home range estimates using different techniques

Radio-telemetry is one of the most used methods to measure the home range of animals; it has been used for many years and most home range analyses were developed for use on radio-telemetry data (Kie et al., 2010). In contrast, camera trapping is a recent technique that has been used to monitor different aspects of wild populations (such as behaviour and density) (Burton et al., 2015; Caravaggi et al., 2017) and its value as a possible method to estimate home ranges needs to be validated against the radio-telemetric method. From the six different methods used to calculate home range size based on camera trap data, the two with the highest correlation between radio-telemetry and CRE home range sizes were the grid and ½ AD methods. Both had higher correlations to the CRE method than the radio-telemetry only home range estimate. This is likely because the CRE contains some of the camera trap locations, so the camera locations are not completely independent of the CRE, unlike the radio-telemetry home range estimate. The grid method underestimated larger home range sizes, whereas the ½ AD method was highly correlated with the CRE data, however, it tended to overestimate home ranges that were between 250-300 ha. The ½ AD method was calculated using half of the average distance measured between consecutive captures on different camera trap locations, which was used as a buffer around each camera. It is likely that this method overestimated the distances moved by the cats, as they are less likely to pass cameras given their smaller home range, which produced large buffers around the cameras (from the ½ AD method), causing this overestimation of home range size.

Using camera trap data to estimate home range sizes requires caution, though, as it is a fixed position sampling technique (Foster & Harmsen, 2012; Burton et al., 2015; Meek et al., 2015). Animals that move out of the camera trap grid would have their home range underestimated, so this method requires that camera trap grids are larger than the home range size of the animals being monitored. Supplementing the radio-telemetry location data with the camera trap data did increase estimates of home range size of the Ponui Island cats. With the high correlation between the different home range estimate methods, there is the potential to develop a method for using camera locations alone to estimate home range size, but more work needs to be done developing this technique.

Management

Given the large cost of eradication and control programmes, and the continued threat to our native species posed by invasive species, increasing the efficiency of control programmes would be beneficial. Knowledge of an invasive species' home range and how it responds to changes in population density is of value to help optimise control programmes (Smith et al., 2015), and the results from this study have interesting implications for management. Firstly, the home ranges of the cats studied on Ponui Island were comparable or slightly larger to those of feral cats in most of the mainland studies, suggesting trap placement for mainland feral cat operations may be sufficient in some island operations. Secondly, the home range versus density relationship could be used to fill in knowledge gaps on either the home range size or the density of feral cat populations. For example, if the home range of the cats is known, then the number of cats in the control area can be estimated. If the density is known, then the home range could be estimated and used to estimate ideal capture trap placement. Bengsen et al. (2012) recommends that traps should be spaced based on the radius of the smallest home range. If the only available information is the average home range size of the population, then traps should be spaced based on the radius of the average home range size, e.g. an average home range size of 116 ha (such as that in the Orongorongo Valley, Wellington (Fitzgerald & Karl, 1986)), means that traps should be placed at a maximum of 600 m spacing (assuming a circular home range). Ideally, traps should be spaced so that there are at least two traps in every cat's home range to increase the chances of the cat encountering it.

The results from the cat removal study, particularly the second removal, pose an interesting management question: could this manipulation be used to produce *attractive sink patches* within an area (Delibes et al., 2001; Bryce et al., 2011) that could be used for cat control? The term *attractive sink* as used here refers to an area of equal or similar habitat quality that has been cleared of resident cats and thus acts as a vacuum (Gibson et al., 2002), drawing new cats into the area. Such an area could work in cat management; for example, an area could be trapped, the resident cats removed, and two or three months later, when the non-resident cats have moved in, they could be captured in this area. This approach may be most effective when population turnover is low, with low recruitment, such as occurs on Ponui Island (Chapter 4). A high recruitment rate would mean that the cats in the area are repeatedly replaced by new, young individuals, and creating *attractive sinks* would likely have no effect on reducing the population size. Studying the reproduction and recruitment rate of the population would be necessary before implementing this type of management strategy.

The advantage of creating a vacuum effect and drawing cats into an area would be that it would decrease trapping effort, as capture traps and resources could be set up at high density in one area that is used repeatedly, potentially obtaining similar results to normal trapping procedures. However, it is possible that the non-resident cats could be more interested in scent-marking the new areas rather than responding to the control we want to impose, for example entering capture traps for culling. So, while there could be more cats in an area, they may not be trappable and/or may avoid control measures such as trapping. These un-trappable cats may be able to be removed through shooting, which has been a standard procedure in control operations in past eradications (Campbell et al., 2011).

In conclusion, this study has important implications for the management of feral cats. There is support for the use of the home range versus density relationship for calculating missing information within a population. I have taken the first steps towards developing techniques for estimating home range using camera traps, which could be used as a less invasive technique for home range studies. More manipulations of the home range versus density relationship should be carried out, especially to look at the effects of removing females too. There is also a need to establish the key parameters that determine the population density and the home range size of feral cats. Further research on the potential to create *attractive sinks* within cat habitat by removing resident cats should be explored as a potential technique for control programmes by managers. Here I have outlined some interesting concepts that could be used for feral cat management, though further research on applicability would be needed. Home range size can be used to determine trap placement for feral cat control operations, though information on the activity patterns of feral cats is required to determine when live-traps should be set and checked to target feral cats. The following chapter (3) investigates activity patterns of the feral cats on Ponui Island.

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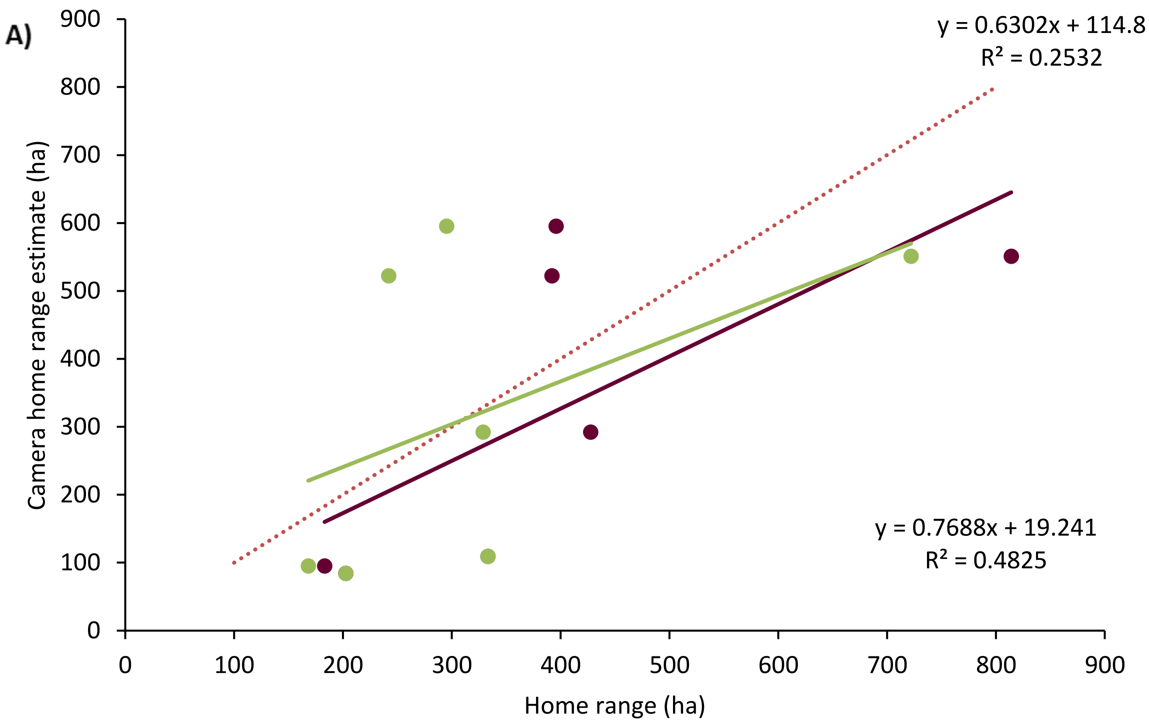
Supplementary material

Table S1: Summary of home range studies of feral cats in New Zealand, on islands, and elsewhere. * Not stated in study.

	Study	**Location**	**Technique**	**Cat #**	**Method**	**Location Fixes**	**Male Max. (km²)**	**Male Min. (km²)**	**Male Mean (km²)**	**Female Max. (km²)**	**Female Min. (km²)**	**Female Mean (km²)**	**Average of males and females (km²)**	**Density (cats per km²)**
New Zealand	Fitzgerald & Karl (1986)	North Island, NZ	VHF	9	Honing in to within 10m	2x daily in 1-6 months	3.1	0.5	1.55	1.7	0.2	0.84	1.16	1.1
	Gillies et al. (2007)	Trounson Park, Northland, NZ	VHF	21	Triangulation, MCP 100	Average of 30.8 fixes per cat	10.53	1.22	4.46	2.74	0.19	1.17	3.36	*
	Harper (2007)	Rakeahua Valley, Stewart Island	VHF	22	Triangulation, 100% MCP and 95% kernel	1-2x daily for up to 4 weeks each season	*	*	20.83	*	*	11.09	*	0.19
	Moller & Alterio (1999)	Otago Peninsula, NZ	VHF	11	Triangulation, MCP 100	1-2 locations each night or day	3.58	0.9	*	1.86	0.75	*	1.89	*

	Norbury et al. (1998b)	South Island, NZ	VHF	28	Helicopter, MCP 100	Once every 7-34 days, average 17 locations per cat	7.42	0.42	1.89	8.40	0.79	2.49	2.25	0.6-1.4
	Recio & Seddon (2013)	Mackenzie Basin	GPS	21 (11m, 10f)			*	*	8.27	*	*	2.66	5.54	*
	Recio et al. (2010)	Tasman Valley, NZ	GPS	5 (one tracked twice), one female	GPS	3478 (295 – 1232 per individual)	24.86	1.78	8.76	16.07	16.07	16.07	9.98	*
Islands	Dowding (1998)	Motuihe Is.	VHF	14	Honing in	Average of 31 fixes per cat	0.74	0.47	0.16	1.41	0.12	0.46	0.47	16.8
	Bengsen et al. (2011) (2012)	Kangaroo Is. Australia	GPS	13	MCP 100		19.22	1.94	7.8	8.18	2.87	4.8	7.39	0.4-0.7
	Konecny (1987)	Galapagos Islands	VHF	14 (2 populations)	Honing in and visualisation	2613 (20-600 per individual)	7.6	0.35	3.04	2.10	0.21	0.82	2.41	2.2-2.5
	Martin et al. (2013)	Kerguelen archipelago, Sub Antarctic Islands	GPS	3 young males	GPS	10,391	0.73	0.30	0.58	*	*	*	*	*

Elsewhere	Biró et al. (2004)	Godollo, Hungary	VHF	3 (1 male)	Triangulation, MCP 100	145 (51-46 per cat)	1.49	1.49	1.49	3.28	0.41	1.845	2.96	*
	Edwards et al. (2001)	Northern Territory, Australia	VHF	19 (only used 4 for home range estimates)	Honing in, MCP 100	25-50 per cat	*	*	*	22.10	*	*	*	0.1
	Horn et al. (2011)	USA	VHF	16	MCP 95		5.47	0.01	1.57	2.41	0.14	0.57	0.35	*
	Jones & Coman (1982)	Vic, Australia	VHF	6	Honing in and visualisation	55-125	9.9	3.3	6.15	2.7	0.7	1.7	4.67	0.6
	Molsher et al. (2005)	NSW, Australia	VHF	21 (15 for mean)	Triangulation, MCP 100	730 (13-54 in individuals)	7.47	0.18	4.23	3.85	1.51	2.38	3.74	*
	Moseby et al. (2009)	Arid Recovery Reserve, South Australia	VHF and GPS	13	GPS, MCP 95	3568 (23-550 per individual)	131.98	0.55	32.32	35.65	2.60	20.78	28.86	*



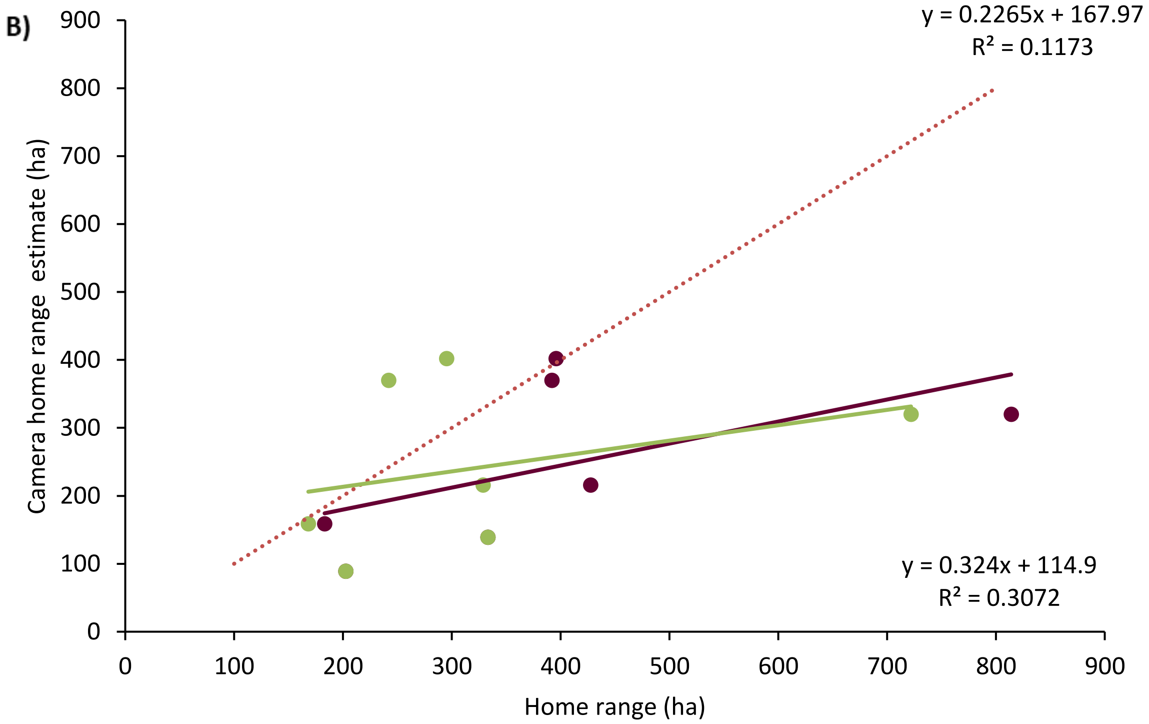


Figure S2: Correlation in home range size (ha) between **A)** ½ max, and **B)** average distance (AD), (see methods section). The orange line represents the line of equality. Home range estimation from camera traps based on the camera trap technique compared to the combined range estimate (CRE) (maroon) and radio-telemetry (green) (100% MCP). The equation and R^2 value are shown for the radio-telemetry data (top) and CRE (bottom).

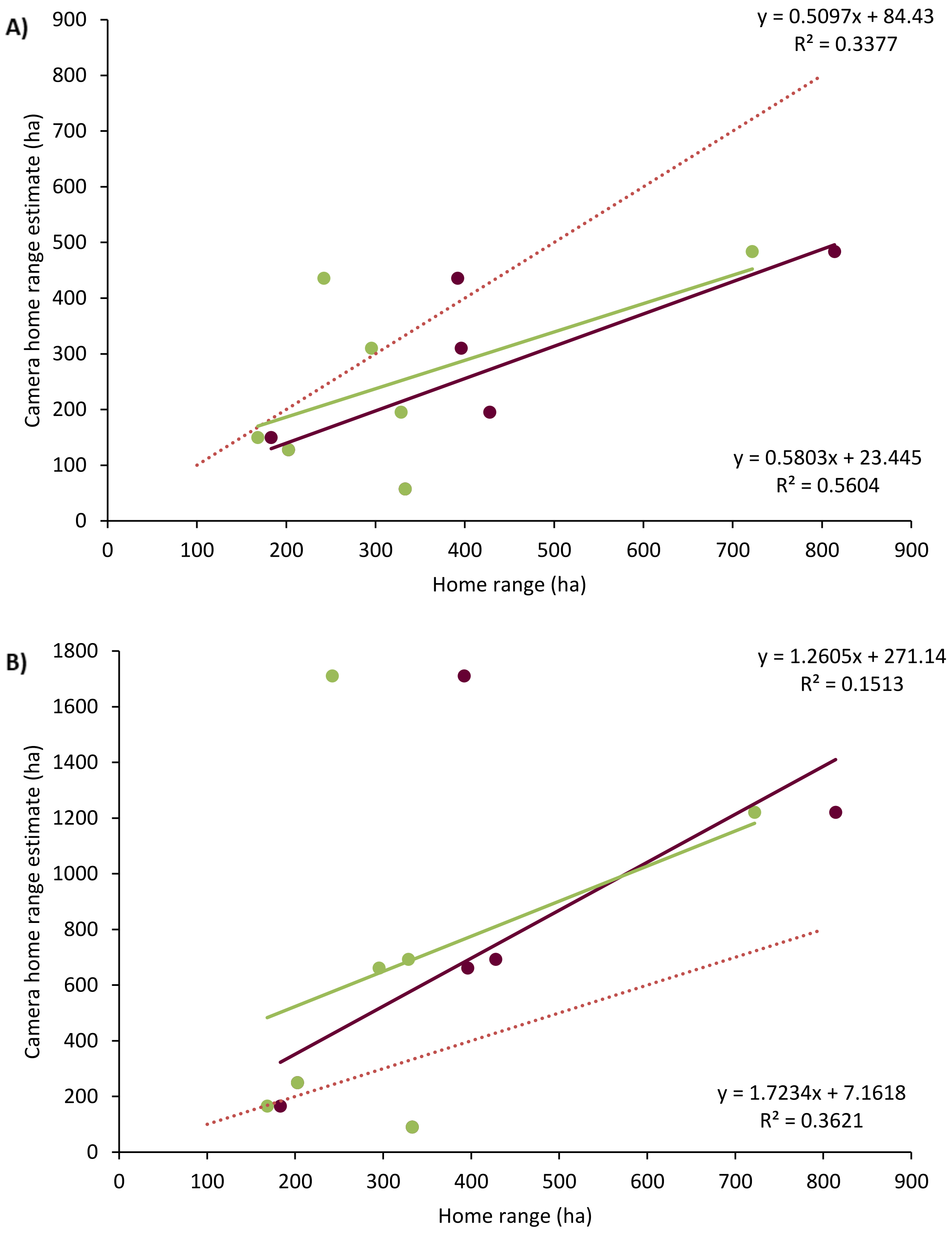


Figure S3: Correlation in home range size (ha) between **A)** 100m buffer camera trap technique and radio-telemetry (blue) and the combined range estimate (CRE) (maroon) (100% MCP), and **B)** 2.45 sigma camera trap technique and radio-telemetry (green) and CRE (maroon) (95% KDE). The orange line represents the line of equality. The equation and R^2 value are shown for the radio-telemetry data (top) and CRE (bottom).

Table S4: Home range estimates for individual cats monitored through radio telemetry and camera traps, and the estimates of their home range from camera trap data only using different techniques (see methods for details on calculations). No. of cameras is the total number of cameras the cat was detected on from September 2015 – March 2017. CRE = Combined Range Estimate which is the home range size of the cat estimated through camera trap locations and radio-telemetry. All measurements of home range are given in hectares (ha). *Not included in graphs or calculations.

Cat	No. cameras	CRE	Telemetry	½ Max	AD	½ AD	2.45 σ	Grid	100m
Cleo	7	183	168	95	159	220	165	175	150
Patches	5	333	333	109	139	150	90	125	58
Socks	7	203	203	84	89	216	249	175	128
Midnight	17	392	392	522	370	671	1710	425	435
Tigger	21	814	722	551	320	725	1220	525	484
Mittens	11	396	295	595	402	533	661	275	310
Salem	9	428	329	292	216	405	692	225	195
Sylvester*	3	550	550	304	486	359	-	75	97
Shadow*	8	75	2	203	163	214	2150	200	112

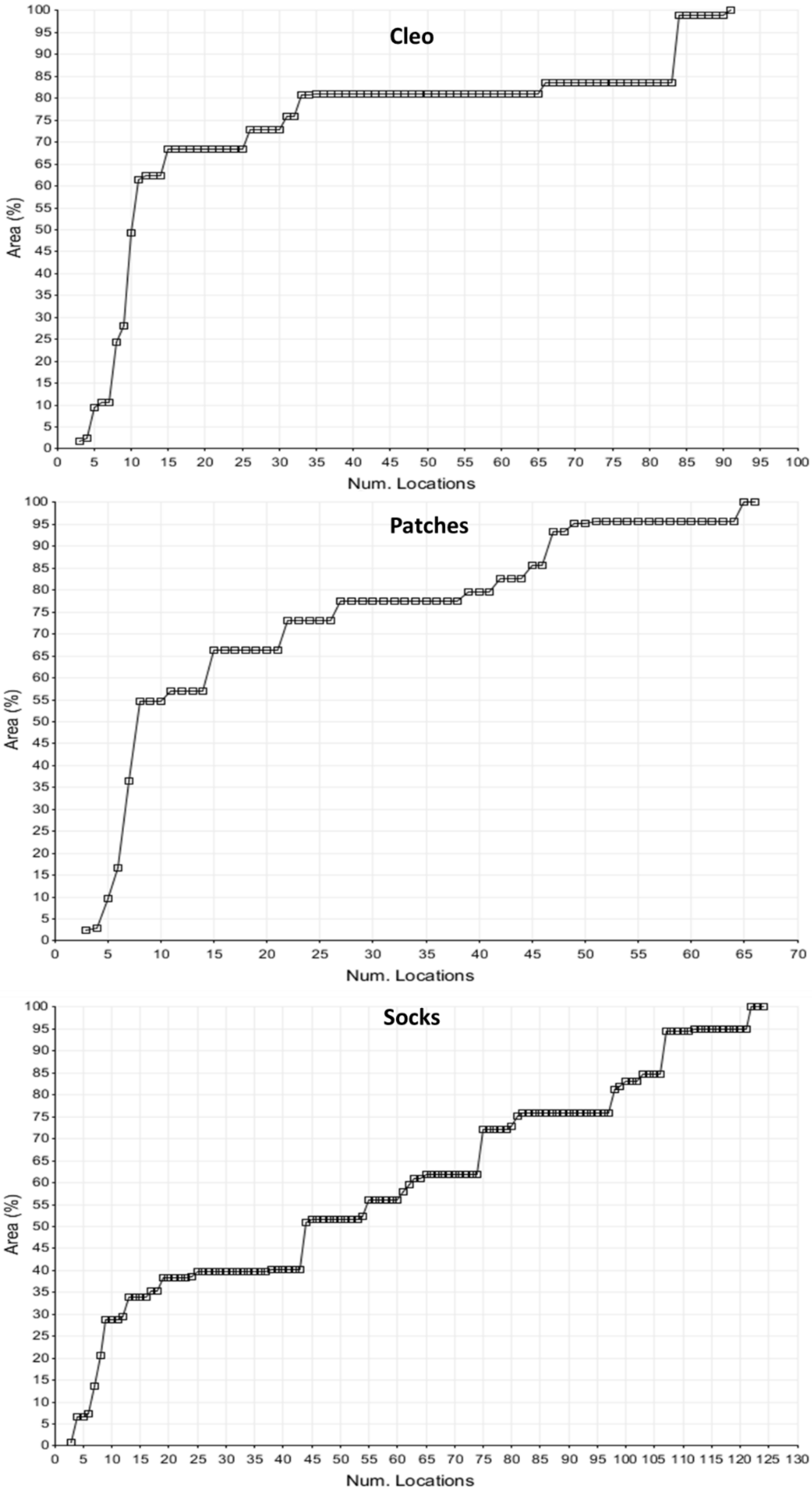


Figure S5: Incremental increase analysis showing the change in home range size with each additional location point for three of the female cats monitored in this study. All telemetry data was used, however for the camera trap data only the first time the cat was seen on that camera trap location was used.

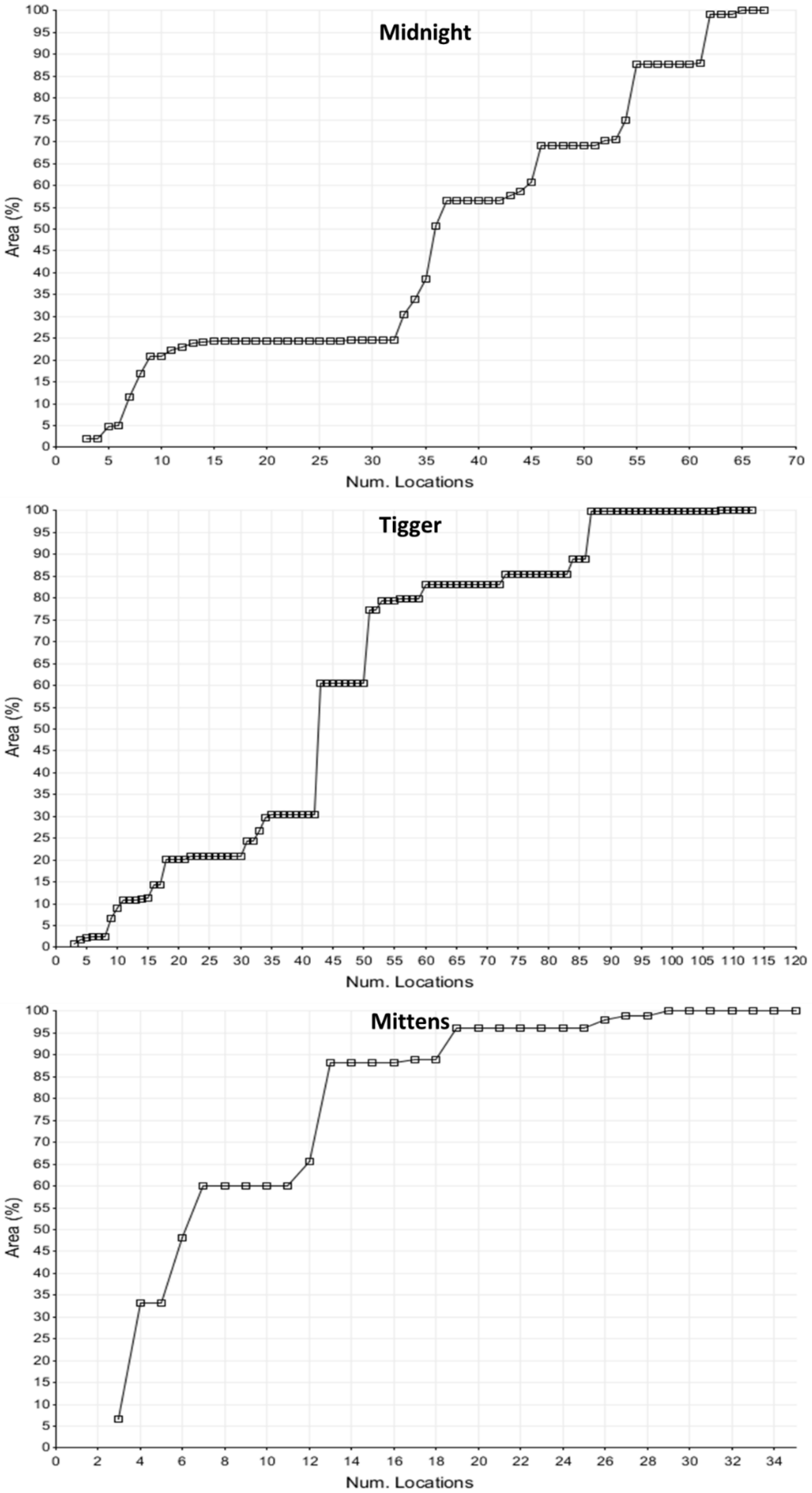


Figure S6: Incremental increase analysis showing the change in home range size with each additional location point for three of the male cats monitored in this study. All telemetry data was used, however for the camera trap data only the first time the cat was seen on that camera trap location was used.

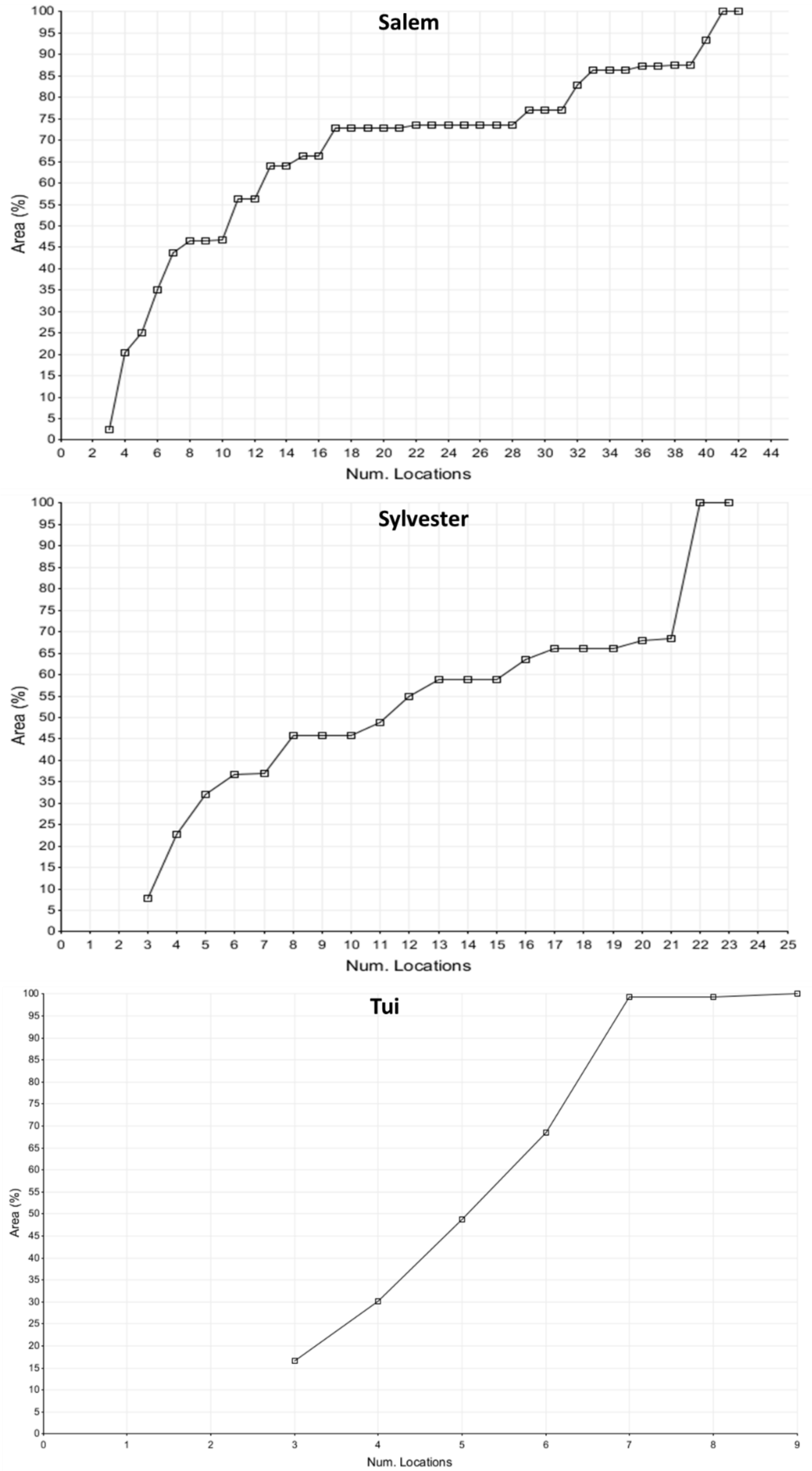


Figure S7: Incremental increase analysis showing the change in home range size with each additional location point for three of the male cats monitored in this study. All telemetry data was used, however for the camera trap data only the first time the cat was seen on that camera trap location was used.

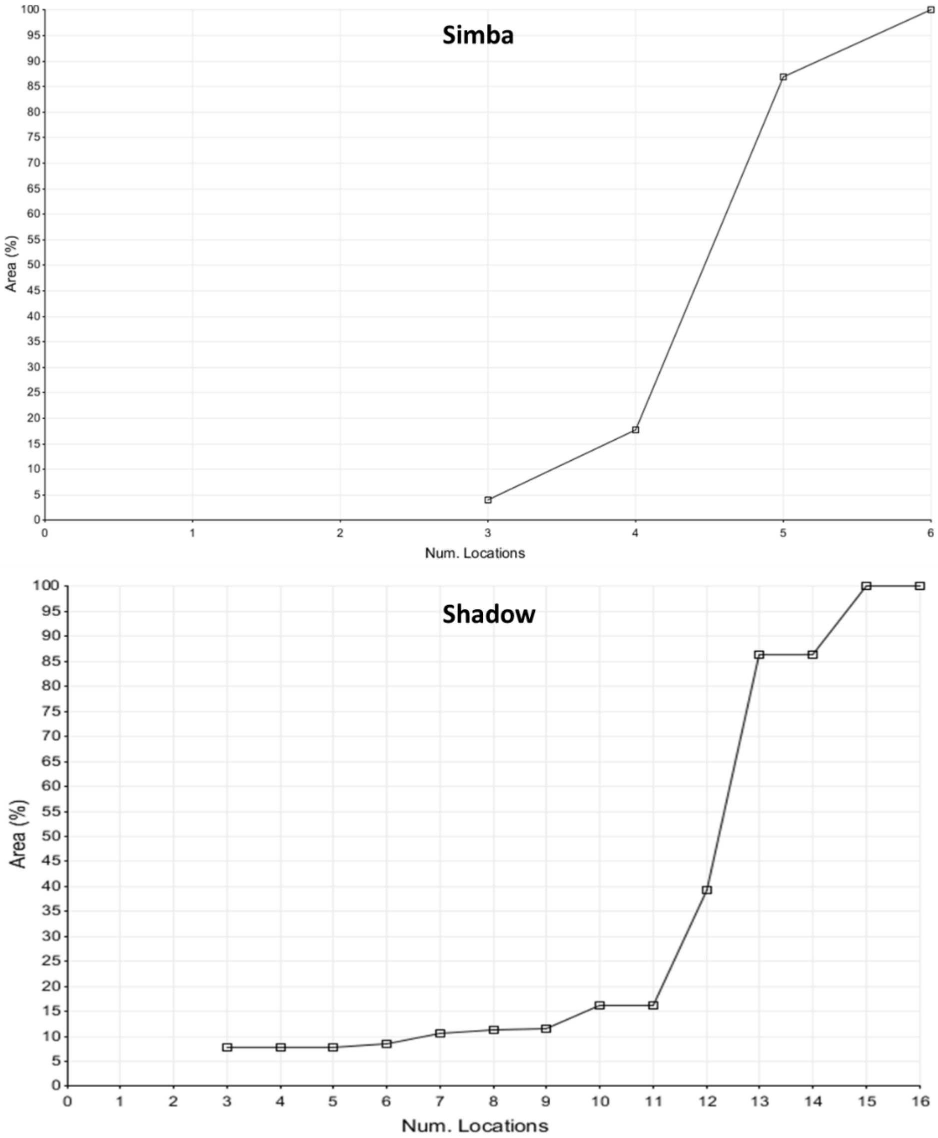


Figure S8: Incremental increase analysis showing the change in home range size with each additional location point for one male cat (top) and one female cat (bottom) monitored in this study. All telemetry data was used, however for the camera trap data only the first time the cat was seen on that camera trap location was used.

Table S6: Summary of feral cat morphometrics in New Zealand. The morphometrics from this study on Ponui Island are included. – represents data that was not included in the study.

Reference	Location	Latitude		Weight (kg)		Head-body Length		Tail Length	
				M	F	M	F	M	F
Fitzgerald (1990)	Raoul Island	29ºS	mean	2.46	1.74	491	447	265	246
			range	1.1-3.9	1.2-2.1	376-565	392-495	165-320	220-270
			n	59	17	3	5	57	17
Gillies unpubl. cited in Gillies & Fitzgerald (2005)	Northland	36ºS	mean	3.39 ± 0.08	2.54 ± 0.07	-	-	-	-
			range	1.35-5.5	1.3-3.7	-	-	-	-
			n	128	52	-	-	-	-
Veitch (2001)	Little Barrier Island	36ºS	mean	2.95	2.23	473	440	283	252
			range	1.6-4.1	1.5-3.8	370-530	380-550	250-320	210-300
			n	18	35	21	40	21	40

DOC unpubl. cited in Gillies & Fitzgerald (2005)	Okiwi Reserve, Great Barrier Island	36ºS	mean	2.35 ± 0.12	2.14 ± 0.08	-	-	-	-
			range	1.2-4.8	1.1-4	-	-	-	-
			n	53	49	-	-	-	-
Strang, this study	**Ponui Island**	**36ºS**	**mean**	**3.6**	**2.3**	**546**	**486**	**290**	**265**
			range	**3.0-4.3**	**1.8-2.7**	**502-569**	**453-525**	**262-313**	**243-289**
			n	**8**	**4**	**8**	**4**	**8**	**4**
Dowding DOC report cited in Gillies & Fitzgerald (2005)	Tuhua (Mayor) Island	37ºS	mean	3.67 ± 0.2	2.15 ± 0.09	497 ± 7	432 ± 10	-	-
			range	3.35-4.05	2-2.3	485-510	412-445	-	-
			n	3	3	3	3	-	-
King et al. (1996)	Pureora NP, Central North Island	39ºS	mean	3.3	2.06	501	421	-	-
			range	2.7-3.9	1.14-2.95	463-540	383-465	-	-
			n	2	5	2	5	-	-

DOC unpubl. cited in Gillies & Fitzgerald (2005)	Boundary Stream, Hawke’s Bay	39°S	mean	3.68 ± 0.11	2.69 ± 0.11	518 ± 18	441 ± 25	-	-
			range	1.75-5.3	1.15-3.5	380-620	360-490	-	-
			n	44	30	13	5	-	-
Murphy et al. (2011)	Ngamatea Station, Central Plateau, North Island	39°S	mean	3.28	2.70	-	-	-	-
			range	1.41-4.52	1.35-3.52	-	-	-	-
			n	11	13	-	-	-	-
Fitzgerald (1990)	Orongorongo Valley	41°S	mean	3.67	2.72	514	477	283	247
			range	2.1-5.1	2.2-3.5	501-525	415-505	270-295	180-280
			n	12	15	3	5	3	5
Recio et al. (2010)	Tasman Valley	43°S	mean	3.75	2.97	-	-	-	-
			range	-	-	-	-	-	-
			n	-	-	-	-	-	-

Pierce unpubl. in Gillies & Fitzgerald (2005)	McKenzie Basin	44°S	mean	3.75	2.97	562	496	-	-
			range	2.07-7	1.6-4.6	530-590	435-570	-	-
			n	29	34	3	6	-	-
Mills (1994)	McKenzie Basin and Central Otago	44-45°S	mean	3.69 ± 0.13	2.63 ± 0.07	-	-	-	-
			range	1.92-6	1.52-4.43	-	-	-	-
			n	50	74	-	-	-	-
Baker (1989)	Middlemarch, Central Otago	45°S	mean	3.74 ± 0.38	2.76 ± 0.19	-	-	-	-
			range	1.08-6.25	1.18-4	-	-	-	-
			n	15	17	-	-	-	-
Fitzgerald & Veitch (1985); Fitzgerald (1990)	Herekopare Island	46°S	mean	3.36 ± 0.23	2.75 ± 0.3	502	471	247	232
			range	2.8-3.6	2.3-3.3	475-525	445-495	230-260	210-255

			n	12	8	12	8	12	8
Harper (2002) cited in Gillies & Fitzgerald (2005)	Freshwater and Rakeahua Valleys, Stewart Island	47ºS	mean	3.36 ± 0.5	2.63 ±0.43	518 ± 27	461 ±30	-	-
			range	2.68-4.09	2.16-3.25	460-560	435-500	-	-
			n	13	7	13	7	-	-

Chapter 3: Camera traps versus accelerometry: Do they tell the same story?

Plate 3: Still from a camera trap video of Mittens captured on Ponui Island.

Introduction

Feral cats have previously been shown to be nocturnal (Recio et al., 2010; Garvey, 2016) or crepuscular (Jones & Coman, 1982; Konecny, 1987), and their activity patterns are influenced by prey availability (Konecny, 1987; Garvey, 2016), the presence of people (Bogdan et al., 2016), and other predators (Brook et al., 2012; Kennedy et al., 2012). In New Zealand, Garvey (2016) found that cats were more diurnally active in areas where birds and lagomorphs were the main available prey, whereas, in areas of high rodent availability, cats were almost exclusively nocturnal.

Live-traps are a common method used for population control in feral cats. Knowledge of home range size is often used to increase the likelihood of cats encountering live-traps (Chapter 2). Trapping efficiency can be further increased by using knowledge of the daily activity patterns of feral cats. A large proportion of feral cat control is through live capture due to the risk of killing pet cats or non-target species in traps (Molsher, 2001; Nogales et al., 2004; Campbell et al., 2011) or through poisoning, which are common control measures used with other species. However, live-traps are labour intensive, requiring frequent checks to satisfy welfare concerns (New Zealand Government, 1999). Nevertheless, species are most likely to visit traps when they are the most active and identifying the activity patterns of feral cats could be used to find the optimal time to set and check cage traps. This would potentially increase the capture rates of feral cats and increase overall trapping efficiency.

The success of feral cat eradication programmes is often assessed by comparing the number and detection rate of feral cats captured on cameras before, during, and after control (Campbell et al., 2011). Felids (including feral cats) often use trails to move throughout their habitat, which has led to recommendations to set up camera traps on trails to increase their capture probability (O'Connell et al., 2010; Meek et al., 2012; Rovero et al., 2013; Cusack et al., 2015). Hotspots of feral cat activity may appear throughout a study site based on habitat qualities, and identifying these habitat features could allow future studies to set up cameras in areas with the highest chances of detecting feral cats.

Feral cats, being a common species, may be an appropriate model for estimating the quantity of camera trap data that is required to also be able to accurately infer the activity of non-domestic felids. Feral cats share traits with other small non-domestic felids, such as similar home range sizes, activity patterns, and habitat use (Biró et al., 2004; Germain et al., 2008; Luna-Mendoza et al., 2011; Manfredi et al., 2011). Worldwide, populations of non-domestic felids are declining with the major threats being poaching and habitat destruction (McCarthy et al., 2015). These population declines, and the elusive nature of small non-domestic felids, has resulted in sparse data on their range distribution and ecology (Lucherini et al., 2004; Brodie, 2009). Infrequent sightings and camera trap detections result in inferences on the behaviour and activity of non-domestic felids being made based on small datasets (Di Bitetti et al., 2006; Cheyne & Macdonald, 2011), which could lead to misguided management decisions.

Camera trapping is a tool that is becoming more commonly used in wildlife studies in recent years (Burton et al., 2015; Caravaggi et al., 2017), mainly due to technological advances that have allowed camera traps to remotely trigger based on heat-in-motion (passive infrared cameras) (Meek et al., 2015). Camera traps are, however, a fixed point sampling method with small detection zones relative to a study site (Burton et al., 2015), and the detection of an animal is reliant on it walking in front of the camera. The small detection zones of camera traps and the potential for avoidance behaviour mean the activity patterns obtained by camera traps may not reflect the true activity pattern of the study species. In two studies, one of kinkajous (*Potos flavus*) and one of tigers (*Panthera tigris*), the animals progressively avoided camera trap sites, however both of these studies used cameras with a white flash (Wegge et al., 2004; Schipper, 2007). Increased use of infrared cameras for research has led to reduced reports of camera trap shyness, however, infrared cameras can still be detected by animals due to the sound they emit, and study animals stop and look at the camera traps (Meek et al., 2014a; Meek et al., 2016). With this potential for animals to become camera trap shy and avoid cameras, there is a need to determine whether the activity described by camera trap data is similar to that obtained through other methods.

Numerous studies have reported the activity patterns of various species from camera trap data, particularly carnivores (Paviolo et al., 2009; Ilemin & Gürkan, 2010; Kolowski & Alonso, 2010; Gray & Phan, 2011; Monteverde & Piudo, 2011; Akbaba & Ayaş, 2012; Oliveira-Santos et al., 2012; Wallace et al., 2012; Kuhnen et al., 2013; Ohashi et al., 2013), however there is a lack of consistency in the collection of data and the amount of data used to describe activity, creating difficulties in comparing studies. There are studies with recommendations on camera trap placement for animal detection, measures of occupancy, and reporting data (Glen et al., 2013; Claridge & Paull, 2014; Jansen et al., 2014; Meek et al., 2014b), however, there are no studies on the quantity of data needed to obtain an accurate representation of activity patterns. Emphasis is often placed on camera trap effort (the number of cameras and the number of nights the cameras are recording) for estimating population density. In turn, this has led to studies describing activity patterns also focusing on camera trap effort rather than the number of encounters (videos/photos) of the study species. The number of encounters of a species on camera traps is dependent on the density and behaviour of the species, therefore, emphasis for data collection for describing activity should be placed on the number of encounter events rather than the camera trap effort.

Tri-axial accelerometry devices are another method used to describe activity, and their use for monitoring activity has been validated in several felids, including domestic cats (Watanabe et al., 2005; Lascelles et al., 2008; Shepard et al., 2008; Grünewälder et al., 2012; Andrews et al., 2015). Tri-axial accelerometry devices contain data-loggers that record the body movements of an animal based on changes in the acceleration along three axes (Watanabe et al., 2005; Wilson et al., 2013a). Accelerometers have been used in many wild animal studies (Nathan et al., 2012; Wang et al., 2015; Pagano et al., 2017), but their use is not always feasible. Many of the commercially available devices were originally developed for use on domestic pet animals (Watanabe et al., 2005; Lascelles et al., 2008), and either require the device to be retrieved for manual download of data, or for the device to be very close to a downloading receiver. Because owners can remove and reset the device regularly, the storage capacity is generally less than 30 days of continuous monitoring and this limits their usefulness for studies on wild animals (Wilson et al., 2013b; Wang et al., 2015; Pagano et al., 2017).

The advantages of using camera traps, where information can be collected on a larger number of individuals and are non-invasive (Burton et al., 2015; Caravaggi et al., 2017), may outweigh the benefits of accelerometers that monitor activity at a finer scale, but are less logistically feasible for monitoring activity in wild felids. For these reasons, there is a need to determine whether the activity from camera trap data is similar to that described from accelerometry.

In this study, I compare the activity of feral cats measured using camera traps and accelerometry, and measure the amount of camera trap data that is needed to describe feral cat activity using this method. I also aimed to describe feral cat activity around live-traps with the hope of using this knowledge to make feral cat trapping more efficient. I aim to see if there are particular habitat or trail features that increase the number of captures of feral cats on camera traps in order to recommend placement of camera traps for future studies.

Methods

Accelerometers

Feral cats in the study site were already part of a radio-tracking study and had been fitted with radio collars as described in Chapter 2. The accelerometers used in this study (Heyrex™, Say Systems, Wellington, New Zealand) measured the acceleration of the body in three axes, and these vectors were summed into a total change in acceleration over 15-minute epochs, which was expressed relative to standard gravity (delta-g/15 minutes). The delta-g measured the change in acceleration between the current and the previous data point.

Modifications were made to reduce the weight and size of the devices because the accelerometers were originally designed for dogs. The accelerometers were modified by placing them in resin with a moulded ABS (acrylonitrile butadiene styrene) plastic on the outside. The devices were also adapted to be attached to a radio collar by adding zip ties set in the resin. The modified devices weighed 20 g and measured 65 mm in length and 21 mm at its widest point. An additional zip tie was placed around the middle of the accelerometer and over the radio collar to ensure the device was secure (Figure 1). Accelerometers were placed on the opposite side of the collar to the radio transmitter to distribute the weight evenly. The accelerometers collected data continuously over approximately ten days, with the information stored on the device until it was downloaded. All prior existing data were removed before attaching the device to the cats.

Feral cats were live-trapped to attach accelerometers from December 2015 - July 2016 using the same methods outlined in Chapter 2. Four accelerometers were placed on cats in December 2015, one in January 2016, one in March 2016, and one in each of June and July 2016.

I used two methods in the field to attempt to remotely download the data stored in the device. The accelerometers had an open-air range of 30 m over which the device could connect to the receiver. This made downloading the data from the device difficult. Antennas were constructed in an effort to extend the range of the receiver, but these proved unsuccessful in field trials due to obstruction of the signal by vegetation. I then opted to re-trap the cats so that the receiver could be placed close enough to them to enable the accelerometry data to be downloaded. Once a cat was captured a blanket or a towel was placed over the cage and the cat was otherwise left undisturbed until the data were downloaded, and then the cat was released. I downloaded the data from the accelerometers by attaching a receiver to a Linux laptop running the proprietary software, which was placed close to the cage. The accelerometer took one hour to download ten days of data.

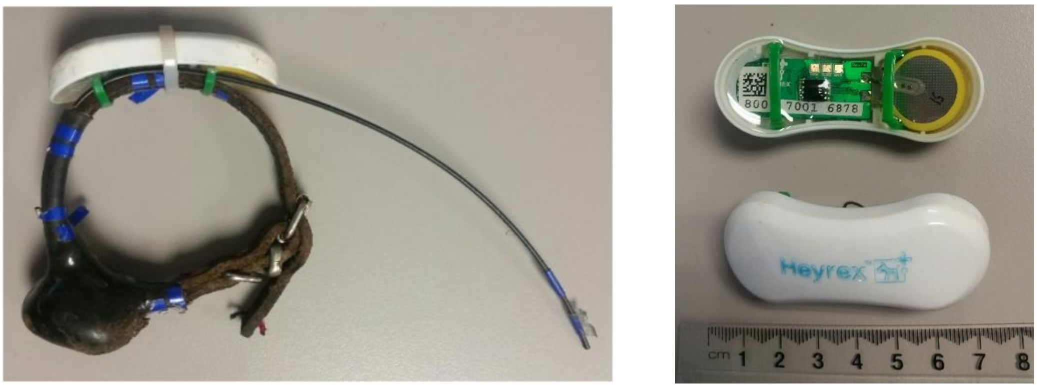


Figure 1: Left – Radio collar with an accelerometer attached which had been deployed on a cat. The accelerometer was attached using zip ties. Reflective tape was placed around the radio collar in a unique pattern for each cat for identification on camera traps. **Right** – Heyrex accelerometer device with the modifications made for this study (described in methods section). Zip ties were set in resin for attachment to the radio collar. Photos by author.

Analysis of accelerometry data

Delta-g/15 minutes was summed over an hour time frame for each individual cat, which was used as an estimation of total activity over that time period (delta-g/hour). Data collected by the accelerometer device 1-2 hours after the cat was released from the cage trap (if it had been anaesthetised, e.g. when the accelerometer was first attached to the cat) was ignored due to the effect of anaesthesia on the animal's movement (Fahlman et al., 2005). There was the chance that the accelerometer did not completely record all of the cat's movements in the last hour of collection (as it reached its storage capacity), therefore, the last hour of data collected by each device was excluded from analysis.

Camera traps

Camera trap footage was collected as outlined in Chapter 2. All independent feral cat videos were used that were collected from January 2014 - March 2017 unless otherwise stated. Independent videos were where only the details from the first video was used (if the cat stayed in front of the camera for multiple videos), or an individual cat reappeared on the camera more than ten minutes after its last video. Footage from baited camera traps was not used for describing seasonal activity or for comparing activity patterns between camera trap data and accelerometry.

Analysis

Feral cat activity

The accelerometry devices collected between 7-10 days of movement data for each cat over a collection period, which was typically one month or until the cat could be trapped again and the data cleared from the device. The daily activity patterns of the four cats that had activity data collected over December 2015 were graphed showing the average delta-g/hour ± SE. The average delta-g/hour was calculated for each cat by averaging the delta-g value for each hour over the 7-10 days of data collection.

Average delta-g/hour (± SE) was compared between sexes using all available accelerometer data for males and females, regardless of month of collection. The area under the curve was calculated by summing the average delta-g/hour over the 24 hour time period for each sex. To determine the overall hourly activity of feral cats from accelerometry, all accelerometer collection periods (11) were used (a total of 2547 hours), and the average delta-g/hour ± SE graphed.

To test the validity of the data (due to repeated measures and biases towards the collection of accelerometry data towards certain individuals), I first compared the hourly activity patterns of the cats that were collected during December 2015, to determine whether there were any large differences in activity between the individual cats. As the data was then compiled to look at sex differences in activity patterns, I visually assessed whether the pattern was consistent with that seen between the two male and two female cats that had data collected in December 2015.

Differences in activity between seasons were evaluated using camera trap videos only, due to the small sample of accelerometry data. The videos were divided into season across all years: summer (December – February), autumn (March – May), winter (June – August), and spring (September – November). The number of videos for each season was counted, and the number of cat videos captured each hour was expressed as a percentage of the total number of cat videos for that season and graphed. Time of sunrise and sunset was provided by Thorsen (2017) for the Auckland region during the different seasons.

Comparing activity patterns from camera traps to accelerometry

The correlation between activity as detected by camera traps with activity recorded by accelerometry was tested using linear regressions in R (R Development Core Team, 2008). The overall average hourly activity calculated above (using 2547 hours of accelerometry data) was used for the comparison between accelerometry and camera trap data. Correlations between the two methods were calculated using number of videos, months of collection, and number of camera trap nights. Only feral cat videos collected from September 2015 – March 2017 (where cameras were set up in a 500 x 500 m grid system), were used for this analysis (a total of 1,028 videos). Videos were not included in the analysis where the cameras were baited for trapping during this time.

Feral cat activity around live-traps and cameras

To describe the activity of feral cats around traps and baited cameras, I only used the camera trap videos that featured a cat eating bait to determine the hour that cats visited these baited cameras and traps (322 videos). Where there were sequences of videos where a cat was at a cage trap eating bait, only the first video of the sequence was used for describing the activity pattern. I also compared this camera trap data to the overall hourly activity (accelerometry data) described above to determine whether feral cats visited traps when they were the most active.

I used generalised linear models (GLM) in R using the MASS package (R Development Core Team, 2008) to test if habitat and location traits associated the camera trap site influenced the number of cat videos, and the number of individual cats, captured at different camera trap locations. These included: trail length, trail width, habitat, and location (gully or ridge) (Table 1). Four home range calculations were also used from the home range analysis in Chapter 2. This included the number of resident cats, which was the number of cats that had a home range that overlapped the camera site (100% MCP), and this was split into sex also; the number of resident males and the number of resident females. The number of core ranges was also tested for; the number of cats that had a core home range (50% MCP) that overlapped the camera. I only used videos (n = 1028) that were collected from September 2015 – March 2017 when the 28 cameras were set up in the 500 m x 500 m grid in the study site. Videos captured when the camera was set up on a baited live-trap were not used for the model.

Due to over-dispersion in the data, a GLM using negative binomial probability distributions was used for the number of cat videos at camera trap locations (Crawley, 2013). A GLM with a Poisson probability distribution was used for the number of individual cats captured at camera traps. A stepwise elimination was carried out for both models based on Akaike Information Criterion (AIC) values to identify the most important habitat features. These models allowed me to determine if there were hotspots of cat activity.

GLMs using Poisson probability distributions were also used to determine if there were habitat and trail features associated with camera trap locations that were drivers for the number of male cat videos and for female cat videos. As above, only videos that were collected from September 2015 – March 2017 were used for the models. Videos captured when the camera was set up on a baited live-capture trap were excluded. All cat videos were used where the sex of the cat could be determined (n videos = 242 female, 498 male). These models only incorporated habitat, location (gully or ridge), trail length, and trail width in the analysis (Table 1). Heat maps were produced using QGIS (geographic information system) of camera trap activity reflected by; number of cat videos, and number of individual cats at each camera trap location.

Table 1: Habitat and location features associated with the 28 camera trap locations used in this study that were tested as predictors for the number of individual cats and the number of cat videos captured at each location. Home ranges were 100% Minimum Convex Polygon (MCP), and core home range was 50% MCP.

Predictor	**Levels**	**Categorisation**
Habitat	Pasture	Camera set up in a forest/scrub fragment but the camera points towards open pasture.
	Scrub	Mix of kanuka (*Kunzea ericoides*) and manuka (*Leptospermum scoparium*) and other small shrubs
	Forest	Broadleaf and kauri (*Agathis australis*) forest
Location	Ridge	Camera set up on a ridge
	Gully	Camera set up in a gully
Trail length	None	Camera was not set up on a trail
	Short	Trail less than 100 m long
	Medium	Trail length between 100-399 m long
	Long	Trail 400 m or more in length
Trail width	None	Camera was not set up on a trail
	Narrow	Trail 1 m wide
	Medium	Trail 2-3 m wide
	Wide	Trail 4 or more metres wide
Resident cats	Low	1-3 cats overlapped the camera location in home range
	Medium	4-5 cats overlapped the camera location in home range
	High	6-8 cats overlapped the camera location in home range
Females	None	No resident females had home ranges overlapping the camera trap
	One	1 resident female had a home range overlapping the camera
	Two	2 resident females had home ranges that overlapped the camera
Males	Low	Less than 3 resident males had home ranges overlapping the camera
	Medium	3-4 resident males had home ranges overlapping the camera
	High	5 or more resident males had home ranges overlapping the camera
Core	Yes	Camera was set up in a feral cat’s core home range
	No	Camera trap was not set up in a feral cat’s core home range

Results

Feral cat activity

Accelerometry

Accelerometry devices were fitted to a total of eight cats after live-trapping and anaesthetising. Accelerometry data was subsequently collected from five cats, resulting in 11 periods of collection (109 days) and 2547 hours of activity data (Table 2). The three remaining cats were not recaptured, due to them avoiding live-traps, to enable downloading of data.

Over the same time period (December 2015), the two males had higher levels of activity (represented by higher delta-g/hour) than the two females (Figure 2). The males had similar activity patterns, and all four cats had a drop in activity in the early morning after sunrise (7:00-10:00 h). One of the females (Cleo) had higher activity than the other cats during the afternoon (Figure 2).

Over all hours of activity collected from December 2015 - July 2016 (males = 1093 hours, females = 1454 hours), both males and females were active during similar hours (Figure 3). Both sexes were most active during night hours, and had a reduction in activity at 08:00-9:00 h. Males had a higher average delta-g/hour than females, and were 50% more active than females (area under the curve (delta-g/hour); males = 60351, females = 40003) (Figure 3).

Combining all activity data for the feral cats (2547 hours), regardless of sex or month of collection, a similar pattern of activity was found where, overall, the feral cats were most active at night, with a peak of activity during the first few hours of darkness (Figure 4). Their lowest activity was in the early hours of the morning, between 7:00-10:00 h, which was also when there was the smallest amount of variation in activity between the cats.

Table 2: The days and months that accelerometry data was collected for each cat. Data was collected by re-capturing the cats in live-traps and remotely downloading the data while the cat was in the trap. The sex of the cat is in parentheses.

	Cleo (F)	Midnight (M)	Socks (F)	Tigger (M)	Mittens (M)
December	14th-24th	13th-22nd	13th-23rd	15th-21st	
January/February	24th-3rd	26th-5th	25th-3rd		
March	20th-29th				
April	15th-25th				
July				17th-26th	13th-22nd

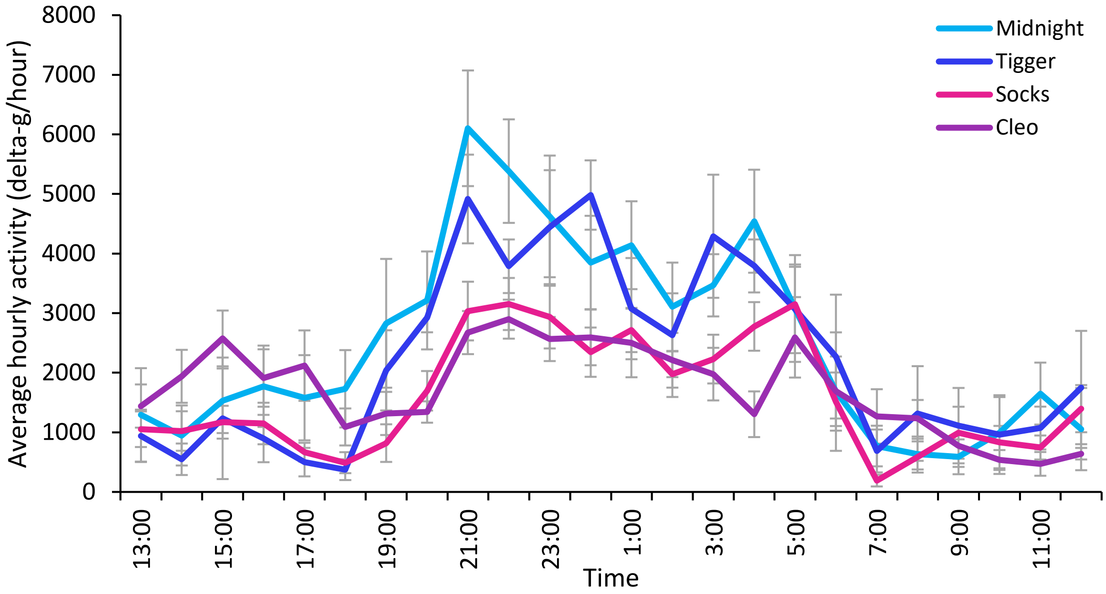


Figure 2: Average hourly activity (delta-g/hour ± SE) collected by collar-mounted tri-axial accelerometry devices from four cats (two males and two females) recorded in December 2015. The total number of hours recorded for each cat differed; Midnight = 239, Tigger = 146, Socks = 235, and Cleo = 243.

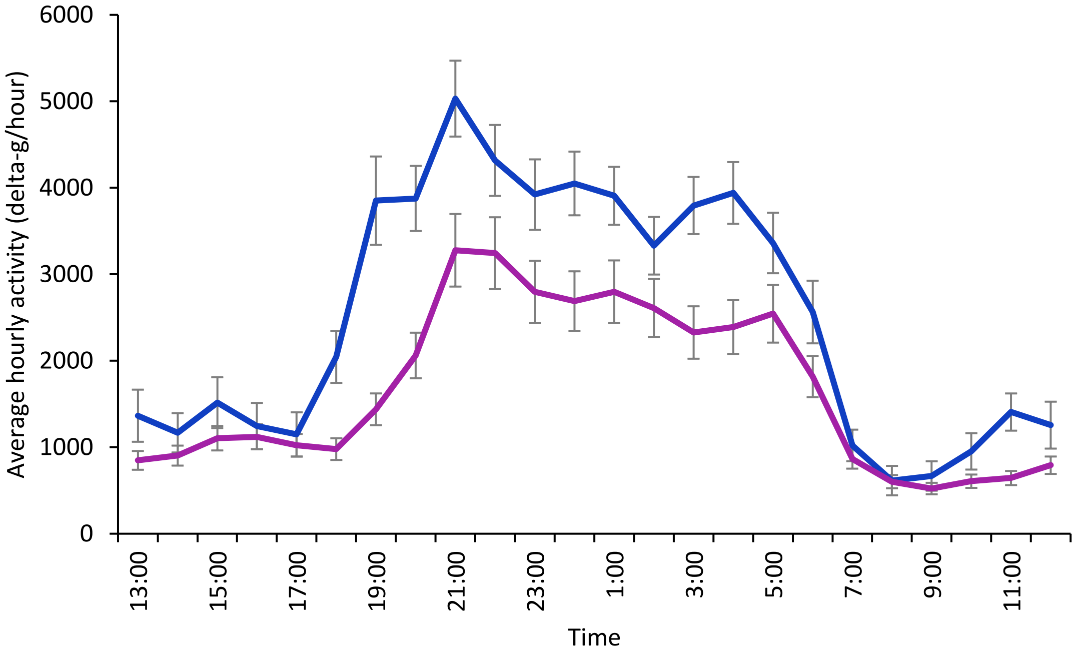


Figure 3: Average hourly activity (delta-g/hour ± SE) collected from December 2015 - July 2016 by collar-mounted accelerometry devices from three males (5 collection periods, 1093 hours) and two females (6 collection periods, 1454 hours). The blue line represents the activity of males and the purple line represents the females.

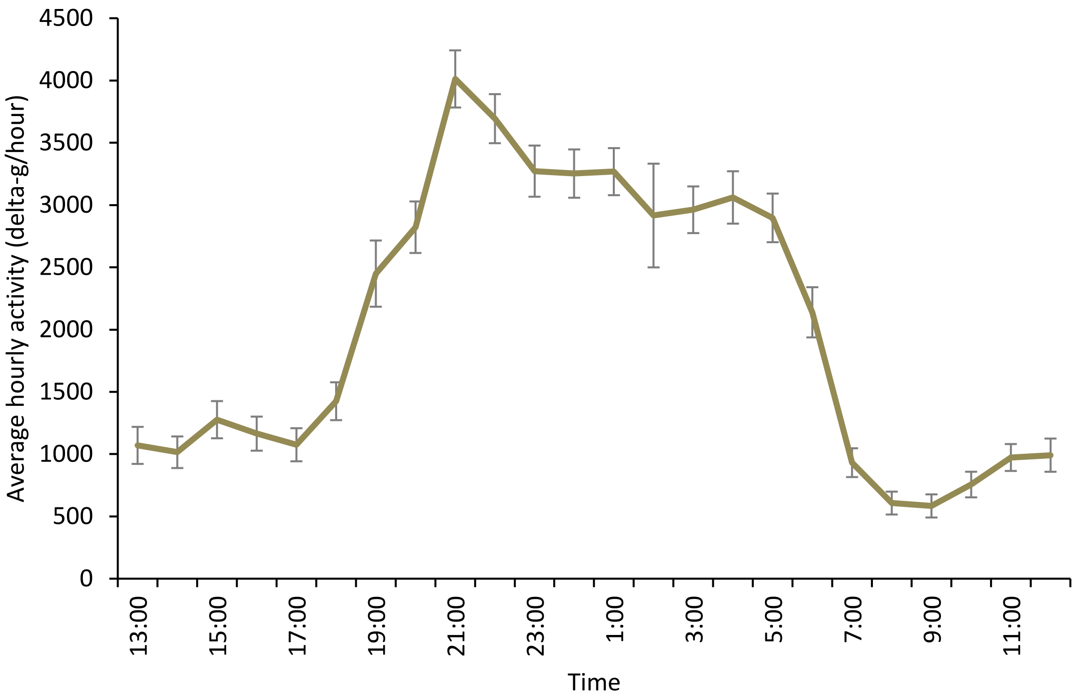


Figure 4: Average hourly activity (delta-g/hour ± SE) collected by the tri-axial accelerometers mounted on radio collars of five feral cats on Ponui Island (11 collection periods, 2547 hours). Data was collected from December 2015 - July 2016.

Camera trapping

Seasonal activity

A total of 174,571 camera trap videos were collected from January 2014 – March 2017, of which 1,642 were independent cat videos. This included 322 feral cat videos where the cameras were filming live-traps that were baited. Of those, 1,028 cat videos were taken from September 2015 - March 2017 when the cameras were set up in a 500 x 500 m grid across the study site, and does not include videos where the camera traps or live-traps were baited.

Regardless of season, most activity captured by camera traps was during the night, with 64-88% of the total daily activity occurring between sunset and sunrise (Figure 5). There was a drop in activity between 08:00-09:00 h in all seasons. The percentage of videos captured at night was highest in autumn (88%) and lowest in summer (64%). Spring and winter had 73-76% of videos captured during the night.

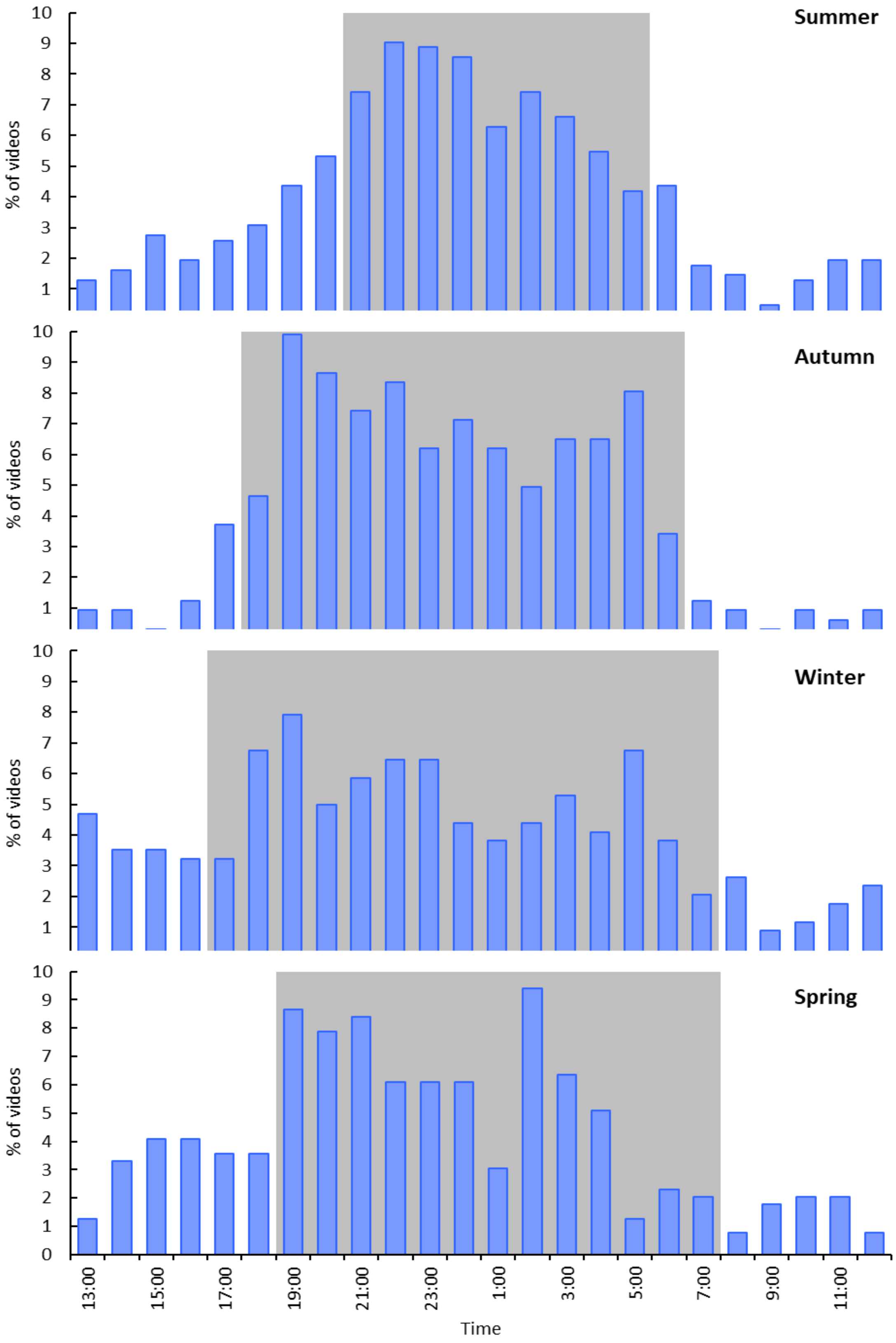


Figure 5: Seasonal pattern of activity shown by the percentage of the total number of camera trap videos captured for each hour during that season. Camera trap data was collected from January 2014 – March 2017. The grey blocks are the hours of darkness for the season (Thorsen, 2017). Summer (n = 620 videos), Autumn (n = 323), Winter (n = 341), Spring (n = 393).

Comparison of camera trap data with accelerometry

The distribution of independent cat videos by hour followed a similar pattern of activity to that recorded by the accelerometers (Figure 6). Both methods showed that the cats were mostly nocturnal, with a peak in activity in the first few hours of darkness, and a drop in activity a few hours after sunrise.

The patterns of activity recorded by accelerometry and camera trapping were highly correlated ($R^2 > 0.9$). When using a grid setup of camera traps, at least 600 videos were needed to reach a high correlation ($R^2 = 0.9$) (Figure 7A). Six months of camera trap videos, or 3000 camera trap nights, were needed to reach an R^2 value of 0.9 (Figure 7B & C). Once a regression value of 0.9 was reached for the correlation between the accelerometry data and the number of videos, number of camera trap nights, or months that the cameras were operating, the correlation plateued and new data did not greatly improve the relationship.

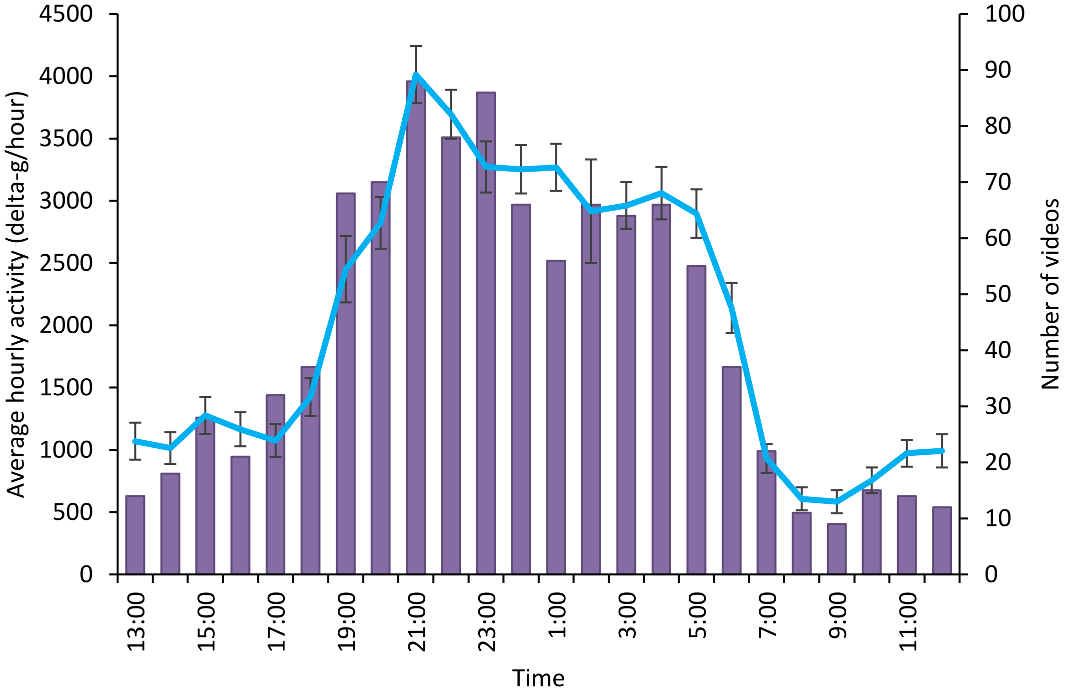


Figure 6: Comparison of daily activity patterns calculated using accelerometry data (delta-g/hour) collected from December 2015 – July 2016 and camera trap data (number of videos) collected from September 2015 – March 2017. Accelerometry data is shown as a line with mean hourly activity ± SE for all 2547 hours of data collected. Camera trap data is shown as bars and includes 1,028 independent cat captures.

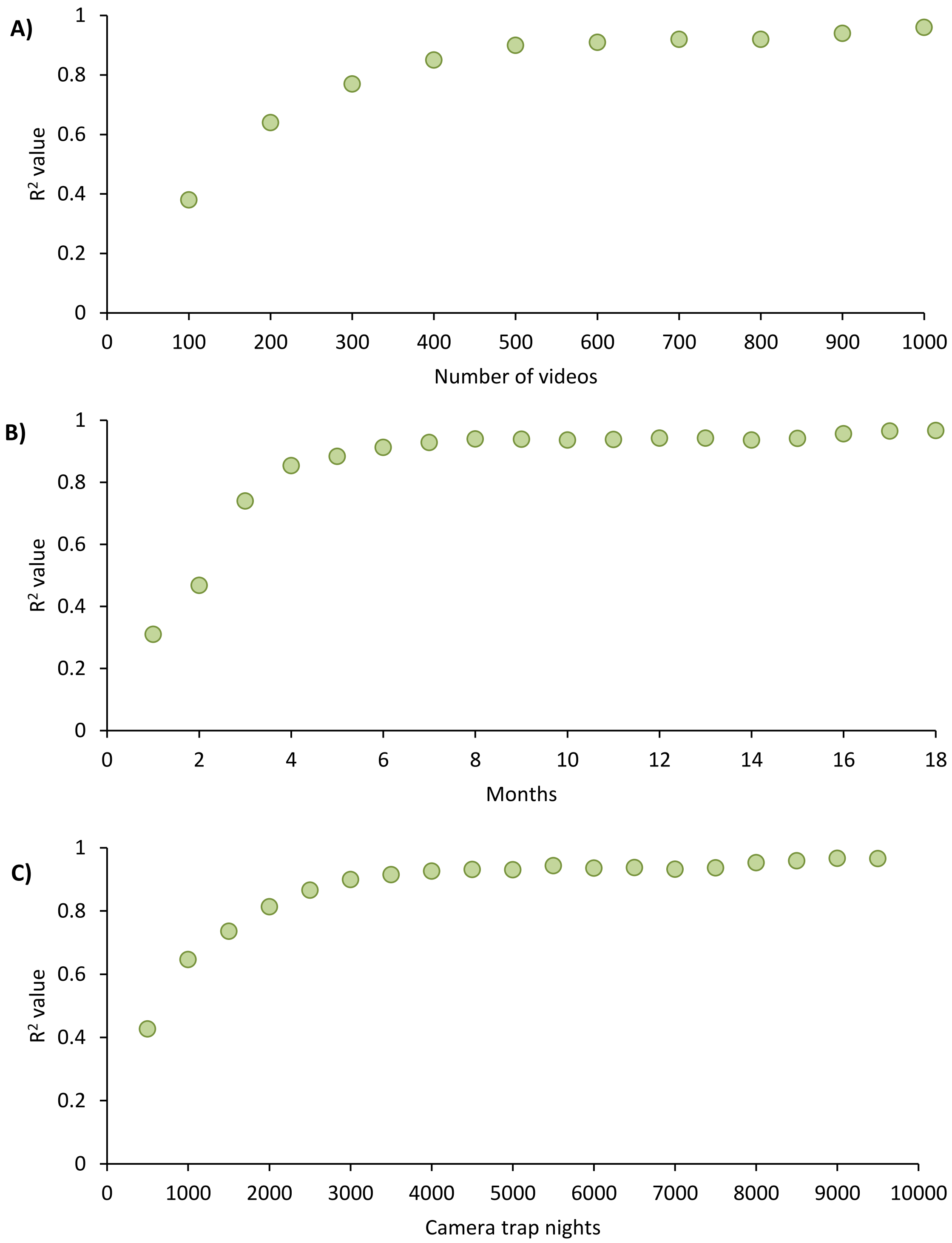


Figure 7: Scatterplots showing the R^2 values for linear regressions performed on the hourly activity patterns described for accelerometry (2547 hours) and camera trap data (1028 videos). Camera trap data used was that collected from September 2015-March 2017 when the cameras were set up in fixed positions in a 500 x 500 m grid across the study site. The videos used for the analysis did not include those where live-traps associated with cameras were baited. Each graph shows how the relationship in hourly activity patterns obtained from the two methods changes with the amount of data accumulated for**:** **A)** number of camera trap videos, **B)** months the camera trap study had been operating, and **C)** number of camera trap nights.

Activity around live-traps

Feral cats visited cage traps and ate bait mainly during night hours. Live-trap visit times were very similar to the overall activity pattern shown by feral cats. Cats were least likely to visit cage traps in the early morning, which is when they were their least active, and visited live-traps more frequently at midnight than any other hour (Figure 8).

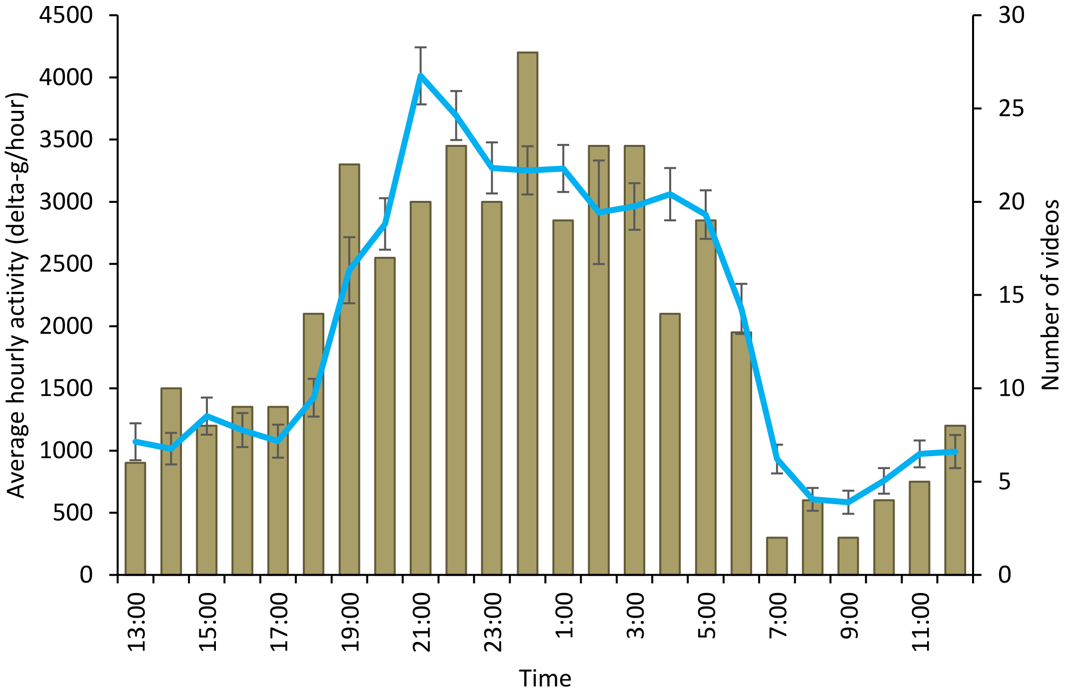


Figure 8: Camera trap videos (n = 322) of cats visiting cage traps, eating bait, or being captured in a live-trap compared to the overall activity pattern detected by accelerometry data (average delta-g/hour ± SE). All accelerometry data was used (n = 11 collection periods, 2547 hours). Camera trap data are shown as the bars, accelerometery data are represented by the line.

Camera trap hotspots

There were hotspots of activity on cameras throughout the study site, reflected in both high numbers of cat videos (Figure 9A) and high numbers of individual cats captured at certain camera trap locations (Figure 9B). The final GLM (based on the lowest AIC) identified four factors that were the most important drivers of the number of cat videos at each camera trap location (Table 3 & Supplementary material: Table S1). These were habitat, location (ridge or gully), the number of resident cats, and trail width. The final model itself was also significant (GLM, p-value <0.001). Cameras set up on ridges had a higher number of cat videos than those cameras set up in gullies (Table 4). Cameras that were positioned on trails more than 3 m wide also had higher numbers of cat videos than those set up on trails 3 m wide or less. Cameras in forested habitat had more camera trap videos of cats than cameras in either scrub or pasture habitats. Camera trap locations that overlapped the home ranges of more than five resident cats had more feral cat videos than those cameras overlapping fewer resident cats' home ranges (Table 4).

The final GLM identified the location (ridge or gully) and the number of resident male cats as the factors that could best explain the variation in the number of individual cats captured on camera traps (Table 5 & Supplementary material: Table S2) (GLM, p-value <0.001). Cameras that were set up on ridges had a higher number of individual cats captured than those cameras set up in gullies (Table 6). Cameras that also had 6-8 resident cats where their home range overlapped the camera location also had a higher number of individuals cats captured on the camera than those cameras that had 5 or fewer resident cats (Table 6).

Table 3: GLM with negative binomial probability distribution results for the overall model on factors driving the number of cat videos captured at camera trap locations (see methods section). The table includes the four factors that were identified in the final model, followed by the factors that were removed in each step of a stepwise backwards elimination. The removed factors are in the order that they were removed, and the AIC values are presented for the models after each removal. df = degrees of freedom.

Factor	**df**	**Deviance**	**p-value**	**AIC**
Overall model			<0.001	260.96
Habitat	2	34.217	0.01	-
Location	1	41.008	<0.001	-
Trail width	3	50.332	0.003	-
Residents	2	49.503	<0.001	-
Females	1	27.730	0.627	261.07
Core	1	27.912	0.674	262.73
Trail length	2	30.684	0.011	265.03
Males	2	28.815	0.556	268.32

Table 4: Results of the final GLM, estimate, standard error (SE), z values, and significance levels for each category as a predictor of the number of cat videos at different camera trap locations. The intercept represents the missing category for the factor; location – gully, habitat – forest, trail width – medium, residents – low.

Factor	**Category**	**Estimate**	**SE**	**z value**	**p-value**
(Intercept)		4.629	0.836	5.538	<0.001
Location	Ridge	1.038	0.289	3.587	<0.001
Habitat	Pasture	-1.342	0.494	-2.718	0.006
	Scrub	-0.977	0.430	-2.273	0.023
Trail width	Narrow	-0.385	0.461	-0.834	0.404
	None	-2.302	0.613	-3.756	<0.001
	Wide	0.211	0.497	0.425	0.671
Residents	High	0.962	0.469	2.049	0.040
	Medium	-0.401	0.463	-0.846	0.387

Table 5: GLM with Poisson probability distribution results for the overall model on factors driving the number of individual cats captured at camera trap locations. It includes the two factors that were identified in the final model, followed by the factors that were removed in each step of a stepwise backwards elimination. The removed factors are in the order that they were removed, and the AIC values for the models after each removal. df = degrees of freedom.

Factor	df	Deviance	p-value	AIC
Overall model			<0.001	122.05
Location	1	8.092	0.004	-
Males	2	8.449	0.015	-
Females	1	0.096	0.967	123.72
Core	1	0.278	0.599	125.18
Habitat	2	2.073	0.355	128.59
Residents	2	3.746	0.154	132.32
Trail width	3	4.194	0.241	135.86
Trail length	2	3.138	0.371	139.33

Table 6: Results of the final GLM, estimate, standard error (SE), z values, and significance level for each category as a predictor of the number of individual cats captured at different camera trap locations. The intercept represents the missing category for the factor; location – gully, males – low.

Factor	Category	Estimate	SE	z value	p-value
(Intercept)		1.378	0.215	6.408	<0.001
Location	Ridge	0.587	0.169	3.481	<0.001
Males	High	0.542	0.246	2.204	0.027
	Medium	0.051	0.240	0.215	0.83

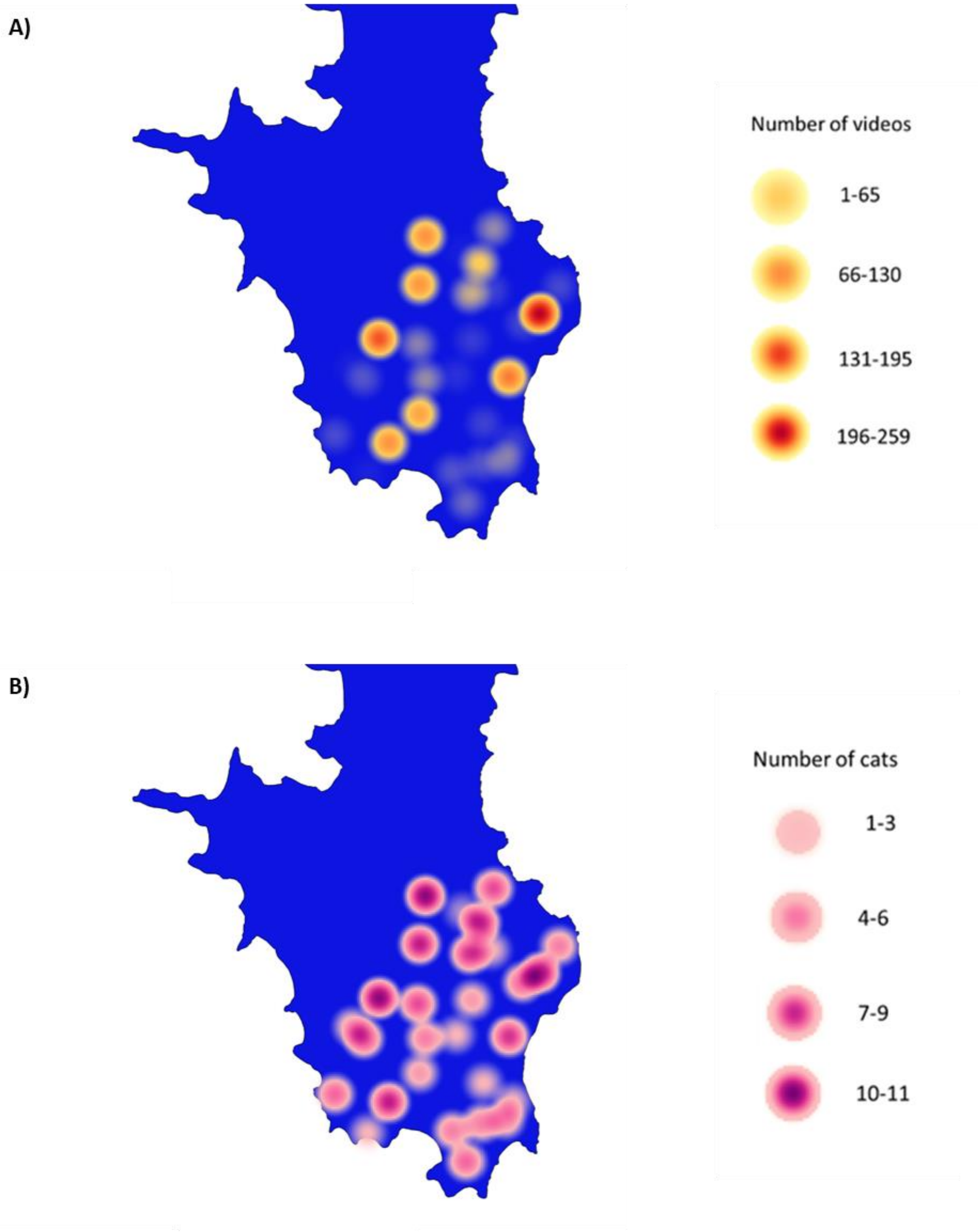


Figure 9: Heat map of feral cat activity on the 28 camera traps set up in a 500 m x 500 m grid system around South Ponui Island. The darker the circle, the higher activity reflected in **A)** number of cat videos (n = 1,320), and **B)** number of individual cats (n = 13). Videos collected from September 2015 - March 2017 were used.

Differences in male and female camera trap hotspots

There were also differences in the number of male and female cat videos that were captured on different camera traps. GLMs run for the number of male cat videos and the number of female cat videos on each camera trap identified all four habitat features to be significant drivers for both sexes; habitat, location (ridge or gully), trail length, and trail width (see Table 1 for a detailed description of the habitat features).

The GLM (AIC = 296.21) run for the number of female cats captured at camera trap sites found that cameras set up in forest had a higher number of female cat videos than cameras in scrub or pasture (Table 7). Females were captured more on cameras that were set up on short trails (less than 100 m long) than trails that were longer, and also on cameras that were set up on a wide trail (≥4 m). Females were also captured more on cameras set up on ridges than those set up in gullies (Table 7).

The GLM (AIC = 292.58) that was run on the number of male cats captured at different camera trap sites also found that cameras in forest habitat, and those set up on ridges, had higher captures of males than those in other habitat types or in gullies (Table 8), a similar finding to that of females. However, males appeared to be captured more on cameras that had different trail features than those identified as important predictors for female feral cats. Males were captured more on cameras associated with a long trail (more than 400 m in length), and also on cameras that were 2-3 m wide (Table 8).

There were individual differences between cats, with Midnight being captured on the most cameras (17) and Patches on the least (5). Females were captured on fewer cameras overall than males (females, n = 4, mean number of cameras = 6.25 ± 0.96 (SD); males, n = 4, mean = 12.75 ± 2.99) (Figure 10). Females had a higher number of captures (mean number of videos ± SD, range; 15.3 ± 29.0, 1-105) on the cameras they were seen on than males (8.2 ± 9.8, 1-46).

Table 7: Results of the GLM with Poisson probability distribution, estimate, standard error (SE), z values, and significance levels for each category as a predictor of the number of female cat videos captured at different camera trap locations. The intercept represents the missing category for the factor; location – gully, habitat – forest, trail width – medium, trail length - long.

Factor	Category	Estimate	SE	z value	p-value
(Intercept)		1.035	0.503	2.057	0.040
Location	Ridge	1.071	0.142	7.531	<0.001
Habitat	Pasture	-1.980	0.432	-4.587	<0.001
	Scrub	-0.9838	0.3436	-2.863	0.004
Trail width	Narrow	-0.723	0.438	-1.650	0.099
	Wide	1.946	0.417	4.670	<0.001
Trail length	None	0.860	0.504	1.705	0.088
	Short	2.139	0.363	5.900	<0.001
	Medium	1.181	0.188	6.267	<0.001

Table 8: Results of the GLM with Poisson probability distribution, estimate, standard error (SE), z values, and significance levels for each category as a predictor of the number of male cat videos captured at different camera trap locations. The intercept represents the missing category for the factor; location – gully, habitat – forest, trail width – medium, trail length - long.

Factor	Category	Estimate	SE	z value	p-value
(Intercept)		3.893	0.249	15.610	<0.001
Location	Ridge	0.660	0.122	5.401	<0.001
Habitat	Pasture	-2.022	0.209	-9.669	<0.001
	Scrub	-0.856	0.148	-5.761	<0.001
Trail width	Narrow	-0.297	0.237	-1.253	0.21
	Wide	-0.003	0.242	-0.013	0.990
Trail length	None	-1.916	0.278	-6.882	<0.001
	Short	0.224	0.173	1.300	0.194
	Medium	-0.371	0.137	-2.704	0.007

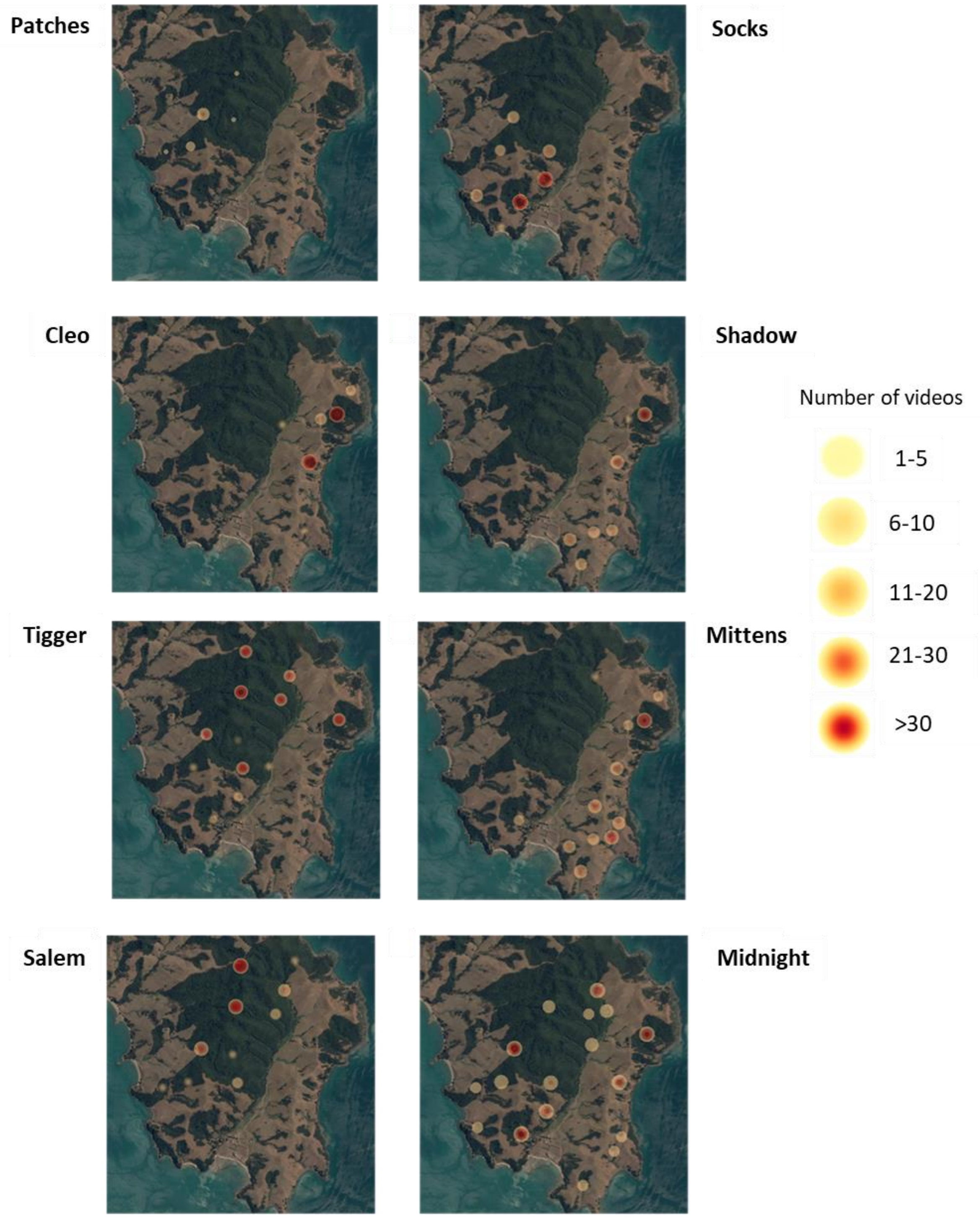


Figure 10: Heat maps for individual study cats of the number of videos captured at the 28 camera locations set up in a 500 m x 500 m grid system in South Ponui Island. The top four cats are females, and the bottom four cats are male. Videos collected from September 2015 - March 2017 were used.

Discussion

Camera versus accelerometer comparison

One of my aims of this study was to compare the activity patterns of feral cats based on camera trap and accelerometry data. I found that there was a very high correlation (R^2 >0.9) between the number of camera trap videos captured each hour and the accelerometer data (delta-g/hour). The correlation (R^2 >0.9) between camera trap and accelerometry data did not plateau until at least 600 videos had been recorded. This study suggests that to accurately identify the activity patterns of feral cats from camera trap data, at the densities found on Ponui Island (1.17 cats/km^2 - Chapter 2), a large number of videos are needed. Correlation coefficients were high (R^2 >0.9) when activity patterns were calculated from over 600 videos, and low (R^2 = 0.37) when there were fewer than 100 videos analysed. Despite the vast number of camera trap studies, few have estimated activity patterns using datasets of over 600 videos (Maffei et al., 2005; Barrueto et al., 2014).

Several studies have used fewer than 100 capture events to report on activity patterns of non-domestic felids (Di Bitetti et al., 2006; Cheyne & Macdonald, 2011; Akbaba & Ayaş, 2012; McCarthy et al., 2015). Those studies made broad statements about activity, reporting mainly whether the animals were diurnally or nocturnally active (Di Bitetti et al., 2006; Cheyne & Macdonald, 2011; McCarthy et al., 2015). Using broad statements on activity (diurnal versus nocturnal) will reduce the inaccuracy of reporting on activity with a small dataset. However, for reporting on hourly activity, I have shown that there is a large amount of camera trap data that is required, at least for describing the hourly activity of feral cats. Therefore, studies that report on hourly activity using small datasets may need to be interpreted appropriately now that it is evident that conclusions drawn from small datasets may misrepresent activity patterns.

With my camera trap grid set up (one camera per 25 ha) there was a high correlation between accelerometry and camera trap data when I used 3000 camera trap nights or six months of camera trapping. I would argue that emphasis should be placed more on the number of encounter events than on the camera trapping effort or how long the camera trap study had been operating. This is because there is a large amount of variation in the probability of detecting an animal on a camera trap (detection probabilities), even within the Felidae family, which would affect the number of encounter events obtained over time (Cheyne & Macdonald, 2011). This is not only due to differences in the density of the species, but also due to behavioural differences that reduce the chances of the species encountering a camera, such as the semi-arboreal nature of the clouded leopard (*Neofelis nebulosa*) (Cheyne & Macdonald, 2011; Brodie & Giordano, 2012). Due to differences in the capture rates of animals and camera trap setups (Cheyne & Macdonald, 2011; Burton et al., 2015), activity studies should meet minimum video/photo acquirement rather than the recommended camera trapping effort for density studies. Studies should show that they have the optimum number of camera trap videos.

Camera trap technology could be used to accurately estimate hourly activity patterns of other members of the Felidae family. Feral cats show similar patterns in activity to other studied felids; jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Harmsen et al., 2011), ocelots (*Leopardus pardalis*) (Kolowski & Alonso, 2010; Porfirio et al., 2016), and Geoffrey's cats (*Leopardus geoffroyi*) (Manfredi et al., 2011) were mostly nocturnal with a peak in activity soon after sunset. The high correlation between the camera trap data and the accelerometry data found in this study provides support for using camera traps to estimate feral cat activity. Similarities between feral cats and non-domestic felids suggest that camera trapping could be applied in a similar fashion for studying non-domestic felids. Although, further study with a larger sample size and replicating this study with non-domestic felids is required to be able to show this proof of concept.

The use of accelerometry devices in wildlife studies is not always feasible, and the difficulties of using accelerometers on wild animals mean they may not be the most efficient method for investigating activity patterns. Sample sizes of wildlife accelerometry studies are often small due to the invasiveness of the procedures needed to capture animals to deploy and retrieve accelerometers (Shepard et al., 2008; Grünewälder et al., 2012; Wang et al., 2015; Pagano et al., 2017). The small accelerometry dataset for this study was mainly due to not being able to download data from a distance, and therefore the requirement to recapture the study cats. However, some of the cats could not be recaptured to download the accelerometry data, leading to a bias in the representation of certain individuals based on the number of times that the cat could be recaptured. Small sample sizes and over-representation of certain individuals can lead to misrepresentation of activity patterns in the wider population or species due to the high levels of individual variation in activity (Gervasi et al., 2006; Andrews et al., 2015; Hertel et al., 2017).

This presented some challenges for statistically testing the correlation in the hourly activity pattern shown by the acclerometry and camera trap data. Linear regressions assume that the data is independent and is not usually used to test repeated measures. Unfortunately, there was no way to bypass this issue. I looked at whether the individual activity pattern of the cats was similar over the same time period to determine if large individual differences in activity could affect or misrepresent the overall activity pattern of feral cats described in this study. As the hourly activity pattern was similar between individuals, I did not foresee issues with using the data in this way. However, this was a large limitation to this study, and I would recommend the correlation in activity patterns between accelerometry and camera trap data to be studied in more depth, with a larger sample size used for the accelerometry device deployment to make this statistically sound.

Feral cat activity pattern

I found that feral cats were most active at night, with a peak in activity in the first hours after dusk. These are similar results to previous studies, which also report a nocturnal activity pattern for feral cats (Jones & Coman, 1982; Page et al., 1992; Alterio & Moller, 1997; Hilmer et al., 2010; Horn et al., 2011; Wang & Fisher, 2012; Cove et al., 2017). This likely reflects the prey that feral cats are hunting and the prey that they evolved hunting, since nocturnal behaviour appears to be an ancestral trait for the *Felis* genus (Mattern & McLennan, 2005). Previous studies in New Zealand have found that the feral cat diet comprises mainly small mammals, with birds, reptiles, and invertebrates being important secondary prey (Dilks, 1979; Fitzgerald & Karl, 1979; Langham, 1990; Fitzgerald et al., 1991; Alterio et al., 1996; Harper, 2002). Rats (*Rattus rattus* and *R. norvegicus*) and mice (*Mus musculus*) are nocturnal (Calhoun, 1962; Macdonald et al., 1999; Innes, 2005a; Ruscoe & Murphy, 2005), and were a main prey for Ponui Island cats (Chapter 6), therefore feral cats may be active during similar hours as prey to increase hunting opportunities (Harmsen et al., 2011; Brook et al., 2012; Bogdan et al., 2016; Porfirio et al., 2016).

Male and female feral cats were active during similar hours, though males had higher peaks in activity. Sex differences in activity have also been identified in Geoffrey's cats (Manfredi et al., 2011), and Iriomote cats (*Prionailurus iriomotensis*) (Schmidt et al., 2008). This may be due to sexual dimorphism in body weight of feral cats, where males have higher body weights than females (Fitzgerald et al., 1991; Mills, 1994; King et al., 1996; Gillies & Fitzgerald, 2005), which would increase their energetic requirements (Scott & Scott, 1967; MacDonald et al., 1984; Fettman et al., 1997; Zoran, 2010). These increased energetic requirements could result in male feral cats needing to ingest more prey per day, thus requiring more activity to either hunt more prey, or larger prey (MacDonald et al., 1984).

Male cats also tend to have larger home ranges than females, and a greater area to utilise and hunt in (Chapter 2) (Fitzgerald & Karl, 1986; Gillies et al., 2007; Harper, 2007). This was reflected in the larger number of camera traps that males were captured on in the study site compared to females. Male feral cats may move around the entirety of their home range more often than females (see Chapter 2), leading to the higher activity levels detected in this study.

Seasonal patterns in activity

Feral cats showed a seasonal pattern to their activity, with their activity following photoperiod. Seasonal differences in activity have been identified in most carnivores, including felids, with seasonal variations related to prey activity or reproductive status (Schmidt, 1998; McCarthy et al., 2005; Manfredi et al., 2011; Podolski et al., 2013). For example, Zielinski et al. (1983) found that pine martens (*Martes americanus*) were more nocturnal in winter but diurnal in summer, which coincided with the seasonal availability of prey.

Cats showed more nocturnal activity in autumn than the other seasons, represented by a higher percentage of videos captured at night than day. There may be several explanations for this, one of which may be that most kittens were born in autumn, which would place higher energy requirements on the females and may lead to higher levels of nocturnal hunting in order to provide enough food (Chapter 4). It may also be due to prey availability and their activity, because the prey consumed the most by feral cats in autumn are rats, mice, and orthopterans (weta and crickets) (Chapter 6); all of which are nocturnal (Loher, 1979; Lewis, 1994; Innes, 2005a, 2005b; Ruscoe & Murphy, 2005). Feral cats exhibited more diurnal activity in the summer than the other seasons. This might be related to the seasonal change in their diet, where feral cats have higher depredation pressures on birds (which tend to be diurnal) during the summer and spring (Chapter 6).

Feral cats can switch prey between seasons, and target species that are more common (Molsher et al., 1999), and their activity may change with this prey switching. Detecting these seasonal changes in activity patterns may be important for identifying increased risks of predation for vulnerable species. Feral cats are more likely to depredate other prey species that are active at similar times, not just the main prey species. For example, if feral cats are more nocturnally active in areas where rats are their main prey (Garvey, 2016), then this could lead to increased depredation rates on other nocturnal species. On Ponui Island, for example, cats have been reported depredating kiwi (*Apteryx* spp.) (Wilson, 2013) (Chapter 6).

Seasonal changes in activity may also be attributed to reproduction and not just prey availability. Despite the ability to reproduce throughout the year, feral cats show a seasonal pattern of breeding (Shille et al., 1979; Brown, 2011) (Chapter 4). The changes in activity in spring and summer may be due to searching for mates, and females raising litters (Apps, 1983).

Feral cat activity around live-traps and camera trap hotspots

Unsurprisingly, I found that when feral cats were their least active, they were less likely to visit a live-trap. Live-traps were mainly visited at night, with a peak in visits at midnight. Live-traps are often used in areas for feral cat control where there is the risk of accidental capture of pet cats. Checking cage traps can be labour intensive and expensive, because live-traps must be checked 12 hours after sunrise on each day the trap is set in accordance with the Animal Welfare Act (New Zealand Government, 1999). Increasing our knowledge of visitation rates of feral cats to baited traps could increase the efficiency of cage trap checks. Based on the activity pattern I found, cage traps should be set before dusk and checked between 07:00-09:00 h when cats are least likely to be visiting cage traps, to reduce the chances of disturbing a cat that is about to enter a cage trap. Feral cats can be wary, and disturbance at a cage trap may lead to trap shyness (Apps, 1983; Algar et al., 2002). This recommended time for checking live-traps is also in accordance with the Animal Welfare Act (New Zealand Government, 1999).

There was variation in the number of individual cats captured on cameras in relation to the habitat features associated with the camera sites. The location of the camera (ridge or gully), cameras set up in forest, and on wide trails had higher number of cat videos than the alternatives. Based on my results, for future studies targeting feral cats, I recommend that for maximum detection rates, cameras should be placed on ridges if study sites have similar topography to Ponui Island. Also, I recommend that cameras should be placed on trails that are four metres in width or wider. Camera trap locations that target forest or scrub habitats more than pasture will also have higher detection rates of feral cats. This may be due to denser vegetation restricting movement away from trails compared to more open habitat types, increasing the chances of cats passing a camera (Harmsen et al., 2010). Cusack et al. (2015) and Harmsen et al. (2010) both found a high probability of detecting carnivores on trails; trails may help predators move more quickly and quietly.

It was not surprising that the number of resident cats and resident males are significant factors for explaining the hotspots of feral cat activity on cameras. A resident cat is more likely to pass a camera more often than non-resident cats, and the more resident cats that overlap the camera, then the more movements past a camera.

It was interesting to find that males and females may be using areas that have slightly different habitat features. While both sexes appear to be using forested habitats rather than scrub or pasture, and are also found more on ridges than in gullies, they had different capture numbers on cameras based on the length and width of the trail where the cameras were located. It appears as though males may be using trails that are longer than the trails that female cats use. Males may use longer connected trails to move throughout their larger home ranges (Chapter 2). There is the chance that individual cats may bias these results though, because there were individual differences in the camera trap sites that the study cats were captured on.

In conclusion, the high correlation between accelerometry and camera trap data for detecting hourly activity patterns suggests that camera traps can be used to describe activity of feral cats, provided there is enough data. I found that at least 600 independent cat videos were needed with my camera trap set up of 28 cameras (one camera per 25 ha) in a population with 1.17 cats/km^2. Camera traps can be used to describe the activity patterns of felids, though this is dependent on the number of encounter events. Camera trap technology is more feasible for wild felid studies as they are less invasive than other methods for collecting continuous activity data (such as accelerometry), and are likely to be used more in the future. However, I recommend that emphasis should be placed on the number of camera trap videos as opposed to camera trap effort as has been done in past studies, due to the different detection rates of species. I also recommend further studies on other groups of animals if this technology is going to be applied to other species.

The activity patterns described in this chapter can be used for planning effective trapping programmes, however control or eradication programmes will not be effective unless more cats are removed than the number produced (Campbell et al., 2011). Estimating the reproductive rate of feral cat populations and the survival of kittens is important for effective management, and the reproduction of feral cats on Ponui Island was examined in Chapter 4.

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Supplementary material

Table S1: The first GLM results using negative binomial probability distribution for factors driving number of individual cat videos at camera trap locations. df = degrees of freedom.

Factor	**df**	**Deviance**	**p-value**
Habitat	2	10.343	0.006
Location	1	28.329	<0.001
Trail width	3	4.296	0.116
Residents	2	26.781	<0.001
Trail length	2	11.543	0.009
Core	1	0.153	0.696
Females	1	0.014	0.905
Males	2	1.172	0.556

Table S2: The first GLM results using Poisson probability distribution for factors driving number of individual cats at camera trap locations. df = degrees of freedom.

Factor	**df**	**Deviance**	**p-value**
Habitat	2	2.073	0.355
Location	1	8.092	0.004
Trail width	3	0.020	0.989
Residents	2	2.862	0.142
Trail length	2	5.445	0.204
Core	1	0.211	0.646
Females	1	0.071	0.790
Males	2	2.412	0.299

Chapter 4 - Infanticide, recruitment, and kitten growth rates in a population of island feral cats (*Felis catus*).

Plate 4: Photos of two of the kittens found in the study site; Cleo BW from Cleo's May 2016 litter (left), and Pumpkin from Socks' November 2015 litter (right). Photos were taken by the author.

Introduction

Home range and activity (Chapters 2 & 3) can be used to develop a control protocol, but information on the reproduction and reproductive parameters of feral cats can also be used for management purposes. There is a lack of information on the reproductive biology of invasive predators, particularly solitary living feral cats (*Felis catus*). The reproductive rate of feral cats can affect their population recovery rate following control programmes, and knowledge of this can allow managers to make predictions of how fast a population could recover following a reduction in density through control, as has been demonstrated with ferrets (*Mustela furo*) by Byrom (2002).

There are several reproductive parameters that need to be estimated to understand population growth (Noon et al., 1992), including age at first pregnancy, number of litters per year, litter size, and juvenile survival. Most of what is known about domestic cat reproduction is derived from studies on house and colony cats. Domestic cats become sexually mature by one-year-old (Ogan & Jurek, 1997; Fitzgerald & Turner, 2000) but, on average, the females reach puberty at 6-9 months or 75% of their adult body weight (Tsutsui & Stabenfeldt, 1993; Wildt et al., 1998). Oestrus typically lasts 3-16 days (Brown, 2011) and queens (female cats) can come into oestrus up to five times per year, though they normally have only two litters annually (Robinson & Cox, 1970; van Aarde, 1983; Warner, 1985; Ogan & Jurek, 1997; Fitzgerald & Turner, 2000; Nutter et al., 2004). Gestation lasts 58-65 days (Prescott, 1973; Ogan & Jurek, 1997; Fitzgerald & Turner, 2000; Brown, 2011). These reproductive parameters, if maintained in the wild, may allow feral cats to expand their population sizes rapidly.

Feral cats have their kittens in dens, making it difficult to examine offspring in their youngest stages (Fitzgerald & Karl, 1986; Kitchener, 1991). As a result, few studies have described den use by feral cats. Females use multiple types of shelter as dens; Langham (1992) found that some female feral cats took advantage of man-made shelters such as barns, while other females used cavities in trees for dens. Den use by feral cats was also noted by Fitzgerald & Karl (1986) in the Orongorongo Valley (Wellington), where only females with kittens under six weeks old had regular den sites. Neither of these studies described subsequent dens used by a litter.

Estimating survival of juvenile feral cats is difficult. Devices for attaching transmitters need to be modified for expansion with the growth of the animal, and the animal still needs to be recaptured for device removal (Blackwell et al., 1991; Garrison et al., 2007; Clark et al., 2015). Intraperitoneal radio transmitters have been developed that can be inserted into the body, eliminating the need for an expanding device, but deployment typically involves highly invasive procedures (Crawshaw et al., 2007; Léchenne et al., 2012; Moriarty et al., 2012). These limitations have contributed to the paucity of studies that have estimated juvenile feral cat survival and recruitment rates. On Dassen Island, Apps (1983) found that 86% of juveniles survived until they were 5-6 months-old, and 75% of juveniles survived until they were 7-10 months-old. The Dassen Island feral cat population had a high rate of recruitment illustrated by at least half of the cats in the population being less than one-year-old, and the population was steadily increasing in numbers following previous control operations (Apps, 1983). This high recruitment rate may have been due to density-dependent population growth. Melero et al. (2015), for instance, reported for American mink (*Neovison vison*) that changing densities of females affected their reproductive output including their probability of conceiving and litter size. Recruitment rates and reproductive parameters of feral cats may be different in populations that are stable and at carrying capacity when compared to those that are recovering from control.

Very little information on causes of juvenile mortality in feral cats is available in the literature. Apps (1983) found six kittens that had died from natural causes, three of which had upper respiratory tract infections. Studies on other felids suggest infanticide and starvation are the most common causes of juvenile mortality (Palomares et al., 2005; Farhadinia et al., 2009; Mills & Mills, 2014). Infanticide is defined as the killing of conspecific young, and also includes maternal behaviour (such as reduced parental investment) that causes the death of an infant (Supplementary material; Table S1) (Hrdy, 1979; Packer & Pusey, 1984; Balme & Hunter, 2013). Juvenile development and maternal behaviour are similar within the Felidae family; females use dens to protect altricial kittens while the mother is out hunting, and offspring learn to hunt with the mother once they are fully ambulatory. Information on causes of juvenile mortality could provide information on the factors that naturally limit feral cat recruitment rates.

No published studies report the growth rates of feral kittens. In colony conditions, kittens gain approximately 76 grams per week (Dickinson & Scott, 1956). Colony cats do not need to hunt for their food, while in the wild, maternal food intake could restrict lactation and the provisioning of food to the offspring, thus hindering their growth (Laurenson, 1995). Therefore, the growth rates of colony-raised kittens may not reflect the growth rates of feral kittens, where the growth rates may be influenced by food availability.

In many species, females have reduced movements when they have dependent young, and may not be able to move very far from the den. This has not been studied previously in feral cats, though Jedrzejewski et al. (2002) found that Eurasian lynx (*Lynx lynx*) had different ranging movements based on whether or not they had kittens. Female lynx moved shorter distances when they had kittens than when they did not (Jędrzejewski et al., 2002). This reduced movement based on reproductive phase is important to understand in feral cats in terms of management, because reduced movements may mean that females are less likely to encounter traps during control operations.

Here, I investigated the reproduction of a population of feral cats that were likely to have reached carrying capacity, and where there was limited migration. My aims were five-fold: 1) to describe the characteristics of dens and determine how often kittens are moved between dens; 2) to describe the growth rate of feral kittens and compare it to the growth rates of colony-living kittens; 3) to describe the causes of mortality in feral kittens; 4) to determine the movements of queens in different reproductive phases; 5) to estimate recruitment rate for the Ponui Island feral cat population.

Methods

Detecting pregnancies

This study was conducted on the Ponui Island feral cat population. Videos of female cats from camera trap videos (Chapter 2) were examined for any signs of pregnancy or lactation. Signs included an increase in size around the abdominal region, a distended abdomen, or visibly prominent nipples.

Finding den sites and processing kittens

Female cats in the study site had previously been fitted with radio collars (Chapter 2). When it was suspected (from camera trap footage) that a female was in the late stage of pregnancy or was lactating, she was located using radio-telemetry and observed directly. On all occasions, the queen ran off after detecting my presence and I then searched for the den and determined whether or not she had kittens.

Latex gloves were worn while holding the kittens, and the time spent handling them was kept to a minimum in order to reduce their stress. The kittens were sexed and weighed, coat colour and body condition scored (based on the 5-point scale (Lund et al., 1999)), and any other observations noted. Kittens were aged based on whether their eyes and ears were open, and their ease of movement (Baerends-van Roon & Baerands, 1979; Villablanca & Olmstead, 1979; Beaver, 1980; Levine et al., 1980). Those estimated to be aged four weeks or older had a microchip injected under the skin in the back of their neck. Kittens were then placed back into the den. The following day the female was tracked from a distance to confirm that she had returned to the den.

Recorded den details included: habitat type, the type of nest material used, and den type. A photo was taken for future reference. Coordinates were also taken using a GPS device and marked in Google Earth Pro.

Kittens were measured as often as possible to follow their growth. For example, one litter was measured once a week until they were six-weeks-old. The queen then moved them, after which they could not be found again.

Tracking queens and estimating core home range

Locations of the two radio-tagged females were estimated using similar signal triangulation methods as that outlined in Chapter 2. Locations for the females were recorded for at least five days per month from May 2015 - December 2016 and mapped using Google Earth Pro. Camera trap footage was used to determine in which months the females had kittens.

The average monthly home range of two females was calculated, using radio-telemetry and camera trap data from Chapter 2. The home ranges (100% MCP) were mapped in Google Earth Pro and the area estimated for the females when they were in different reproductive stages: pregnant, with kittens, breeding (during the breeding season identified from Figure 1; August - April), and non-breeding (May - July).

The distance moved by the female from the den in different reproductive phases was also recorded. The reproductive phase was determined through analysis of camera trap footage of the female cats, and were: pregnant, denning (when the kittens were less than eight-weeks-old), kittens venturing out of the den with their mother (8-14 weeks-old), and weaning (14-weeks and older). Movements during the pregnant phase were determined as distance moved from the natal den where the female had her kittens. Location points (radio-telemetry and camera trap) for the females were used from Chapter 2, and distances from each location point of the cat to the den were measured using Google Earth Pro.

The core home ranges (50% Minimum Convex Polygon (MCP)) of the two females were calculated using locations of the individual cats from camera trap and radio-telemetry data. The core home ranges of 50% MCP were estimated using Ranges 9 and a convex polygon produced and mapped in Google Earth Pro.

One juvenile cat was radio-collared in December 2015 using a V2L transmitter (Sirtrack®, Hawke's Bay, New Zealand) on an expandable elastic collar. Locations from radio telemetry were determined by honing in using the radio signal. Juvenile radio frequencies were tracked using a Telonics TR4 receiver (Kiwi Track Ltd., Havelock North, New Zealand). Additional locations of the sub-adult were also provided from camera trap data.

Colony cats

Body weights for colony cats and kittens weighed from 2002-17 were obtained from the Massey University Feline Unit, Palmerston North, New Zealand. Kittens and adult cats were weighed weekly by colony staff. All cats were fed *ad libitum* diets consisting mainly of wet food. Queens were given access to commercial wet food and cat biscuits during lactation, which the kittens also had access to. If the queens did not produce enough milk, or the kittens were unable to feed properly, the kittens were bottle-fed kitten milk formula. The kittens were not weaned until they were at least six-weeks-old. Weaning started with the kittens being separated from the mother for a few hours each day, which was then gradually increased. Full weaning occurred when the kittens were at least ten-weeks-old or older. After weaning, the kittens were fed *ad libitum* kitten formula wet food. At approximately six-months-old, males were neutered, and all of the kittens were integrated into the rest of the colony, which consisted of large colony cages. Cats were kept in mixed-sex groups. For the comparison in body weight between feral cats and colony cats, both neutered and entire cats from the colony were used in the analysis. This was because most of the males were neutered in the colony, and most of the females were intact, therefore the effect of neutering could not be distinguished from the effect of sex in this colony (Cave et al., 2018). Only the weights of adults aged between 3-6 years-old were used for this analysis as this was the approximate age range of the feral adults from Ponui Island.

Post-mortems

The radio transmitters had an in-built mortality function (Chapter 2). If a transmitter was in mortality mode then the cat was located as quickly as possible. Photos were taken of the cat and the habitat in which it was found. A similar protocol was taken for any dead cats not wearing radio-collars or kittens found around the study site. If the animal was still intact and not decomposed, then head-body length measurements, body condition score, and the body weight were recorded. Any external marks or obvious bruising on the animal were also noted. Dead cats and kittens were stored in the freezer at -20°C until a post-mortem could be performed. If only the bones were found of a dead cat, and there was suspected depredation, then bones were examined under a microscope to determine the most likely predator based on the size and shape of holes in the bones.

Adult dead cats had a gross post-mortem performed in the field. A ventral cut was made down the thoracic and abdominal region, and the amount of subcutaneous fat was noted. Five-millimetre slices of kidney, intestine, spleen, and lung, as well well the whole thyroid gland were taken and stored in 10% formalin for histology. The cat carcass and the rest of the organs were stored at -20°C for a more in-depth post-mortem by a pathologist to determine the cause of death.

Statistical analysis

Mann-Whitney U tests were calculated using R (R Development Core Team, 2008) to test for the difference in the monthly home range sizes (100% MCP) of two queens when they had kittens and when they did not. Mann-Whitney U tests and a Kruskal-Wallis test were used to test for differences in the distance moved by queens during pregnancy and different ages of kittens.

Results

Ten cats were live-trapped and followed throughout this study (January 2014 – March 2017) (Chapter 2). Two adult males died, and another disappeared and was presumed dead (Table 1). The feral cats in this study had low body condition scores (Chapter 2), though some males had a condition score of 3, and one of the females had a condition score of 1 (Table 1). All female cats that were captured throughout the study were capable of reproducing, as evident by their observed pregnancies throughout the study. One male cat had cryptorchidism in one testicle, and another male that was found dead had testicular atrophy, which was apparent on histological analysis following his post-mortem (Table 1).

Seasonal pregnancies

During the 39-month study, a total of 18 pregnancies were detected in five females. There was a seasonal pattern to feral cat pregnancies, with over half occurring from January – March and a smaller peak in pregnancies from September - December (Figure 1). Only one pregnancy was observed outside of those seasons, in June 2014. The majority of pregnancies were during seasons where rat densities were an average of 6-10 rats/ha, however, most kittens were weaned when rats were seasonally at their highest density (16-22 rats/ha) (Table 2).

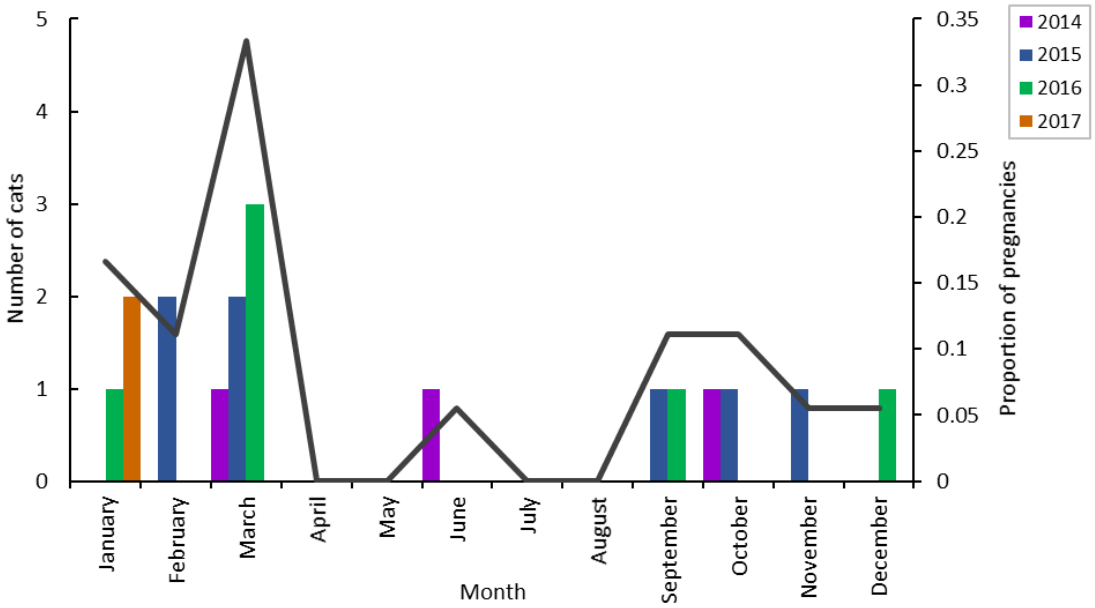

Figure 1: Number of female cats that were pregnant and the first month that the pregnancy was detected from January 2014 - March 2017. Pregnancies were seen in a total of five females. The line shows the proportion of pregnancies for each month from the total number of pregnancies detected for the three years.

Table 1: General information on the adult feral cats that were live-trapped in South Ponui Island. This includes information on conditions that were detected in the cats that might have affected the reproductive ability of the cat. Median body condition score was based on the 5-point scale (Lund et al., 1999).

Cat ID	Sex	Body weight (kg)	Median body condition score	Comments
Cleo	Female	2.7	1	7 pregnancies
Patches	Female	2.3	2	4 pregnancies
Socks	Female	2.3	2	4 pregnancies
Midnight	Male	4.3	3	Died February 2016
Tigger	Male	4.1	3	No observed health conditions
Tui	Male	3.8	3	Disappeared June 2015 (presumed dead)
Mittens	Male	3.5	2	Testicular atrophy, died September 2016
Salem	Male	4.0	2	No observed health conditions
Sylvester	Male	3.2	2	Cryptorchidism in one testicle
Snowball II	Male	3.0	2	No observed health conditions

Table 2: Number of cats that were pregnant each month and the corresponding months the kittens would have been born and weaned. Rat densities are from Shapiro (2005) and Latham (2006) for Ponui Island, however, because the Ponui Island rat population had not been monitored for all seasons, rat densities from Efford et al. (2006) for mainland populations was used to fill in gaps. High densities are between 16-22 rats/ha and low densities are 6-7 rats/ha. Upwards and downwards facing arrows represent increasing and decreasing rat densities respectively.

Month	No. pregnancies detected	Rat density at pregnancy	Kittens born	Rat density at birth	Weaning	Rat density at weaning
January	3	↓	March	↑	June-July	High
February	2	↑/Low	April	↑	July-August	High
March	6	↑	May	↑	August-September	High/↓
April	0	↑	June	High	September-October	Low/↑
May	0	↑	July	High	October-November	Low
June	1	High	August	High	November-December	↓
July	0	High	September	Low	December-January	↓
August	0	High	October	↑	January-February	↓
September	2	Low	November	↓	February-March	↑/Low
October	2	↑	December	↓	March-April	↑
November	1	↓	January	↓	April-May	↑
December	1	↓	February	↑/Low	May-June	↑

Litter size and kitten growth

I found three occupied dens where the kittens were less than three-weeks-old. Litter sizes were 3, 3 and 4 kittens. Four other litters were seen via camera traps before weaning (6-16 weeks old), where litter size varied from one to two kittens. Kittens were first seen on camera traps with the mother when they were 6-8 weeks-old. It is estimated that this is the time the kittens start to leave the den with their mother because kittens aged less than six-weeks-old were only seen in the den. Kittens were still seen with the mother when they were 12-16 weeks-old and were not weaned until after that. This was the estimated age at weaning as kittens were seen on camera traps suckling from the mother when they were 16-weeks-old.

Male and female feral kittens ($n = 7$) weighed more than colony-raised kittens in the first five weeks of life (Figure 2). The average (± SE) weight for colony raised kittens at four weeks of age was 360 ± 14 g for males and 343 ± 9 g for females. The three feral kittens weighing less than this at four-weeks-old all died (Figure 2). Male kittens weighed more than females of the same litter. Between 22-50 weeks old, the male and female sub-adults ($n = 2$) caught weighed less than the colony-raised cats. Both feral adult males and females weighed less than colony adult cats (Figure 3).

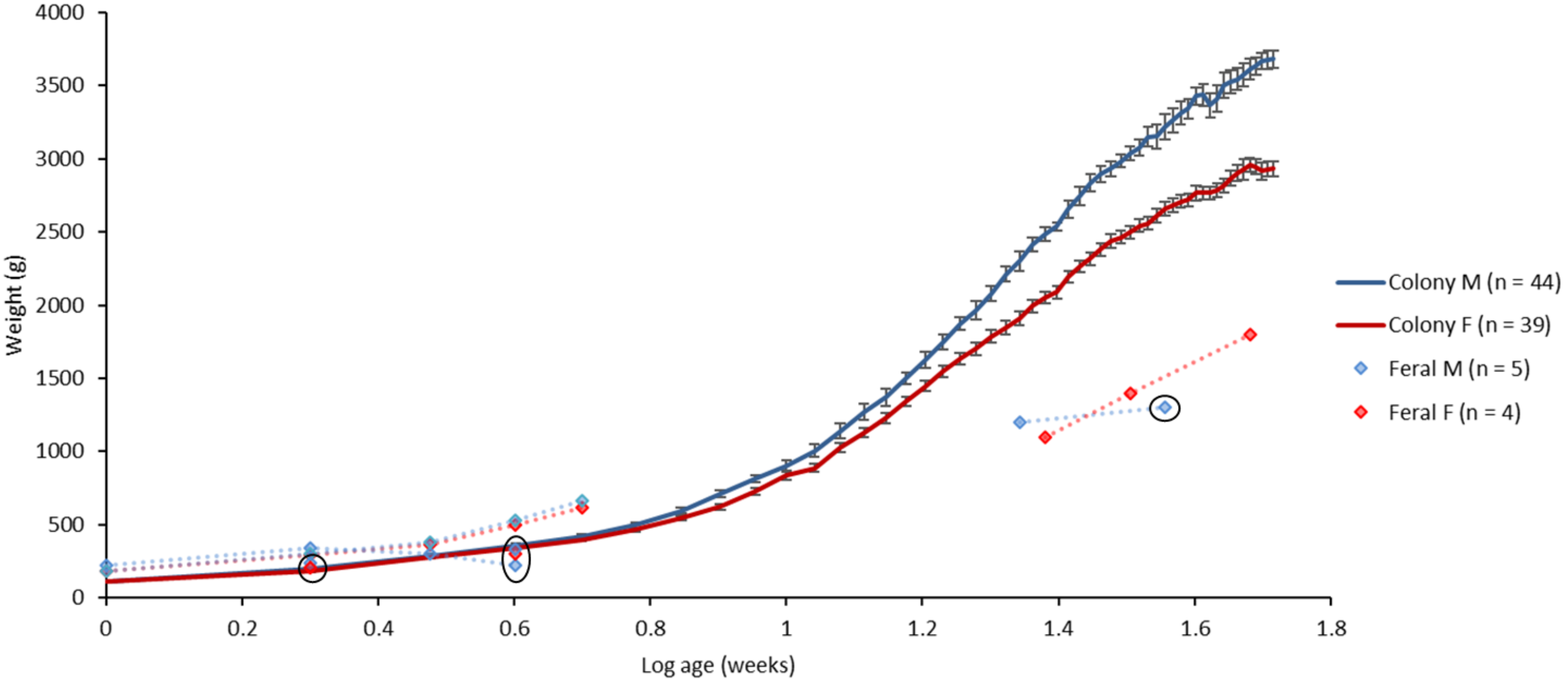

Figure 2: Growth rates of feral and colony raised cats (fed *ad libitum*) during the first year of life. Age (in weeks) is presented in a logarithmic scale. The solid lines are the average body weight of colony raised kittens (males = blue, females = red) with error bars representing standard error. The blue diamonds are the body weights of measured feral male kittens, and the red diamonds are feral female kittens. Dashed lines connecting diamond points are repeated measurements for an individual. The feral kittens and sub-adult that died are circled. Sample size for each category is shown in parentheses in the legend.

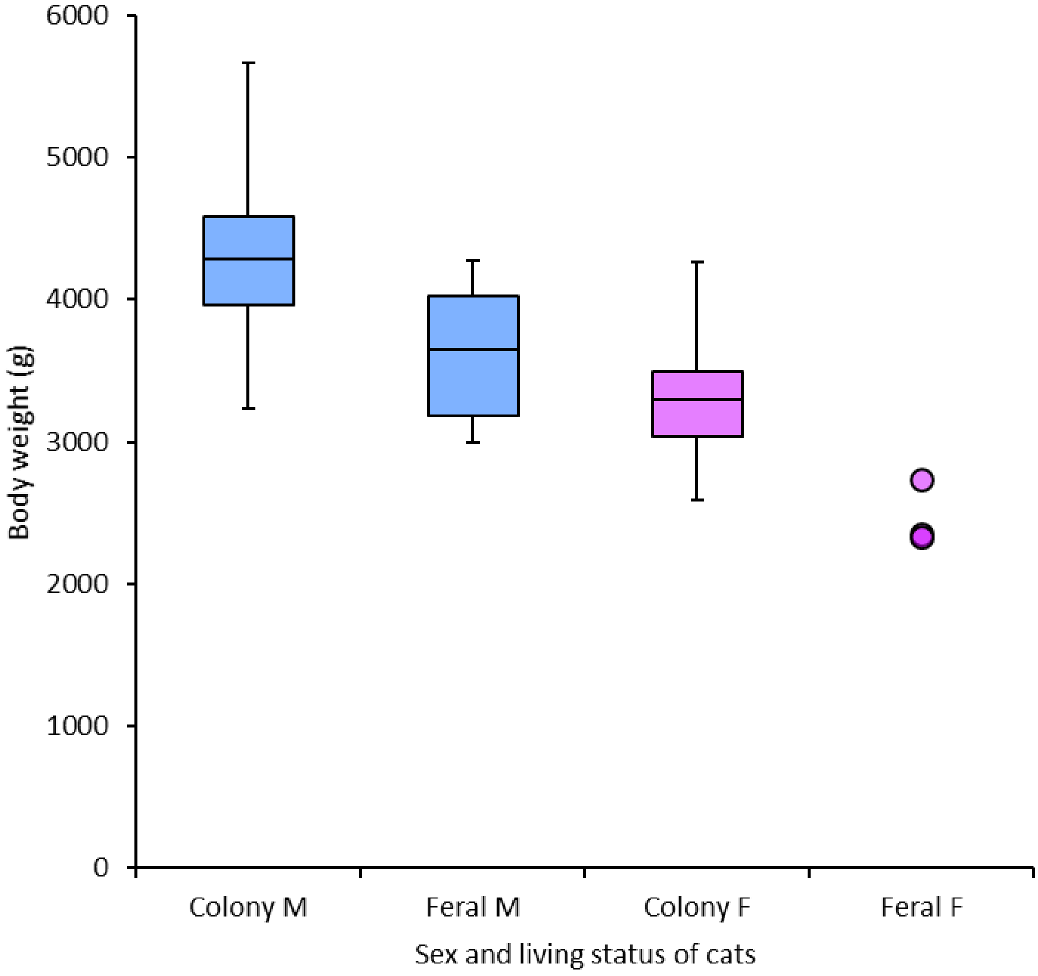

Figure 3: Comparison of the range of adult body weights between colony raised adult (n = 49 males, 59 females) and feral adult cats (n = 8 m, 3 f). Measurements for males are in blue, and those for females are in pink. Both intact and neutered cats were used for the colony measurements, and only weights of adults aged between 3-6 years old. Note: two of the Ponui Island female points are overlapping.

Movements

Queen's movements

I monitored the home ranges of two adult females during different reproductive phases (pregnant, with kittens, breeding, and non-breeding). There was no significant difference in the average monthly home range size (100% MCP) of either female monitored when they had kittens and when they did not (Cleo: Mann-Whitney U-test, df = 1, W = 28, p-value = 0.662; Socks: Mann-Whitney U-test, df = 1, W = 28, p-value = 0.703). Cleo and Socks both had larger home range sizes during the breeding season, followed by the seasons when they had kittens (Table 3). The smallest home range size for the females was during the non-breeding season.

I also looked at the distance moved by the queen away from the den when the queen was pregnant, and when the kittens were different ages. Queens were found the furthest from their dens while they were pregnant and remained close to the dens when the kittens were between 0-7 weeks-old (Figure 4). They started ranging further from the dens when the kittens were between 8-16 weeks-old. The distance moved from the den during different reproductive phases was significantly different for Socks' November 2015 litter (Mann Whitney U-test, n = 84, df = 1, W = 460.5, p-value = 0.027) and Cleo's May 2016 litter (Kruskal-Wallis, n = 134, df = 3, x^2 = 23.9, p-value <0.001) but was not significant for Cleo's February 2016 litter (Mann-Whitney U-test, n = 73, df = 2, W = 256.0, p-value = 0.192).

Table 3: The average (± SE) monthly home range size (ha) (100% MCP) for the two females followed during different reproductive phases. Locations used for the home range analysis were from radio-telemetry and camera trap data. The total number of locations used for Socks was 250 (average = 14 locations per month, range = 3-48) and for Cleo was 285 (average = 19 locations per month, range = 3-46).

Phase	Socks	Cleo
Pregnant	35.4 ± 25.6	16.4 ± 1.7
With kittens	40.5 ± 19.0	21.5 ± 5.2
Breeding	51.5 ± 8.4	30.7 ± 19.2
Non-breeding	26.9 ± 8.5	17.5 ± 1.2

Sub-adult movements

One sub-adult (Shadow) was followed using radio-telemetry. At 6-7 months-old Shadow spent most of her time in her mother's home range (Figure 5 insert). When she was 9-12 months-old she moved between 1.5-2 km south down the island and remained in an area that was previously unoccupied by a female (Figure 5). After relocating, she was rarely seen in her mother's home range area.

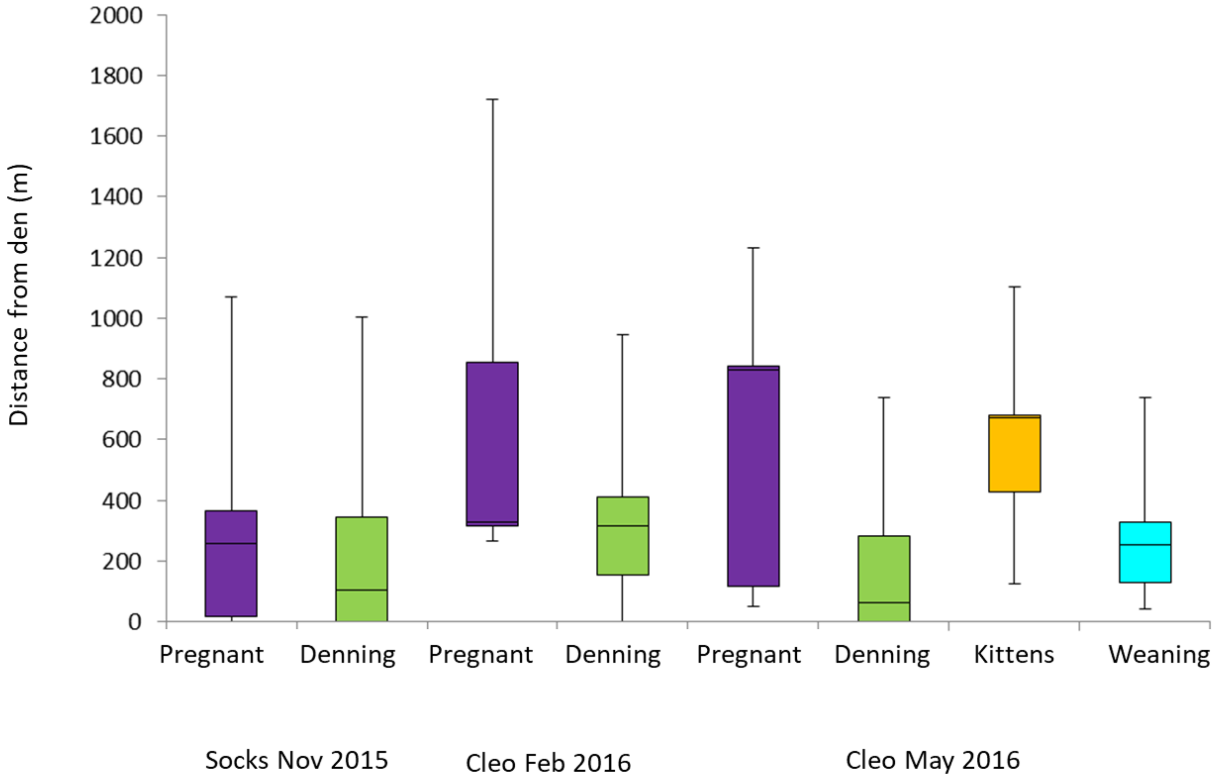

Figure 4: Boxplot showing the distance moved (m) from the den during different reproductive states of two female cats (Socks and Cleo) for three litters: Socks November 2015, Cleo February 2016, and Cleo May 2016. Locations of the adult females were from radio-telemetry and camera trapping. The distance was calculated from the den to the female's location using Google Earth Pro. Pregnant (purple box) was when the cat was from (an estimated) -66 to -1 days of having kittens; denning (green box) was when the kittens were mainly in a den and were aged between 0-7 weeks-old; with kittens (orange box) was when the kittens started to leave the den with the mother and were aged from 8-16 weeks-old; weaning (blue box) was when the kittens became independent of the mother and were between 16-24 weeks-old.

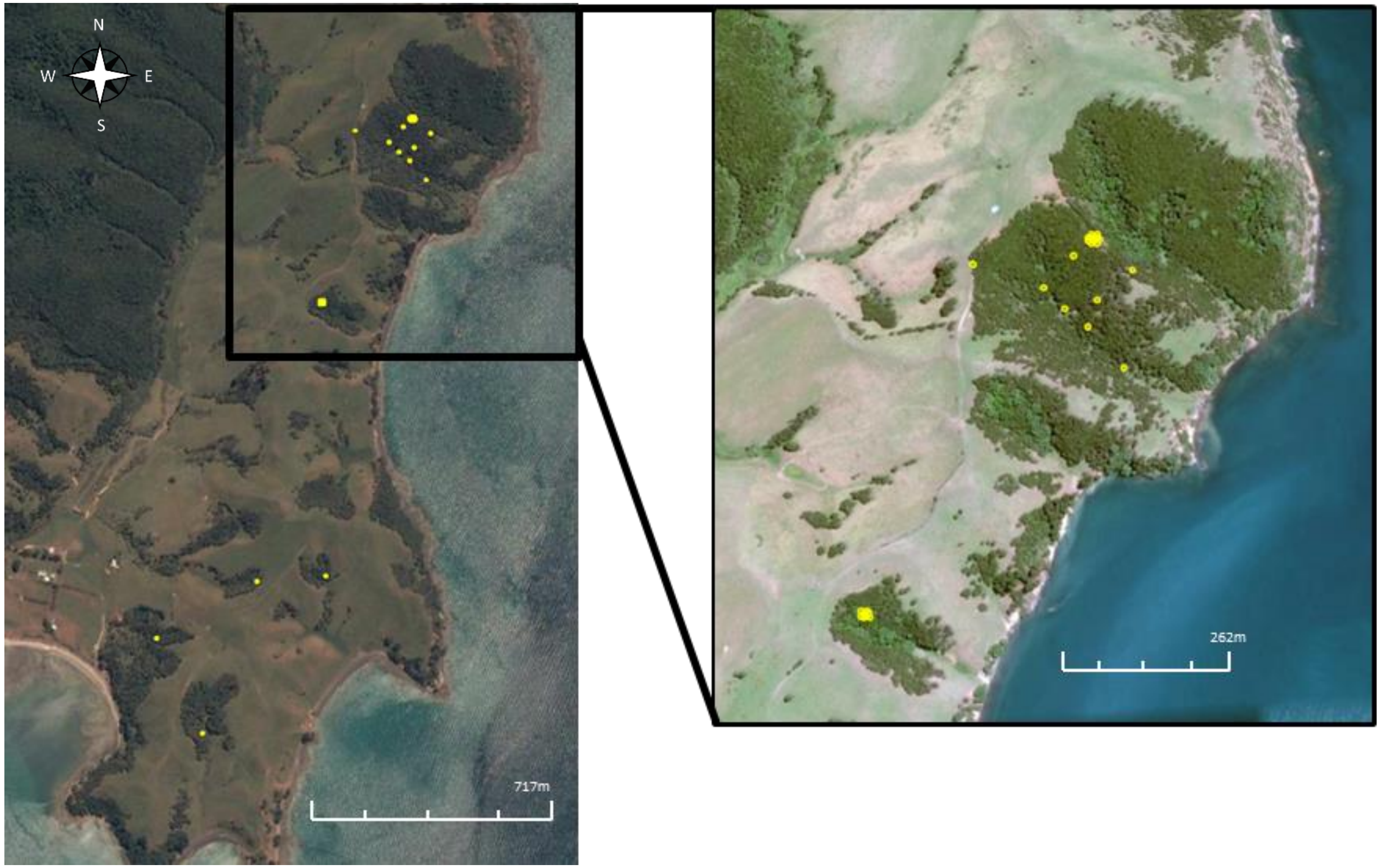

Figure 5: Locations of the sub-adult (Shadow) when she was between 6-12 months-old in South Ponui Island. Locations are from both radio-telemetry and camera trap data when Shadow was between 6-7 months-old. When Shadow was between 8-12 months-old, only camera trap locations were collected. Multiple points in the same area are from camera trap data. **Insert** – Shadow's movements from 6-7 months-old.

Den sites

Eight den sites were located for three different litters (two different queens). Den sites were mostly located in each female's core home range (50% MCP) except for Cleo's February 2016 natal den. All of Cleo's dens were located in forest/scrub-covered gullies, whereas Socks had dens in scrub gullies and pasture (Figure 6). Socks used two dens located in pampas grass, whereas Cleo twice used holes at the base of trees as dens, and moved her kittens to scrub-covered areas (Table 4). Three of the dens had dead leaves or shredded pampas grass lining the den. The time that kittens spent in one den varied from a few days to two weeks (Table 4). At 3-4 weeks-old, two of the litters were moved to open dens in the scrub. Kittens were moved short distances between dens, with an average of 107 ± 51 m (mean ± SE), and the longest distance kittens were moved between dens being 285 m by Socks.

Figure 6: Den site locations for three different litters. Circles represent the natal den. Diamonds represent maternal dens. Lines join the dens for three litters of two cats. Yellow represents Socks' December 2015 litter; green is Cleo's February 2016 litter; and white is Cleo's May 2016 litter. The pink area shows the core home range (50% MCP) of Socks, and the blue area shows the core home range (50% MCP) of Cleo.

Table 4: Description of habitat type, materials used in the den, age that the kittens were first found in the den, and the distance from the last den, for three different litters. The distance between dens was mapped and measured using Google Earth Pro. Natal dens are where the kittens were born, and maternal dens are subsequent dens that kittens are moved to.

Queen	Litter	Name of den	Habitat	Natal or maternal?	Type	Lining material	Age of kittens	Distance to last den (m)	Maximum distance queen detected from den during den occupancy (m)
Cleo	February 2016	Feb den	Scrub	Likely natal	Hole at bottom of stump	Dirt	1-2 weeks	-	947
Cleo	May 2016	May 1	Forest	Natal	In fork of pohutakawa tree	Leaves	0-2 weeks	-	130
Cleo	May 2016	May 2	Scrub	Maternal	Under log and scrub	Grass underneath	2 weeks	159	Only found at den
Cleo	May 2016	May 3	Scrub	Maternal	In hole base of stump	Dirt	2 ½ weeks	22	695
Cleo	May 2016	May 4	Scrub	Maternal	Under scrub at base of tree	Grass underneath	4-5 weeks	24	667
Socks	December 2015	Dec 1	Pasture	Natal	Hole in pampas grass	Shredded pampas grass	0-2 weeks	-	Only found at den
Socks	December 2015	Dec 2	Pasture	Maternal	Hole in pampas grass	Shredded pampas grass	2-3 weeks	44	378
Socks	December 2015	Dec 3	Scrub	Maternal	Under scrub and log	None (grass underneath)	3-4 weeks	285	698

Recruitment rate

The litter size at birth was estimated to be 3-4 kittens for this population. This was estimated from the three litters found at less than two-weeks-old. Based on this litter size, and the 18 pregnancies seen during the study, I estimated 54-72 kittens to have been born in the study site from March 2014 - January 2017. There appears to be a high mortality rate for kittens from birth to two-weeks-old, as only 15 kittens were seen (Figure 7). Less than half (n = 7) of the kittens survived from two-weeks-old to weaning (14-16 weeks-old) (Figure 7). Only two kittens (one female, one unknown) were known to be recruited into the population. Juvenile survival to recruitment (one-year-old) was estimated to be 3-4% for kittens monitored from January 2014 - December 2016. Though recruitment rate was low, the density of cats stayed the same throughout the study due to deaths of four cats, the immigration of two adults from the northern part of the island into the population, and the recruitment of two sub-adults.

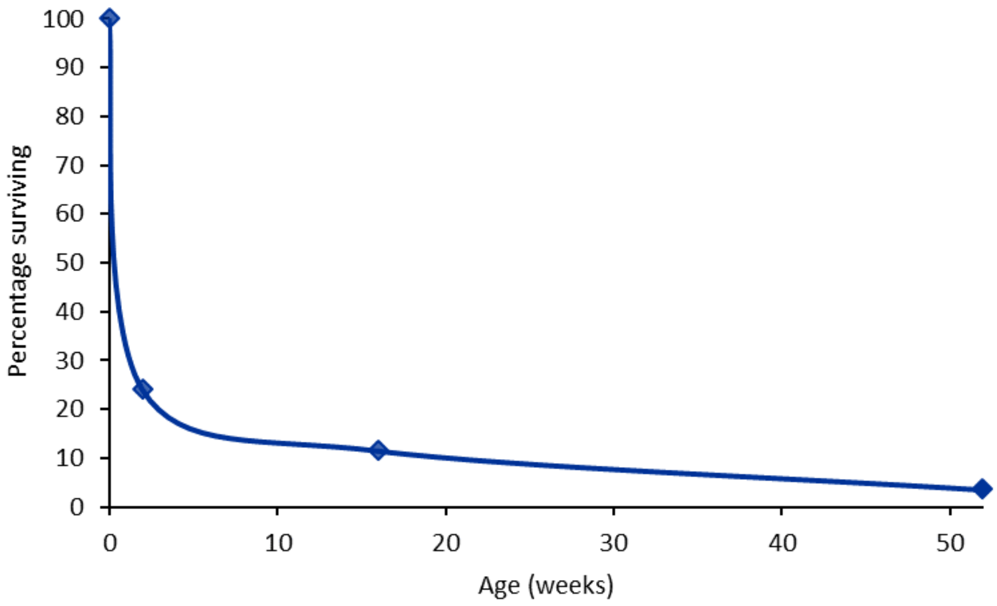

Figure 7: Estimated survival of feral kittens in their first year of life given as the percentage of kittens seen alive at 2 weeks old, weaning (16 weeks old), and recruitment age (one-year-old) from the estimated number of kittens born (54-72 kittens) during January 2014 - March 2017.

Causes of mortality

The cause of death was found for seven kittens, one sub-adult, and three adults (Table 5). Infanticide and depredation were the cause of death for the majority of kittens (six of the seven kittens found dead). Two adult males died from pyothorax. Patches disappeared a week after being seen on camera showing possible signs of feline infectious peritonitis. These signs were an enlarged, distended abdomen, swollen right front leg, a large lump on the left inner hock, and reddened right eye.

Table 5: Causes of mortality in seven kittens, one sub-adult, and three adults found on Ponui Island. Approximate ages could not be given for adults but they were at least two years old. Cause of death was provided from post-mortems and histological assessment by a pathologist.

Litter name	Age	Number of individuals	Cause of death
Socks November 2015	~0 days	1	Stillborn or died soon after birth
Cleo February 2016	2 weeks	4	Depredation by a male cat (infanticide)
Cleo May 2016	4 ½ weeks	1	Starvation and dehydration from abandonment by the queen (infanticide)
Socks May 2016	5 weeks	1	Depredation by either harrier or adult cat
Cleo December 2014	9 months	1	Secondary cholecalciferol poisoning from rat
Midnight	>2 years	1	Pyothorax
Milo	>2 years	1	Pyothorax
Patches	>2 years	1	Suspected Feline Infectious Peritonitis (FIP)

Infanticide

Two incidences of infanticide were recorded; one by a male (n = 4 kittens), and the other by the mother of the litter (n = 1 kitten) (Table 6).

Male infanticide

Cleo was found on 16/02/2016; she had four black kittens in a den in the hole in the ground. The kittens were approximately two-weeks-old. Cleo ran off, and a camera was set up which looked into the entrance of the den. The camera trap footage showed that Cleo did not come back that night. A non-resident adult male cat, Simba, killed the kittens while Cleo was away from the den (Table 6).

Three of the kittens were found the next day under the scrub next to the den. One kitten had been eaten from the back end up to the caudal end of the thorax, with the heart and lungs removed (Figure 8). The other two kittens had not been eaten, and the fourth kitten was not found. All kittens had multiple bite marks over the head, neck, and shoulders. Bite marks ranged from a width of 15 to 23 mm. A post-mortem showed that all three kittens had fractured skulls.

After Cleo lost her February 2016 litter to infanticide, she became pregnant shortly after and had her kittens an estimated 74 days after the infanticide event.

Table 6: Description of the behaviours by both the infanticidal male (Simba) and the queen (Cleo) for the male infanticide event from camera trap footage.

Date	Time	Behaviour
16/02/2016	23:52	Simba entered the den and could be seen grabbing a kitten near the head. The kitten was seen moving around when he grabbed it.
17/02/2016	00:01	There was no movement from the kittens.
	00:20	Kittens were no longer seen in the den, and Simba is presumed to have moved them.
	00:20-01:15	Simba was seen on and off camera, where he was investigating the den.
	06:20	Simba seen in the den, where he sniffed and investigated the den and left soon after.
	07:04	Cleo returned to the den. She entered the den, looked to where the kittens were when she left them, and sat down.
	07:35-07:55	Cleo was seen standing at the entrance of her den and calling periodically.
	07:55-09:33	Cleo continued to sit at the entrance of the den.
	10:30	Cleo was radio-tracked and seen sitting on a log next to the den. She ran off.

Figure 8: Photo of a kitten from Cleo's February 2016 litter that died from infanticide by a male cat and was partially eaten. Photo by author.

Female infanticide

Cleo was tracked using radio-telemetry and was seen running off from near a pohutakawa (*Metrosideros excelsa*) tree. She proceeded to stay in the area. Her litter of three kittens were found two metres up the pohutakawa in a dip in the tree where the branches met the trunk. The kittens were a few days old. There were two males and one female, and one of the males was the heaviest of the litter by 40 g. One and a half weeks later the tree den was checked again. Only one kitten was in the den, which was the heaviest male. The two other kittens had been moved to a new den over 100 m away. A camera trap was set up looking into the entrance of the tree den to observe whether Cleo returned to the den.

The kittens were checked again half a week later. The two kittens were once again moved to another den, however, the lone male kitten remained in the first den; the tree den. It had lost 40 g in body weight, whereas the other two kittens had gained between 70-80 g.

The kittens were found another one and a half weeks later, when the kittens were approximately four-weeks-old. The lone male kitten was found dead in the tree den. It weighed the same amount as it had 23 days prior. The two other kittens had gained between 140-150 g. Camera trap footage showed the kitten calling, though there was no footage of the queen returning to the tree den.

The post-mortem of the kitten showed that it had very little subcutaneous fat. There were no external injuries, and all organs looked formed and normal. There were no signs of congenital diseases or physical abnormalities. The kitten had died from starvation and dehydration (Table 5).

The three kittens gained between 12-20 g/day in body weight over the first two weeks of their life. In the two remaining kittens, their body weight gained per day increased from 12-13 g/day to 17-20 g/day when the litter size decreased from three kittens to two.

Discussion

This chapter describes reproduction of the feral cat population on Ponui Island, and there are several main findings of this chapter. One of my main objectives was to estimate the recruitment rate and reproductive parameters in a stable feral cat population. This feral cat population had a very low recruitment rate of kittens, with only 3-4% of the estimated kittens that were born during the study surviving to one-year-old. I found a seasonal trend to pregnancies in female feral cats. The feral kittens weighed in this study were surprisingly heavier when aged between 1-5 weeks-old than kittens born into a colony. I also found that the movements of female cats changed throughout different reproductive stages, and several den sites were used for different litters. Additionally, two incidences of infanticide were recorded in this population of solitary-living feral cats.

Seasonal pregnancies and recruitment rate

Females had between three to four kittens per litter; this is similar to colony raised female cats which tend to have an average litter size of approximately four kittens per litter (Hall & Pierce, 1934; Robinson & Cox, 1970). Most pregnancies occurred between September - March, with only one litter born outside of this season. This seasonality is similar to that found in previous studies, with a peak in pregnancies in spring and summer (van Aarde, 1978; Apps, 1983; Brothers et al., 1985; Warner, 1985; Read & Bowen, 2001; Ortega-Pacheco et al., 2012). Ovarian activity in cats increases with increasing day length, which could explain the seasonality in this island population far from the equator (Faya et al., 2011). Read & Bowen (2001) found that the peak in pregnancies in a feral cat population coincided with the spring reproduction cycle of rabbits (the main prey) and birds, as well as an increase in the activity of reptiles (a main secondary prey). On Ponui Island, the main prey of the feral cats is rodents (*Rattus rattus* and *Mus musculus*) and birds, with invertebrates being important secondary prey (Chapter 6). While most New Zealand birds do breed in spring (Cockrem, 1995), and there is an increase in invertebrate biomass during summer (Dixon, 2015), the peak in pregnancies of Ponui Island feral cats did not coincide with the highest density of ship rats (Shapiro, 2005; Efford et al., 2006; Latham, 2006). The highest density of rats is during the winter both on Ponui Island (Shapiro, 2005; Latham, 2006) and on the mainland (Efford et al., 2006). By breeding in the spring/summer, the weaning of kittens (when they are 14-16 weeks old) coincides with the peak in rat density (Table 2).

The highest level of mortality occurred between birth and when the kittens were two-weeks-old; only half of the pregnancies resulted in kittens being detected. Half of the kittens that were alive at two-weeks-old survived and were weaned. The time the kittens became independent and were no longer obtaining nutrients from their mother (weaning) was also a time of high mortality; only two of the seven kittens that were weaned survived (28%). This was a similar mortality rate to that observed by van Aarde (1983) on Marion Island, where sub-adults were predicted to have 80% mortality rates. By weaning the kittens during the season of highest rat availability, the Ponui Island kittens may have a better chance at survival.

The overall estimate of kitten survival to recruitment age estimated at 3-4% is lower than that estimated for feral cats on Marion Island (van Aarde & Skinner, 1981; van Aarde, 1983) and Dassen Island (Apps, 1983). While Marion Island had similar mortality rates in sub-adults to my study, they still found that 40% of their population were cats that were less than one-year-old, which was similar to the feral cat population on Dassen Island (51-56%) (van Aarde, 1975; Apps, 1983). The high number of sub-adults in the Dassen Island and Marion Island populations suggests a higher recruitment rate than that found in the Ponui Island population studied here. These differences are likely due to both the Dassen Island and Marion Island cat populations increasing in size, with the Dassen Island population recovering from a control operation (Apps, 1983; van Aarde, 1983), resulting in higher recruitment rates. The lower recruitment rate found in this study may be due to the population being relatively stable and at carrying capacity.

Growth rate differences between feral and colony kittens

Surprisingly, I found that during the first few weeks of life feral kittens grew in body weight faster than colony raised kittens where the mothers were fed *ad libitum*. The two kittens from the Cleo May 2016 litter that were weighed until they were five-weeks-old fitted in the 50-75th percentile weight class of colony-raised kittens (Cave et al., 2018) when they were three-weeks-old or younger. At 4-5 weeks-old, the two kittens were in the 95th percentile weight class of colony kittens (Cave et al., 2018). In this study, those kittens that were at a similar body weight, or had a lower body weight, to the Massey University colony kittens of the same age, were the ones that did not survive to weaning. This difference has not been found before between wild and captive felids, although Laurenson (1995) found that cheetah cubs grew at similar rates to captive cubs, despite their mothers having a lower body condition. This seems counter-intuitive, considering the colony queens were fed *ad libitum* food, so should be in better condition than feral queens, and have more resources for lactation. There are several explanations that may describe the different growth rates observed between feral and colony kittens, including genetic, diet, and environmental differences.

Genetic differences between populations and breeds can produce different growth rates (Lunstra et al., 1978), however, these growth differences are normally the result of artificial selection for increased body weight gain (MacArthur, 1949). Cats were introduced into New Zealand in only 1769 (Fitzgerald, 1990), and feral cats are similar genetically to house cats (Driscoll et al., 2007). However, the growth differences between colony and feral kittens is consistent; the Ponui Island kittens were on average heavier at five weeks old than those measured by Jacobsen et al. (2004) at a colony in the USA, and by Loveridge (1987) at a colony in the UK. These consistent differences in growth between feral and colony kittens is most likely due to an environmental effect rather than genetics.

The differences may be due to diet, since colony cats are fed a different diet to feral cats. In a study by Jacobsen et al. (2004), mothers fed either a high or low fat diet had significant differences in milk composition. Studies have shown that the milk composition of rats and mice fed low energy and protein diets during lactation were different than those fed a normal diet (Nicholas & Hartmann, 1991; Pine et al., 1994). However, these diets were very restrictive (Nicholas & Hartmann, 1991; Pine et al., 1994), and are unlikely to reflect the difference in diet between colony and feral cats. Differences in milk composition did not always result in growth rate changes in kittens either. Although Jacobson et al. (2004) found a change in milk composition for queens fed different diets, the weight gain by kittens was not significantly different. However, another study by Remillard et al. (1993) found there was a significant difference in weight gain between kittens fed a milk replacement that was higher in protein compared to kittens feeding on their queen’s milk. These weights were still smaller than some of the weights of kittens measured in this study of the same age. Thus, it is unlikely that there is a large enough difference in diet of feral and colony cats that would produce a significant difference in milk composition between queens, affecting the growth of the kittens.

Laurenson (1995) found that wild cheetah (*Acinonyx jubatus*) cubs had similar growth rates to captive cubs when it was expected that the wild cubs would grow slower since the mothers did not have *ad-libitum* food resources. She concluded that wild born cheetahs needed to achieve high growth rates due to the threat of depredation on juveniles, and that cheetahs needed to be able to move young between dens (Laurenson, 1995). By having cheetah cubs that grew faster, it would reduce the amount of time that a juvenile was extremely vulnerable (Laurenson, 1995). This may be what is happening to feral kittens in this study and suggests that it is an environmental factor that is causing wild animals to grow at similar rates or faster than colony/captive animals.

Several studies have found that a stressful environment can change the metabolic rate of offspring so they have increased energy storage, as seen in guinea pigs (Schopper et al., 2012), humans (Gluckman & Hanson, 2004; Gluckman et al., 2008), and macaques (Berghänel et al., 2016). The low body condition of the female feral cats might have a similar effect, and result in gestational programming where there are changes in the metabolism of the kittens (Ross & Desai, 2005). This would cause the kittens to store more body fat reserves and better utilize energy sources in preparation for an environment with low food availability (Ross & Desai, 2005). This has been documented in men and women who were prenatally exposed to famine, such as the well-studied case during the Dutch famine (Ravelli et al., 1976; Ravelli et al., 1999; Martorell et al., 2001). The Dutch famine was during World War II, lasted five months, and daily food rations were as low as 400-800 kcal (Ravelli et al., 1999). Those women whose mothers were malnourished during early gestation had higher rates of obesity later in life than those women where their mothers were healthy (Ravelli et al., 1999). This metabolic change during gestation may be occurring in feral cats, resulting in the faster weight gain observed in the feral kittens in this study compared to colony-raised counterparts. Faster weight gain in feral kittens would reduce the time that they are the most vulnerable to infanticide. The majority of kittens during the study were born when rat densities (one of the main prey – Chapter 6) are seasonally increasing. Faster kitten growth would also mean that the feral queen could easily move the kittens to different dens as they became more mobile, shortening the time until kittens could move with their mothers, thereby reducing the chances of infanticide.

The female feral cats in this study were within the smaller weight range of the colony females, whereas the male feral cats overlapped in weight with the colony raised males (though only the lower weight ranges of the colony males). The small sample size of feral cats makes it difficult to draw conclusions, but it may be that the feral female cats have a lower adult body weight than the colony raised-adults because of the metabolic cost of pregnancy and lactation (Oftedal & Gittleman, 1989; National Research Council, 2006). The females in the studied population generally had two litters per year and long lactation periods, which would have a higher metabolic cost than the colony raised females, which breed only a few times over their lifetime, and the kittens are weaned or provided with solid food at eight-weeks-old. The feral females would also need to hunt more when the kittens start on solid food to provide enough resources for growth, also adding to her energy demand (Oftedal & Gittleman, 1989). Feral cats start breeding at young ages, and the added energy demand of pregnancy and lactation could lead to a lower adult body weight (Dickerson, 1978).

Movements of the sub-adult and queens

The sub-adult followed in this study initially moved within the maternal home range, before occupying an area that was, at the time, unoccupied by a female. For many felid species, such as leopards (*Panthera pardus*) (Stander et al., 1997; Farhadinia et al., 2009), Eurasian lynx (Zimmermann et al., 2005; Samelius et al., 2012), bobcats (*Lynx rufus*) (Janečka et al., 2006), and kodkods (*Oncifelis guigna*) (Dunstone et al., 2002), the sub-adults spend time in or close to the maternal home range before dispersing to new areas. Zimmermann et al. (2005) found that some sub-adult Eurasian lynx spent up to seven months after becoming independent from their mother in their maternal home range, before dispersing and forming their own home range. The familiarity of the maternal home range may increase the sub-adult's chances of prey capture, aiding in honing their prey capture skills before moving into unfamiliar territory (Zimmermann et al., 2005).

Dispersal from the maternal area is risky and has a high energy cost (Johnson et al., 2009). The sub-adults in this study weighed less than the colony sub-adults, and there was a high mortality rate from weaning to recruitment. Zedrosser et al. (2007) found a possible relationship between the body weight and mortality rate of sub-adult brown bears (*Ursus arctos*), where individuals with lower body weight were more likely to die. Staying close to the maternal home range may allow the sub-adult to gain enough weight before dispersing, as well as reducing aggressive interactions with unrelated adults (Zedrosser et al., 2007).

One of my objectives was to determine whether the movements of females changed with different reproductive phases. I found that females had larger home ranges during the months they would have been cycling/breeding than any other reproductive phase (non-breeding, pregnant, or with kittens). This has not been studied in feral cats before, however Jedrzejewski et al. (2002) found this in Eurasian lynx. This is most likely because the females could be looking for males to copulate with. Covering more of their home ranges in that time would increase the female's chance of meeting a male. The reproductive phase where females moved the longest distances was during pregnancy, which may be due to females looking for appropriate den sites to have their kittens. They may also need to move further to be able to find enough food to meet the higher demand of pregnancy (MacDonald et al., 1984).

The queen had reduced movements from the den when she had kittens between 0-7 weeks-old as she stayed closer to the den. It is known that the milk intake in kittens is constant over the first four weeks of life (Hendriks & Wamberg, 2000), so the queens would be limited in the distance they can move away from dens. When kittens are older (six-weeks or more) they start to move away from the den with their mother, which is also when the queen starts to move further from the den. Though the kittens are travelling with the queen, and are starting to eat solid food, the queen will be restricted with how far she can travel from the den based on how far the kittens can move. The queen would also need to move further from the den for hunting opportunities. With the kittens eating prey, and the added demand to feed the kittens, the queen may need to venture further from the den to be able to catch enough prey.

When kittens were weaned, the queen did not move as far from the last known den, which was an unexpected result. This may be because the queen is sharing part of her home range with her independent sub-adults, and by restricting her movements it allows the sub-adults to utilise their mother’s home range more. This has been observed in Eurasian lynx (Zimmermann et al., 2005) and leopards (Farhadinia et al., 2009).

Movements of kittens between dens

Three litters were monitored throughout the first few weeks of their life, and in that time, the queen moved their litters between several different den sites. The type of natal den varied between females, as one female had her kittens up a tree, and the other had her kittens in a tunnel in pampas grass. Felids often move young between several different dens in the wild, though the reasons for this is not known, but several hypotheses have been put forward. These include choosing dens that are enclosed to reduce the exposure of kittens to extreme weather; dens that protect kittens during vulnerable stages of development from depredation or infanticide; moving kittens to reduce disease risk and the build-up of ectoparasites; and moving kittens between dens after human disturbance (Butler & Roper, 1996; Fernández & Palomares, 2000; Fernández et al., 2002).

Fernández & Palomares (2000) and Fernández et al. (2002) hypothesised that Iberian lynx (*Lynx pardinus*) moved dens based on the development of the young, moving to more spacious dens once the kittens become more mobile. Tight, enclosed dens are often used more for natal dens (Stander et al., 1997) that may reduce exposure of new-born kittens to extreme weather; kittens are unable to thermoregulate well (Olmstead et al., 1979; Fernández et al., 2002). At birth, kittens are altricial, and are blind and deaf (Spotte, 2014). Kittens start to become more mobile as their visual and auditory senses develop when they are 1-2 weeks-old, but are not fully ambulatory until 5-6 weeks-old (Baerends-van Roon & Baerands, 1979; Villablanca & Olmstead, 1979; Beaver, 1980; Levine et al., 1980). The dens chosen by the queen may reflect these changes in the development of the kittens. The last dens used by kittens in this study were mainly scrub areas as opposed to the enclosed holes used for natal dens. Kittens were moved to scrub areas at around 4-5 weeks-old. At that age, kittens become more mobile and able to thermoregulate better (Olmstead et al., 1979), which may reduce the need for enclosed areas.

Enclosed dens would also conceal the vulnerable young from potential predators (Laurenson, 1994). Two of the three natal dens found in this study were enclosed or difficult to reach areas. Camera trap footage of one den situated two metres up a tree revealed the queen moving two of the kittens away from the edge of the den, where they could have fallen to the ground. Soon after this, the female moved the kittens to a new den. It may be that there is a trade-off with the natal den, where it needs to be in a difficult to access area (to reduce infanticide or depredation) (Schmidt, 1998), but it can only be used when kittens are young and less mobile. The first natal den used by one female was in a hole in the ground at the base of a fallen tree and was fairly accessible, and the litter born there succumbed to infanticide. The next den chosen by that queen for a natal den was two metres up a tree. This observation might support the idea that the natal den is chosen to also reduce the chance of an infanticide or depredation event.

In terms of moving dens to fend ectoparasites, Butler & Roper (1996) found that European badgers (*Meles meles*) avoided burrows with high ectoparasite load. There is a high prevalence of ectoparasites on stray and feral cats, including fleas, ticks, and lice (Akucewich et al., 2002; Borji et al., 2011; Mendes-de-Almeida et al., 2011). A high parasite load can cause anaemia in animals, particularly in young (Akucewich et al., 2002). Ectoparasite load was not measured in this study, and further investigation of this hypothesis is needed for feral cats.

Moving kittens between different dens may also be due to human disturbance. It has been found that Iberian lynx choose den sites that are least likely to be disturbed by humans, and sometimes move their litter after human disturbance (Fernández et al., 2002). It is possible that the queens moved their litters after I had handled the kittens. However, one of the females picked a natal and maternal den close to the farm house, in an area where vehicles and farm dogs frequently went past, and the kittens were not always moved after I had visited the den. This may mean that human disturbance may not be as an important factor to den choice in the feral cats studied on Ponui Island. Boutros et al. (2007) also found that female Eurasian lynx moved their kittens to different dens regardless of whether the researchers had visited the den or not.

Knowing the type of dens females choose to use as natal (where the queen gives birth to the kittens) and maternal dens (sites the kittens are moved to after the natal den) allows us to determine the habitat type that is important for females and the areas where they may have an increased reproductive output. The queens may also hunt prey close to the dens, and will have higher energy demands due to the expense of pregnancy and lactation (Laurenson, 1995; Fernández & Palomares, 2000). By identifying these den site areas and habitats most frequently used, we can identify species that may be at risk of depredation pressures.

Infanticide

In my study, I found two incidences of infanticide in this population of solitary-living feral cats, one by a male cat and the other by the queen of the litter. There are five main hypotheses proposed for explaining how infanticidal behaviour may have evolved; exploitation, resource competition, parental manipulation, sexual selection, and social pathology (Hrdy, 1979; Hausfater & Hrdy, 1984). For each hypothesis outlining infanticidal behaviour, there are predictions for the relationship and age of the infant (Supplementary material: Table S1). Infanticide has been reported in farm cats by Macdonald et al. (1987), and Pontier & Natoli (1999). However, farm cats often form groups, adopting a different lifestyle to that seen in the solitary-living feral cat (Macdonald et al., 1987). This behaviour has not been described before in feral cats, although Harper (2005) found evidence of a kitten being eaten from his dietary analysis of cat scats collected from Stewart Island. Infanticide is difficult to observe, and this behaviour may not be an uncommon practice in feral cats despite its lack of reporting.

There are two hypotheses to explain the infanticidal behaviour demonstrated by the male seen in this study (Hausfater & Hrdy, 1984; Balme & Hunter, 2013). These are: exploitation of an infant as a resource, and sexual selection. There are two conditions associated with the hypothesis that an infanticide event was to exploit an infant as a resource; the infanticidal adult has a nutritional gain, and the killing of infants is normally associated with low prey availability (Hausfater & Hrdy, 1984; Balme & Hunter, 2013). An example of this has been seen in polar bears (*Ursus maritimus*), where Stone & Derocher (2007) observed a male in poor body condition killing and eating a seven-month-old cub. For the infanticide event observed in this study, the male ate one and a half of the kittens, but not all of them. Though he was still present at the den six hours after the killing, he did not eat the two other kittens that he killed. While the rat density on Ponui Island is at its lowest in February (6 rats/ha) (Shapiro, 2005), alternative prey are available that are eaten during these seasons (Chapter 6). Therefore, low prey availability may not have been the primary cause.

In this case, there is more support for the hypothesis of sexual selection, where the perpetrator is normally a male, the kittens are unweaned and highly dependent on the mother, and the whole litter is killed (Hausfater & Hrdy, 1984; Balme & Hunter, 2013). By doing this, it is expected to shorten the interbirth interval of the mother and increase the breeding opportunity of the infanticidal male (Hausfater & Hrdy, 1984; Balme & Hunter, 2013). If Cleo's litter had not been killed, then she would have been in lactational anoestrus until May-June 2016. Because of the seasonal pattern of pregnancies in feral cats, Cleo would possibly not have become pregnant until September-October. The loss of the whole February litter meant that Cleo cycled earlier than she would have, and became pregnant in March-April, shortening her interbirth interval. This would have been beneficial for the unrelated male because it could have increased his chances of mating with the female and increasing his reproductive output, lending support towards the sexual selection hypothesis of infanticide. Finding out if the infanticidal male obtained paternity in the female's next litter could be used as support of this hypothesis.

An alternative hypothesis of infanticide is that males may use this behaviour to reduce or eliminate the genes of sexual rivals. This hypothesis, along with the sexual selection hypothesis were tested using observations of infanticide in howler monkeys (*Alouatta seniculus*) (Crockett, 2003). Males that killed competitor's young were unlikely to benefit because the infanticidal male would most likely have dispersed or died before the young attained reproductive age (Crockett, 2003). There would be a greater benefit for the male to kill the unrelated young and copulate with the mother, and an additional benefit would be reducing competitor's genes (Crockett, 2003). Therefore, Crockett (2003) concluded that there was more support for sexual selection being a driving force for infanticidal behaviour.

In this study, I found that the litter size was between three and four kittens from the three litters that were found. However, when kittens were seen out with their queens at five to sixteen weeks old, the litter size was one or two kittens. Females might reduce their litter size by leaving one or two kittens to die at an early age, reducing the energy demand on the queen, since lactation has a high energy cost (Wichert et al., 2009). This is called parental manipulation, and is where the death of an offspring can improve the chances of survival for the existing young, or for the mother (Hrdy, 1979; Hausfater & Hrdy, 1984). This would increase the chances of at least one or two kittens from the litter surviving until weaning, and ensure they are in a better condition at weaning than they would have been if the queen continued raising the whole litter (Mendl, 1988; Deag et al., 2009). This would also allow the queen to maintain a degree of body condition that ensures her survival; the females observed in this study were in poor condition, as were female feral cats studied in Florida (Scott et al., 2002) supporting this idea. Additionally, the kitten that was abandoned by its queen in this study was the largest of the litter, and was abandoned at 2-3 weeks-old. Hendriks & Wamberg (2000) found that queens had a higher weight loss in the third and fourth weeks of lactation than in the earlier weeks. By abandoning the kitten the queen may have been able to conserve more energy and invest in the other kittens to ensure their survival. Grizzly bears (*Ursus arctos*) have also been hypothesised to abandon litters where there is only one cub, as a tactic to increase their own reproductive output by putting their energy into raising another litter (with more than one cub) (Tait, 1980).

It cannot, however, be dismissed that the abandonment of the kitten may have been caused by human disturbance at the den, though this seems unlikely. Evidence of den abandonment by carnivoran mothers following human disturbance have resulted in the abandonment of the whole litter, and there have been no cases reported where a portion of the litter were abandoned and the mother relocated the others. For example, bears (*Ursus* spp.) that were disturbed in dens with cubs did not return to the dens, and the entire litter was abandoned (Elowe & Dodge, 1989; Linnell et al., 2000). In the case of female abandonment observed in this study, the female returned to the den following the disturbance, and only abandoned one kitten. This leads further support to the conclusion drawn above, that that the kitten died from infanticide via parental manipulation.

Management considerations

The reduced movements of the females in different reproductive phases I observed needs to be considered by managers when designing control programmes. The females are covering shorter distances when they have young or recently weaned kittens. This means that those females are less likely to encounter traps, and that additional traps may need to be set in the area during these seasons. Based on the seasonality of pregnancy in feral cats, it can be predicted that females are unlikely to be captured from November - June.

I have confirmed that infanticide occurs in solitary-living feral cat populations and that males may use this as a reproductive tactic. Male feral cats may be more likely to be trapped, because they encounter more traps due to their larger home ranges (Chapter 2) (Fitzgerald & Karl, 1986; Moller & Alterio, 1999; Gillies et al., 2007; Recio & Seddon, 2013). We need to be careful removing mainly males, since they may be reducing the survival of kittens through infanticide. Removing mainly male feral cats may lead to less infanticide and competition between males for mating opportunities. This could lead to more kittens surviving, and subsequently an increase in population size, or rapid population recovery following feral cat control. These indirect effects need to be taken into account in control programmes for feral cats.

The recruitment rate in this population of feral cats was very low compared to previous studies (Apps, 1983; van Aarde, 1983), however, this is likely to be because the population is at carrying capacity on Ponui Island. Taking into consideration the reproductive parameters found in the Ponui Island feral cat population, where there are a high number of pregnancies, and three to four kittens produced per litter, feral cats have the ability to rapidly recover from control operations. This means that reducing feral cat populations and keeping them suppressed may not be possible, and eradication, if possible, may be more effective long-term.

The infanticide event by the male observed in this study has led to the need to study the parentage of the kittens on Ponui Island to determine whether the infanticide was likely used as a reproductive tactic by the male. Another important aspect to investigate for feral cat management is whether the population is closed and has no immigration, because these closed populations are likely to be able to be successfully eradicated and not re-establish. The population genetics of the feral cats caught on Ponui Island, and the parentage of kittens found in this study, was investigated in the next chapter (Chapter 5).

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Supplementary material

Table S1: Infanticide hypotheses with their predictions for the relationship, age of the infant, characteristics of the killer, and the potential gain. This has been written with regards to wild felids where the female invests more in parental care. This table is modified from Hausfater & Hrdy (1984) and Balme & Hunter (2013).

Hypothesis	**Relationship**	**Characteristics of infant**	**Characteristics of the perpetrator**	**Potential gain**	**Expected observations**
Exploitation of infant as a resource	None	Size and vulnerability	Male or female which is large enough to overtake the infant.	Nutritional	Infants are eaten. Rate of infanticide is related to prey abundance.
Potential competitor or resources	None	Vulnerability	Male or female, usually adults	Increased resource availability	Rate of infanticide related to resource abundance and to cat population density.
Sexual selection	None	Unweaned and still dependent enough on the mother to hinder ovulation	Typically male	Increased breeding opportunity	Whole litter is killed. Interbirth interval is shortened for litters which died earlier. Perpetrator and mother are not mates or close relatives. Perpetrator mates with mother soon after.
Parental manipulation	Close relative	Generally just after birth but could be any age where infant is still dependent on the mother	Typically female	Increased fitness to the parent/s	Increased conditioning of the female. Rate of infanticide related to prey abundance.
Social pathology	Irrelevant	Size, proximity, and vulnerability	Most likely adults who respond aggressively to social or anthropogenic disturbance	Not necessarily to the killer, but may change population density and increase resource availability	High levels of mortality caused by people. Rate of infanticide is related to the cat density.

Chapter 5 – Population genetics of feral cats on Ponui Island and parentage of their kittens

Plate 5: Photo of Cleo's May 2016 litter in their natal den (taken by the author).

Introduction

The observation of infanticidal behaviour and low recruitment rate in the Ponui Island feral cat population (Chapter 4) warrants an investigation of the genetics of the population to determine parentage and whether the population is open or closed with respect to immigration. Population genetics has proved to be an invaluable tool for conservation managers because it can be used to study pest animals' invasion patterns, and identify established, isolated populations of invasive species (Ficetola et al., 2008). Populations that are isolated with little or no immigration are ideal to target for control because they are likely to be comparatively easy to eradicate and have a low likelihood of reinvasion. Eradication of pest species from islands offers excellent examples of this, and the return on investment has often been the successful recovery of endangered or threatened species (Pascal et al., 2005; Donlan et al., 2007; Ratcliffe et al., 2010). Removing invasive pest species from ecosystems is costly, and limited conservation funding restricts the number of locations in which invasive predator management can be implemented (Parkes & Murphy, 2003). Limitation of resources necessitates that management efforts prioritise areas where the pest control will have the greatest benefit for native species (Joseph et al., 2009), and where pest control is most likely to succeed, such as on islands. However, islands can still be connected by migration. Abdelkrim et al. (2005) found that there was immigration of Norway rats (*Rattus norvegicus*) between islands that were geographically close to each other. Genetic analysis is a valuable tool that can indicate how much gene-flow is occurring between geographically close islands. Populations that have high connectivity and migration should be managed and eradicated concurrently to reduce the chances of re-establishment (Abdelkrim et al., 2005). Although cats are unlikely to swim between islands, the establishment of feral cats onto offshore islands has been largely human-mediated (Koch et al., 2016). Thus, offshore islands may not be genetically isolated as there may be continued introductions by humans.

Cats have a long history of association with humans, dating back 10,000 years (Serpell, 2000; Vigne et al., 2004) when cats took advantage of the aggregation of rodents around human settlements and agricultural systems, leading eventually to their domestication (Clutton-Brock, 1999). Cats are often described as being "semi-domesticated" because they are semi-independent as pets, and it is this lifestyle that most likely assisted the establishment of feral cat populations (Serpell, 2000). Feral cats have been identified as an invasive pest due to the detrimental effects they have on native fauna globally (Karl & Best, 1982; Fitzgerald & Veitch, 1985; McLennan et al., 1996; Galbreath & Brown, 2004; Medina et al., 2011; Nogales et al., 2013). Domestic cat dispersal throughout the world has been largely human-mediated (Koch et al., 2016). Cats were frequently taken on voyages to provide rodent control, which resulted in their introductions into widely dispersed and often isolated areas (Fitzgerald, 1990; Gaynor, 1999). Many introductions of cats to continents can be traced back to human intervention. For example, despite the land-bridge between Australia and Asia, genetic analyses have verified that feral cats within Australia are closely related to European cats (Koch et al., 2015; Spencer et al., 2016). The arrival of Europeans to New Zealand also resulted in the introduction of the domestic cat in 1769 (Fitzgerald, 1990).

There are well-developed primers for analysing microsatellite variation in felids (Menotti-Raymond et al., 1999) that allow for measurement of hybridisation between, for example, domestic cats and wildcats (*Felis silvestris*), plus quantification of population genetic diversity and gene-flow (Wiseman et al., 2000; Rueness et al., 2003; Beaumont et al., 2008; Eckert et al., 2010). The domestic cat is genetically and morphologically similar to the wildcat that is distributed throughout Africa, Europe, and Asia (Driscoll et al., 2007). Recent genetic analyses have found that both the Near Eastern and the Egyptian cat lineages contributed to the genetic make-up of the domestic cat (Driscoll et al., 2007; Ottoni et al., 2017), leading to the high genetic diversity of the modern-day domestic cat (Lipinski et al., 2008).

Little is known about the mating systems of feral cats including multiple paternity, although mating systems of feral cats range from polygynous to promiscuous depending on the density of the population (Say et al., 1999; Say et al., 2002a). The home ranges of male feral cats tend to overlap those of several females (McGregor et al., 2015), allowing opportunity for paternity to change in subsequent litters, or even differ within a litter. For example, Say et al. (1999) found higher rates of multiple paternity within litters in cat populations at high densities (2091 cats/km^2).

Understanding mating systems in feral cats is important because control methods such as trapping can be sex-biased towards males (Lofroth et al., 2008) (Chapter 7 and Appendix B). Male feral cats may limit the survival of feral kittens through infanticide, and evidence for infanticide has been reported in solitary-living feral cats on Ponui Island (Chapter 4). Infanticide is a behaviour where an animal kills the young of a conspecific and such action can be used as a reproductive technique (Hrdy, 1979; Hausfater & Hrdy, 1984; Balme & Hunter, 2013). Infanticidal behaviour can be adaptive when the young are unrelated to the infanticidal male since this behaviour effectively reduced a competitor’s genes within the population gene pool and can increase his own reproductive output by copulating with the mother of the killed young with her return to oestrus (Hrdy, 1979; Steyaert et al., 2014). Eutherian females can have lactational anoestrus that reduces the likelihood that a female with dependent young (suckling from the female) will become pregnant (Short, 1976). A male that kills a whole litter or all of the dependent young could reduce the lactational anoestrus (Steyaert et al., 2014; Palombit, 2015). The male would have a greater opportunity of mating with the female, thereby potentially increasing his own reproductive output (Steyaert et al., 2014; Palombit, 2015).

Due to the mating systems of domestic cats, infanticidal behaviour may be more common in cats than has been observed (Macdonald et al., 1987; Pontier & Natoli, 1999). Females may mate with many males to confuse paternity, or reproduce with the most dominant male; these strategies could be used to counteract infanticide (Agrell et al., 1998; Wolff & Macdonald, 2004; Palombit, 2015). Wolff & Macdonald (2004) reviewed the hypotheses explaining the evolution of multi-male mating in mammalian species, and concluded that the most likely drivers of selection for this behaviour were its ability to confuse paternity and thereby reduce infanticidal behaviour and to reduce sexual harassment by males. For these reasons, multiple paternity may be seen within a population where infanticidal behaviour occurs.

There have been few studies on multiple paternity of litters in cats, and these have often had small sample sizes or successive litters have not been sampled (Soares et al., 2006; de Pinho et al., 2014). Say et al. (1999) found differences in levels of multiple paternity within litters with differing cat population densities, but their study was carried out on urban and rural cat populations that have higher densities than those seen in feral cats (Jones & Coman, 1982; Fitzgerald & Karl, 1986; Konecny, 1987; Norbury et al., 1998). Only one study has focused directly on multiple paternity in feral cats (Say et al., 2002a), and there was no evidence of multiple paternity within litters. The genotypes of potential fathers were not known and were predicted through the genotypes of the kittens (Say et al., 2002a).

I investigated the population genetics of feral cats on an offshore island in New Zealand. Cats were first taken to Ponui Island in the 1850s as pets (Bellingham, 1979; Fitzgerald, 1990), and it is not known whether it was from these original cats or subsequent invasions that a feral cat population established. Ponui Island is close (<4 km) to the mainland and to other inhabited islands (Chapter 2), so my goal was to investigate whether the Ponui Island feral cat population has received any new introductions of cats in more recent times. There is the potential for islands that are close to the mainland to be sites for cat dumping (Atkinson, 1973). I have used the Ponui Island feral cat population as a proxy to determine whether the eradication of the feral cat population would be successful in the long term, by identifying whether the population has existed in isolation or had new introductions. Due to the overlapping home ranges between females and several male feral cats studied on Ponui Island (Chapter 2), and evidence of infanticide in the population (Chapter 4), I also decided to investigate the parentage of the kittens sampled within this population. Therefore, my aims were two-fold for this study: 1) to investigate the population genetics of Ponui Island feral cats; and 2) to determine the parentage of kittens.

Methods

Sample collection

I collected samples for DNA extraction from 28 Ponui Island cats; 11 adults (>12 months old), two captured and sampled as sub-adults (6-12 months-old), 11 kittens (<6 months-old), and four cats caught wild on Ponui Island but kept as pets. Blood was preferentially used for DNA extraction when it had been collected, followed by tissue (muscle and cartilage), hair, then bone. (Table 1). The pet cats were originally caught as kittens (before they were of breeding age) so did not breed and contribute to the feral cat population on Ponui Island. Samples from a captive cheetah, two cats from a research-colony, two Northland feral cats, and two Mataia feral cats were collected to be used as outgroups for comparison, and for testing the PCR, fragment analysis, and clustering techniques (Figure 1A).

Ponui cats

The main study site was Ponui Island (Chapter 2), located near Kawakawa Bay, Hauraki Gulf, New Zealand (Figure 1A). The island is in close proximity to human populated areas, particularly Auckland city and Waiheke Island (Figure 1B). Kawakawa Bay has substantial boat traffic, and the areas surrounding Ponui Island are popular with recreational fishers.

Cats were trapped in the southern part of the island from April 2015 – January 2017 as part of another study (Chapter 2) and blood and tissue samples collected. In addition, any adult cats or kittens found dead throughout the study site from January 2014 – March 2017 were collected and stored at -20^{o}C, and samples collected for DNA extraction. Details on trapping procedures and blood collection are outlined in Chapter 2. When possible, blood was collected from captured cats, however, due to the vaso-suppressive side effect of anaesthesia, blood could not be collected from all captured cats. For those cats, I used tissue from the ears obtained when adult cats were ear-notched (a triangle of tissue was cut off the ear measuring 5mm each side) for individual identification on the camera traps (Chapter 2). These tissue samples were retained and stored in 99% ethanol. Kittens that were studied in Chapter 4 had hairs plucked for DNA extraction. The hairs were stored in a paper bag with an enclosed bag of silica beads to keep the samples dry. These kittens were identified by their queen’s name, the month and year of birth, sex, and coat colour.

I also used four pet cats that were originally caught on Ponui Island but were removed from the island as kittens and kept as pets. Owners of the cats provided me with hairs that were stored in paper bags containing silica beads and sent to Massey University for DNA extraction.

Mataia and Northland cats

One male and one female feral cat from both Northland and Mataia sites (Figure 1B) that were killed as part of control programmes had ear-notches collected post-mortem for DNA extraction. Cats were used from these locations due to their availability from trappers.

Colony cats

Blood samples were collected from a male and a female cat at the Massey University Feline Unit (Massey University Animal Ethics Committee 16/39). The jugular area was clipped, and lidocaine gel was applied to the venipuncture site. A sample of 3 ml was taken from the jugular vein using a 25 gauge needle and placed in an EDTA tube. The blood was stored at -20°C.

Cheetah

Cheetah DNA was provided by K. Gedye (IVABS, Massey University, Palmerston North, New Zealand) that was collected from Wellington Zoo for another study.

Table 1: Information about the 36 cats sampled for genetic analysis. The name/ID of each cat is listed, as well as the sample type used for DNA extraction. The origin is the population that the cat was from, and cats were given an age class.

Cat	**Sample**	**Origin**	**Age Class**
Cheetah	Blood	Wellington Zoo	Adult
Colony Male	Blood	Massey University Colony	Adult
Colony Female	Blood	Massey University Colony	Adult
Northland Female	Tissue	Northland	Adult
Northland Male	Tissue	Northland	Adult
Mataia Female	Tissue	Mataia	Adult
Mataia Male	Tissue	Mataia	Adult
Cleo	Blood	Ponui Island	Adult
Tui	Blood	Ponui Island	Adult
Socks	Blood	Ponui Island	Adult
Patches	Blood	Ponui Island	Adult
Tigger	Blood	Ponui Island	Adult
Cleo sub/A	Blood	Ponui Island	Sub-adult
Salem	Tissue	Ponui Island	Adult
Mittens	Tissue	Ponui Island	Adult
Tortoiseshell	Tissue	Ponui Island	Adult
Snowball	Tissue	Ponui Island	Adult
Midnight	Tissue	Ponui Island	Adult
Sylvester	Tissue	Ponui Island	Adult
Shadow	Tissue	Ponui Island	Sub-adult
Cleo BW	Tissue	Ponui Island	Kitten
Cleo F kit 3	Tissue	Ponui Island	Kitten
Cleo M kit 2	Tissue	Ponui Island	Kitten
Cleo ½ kit 1	Tissue	Ponui Island	Kitten
Socks S/B	Bone	Ponui Island	Kitten
Woolshed juvie	Bone	Ponui Island	Kitten
Ponui	Hair	Ponui Island	Adult pet (off-island)
Socks F	Hair	Ponui Island	Kitten
Cleo TS	Hair	Ponui Island	Kitten
Cleo black	Hair	Ponui Island	Kitten
2nd bay juvie	Hair	Ponui Island	Sub-adult
Silver	Hair	Ponui Island	Pet
Mogli	Hair	Ponui Island	Adult pet (off island)
Pumpkin	Hair	Ponui Island	Kitten
Kim	Hair	Ponui Island	Adult pet (off island)
OH juvie	Hair	Ponui Island	Sub-adult

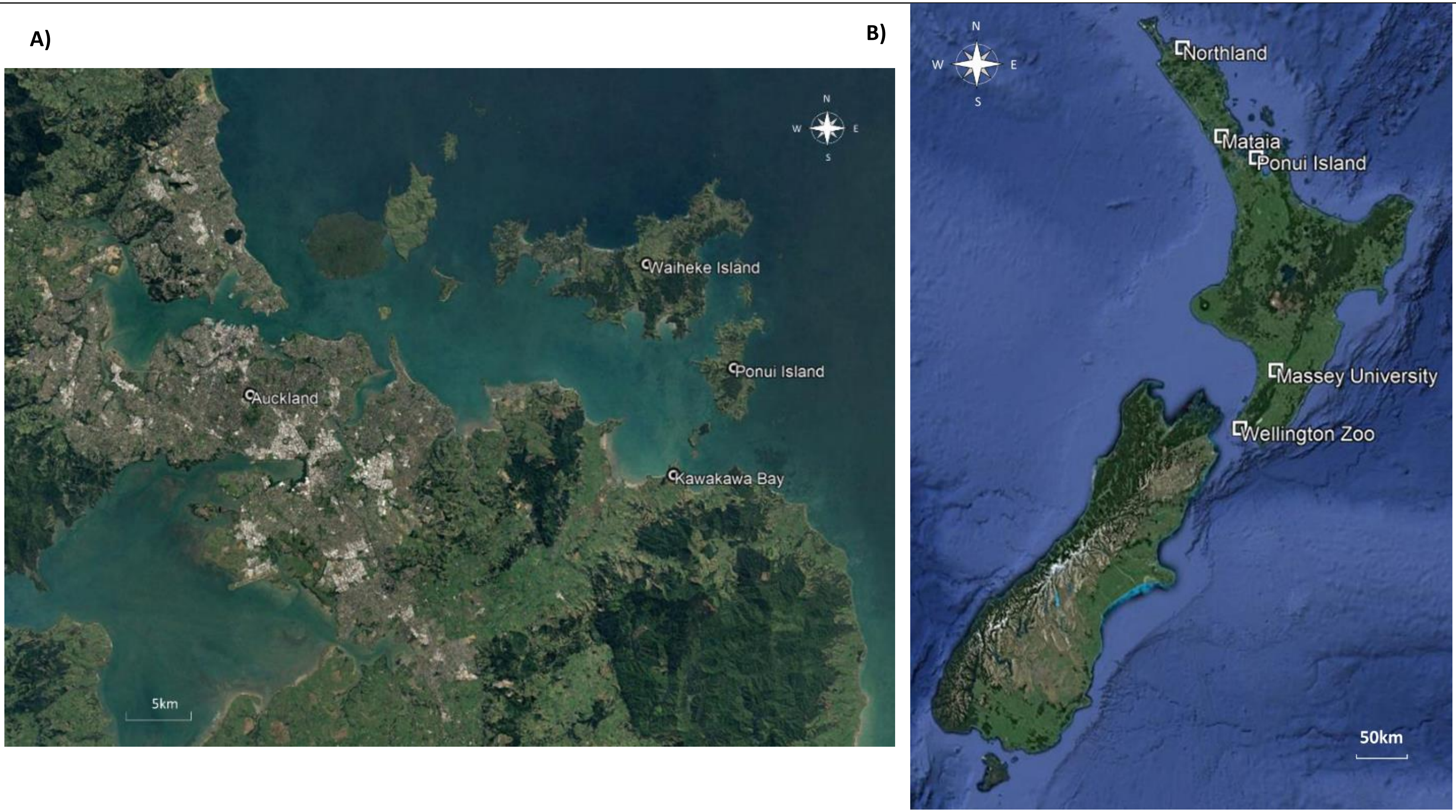

Figure 1: A) Location of Ponui Island (the main study site) and distances to populated areas and cities as potential sources of immigration into the feral cat population. **B)** Location of genetic samples used in this study.

DNA Extraction

Blood

DNA was extracted from 250 µl of cat blood, using 250 µl of an SDS lysis buffer (20 mM EDTA-$NA_2.2H_2O$, 60 mM Tris HCl, 1% Sodium dodecyl sulphate, 1% Triton X-100, pH 8.0), and Proteinase K at 0.5 mg/ml (Roche Diagnostics, Switzerland). This mix was incubated at 56°C for 30 minutes and equal volumes of phenol:chloroform:iso-amyl alcohol (25:24:1, Sigma, MO, USA) were added. Aqueous and organic phases were separated by centrifugation at 13,400 x g for 15 minutes at 4°C. DNA was precipitated using a 10:1 solution of ice-cold 100% ethanol and 3M Sodium acetate (Sigma, MO, USA). The DNA was washed twice with 70% ethanol, allowed to air dry, and resuspended in R40 (40 µg/ml RNase A [Sigma, MO, USA] in TE [10 mM Tris, 1 mM EDTA, pH 8.0]) overnight at 4°C. Extracted DNA was quantified with a Nanodrop (Thermo Scientific, MA, USA) and stored at -20°C.

Tissue

Stored ear-notch tissue was removed from ethanol and stored frozen at -20°C overnight to remove the ethanol so hair could be removed from the tissue easily. Hair was scrapped from the tissue using a scalpel. The tissue was cut in to small strips in an Eppendorf tube, with 500 µl of rat tail lysis buffer (100 mM Tris.Cl pH 8.0, 5 mM EDTA, 0.2% SDS, 200 mM NaCl) (protocol from Tsai Laboratory (2014)) and 10 µl of 20 mg/ml Proteinase K. Samples were put in a water-bath at 55°C overnight, then vortexed. Any samples that were not fully digested were kept in the water-bath for another 24 hours. Dry tissue samples were incubated at 4°C overnight with 500 µl of rat tail lysis buffer. Proteinase K was then added and incubated in the water-bath at 55°C overnight. Samples were then stored at -20°C.

Hair

For each sample, a minimum of five hairs were placed into 1.5 ml Eppendorf tubes with 40 µl of INRA solution A (200 mM NaOH) added and vortexed. Samples were put into the thermocycler for 1 minute at 75°C, 2 minutes at 80°C, 1 minute at 90°C, 10 minutes at 97°C, ending at 4°C. The samples were removed and had 40 µl INRA solution B (200 mM HCl, 100 mM Tris-HCl, pH 8.5) added and mixed. Samples were then stored at 4°C overnight.

Alternatively, hair was treated to a modified Chelex® 100 extraction protocol (Martín-Platero et al., 2010). For each individual cat, six hairs were placed in a 1.5 ml Eppendorf tube and incubated with 10 µl of water, 40 µl of 6% Chelex 100 w/v (Bio-Rad, Hercules, CA, USA), and 1 µl of Proteinase K 20 mg/ml (Roche, Switzerland) and vortexed for 10 seconds. The samples were incubated at 56°C for 1 hour and 98°C for 8 minutes, vortexed and stored at -20°C.

Bone

Femur bones were cut and smashed into 6 mm pieces and put into a 6775 freezer/mill® cryogenic grinder (SPEX®SamplePrep, NJ, USA). Bone fragments were crushed under liquid nitrogen to a fine powder. Approximately 0.5 g of bone powder was incubated with 500 µl of rat tail lysis buffer and 10 µl of 20 mg/ml Proteinase K. DNA extractions were purified using a phenol:chloroform:isoamyl alcohol extraction. DNA was suspended in 50 µl of elution buffer, then stored at -20°C.

Genotyping

A total of 19 microsatellite loci were targeted using primers developed to investigate genetic variation among domestic cats, and were selected from Menotti-Raymond et al. (2005) and Lipinski et al. (2007) (Table 2) (sourced from Integrated DNA Technologies (Iowa, USA)). Primers had been tested and validated by Menotti-Raymond et al. (1999) to ensure the correct microsatellite locus was amplified. The primers selected for this study were those that showed the highest heterozygosity because parentage analysis requires heterozygosity in order to identify alleles inherited by the offspring from the parents (Selkoe & Toonen, 2006; Tokarska et al., 2009). Each primer pair (forward and reverse) targeted one locus and there were 19 primers used. All selected primers targeted the highly conserved flanking regions of microsatellite repeats, which are non-coding and non-expressed regions that occur throughout the genome (Menotti-Raymond et al., 1999; Selkoe & Toonen, 2006; Lipinski et al., 2007; Vieira et al., 2016). Microsatellites are widely used for parentage and population genetics analysis due to their instability and high mutation rates (Selkoe & Toonen, 2006; Vieira et al., 2016). The repeating sequences for the microsatellites targeted in this study were either dinucleotide or tetranucleotide (Menotti-Raymond et al., 2005; Lipinski et al., 2007), and the observed base pair size for each allele amplicon ranged from 110 to 423 (Table 2).

Extracted DNA was amplified using polymerase chain reaction (PCR) for each cat with each of the nineteen primers in 20 µl reactions. Only one primer was used in each reaction. Reactions comprised of 1 µl DNA, 4 µl of 5x Hot Firepol Blend Master Mix (1x concentration) (Solis Biodyne, Tartu, Estonia), 0.6 µl of the forward and reverse primer (0.3 µM), and 13.8 µl sterile water. This was then put in a thermocycler (Applied Biosystems Veriti, Foster City, California, USA) for 15 minutes at 94°C, followed by 45 cycles of: 30 seconds at 94°C; 30 seconds at 54°C; 30 seconds at 72°C, then 7 minutes at 72°C, finishing at 4°C. Two samples of each primer and the negative water control (5 µl) were run through a 2% agarose gel (Bioline, London, UK) visualised with Redsafe (iNtRON, Korea) for 15 minutes at 60 V to check for amplification. PCR products were stored at -20°C.

PCR products were separated by microfluidics capillary electrophoresis in the Massey Genome Services (Palmerston North, New Zealand), Perkin Elmer (Akron, Ohio), LabChip GX Touch HT, using the DNA High Sensitivity LabChip® Assay with internal size standards. Results were analysed using the LabChip GX receiver software that identified peaks that were visually designated as microsatellite alleles (Figure 2). In some samples, portions of the DNA was degraded and there appeared to be an inaccuracy of 2 bp due to potential genotyping errors where the entire allele did not amplify. This problem is common with degraded DNA or samples containing low levels of DNA (Broquet & Petit, 2004; Pompanon et al., 2005), and has been reported with using felid samples typically collected non-invasively (e.g. hair) (Coomber et al., 2007; Wultsch et al., 2014).

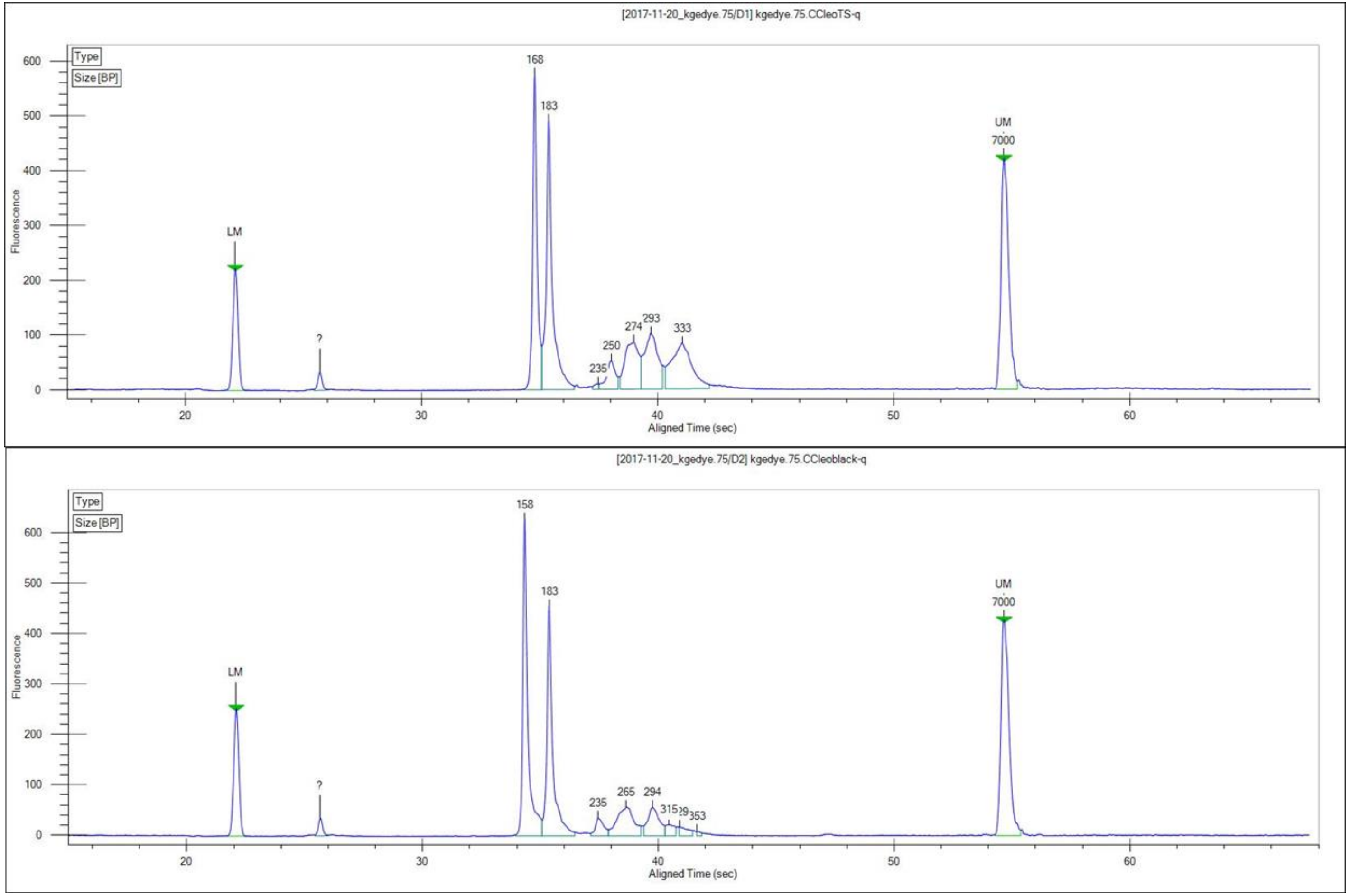

Figure 2: Electropherogram of two kittens from the same litter, Cleo TS and Cleo Black, showing allele amplicon size (bp) for locus F53. Large peaks represent the alleles. The lower and upper markers (LM and UM respectively) show the internal standards.

Table 2: The nineteen primer pairs used for genotyping, length of the repeating sequence, and the observed base pair (bp) range found for all Ponui Island and outgroup samples (n = 36).

Marker	Forward primer	Reverse primer	Repeat motif	Observed size (bp)	Source
FCA069	AATCACTCATGCACGAATGC	AATTTAACGTTAGGCTTTTTGCC	Dinucleotide	110-164	Lipinski et al. (2007)
FCA075	ATGCTAATCAGTGGCATTTGG	GAACAAAAATTCCAGACGTGC	Dinucleotide	140-185	Lipinski et al. (2007)
FCA105	TTGACCCTCATACCTTCTTTGG	TGGGAGAATAAATTTGCAAAGC	Dinucleotide	206-256	Lipinski et al. (2007)
FCA149	CCTATCAAAGTTCTCACCAAATCA	GTCTCACCATGTGTGGGATG	Dinucleotide	130-168	Lipinski et al. (2007)
FCA220	CGATGGAAATTGTATCCATGG	GAATGAAGGCAGTCACAAACTG	Dinucleotide	224-263	Lipinski et al. (2007)
FCA229	CAAACTGACAAGCTTAGAGGGC	GCAGAAGTCCAATCTCAAAGTC	Dinucleotide	167-209	Lipinski et al. (2007)
FCA310	TTAATTGTATCCCAAGTGGTCA	TAATGCTGCAATGTAGGGCA	Dinucleotide	138-200	Lipinski et al. (2007)
FCA441	ATCGGTAGGTAGGTAGATATAG	GCTTGCTTCAAAATTTTCAC	Tetranucleotide	139-178	Lipinski et al. (2007)
FCA678	TCCCTCAGCAATCTCCAGAA	GAGGGAGCTAGCTGAAATTGTT	Dinucleotide	190-255	Lipinski et al. (2007)
FCA723	TGAAGGCTAAGGCACGATAGA	CGGAAAGATACAGGAAGGGTA	Tetranucleotide	190-303	Menotti-Raymond et al. (2005)
FCA731	GATCCGTCTATCCATCTGTCC	ATGCTCCCCTGAAGCTGTAA	Tetranucleotide	297-423	Menotti-Raymond et al. (2005)
FCA733	GAAGATGTGGGATAGATACACCA	TGTTCAGAGGGCAAATTTCA	Tetranucleotide	200-267	Menotti-Raymond et al. (2005)
FCA736	ACCGAGCTCTGTTCTGGGTA	CAGACTGCACCACTGCCTAA	Dinucleotide	236-396	Menotti-Raymond et al. (2005)
FCA740	CACTTTCTGAAGGAGCAGCA	AACCAAATGGGAGTTTGTGG	Tetranucleotide	183-335	Menotti-Raymond et al. (2005)
FCA742	TCAATGTCTTGACAACGCATAA	AGGATTGCATGACCAGGAAC	Tetranucleotide	127-196	Menotti-Raymond et al. (2005)
FCA749	CTGGGGGAGGAGCTTACTTA	GATTTGAAAGAGGCCAGCAG	Tetranucleotide	158-279	Menotti-Raymond et al. (2005)
F53	GTTGGGAGTAGAGATCACCT	GAAAAAGACTCCTGCTTGCA	Tetranucleotide	149-269	Menotti-Raymond et al. (2005)
F85	TCTGGTCCTCACGTTTTCCT	ATGTCTGTATGAGATGCGGT	Dinucleotide	209-375	Menotti-Raymond et al. (2005)
F124	TGCTGGGTATGAAGCCTACT	ATTGCCTCAACTACCTAGGC	Tetranucleotide	199-302	Menotti-Raymond et al. (2005)

Analysis

Microsatellites are more likely to have a repeating sequence (dinucleotide or tetranucleotide) addition or deletion for the loci used in this study (Levinson & Gutman, 1987; Menotti-Raymond et al., 2005; Lipinski et al., 2007). For this reason, allele sizes were rounded up to the nearest 2 base pair (bp), or rounded to the nearest 4 bp addition or deletion for the loci (Table 2). The genotyping methods identified the length of the allele for the locus, but did not show the sequence. Therefore, a base pair addition or deletion would be detected, but not a base pair substitution.

Data was analysed using MICROCHECKER 2.2.3 (Van Oosterhout et al., 2004) to check for null alleles. Null alleles are alleles that do not amplify by PCR techniques to levels that can be detected, and the individual is misclassified as being homozygous for that locus (Dakin & Avise, 2004; Selkoe & Toonen, 2006). The presence of null alleles was identified for locus F85, and this locus was removed for subsequent analyses.

GENEPOP 4.7.0 (Rousset, 2008) was used to estimate deviance from Hardy-Weinberg equilibrium, which is used to determine whether a population has allele and genotype frequencies that have reached equilibrium (Frankham et al., 2010). It assumes the population has random mating, and a lack of mutation, migration, and selection (Frankham et al., 2010). Under those conditions, the population reaches equilibrium in allele/genotype frequencies after one generation and remains constant (Frankham et al., 2010). To test for Hardy-Weinberg equilibrium in the Ponui Island feral cat population the dememorization number, batch number, and iteration number were all set to 1000, following methods used by Cross (2016).

Expected and observed heterozygosity was calculated using GENEPOP. Expected heterozygosity is calculated based on the allele or genotype counts that are expected for a population under Hardy-Weinberg equilibrium using the assumptions described above, and is a measure of allele frequency ‘evenness’ (Raymond, 1995; Rousset, 2008; Hale et al., 2012). In contrast, observed heterozygosity is the allele or genotype frequency that is actually detected in the population (Raymond, 1995; Rousset, 2008; Frankham et al., 2010). A sample size of 25-30 individuals from a population is sufficient for describing population genetics from microsatellite data (when testing 5-9 loci) (Hale et al., 2012).

Allele richness and the inbreeding coefficient (F_{IS}) was estimated for the Ponui Island results using FSTAT 2.9.3 (Goudet, 2001). GENEPOP and FSTAT analysis was repeated using 10 loci (FCA441, FCA723, FCA731, FCA733, FCA736, FCA740, FCA742, FCA749, F124, and F53) to allow direct comparison with results obtained by Cross (2016) for a Southland feral cat population.

This was repeated again using 7 loci (FCA441, FCA723, FCA731, FCA733, FCA740, FCA742, and F124) for comparison with a study on a feral cat population in Hawaii (Hansen et al., 2008). These two populations were used because they used similar loci to those used in this study. The Southland population studied by Cross (2016) allows comparison to a New Zealand mainland feral cat population that is likely to have higher migration rates and less isolation compared to an island population.

To assess genetic structure against a null hypothesis of homogeneity I used STRUCTURE 2.3.4 (Pritchard et al., 2010) to estimate the optimal number of genetic clusters (K). STRUCTURE uses a Bayesian assignment approach to identify potential population genetic structure using allelic frequencies for a given set of loci among samples, and assigns the individuals to the set number of genetic clusters (Porras-Hurtado et al., 2013). The programme is often used to investigate variation in microsatellite data (Dutta et al., 2013; Koch et al., 2015; Steyer et al., 2016).

I tested for one to seven clusters using an admixture model with correlated allele frequencies using the microsatellite data from the outgroups and the Ponui Island feral cat population, with a location prior (LOCPRIOR) set to the population sites. This analysis was then repeated for Ponui Island cats only but testing for one to five clusters; a location prior was not included because all of the individuals were sampled from the same location. Both analyses were run for 10 iterations, with an MCMC length of 1,000,000 generations with a 10% burn-in of 100,000. Results from STRUCTURE were run through the web-based programme STRUCTURE HARVESTER (Earl & vonHoldt, 2012), where the most likely K value was selected using the “Evanno method” (Evanno et al., 2005). Results were averaged across the 10 iterations and analysed using CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007). Output graphs were generated using DISTRUCT 1.1 (Rosenberg, 2004).

For parentage, only litters or kittens where the mother was known were used. I manually matched up the alleles from the kittens with the known mother. To ensure that the known mother was correctly identified using genetic techniques, alleles from the kittens were also compared to the two other females in the site. This was to provide support for using this technique to estimate parentage. Paternity was manually determined by matching up alleles from the kitten with potential fathers. Due to the potential genotyping errors, one (for loci with a tetranucleotide repeat sequence) or two (for loci with a dinucleotide repeat sequence) allele deletion or addition either side of the kitten was used to match up with the potential parent. For example, if the kitten had an allele size of 200 for loci FCA740 (that has a tetranucleotide repeating sequence) then males with either 196, 200, or 204 alleles were classed as a match for that locus.

To avoid potential parentage mismatch due to possible null alleles being present, and because homozygous loci do not provide a lot of information on parentage (Coomber et al., 2007; Pemberton et al., 2008), only microsatellite markers that were polymorphic and had high levels of heterozygosity were used for the parentage analysis (n = 13). Loci where the mother or the kitten were homozygous were removed from the parentage analysis. The microsatellite markers FCA441, FCA742, FCA749, F53, F85, and F124 were not used.

The home ranges of the queens of the litters and the potential fathers were obtained from Chapter 2. The 100% MCP (Minimum Convex Polygon) was created for each cat using radio-telemetry and camera trap locations (Chapter 2). Home ranges were mapped using QGIS (geographical information system) where the queen's home range was overlapped with each potential father. This was used to determine the level of overlap between the queen and the males in the study site and determine whether the most likely father of the litter was the male that overlapped in home range the most with the queen. To determine whether the most likely fathers of the litters were the heaviest, body weights of the males were obtained from Chapter 2.

Results

All 35 domestic cats and one cheetah were successfully genotyped for 11 out of the 19 microsatellite loci tested; eight of the domestic cats had one locus that did not amplify, and six of the Ponui Island feral cats had two or more loci that did not amplify (Supplementary material: Table S6 & S7). The cats that had two or more loci that did not amplify had DNA extracted from hair (4), blood (1), and tissue (1). There was evidence of null alleles for F85 which was removed for the subsequent analyses.

Genetic diversity

The Ponui Island feral cat population had an average of 11.8 ± 5.2 (SD) alleles per loci, and a range of 3-21 for the 18 loci used in the analysis. Observed heterozygosity (H_o) (0.758) was lower than the expected heterozygosity (H_e) (0.829), suggesting that the Ponui Island population has a lack of heterozygotes across the 18 loci sampled. Indeed, the population had significant deviance from Hardy-Weinberg Equilibrium (p-value <0.005). The Ponui Island population sampled had a low inbreeding coefficient (F_{IS}) of 0.087.

When compared to Southland cats using the same loci (n = 10) the Ponui Island cats had higher allele diversity (mean number of alleles per loci) despite a smaller number of cats sampled. The Ponui Island feral cats had an average of 10 ± 5.9 (SD) alleles per locus whereas the Southland population had an average of 7.6 ± 0.7 alleles across the ten loci tested (Table 3). The Ponui Island results were more varied, shown by a higher standard deviation than the Southland population. There was a greater difference between the observed and the expected heterozygosity in the Ponui Island feral cat population compared to the Southland population (Table 3) (Cross, 2016), suggesting that there has been some loss of heterozygosity in the loci tested in the Ponui Island population.

The Ponui Island population had similar allelic diversity across seven loci tested to the Hawaii feral cat population (Table 3). However, similar to the Southland feral cat population, the Hawaii population has similar observed heterozygosity to the expected heterozygosity, whereas the Ponui Island population appears to have a deficiency of heterozygotes in the loci tested (Table 3).

Table 3: Comparison of genetic parameters across loci between the Ponui Island cats sampled, mainland Southland population analysed by Cross (2016), and Hawaii population analysed by Hansen et al. (2008). N = number of cats sampled, A = mean number of alleles per loci ± SD, H_o = observed heterozygosity, H_e = expected heterozygosity, F_{IS} = inbreeding coefficient.

Population (No. of loci)	N	A	H_o	H_e	F_{IS}
Ponui (10)[1]	29	10 ± 5.9	0.541	0.707	0.243
Southland (10)[1]	157	7.6 ± 0.7	0.71	0.77	0.081-0.101
Ponui (7)[2]	29	9.71 ± 4.4	0.581	0.731	
Hawaii (7)[2]	85	8.48 ± 3.2	0.703	0.736	

[1] Loci used: FCA441, FCA723, FCA731, FCA733, FCA736, FCA740, FCA742, FCA749, F124, and F53.

[2] Loci used: FCA441, FCA723, FCA731, FCA733, FCA740, FCA742, and F124.

Relationships between cats on Ponui Island and other populations

Bayesian analysis clustered the Ponui Island feral cat population separate to the four outgroups (Figure 3). The estimated optimal number of genetic clusters (K) based on the Evanno method (the change in likelihood score (Evanno et al., 2005)) was two. However, clustering of three groups placed the four outgroups separate to the Ponui Island population. A cluster of four did not separate any more individuals. The clustering of two groups separated some of the Ponui Island cats from each other. Adding a third cluster did not separate the Ponui Island individuals any more from each other, but placed the outgroups into a distinct cluster. This suggests that the Ponui Island feral cats are most genetically similar to each other, so there has been some separation from mainland domestic cats.

Two and three clusters were best supported by the Evanno method (Evanno et al., 2005) when only the Ponui Island cats were analysed, though with low support for both (Figure 4). Most of Cleo's kittens were clustered together along with some of the adult males on Ponui Island (Midnight, Mittens, Tui, and Snowball II). Clustering by three or four groups did not visually separate any more individuals (Figure 4), suggesting that the cats on Ponui Island are genetically similar. Due to the low values of delta K, and the clustering of the known related individuals (kittens from the same litters), it is most likely that the Ponui population forms only one cluster. However, the Evanno method is based on the change in likelihood score, meaning that testing for a cluster of one is not possible (Evanno et al., 2005; Porras-Hurtado et al., 2013).

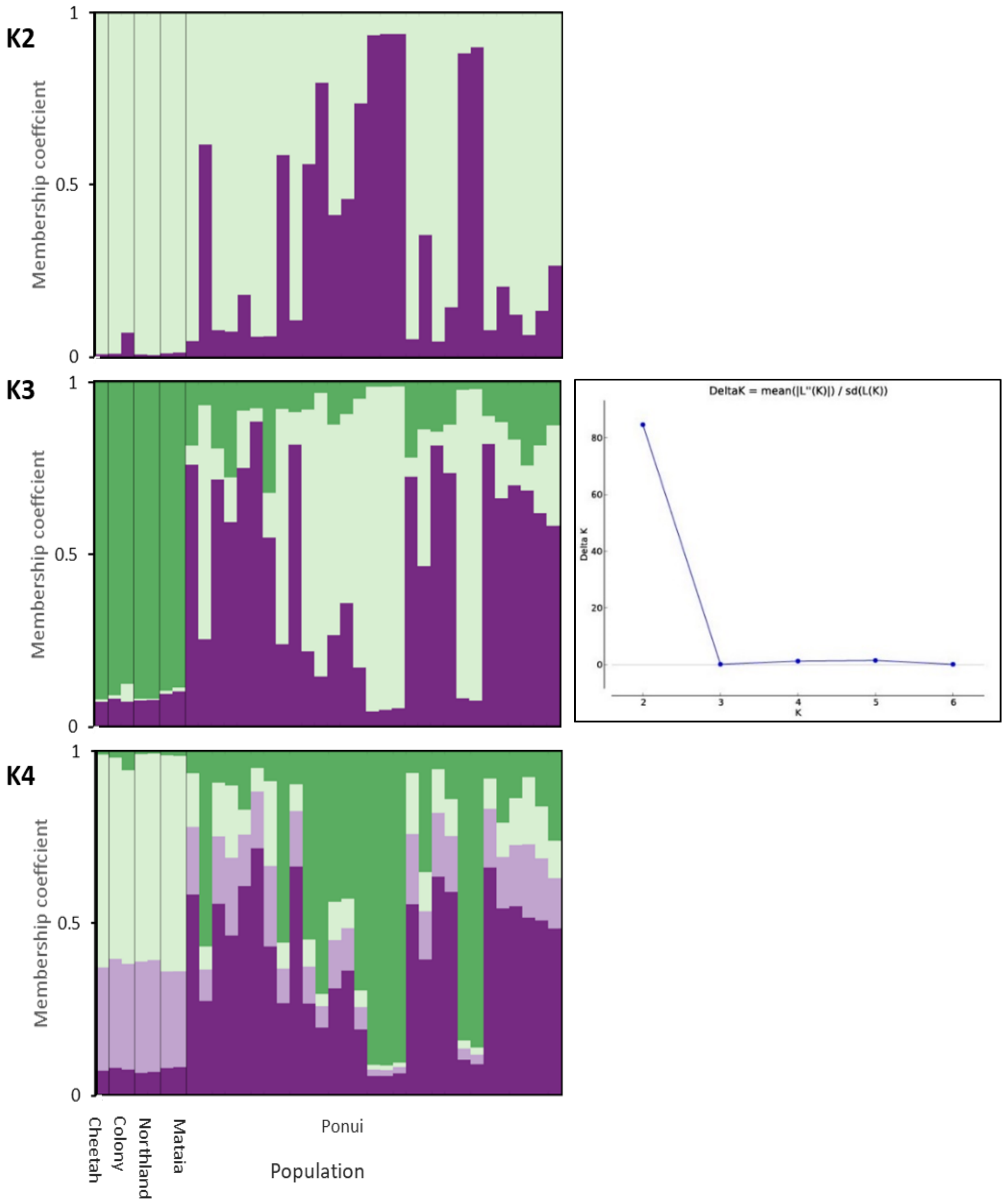

Figure 3: Genetic clusters based on microsatellite data (loci = 18) of individuals sampled from Ponui Island and four outgroup populations (see methods section for more details). Populations are separated by black vertical lines and labelled, and each column represents an individual in the population. Delta K values are shown for each cluster. The colours represent the assignment of the individual to a cluster. Individuals and populations that are genetically similar have a similar column structure in terms of colours.

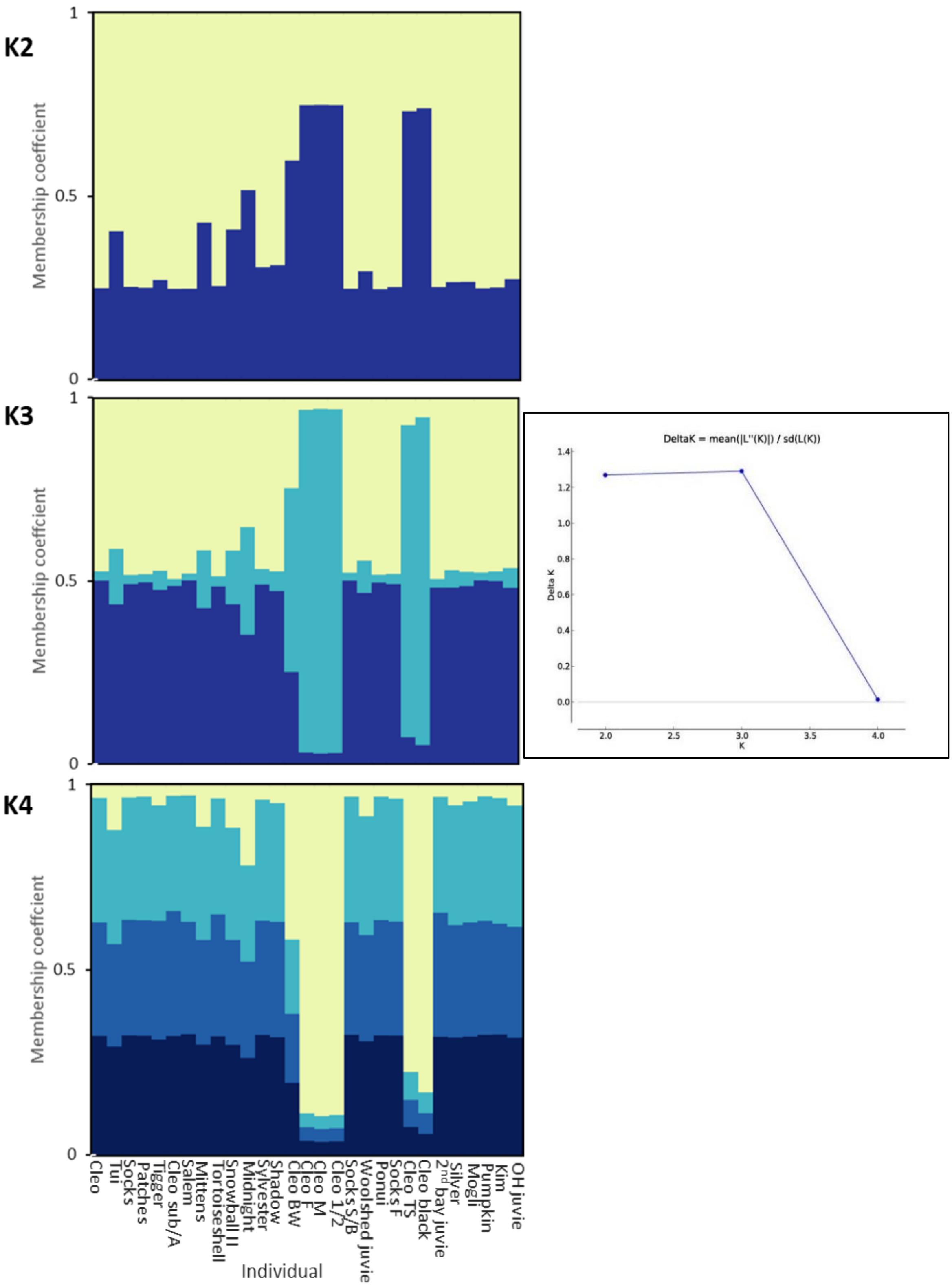

Figure 4: Clustering based on microsatellite data (loci = 18) of 29 individuals sampled from Ponui Island only. Individuals are represented by columns and are labelled. Delta K values are shown for each cluster tested. The colours represent assignment to the clusters. Individuals that are genetically similar have a similar column structure in terms of colours.

Parentage

Ten to eleven polymorphic loci were used for parentage analysis between Cleo, her litters, and the potential fathers. Allele match-up between the kittens and Cleo was for 9 and 11 loci. Ten to 12 loci were used for Socks, resulting in 9-11 alleles matching up between the kittens and Socks for the loci tested. Only four of Cleo's kittens had complete allele match-up for all tested loci, where one allele from each locus matched with Cleo. Socks and Cleo both had kittens that had alleles from 1-2 loci that did not match with the known mother (Table 4), that may be due to genotyping errors due to the degraded DNA. The known mother had more alleles match with the kittens than the other queens in the area (Supplementary material: Table S1-5).

The potential fathers all overlapped with the two queens (Figure 5), except for Snowball II because only one location was detected for him. Potential fathers were based on the male with the highest number of loci matched with the kitten. The fathers (Midnight, Mittens, and Tigger) of Cleo's kittens were the males that overlapped the most with her home range (Figure 5). Tigger, the father of one of Socks' kittens, was one of the males who overlapped Socks' home range the most (Figure 5). Midnight and Tigger were also the largest males in the study site, weighing over 4kg (Chapter 2).

The father of Cleo's first kitten from the November 2014 litter could not be determined (Table 4), due to three males having the same number of alleles matching with the sub-adult. Midnight was the father of Cleo's sub-adult from her second litter analysed (Shadow) and was also the father of all of the kittens in the consecutive litter.

Socks' litter was mostly fathered by a male feral cat that was not trapped during the study, due to the low match-up with the males sampled (Table 4). Tigger is likely to be the father of one of the kittens (Pumpkin).

Snowball II had high allele match-up with some of the kittens (Table 4), although it is uncertain whether he is the father. This male was not seen on camera traps until 6-9 months after the litters were born, and was not seen in an area overlapping Cleo's home range. As Snowball II was unlikely to be in the study site, it is more probable that Mittens is the true father of Cleo BW, and Tigger the father of the other two kittens. There is also the possibility that Simba may have been the father of some of the kittens as well, but this could not be tested because a genetic sample could not be obtained.

Table 4: Number of alleles matched up between the potential father and each kitten for Cleo's four litters and Socks' one litter. The mother column contains the number of alleles matched to the kitten. Kittens are split into the litter they belong to, with the litter labelled with the month and year they were born. Highlighted numbers are the most likely father for the kitten, where dark blue is the most likely, and light blue has the second highest allele match up. Highlighted numbers for Snowball II are when he has high match up with kittens, however, he was not seen in the study site until 6-9 months after the litters were born. – represents males that could not be the father as they died before the approximate date the female would have been mated with (approximately 63 days before birth (Prescott, 1973; Ogan & Jurek, 1997)). Because some of the DNA was degraded there were genotyping errors that meant that there was not a complete match-up in alleles at each locus between the mother and the kitten. Genotyping data was treated as binary, therefore a match in alleles at a locus between the kitten and the mother meant the other allele must have been inherited from the father. See Supplementary material that shows the allele match-ups between each kitten, mother, potential fathers, and the other females in the study site.

Litter	Kitten	Loci scored	Mother	Potential fathers						
			Cleo	Tigger	Salem	Mittens	Snowball II	Midnight	Sylvester	Tui
Nov 2014	Cleo sub/a	11	9	8	5	9	8	9	9	6
Apr 2015	Shadow	11	9	7	6	9	9	11	9	8
Feb 2016	Cleo F	11	10	8	7	10	9	11	8	-
	Cleo M	11	11	9	6	9	10	10	7	-
	Cleo 1/2	11	10	8	7	10	8	11	8	-
May 2016	Cleo BW	10	10	7	6	8	9	-	6	-
	Cleo TS	11	11	10	8	8	8	-	6	-
	Cleo black	10	10	8	5	5	8	-	5	-
			Socks	Tigger	Salem	Mittens	Snowball II	Midnight	Sylvester	Tui
Nov 2015	Socks S/B	11	9	6	6	6	7	6	6	-
	Socks F	12	11	5	5	4	5	5	5	-
	Pumpkin	10	9	8	4	3	4	6	4	-

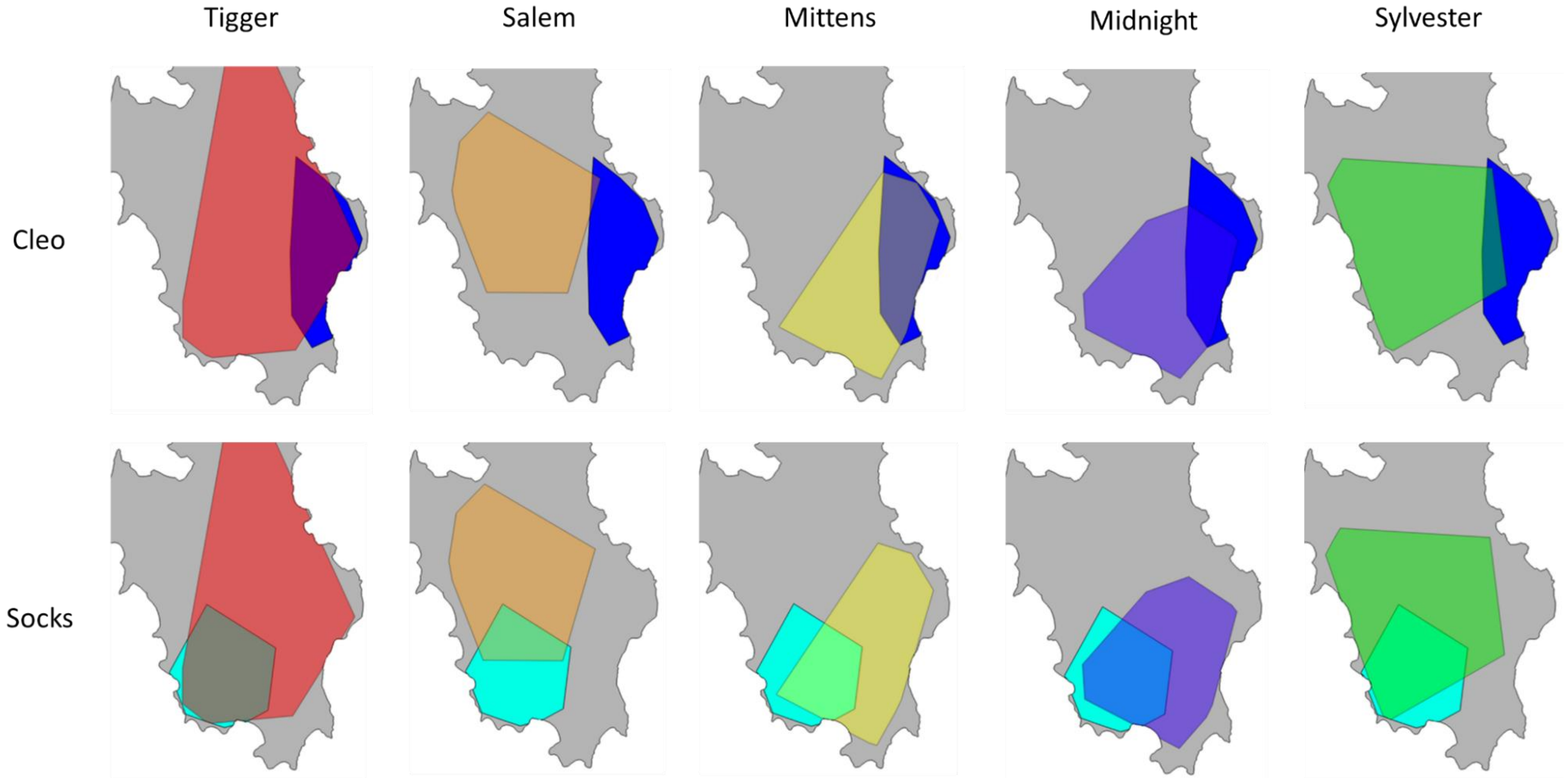

Figure 5: Overlap in home range (100% MCP) between Cleo (female) (dark blue area) and Socks (female) (light blue area) and the potential fathers of their litters. Locations for home ranges were from radio-telemetry and camera trap data collected in Chapter 2.

Discussion

Population genetics and diversity within the Ponui Island feral cats

The high level of genetic diversity (mean number of alleles per loci) and low inbreeding coefficient within the Ponui Island feral cat population was surprising due to the long establishment time of the population (introduced in the 1850s (Gillies & Fitzgerald, 2005)) and presumed prolonged isolation. Genetic parameters were expected to be similar to those observed by Pontier et al. (2005) from the Kerguelen population. The Kerguelen feral cat population has been established for at least 50 years, and is thought to have had a founding population of less than ten cats (Say et al., 2002b). Compared to the Ponui Island feral cat population, the Kerguelen population had lower observed and expected heterozygosity, and there was greater evidence for inbreeding in the Kerguelen population. This may be in relation to the geographical isolation of the Kerguelen population (Pontier et al., 2005), which likely started with a smaller founding population than Ponui Island. This comparison is tentative since Pontier et al. (2005) used different markers than those used for the Ponui Island population.

The Hawaiian feral cat population may allow for a better comparison than that from the Kerguelen (Pontier et al., 2005; Hansen et al., 2008). Though Hawaii is also geographically isolated, it is more accessible for people, resulting in a greater potential for multiple past introductions of cats. The proximity of Ponui Island to the mainland of New Zealand also permits the opportunity for intermittent introductions to the cat population. Allele richness across seven loci was similar between the Ponui Island population and the Hawaii population (Hansen et al., 2008) although there was a much greater difference between the observed and the expected heterozygosity in the Ponui Island population than that detected in the Hawaii population. Hansen et al. (2008) found similar genetic diversity between the Hawaii population compared to European domestic cats (Pierpaoli et al., 2003), suggesting a diverse group of founders or supplementation of the feral cat population with house cats. Similar results were obtained for the feral cat population on Dirk Hartog Island, Australia, with the most probable cause being multiple introductions of genetically diverse cats (Koch et al., 2014).

I found higher allele richness within the Ponui Island population compared to the Southland (Cross, 2016) and the Hawaii populations (Hansen et al., 2008). There is a chance that the higher level of allele richness within the Ponui Island population was due to degradation of the DNA extracted from the samples used in this study. Degraded samples or those with a small amount of DNA (normally collected non-invasively) can contain only a small amount of template DNA for amplification (Broquet & Petit, 2004; Pompanon et al., 2005). This can lead to genotyping errors through allele dropout (where one of the alleles is not amplified leading to a falsely identified homozygote) or where the whole allele is not amplified correctly and the allele is genotyped incorrectly (Broquet & Petit, 2004; Pompanon et al., 2005). These genotyping errors could result in either a higher number of alleles identified per locus, or the misidentification of homozygotes for some loci. Several studies have observed that alleles did not amplify in felid samples with low DNA concentrations or when using less than ideal samples for extraction (faecal and other non-invasive methods) (Taberlet et al., 1999; Bhagavatula & Singh, 2006; Coomber et al., 2007; Janečka et al., 2008; Wultsch et al., 2014).

Higher inbreeding coefficients and lower heterozygosity suggest that the Ponui Island population has received fewer introductions through time than the Southland population (Cross, 2016). This result was expected as island populations experience lower migration and gene-flow than mainland populations (Couvet, 2002; Frankham, 2008). Island populations tend to have less genetic variation due to small sizes of founder populations and subsequent bottle-necking (Frankham, 1997).

The high level of genetic diversity coupled with low heterozygosity of the feral cat population on Ponui Island may have occurred through three situations: 1) a founding event where the individual cats introduced to the island represented high genetic diversity; 2) many introductions of cats to the island when the population was first established; or 3) both. It is most likely that there were both multiple introductions during the founding stage and of very genetically diverse cats. Domestic cats that have been introduced from Europe into Australia, New Zealand, and Hawaii, have formed feral populations that have retained high genetic diversity (Hansen et al., 2008; Cross, 2016; Spencer et al., 2016), due to their multiple origins of domestication (Driscoll et al., 2007; Lipinski et al., 2008; Ottoni et al., 2017). The high genetic variation found in mainland New Zealand feral cats (Cross, 2016) also lends support for genetically diverse cats being introduced to an island.

I found that the population of Ponui Island feral cats was clustered separately to the cheetah and mainland populations of cats. These results suggest that there have been few recent introductions of other cats. This was supported by the Ponui Island cats clustering together, along with Silver, the farmers' 17-year-old pet cat, and low observed heterozygosity. There were no cats from the Ponui Island population that were very genetically different to the other cats. However, there may have been introductions of pet cats on to the island, and such individuals could have been neutered, or were outcompeted by the resident males for access to females, or may have died before breeding. Consequently, these possibilities cannot be ruled out.

Although the Ponui Island cats were separated into two clusters, it is most likely that the population only forms one cluster, yet this cannot be tested using the Evanno method (Evanno et al., 2005; Porras-Hurtado et al., 2013). The small size of Ponui Island (1770 ha) and the large home ranges of the feral cats studied (Chapter 2) also supports the hypothesis that there would only be one cluster. Feral cats have varied mating systems that change with densities (Say et al., 1999; Say et al., 2002a), though the males have home ranges that overlap those of many females, increasing a male's opportunities to mate with more than one female (Liberg et al., 2000; Say & Pontier, 2004). This is similar to females (Chapter 2), providing opportunity for multiple paternity within litters (Say et al., 1999). Given the large home range size, the varied mating system of feral cats, and the STRUCTURE clustering analysis, there is likely to be gene-flow between feral cats throughout the entire island. This provides support for the hypothesis that the feral cat population on Ponui Island forms only one genetic cluster.

Parentage of Ponui Island kittens

The results for paternity testing suggest that there may be a few male feral cats in the population that monopolise the females and mating opportunities. There was no evidence for two of the males (Salem and Tui) tested to be likely fathers of any of the kittens sampled. Male feral cats distribute themselves throughout an area based on many different resources, including the presence of female feral cats (Sandell, 1989; Liberg et al., 2000). The most likely fathers of the kittens for both females were the males that overlapped the most in home range with the females. By spending more time in a female's home range, the males are more likely to come in contact with the female when she is in oestrus, increasing their mating opportunities (Sandell, 1989).

The two heaviest males (Tigger and Midnight) were also the cats that monopolised the females and were the likely fathers of the majority of the kittens tested. Yamane et al. (1996) identified body weight as an important factor in determining the mating success of a free-living male cat. Large male cats tended to win more interactions against lighter males (Yamane et al., 1996). However, larger and heavier cats also tend to have larger home ranges (Chapter 2). Mittens was a smaller and lighter cat than some of the other males that did not breed, supporting the idea that home range overlap may be more important than size (body weight and head-body length) for mating opportunities.

The high allele match-up between Midnight and the kittens from the February 2016 litter means that the infanticidal male (Simba) was unlikely to be the father of the litter that he killed (Chapter

4). These paternity results provide tentative support for infanticide as a reproductive tactic used by male feral cats. Males may commit infanticide to increase their own reproductive output by bringing the female into oestrus sooner (Hrdy, 1979; Hausfater & Hrdy, 1984; Balme & Hunter, 2013). For this to be adaptive, the infanticidal male must be unrelated to the litter (Hausfater & Hrdy, 1984; Balme & Hunter, 2013). My results show that Midnight is likely to be the father of the litter. There is also the possibility that the litter after the infanticide event may have been fathered by Simba but, unfortunately, that could not be confirmed because the infanticidal male's DNA was not obtained.

There may be support for multiple paternity within two of the tested litters (Cleo May 2016 and Socks November 2015) that belonged to two different queens. Multiple paternity has been described in feral cat populations (Say et al., 1999; Say et al., 2002a), and in other felid species (Jewgenow et al., 2006; Gottelli et al., 2007). Say et al. (1999) found that the level of multiple paternity depended on the cat density, finding that the rural cat population that had a density of 234 cats/km^2 had low multiple paternity, whereas the urban cat population of 2091 cats/km^2 had high levels of multiple paternity. No evidence of multiple paternity was found in a feral cat population of less than 1.5 cats/km^2 (Say et al., 2002a). Therefore, the finding of potential multiple paternity in the Ponui Island population was unexpected since it had a density of 1.17 cats/km^2 (Chapter 2), suggesting that despite the lower density of feral cat populations compared to urban and rural cats, there may be multiple paternity within the litters.

The potential finding of multiple paternity within litters in this study is interesting, given the evidence for infanticide in this feral cat population. Multiple paternity can be used by females to confuse paternity and reduce the chances of their litter succumbing to infanticide (Wolff & Macdonald, 2004). Mating with many male cats and having litters with mixed paternity may confuse the males and reduce the number of litters they kill (Ebensperger, 1998; Wolff & Macdonald, 2004; Lyke et al., 2013). This assumes, however, that male feral cats are able to recognise their own young. Soares et al. (2006) found that a male jaguar (*Panthera onca*) killed two cubs that were fathered by him, demonstrating that paternal recognition may be low.

Multiple paternity may also be used as a tactic to increase the genetic diversity of the litter (Wolff & Macdonald, 2004). Murie (1995) found that the litters produced by female yellow-toothed cavy (*Galea musteloides*) (a type of rodent) that mated with more males had higher survival rates. However, there is little evidence for an increase in genetic diversity as a driving force for increased promiscuous behaviour in mammals (Wolff & Macdonald, 2004).

Since all of the males on the island were not sampled, there is a chance that there was not multiple paternity within the litters but rather that an unsampled male fathered all the kittens in the litter. The low heterozygosity and the evidence presented previously that this population of cats is likely to be closed demonstrates the difficulty in determining parentage within this population.

There were some limitations to this study, particularly in terms of having samples with degraded DNA, and using the fragment analyser machine (LabChip GX Touch HT) that has a lower resolution used compared to other studies (Say et al., 1999; Say et al., 2002a). This led to lower allele match-up between the known mother compared to other maternity and paternity studies using high fluorescent tagged primers, where there is complete allele match-up between the alleles of the offspring and the parents (Say et al., 1999; Say et al., 2002a). Despite this, the kittens had more alleles matched with the known mother than the other females in the study site (Supplementary material: Tables S1-5), providing some robustness to the methods used. As this was the case, I expected to be able to identify potential fathers of the litters using similar techniques, though with a degree of uncertainty.

Some of my parentage results suggested that a male (Snowball II), that was not seen in the area at the time, was the likely father of the kittens. The high allele match-up between Snowball II and the kittens may be due to high relatedness between the feral cats on Ponui Island. A high level of relatedness has been found in a population of cats exploiting a rubbish site (Denny et al., 2002). Ecological data are also important when used in combination with genetic data to rule out potential misidentification of paternity (Denny et al., 2002; Jones et al., 2010). However, it is possible that Snowball II could be the true father, as Say & Pontier (2004) found that some male cats were the father of litters from mothers, despite their home ranges not overlapping. This suggests that males made short trips out of their normal home range to find females (Say & Pontier, 2004).

Implications for management

The clustering of the Ponui Island cat population separate from the outgroups and the low observed heterozygosity supports the notion that control or eradication of feral cats on this island is likely to be successful. Koch et al. (2014) reached a similar conclusion after studying the feral cat population on Dirk Hartog Island, in Australia. This study provides a stepping stone and shows a need for the genetic analysis of other offshore island feral cat populations that would allow the identification of the islands with the highest potential success for an eradication or control programme (Robertson & Gemmell, 2004; Abdelkrim et al., 2005). These techniques should also be applied country-wide to mainland populations of feral cats in New Zealand to identify areas of gene-flow between populations, and to aid the identification of areas for eradication (Robertson & Gemmell, 2004).

The results from the paternity testing of the Ponui Island feral cat population have interesting implications for feral cat management. Infanticide may be used as a reproductive tactic by male feral cats to increase their own reproductive opportunities (Pontier & Natoli, 1999). The potential multiple paternity found within some of the litters tested may be a counterstrategy used by females to reduce the chances of their litters being killed by an infanticidal male cat (Wolff & Macdonald, 2004). Potential multiple paternity was found in two of the three litters tested in this study. Wolff & Macdonald (2004) found that multiple paternity may be related to infanticide within mammal populations, so my results may suggest that infanticide might occur more often than has been reported.

The male feral cats with larger home ranges and greater overlap with females tend to be the fathers of the litters. The males that are the largest and heaviest also have the larger home ranges (Chapter 2) and are the cats that are most likely to encounter traps and be removed from the population through control programmes (Gillies et al., 2007; Recio & Seddon, 2013). Rather than decreasing the reproductive rate of the population by removing the males that have higher reproductive rates, this removal could result in a reduction in competition for mating opportunities. This may then eliminate infanticide from the population, and potentially increase the number of kittens that survive to recruitment (Chapter 4). The results from this paternity testing provide more support for these management implications.

The population genetics of the Ponui Island feral cats investigated in this chapter suggests that the population is closed with no recent immigration. This suggests that the eradication of this population would be successful with a low risk of feral cats re-establishing on the island. The last aspect of feral cat ecology to be studied in the Ponui Island feral cat population to determine whether it should be controlled or not is their diet, which is investigated in the following research chapter (Chapter 6).

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Supplementary material

Table S1: Allele match-up between the known queen (Cleo) of the February 2016 litter, potential fathers, and the other females in the study site. Grey is a match up with Cleo, green is a potential father, and pink is other females.

	FCA 069	FCA 069	FCA 075	FCA 075	FCA 105	FCA 105	FCA 149	FCA 149	FCA 220	FCA 220	FCA 229	FCA 229	FCA 310	FCA 310	FCA 678	FCA 678	FCA 723	FCA 723	FCA 731	FCA 731	FCA 733	FCA 733	FCA 736	FCA 736	FCA 740	FCA 740
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238	196	228	324	388			250	362	196	280
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234	196	232	324	392			240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240	192	216	324	324			260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238	196	232	332	380			260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236	200	228	328	380			246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238	196	228	328	380			264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234	200	228	328	380			264	386	200	332
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234	192	208	324	380			248	360	204	320
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248	192	224	328	328			262	370	200	320
Cleo F	132	154	148	178	210	248	132	156	232	260	174	200			210	236	196	228	324	380			260	380	196	284
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238	196	228	324	388			250	362	196	280
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234	196	232	324	392			240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240	192	216	324	324			260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238	196	232	332	380			260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236	200	228	328	380			246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238	196	228	328	380			264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234	200	228	328	380			264	386	200	332
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234	192	208	324	380			248	360	204	320
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248	192	224	328	328			262	370	200	320
Cleo M	132	154	152	178	212	248	132	154	232	260	178	206			212	238	196	228	328	380			246	362	196	276
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238	196	228	324	388			250	362	196	280
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234	196	232	324	392			240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240	192	216	324	324			260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238	196	232	332	380			260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236	200	228	328	380			246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238	196	228	328	380			264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234	200	228	328	380			264	386	200	332
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234	192	208	324	380			248	360	204	320
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248	192	224	328	328			262	370	200	320
Cleo 1/2	132	152	152	180	210	248	132	154	230	258	178	208			212	238	196	228	328	380			260	382	196	280

Table S2: Allele match-up between the known queen (Cleo) of the May 2016 litter, potential fathers, and the other females in the study site. Grey is a match up with Cleo, green is a potential father, and pink is other females.

	FCA 069	FCA 069	FCA 075	FCA 075	FCA 105	FCA 105	FCA 149	FCA 149	FCA 220	FCA 220	FCA 229	FCA 229	FCA 310	FCA 310	FCA 678	FCA 678	FCA 723	FCA 723	FCA 731	FCA 731	FCA 733	FCA 733	FCA 736	FCA 736	FCA 740	FCA 740
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238	196	228	324	388			250	362		
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234	196	232	324	392			240	362		
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240	192	216	324	324			260	370		
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238	196	232	332	380			260	372		
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236	200	228	328	380			246	360		
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238	196	228	328	380			264	386		
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234	200	228	328	380			264	386		
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234	192	208	324	380			248	360		
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248	192	224	328	328			262	370		
Cleo BW	128	148	152	152	212	248	132	152	228	258	174	204			210	236	196	228	328	380			248	364		
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238	196	228	324	388			250	362	196	280
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234	196	232	324	392			240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240	192	216	324	324			260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238	196	232	332	380			260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236	200	228	328	380			246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238	196	228	328	380			264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234	200	228	328	380			264	386	200	332
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234	192	208	324	380			248	360	204	320
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248	192	224	328	328			262	370	200	320
Cleo TS	130	152	152	180	208	248	132	154	228	254	178	204			210	238	196	232	320	388			246	362	196	284
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238			324	388			250	362	196	280
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234			324	392			240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240			324	324			260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238			332	380			260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236			328	380			246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238			328	380			264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234			328	380			264	386	200	332
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234			324	380			248	360	204	320
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248			328	328			262	370	200	320
Cleo black	132	154	152	180	208	246	132	154	230	256	176	204			212	238			316	384			250	360	196	284

Table S3: Allele match-up between the known queen (Cleo) of the kitten (Cleo sub/a), potential fathers, and the other females in the study site. Grey is a match up with Cleo, green is a potential father, and pink is other females.

	FCA 069	FCA 069	FCA 075	FCA 075	FCA 105	FCA 105	FCA 149	FCA 149	FCA 220	FCA 220	FCA 229	FCA 229	FCA 310	FCA 310	FCA 678	FCA 678	FCA 723	FCA 723	FCA 731	FCA 731	FCA 733	FCA 733	FCA 736	FCA 736	FCA 740	FCA 740
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238	196	228	324	388			250	362	196	280
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234	196	232	324	392			240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240	192	216	324	324			260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238	196	232	332	380			260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236	200	228	328	380			246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238	196	228	328	380			264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234	200	228	328	380			264	386	200	332
Tui	128	150	150	178	212	252	134	154	228	256	172	200			208	238	196	232	320	388			250	360	208	288
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234	192	208	324	380			248	360	204	320
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248	192	224	328	328			262	370	200	320
Cleo sub/a	134	160	150	184	212	256	134	160	234	260	178	208			212	242	196	228	328	380			240	374	200	328

Table S4: Allele match-up between the known queen (Cleo) of the kitten (Shadow), potential fathers, and the other females in the study site. Grey is a match up with Cleo, green is a potential father, and pink is other females.

	FCA 069	FCA 069	FCA 075	FCA 075	FCA 105	FCA 105	FCA 149	FCA 149	FCA 220	FCA 220	FCA 229	FCA 229	FCA 310	FCA 310	FCA 678	FCA 678	FCA 723	FCA 723	FCA 731	FCA 731	FCA 733	FCA 733	FCA 736	FCA 736	FCA 740	FCA 740
Cleo	132	160	152	186	208	248	134	158	228	254	178	210			214	238	196	228	324	388			250	362	196	280
Tigger	134	160	146	176	210	248	130	152	228	256	178	204			210	234	196	232	324	392			240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202			212	240	192	216	324	324			260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204			210	238	196	232	332	380			260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202			210	236	200	228	328	380			246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202			212	238	196	228	328	380			264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202			210	234	200	228	328	380			264	386	200	332
Tui	128	150	150	178	212	252	134	154	228	256	172	200			208	238	196	232	320	388			250	360	208	288
Patches	132	156	148	178	210	246	142	142	234	262	174	202			210	234	192	208	324	380			248	360	204	320
Socks	130	152	150	178	210	248	136	160	234	264	174	202			220	248	192	224	328	328			262	370	200	320
Shadow	128	152	150	178	212	250	134	158	230	258	176	204			212	238	192	224	328	380			264	386	204	320

Table S5: Allele match-up between the known queen (Socks) of the November 2015 litter, potential fathers, and the other females in the study site. Grey is a match up with Socks, green is a potential father, and pink is other females. Blank cells represent alleles that did not amplify for that sample at the locus.

	FCA 069	FCA 069	FCA 075	FCA 075	FCA 105	FCA 105	FCA 149	FCA 149	FCA 220	FCA 220	FCA 229	FCA 229	FCA 310	FCA 310	FCA 678	FCA 678	FCA 723	FCA 723	FCA 731	FCA 731	FCA 733	FCA 733	FCA 736	FCA 736	FCA 740	FCA 740
Socks	130	152	150	178	210	248	136	160	234	264	174	202	154	180	220	248	192	224					262	370	200	320
Tigger	134	160	146	176	210	248	130	152	228	256	178	204	170	188	210	234	196	232					240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202	182	190	212	240	192	216					260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204	174	184	210	238	196	232					260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202	174	182	210	236	200	228					246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202	174	184	212	238	196	228					264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202	178	184	210	234	200	228					264	386	200	332
Patches	132	156	148	178	210	246	142	142	234	262	174	202	152	166	210	234	192	208					248	360	204	320
Cleo	132	160	152	186	208	248	134	158	228	254	178	210	170	170	214	238	196	228					250	362	196	280
Socks S/B	130	156	150	184	210	252	138	160	236	264	178	206	142	166	224	256	196	228					238	376	204	324
Socks	130	152	150	178	210	248	136	160	234	264	174	202	154	180	220	248	192	224			212	268	262	370	200	320
Tigger	134	160	146	176	210	248	130	152	228	256	178	204	170	188	210	234	196	232			244	244	240	362	196	276
Salem	126	148	144	172	212	250	140	164	232	260	172	202	182	190	212	240	192	216			216	240	260	370	192	276
Mittens	128	148	150	178	214	252	132	154	236	264	176	204	174	184	210	238	196	232			212	240	260	372	192	276
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202	174	182	210	236	200	228			212	236	246	360	196	280
Midnight	130	150	150	178	210	248	134	156	228	256	174	202	174	184	212	238	196	228			208	260	264	386	200	332
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202	178	184	210	234	200	228			208	232	264	386	200	332
Patches	132	156	148	178	210	246	142	142	234	262	174	202	152	166	210	234	192	208			240	240	248	360	204	320
Cleo	132	160	152	186	208	248	134	158	228	254	178	210	170	170	214	238	196	228			244	244	250	362	196	280
Socks F	132	160	150	184	208	252	136	158	230	258	178	206	156	190	220	246	196	240			216	244	254	378	200	332
Socks	130	152	150	178	210	248			234	264	174	202	154	180	220	248	192	224			212	268	262	370		
Tigger	134	160	146	176	210	248			228	256	178	204	170	188	210	234	196	232			244	244	240	362		
Salem	126	148	144	172	212	250			232	260	172	202	182	190	212	240	192	216			216	240	260	370		
Mittens	128	148	150	178	214	252			236	264	176	204	174	184	210	238	196	232			212	240	260	372		
Snowball II	130	150	150	180	218	254			234	262	172	202	174	182	210	236	200	228			212	236	246	360		
Midnight	130	150	150	178	210	248			228	256	174	202	174	184	212	238	196	228			208	260	264	386		
Sylvester	130	150	142	168	218	254			230	258	174	202	178	184	210	234	200	228			208	232	264	386		
Patches	132	156	148	178	210	246			234	262	174	202	152	166	210	234	192	208			240	240	248	360		
Cleo	132	160	152	186	208	248			228	254	178	210	170	170	214	238	196	228			244	244	250	362		
Pumpkin	130	164	146	178	208	246			230	256	174	206	142	168	208	246	196	208			216	256	258	362		

Table S6: Alleles (bp) for ten loci tested for the outgroups and the Ponui Island cats (n = 36). -9 represents alleles that did not amplify.

	FCA 069	FCA 069	FCA 075	FCA 075	FCA 105	FCA 105	FCA 149	FCA 149	FCA 220	FCA 220	FCA 229	FCA 229	FCA 310	FCA 310	FCA 441	FCA 441	FCA 678	FCA 678	FCA 723	FCA 723
Cheetah	124	144	142	166	212	248	142	166	224	246	168	194	174	184	140	140	190	214	200	212
Colony Male	110	128	146	172	212	248	138	158	238	264	180	206	138	166	176	176	220	246	224	288
Colony Female	110	130	152	178	214	252	132	150	236	264	176	204	174	184	176	176	212	238	200	212
Northland Female	122	146	150	178	206	242	140	166	236	264	178	204	142	168	168	168	210	236	192	284
Northland Male	126	148	146	174	216	254	142	168	234	264	174	202	146	160	172	180	214	238	204	304
Mataia Female	124	146	150	180	208	244	140	166	234	260	176	202	156	182	176	176	210	236	224	232
Mataia Male	130	152	148	176	214	250	140	166	234	262	178	204	154	180	168	168	210	236	192	204
Cleo	134	160	152	186	208	248	136	158	228	254	180	210	142	170	172	172	214	240	196	228
Tui	128	150	150	178	212	252	134	154	228	256	172	200	182	190	164	164	208	238	196	232
Socks	130	152	150	178	210	248	136	160	234	264	174	202	154	188	168	168	220	248	192	224
Patches	132	156	148	178	210	246	142	142	234	262	174	202	152	166	164	164	210	234	192	208
Tigger	134	160	146	176	210	248	130	152	228	256	178	204	170	188	168	168	210	234	196	232
Cleo sub/A	134	160	150	184	212	256	134	160	234	260	178	208	154	170	168	168	212	242	196	228
Salem	126	148	144	172	212	250	140	164	232	260	172	202	182	190	164	164	212	240	192	216
Mittens	128	148	150	178	214	252	132	154	236	264	176	204	174	184	164	164	210	238	196	232
Tortoiseshell	128	152	150	178	216	254	132	168	234	262	172	204	140	170	168	168	212	240	196	224
Snowball II	130	150	150	180	218	254	134	156	234	262	172	202	174	182	164	164	210	236	200	228
Midnight	130	150	150	178	210	248	134	156	228	256	174	202	174	184	168	168	212	238	196	228
Sylvester	130	150	142	168	218	254	140	164	230	258	174	202	178	184	164	164	210	234	200	228
Shadow	128	152	150	178	212	250	134	158	230	258	176	204	144	174	164	164	212	238	192	224
Cleo BW	128	148	150	150	212	250	132	152	230	258	174	204	176	186	168	168	210	236	196	228
Cleo F kit 3	132	154	148	178	210	248	132	156	232	260	174	200	176	186	168	168	210	236	200	228
Cleo M kit 2	132	154	150	178	212	248	132	154	232	260	178	206	176	186	168	168	212	238	200	228
Cleo ½ kit 1	132	152	152	180	210	248	132	154	230	258	180	208	174	186	168	168	212	238	200	228
Socks S/B	130	156	150	184	210	252	138	160	236	264	178	208	142	166	168	168	224	256	196	228
Woolshed juvie	130	156	150	180	208	250	134	160	232	260	176	206	158	182	164	164	214	244	196	236
Ponui	132	158	146	176	208	250	130	156	230	260	178	210	156	180	168	168	212	242	196	256
Socks F	132	160	150	184	208	252	136	158	230	258	178	206	156	190	168	168	220	246	196	240
Cleo TS	130	152	150	180	208	248	132	154	228	254	176	204	176	186	168	168	210	238	196	232
Cleo black	132	154	152	180	208	246	132	154	230	256	176	204	174	184	168	168	212	240	200	200
2nd bay juvie	134	150	148	180	212	256	142	166	230	262	174	204	140	170	168	168	212	242	192	224
Silver	132	154	150	184	214	254	-9	-9	234	262	180	208	142	172	168	168	212	244	192	228
Mogli	134	158	140	140	210	250	-9	-9	228	258	176	204	142	168	168	168	220	248	196	228
Pumpkin	130	164	146	178	208	246	134	134	230	256	174	206	142	168	172	172	208	246	196	208
Kim	136	160	142	172	214	254	130	156	232	260	180	208	158	180	164	164	210	238	196	228
OH juvie	128	154	148	178	-9	-9	-9	-9	230	256	176	208	140	164	172	172	214	244	196	224

Table S7: Alleles (bp) for nine loci tested for the outgroups and the Ponui Island cats (n = 36). -9 represents alleles that did not amplify.

	FCA 731	FCA 731	FCA 733	FCA 733	FCA 736	FCA 736	FCA 740	FCA 740	FCA 742	FCA 742	FCA 749	FCA 749	F53	F53	F85	F85	F124	F124
Cheetah	352	424	212	212	238	352	184	336	128	184	160	248	268	268	292	292	200	208
Colony Male	336	336	212	244	246	284	204	284	136	196	260	268	148	240	262	318	200	304
Colony Female	336	336	208	228	262	380	196	276	136	148	264	280	148	180	260	376	216	296
Northland Female	296	324	224	264	272	396	192	308	144	160	260	260	-9	-9	266	286	236	300
Northland Male	328	336	216	240	264	374	200	316	148	184	260	260	156	156	-9	-9	232	296
Mataia Female	328	328	200	220	262	372	204	324	136	148	252	264	168	176	266	284	220	280
Mataia Male	328	380	200	200	264	382	196	292	144	156	260	260	168	168	266	266	228	288
Cleo	324	392	240	240	250	362	200	280	156	160	276	276	-9	-9	276	292	208	236
Tui	320	388	244	244	250	360	208	288	160	160	272	272	160	160	266	266	220	220
Socks	328	328	212	268	262	370	200	320	152	160	268	268	-9	-9	288	288	216	216
Patches	324	380	240	240	248	360	204	320	152	152	-9	-9	-9	-9	288	288	216	240
Tigger	324	392	244	244	240	362	196	276	160	160	264	264	160	160	270	270	212	212
Cleo sub/A	328	380	216	244	240	374	200	328	156	160	264	264	160	188	262	274	212	236
Salem	324	324	216	240	260	370	192	276	160	160	260	260	-9	-9	270	290	220	220
Mittens	332	380	212	240	260	372	192	276	160	160	268	268	184	184	262	262	216	216
Tortoiseshell	328	380	220	244	240	376	200	328	160	160	264	264	-9	-9	290	290	220	220
Snowball II	328	380	212	236	246	360	196	280	160	160	268	268	168	180	288	288	212	212
Midnight	328	380	208	260	264	386	200	332	160	160	268	268	-9	-9	272	272	204	204
Sylvester	328	380	208	232	264	386	200	332	160	160	268	268	184	184	272	272	212	212
Shadow	328	380	212	240	264	386	204	320	152	160	268	268	160	184	262	290	208	224
Cleo BW	328	380	204	228	248	364	192	192	160	160	268	268	160	188	260	288	204	216
Cleo F kit 3	328	380	228	228	260	380	196	284	160	160	272	272	160	160	288	288	204	212
Cleo M kit 2	328	380	224	248	246	362	196	276	152	160	268	268	160	160	272	288	204	204
Cleo ½ kit 1	328	380	220	248	260	382	196	280	152	152	268	268	160	160	288	288	204	204
Socks S/B	324	380	228	228	238	376	204	324	156	164	268	268	-9	-9	-9	-9	220	220
Woolshed juvie	324	380	220	248	250	382	204	324	164	164	268	268	160	188	274	274	204	204
Ponui	328	380	220	256	238	372	204	328	152	160	260	260	172	188	274	292	216	216
Socks F	328	380	216	244	254	378	200	336	156	160	268	268	184	184	292	292	204	216
Cleo TS	320	388	248	248	246	362	200	284	156	160	272	272	168	184	270	270	204	224
Cleo black	316	384	220	248	250	360	196	284	160	160	272	272	160	184	270	270	204	216
2nd bay juvie	-9	-9	216	244	264	372	204	204	160	160	-9	-9	-9	-9	262	268	216	216
Silver	328	384	216	248	260	372	200	332	160	160	268	268	164	172	274	292	220	220
Mogli	328	380	212	212	246	366	-9	-9	152	160	-9	-9	-9	-9	-9	-9	220	220
Pumpkin	-9	-9	216	256	258	362	212	212	160	160	-9	-9	-9	-9	-9	-9	-9	-9
Kim	328	380	220	248	236	370	200	336	160	160	268	268	164	188	264	292	208	220
OH juvie	-9	-9	220	248	254	378	-9	-9	160	160	268	268	-9	-9	-9	-9	212	224

Chapter 6 – Feral cats on a rat-dominated offshore island: Season and sex differences in diet and impact on brown kiwi

Plate 6: Photo of kereru (*Hemiphaga novaeseelandiae*) prey remains from feral cat depredation in Kauri Bush gully.

Introduction

The population genetic analysis in Chapter 5 showed that the Ponui Island population is most likely genetically isolated, and eradication of this population would be possible with low chances of reinvasion. Dietary analysis is required to determine whether the Ponui Island cats are affecting the native species co-existing on the island, or if the cats are mainly sustained by the rat population that reached high densities.

New Zealand's terrestrial fauna evolved in isolation from mammalian predators, leading to mammal-naïve native species that display ineffective anti-predator behaviour towards these alien invasive species (Holdaway, 1989; Duncan & Blackburn, 2004; Sih et al., 2010). The introduction of mammalian predators into New Zealand thus caused rapid population declines in native species often leading to extinction. Invasive species remain one of the biggest threats to native fauna (Gurevitch & Padilla, 2004; Doherty et al., 2016), and their elimination is a high priority for many species conservation plans (Parkes & Murphy, 2003).

The magnitude of the threat presented by invasive species to native fauna and flora has led to an ambitious New Zealand Government plan (2016) termed Predator Free 2050 (PF2050), to eradicate predators from the country by 2050. Target species include mustelids (*Mustela* spp.: stoats, weasels, and ferrets), rats (*Rattus* spp.: ship, Norway, and Polynesian) and possums (*Trichosurus vulpecula*) (New Zealand Government, 2016). However, feral cats are not included in this long-term goal, possibly reflecting public opposition to lethal feral cat control (Farnworth et al., 2011; Rouco et al., 2017) (Chapter 1). Feral cats have a higher consumption of birds in areas where rats are absent (e.g. Herekopare Island) (Fitzgerald & Veitch, 1985), meaning that the proposal to remove rats from ecosystems where they coexist with feral cats could lead to prey switching of feral cats to birds and reptiles, and greater negative effects on native fauna.

In New Zealand, feral cats may play a part in regulating the numbers of other invasive pest species such as rodents and rabbits (*Oryctolagus cuniculus*), because these species frequently occur in the stomach contents or scats of feral cats (Table 1) (Chapter 1). The prey consumed differs across locations, with rabbits and hares (*Lepus europaeus*) occurring more frequently in the diet of cats studied in the South Island than those in the North Island (Gillies & Fitzgerald, 2005). Rats, birds, and invertebrates have been found to be eaten in similar proportions in both mainland and offshore islands (Table 1). Thus, differences in diet throughout New Zealand seems to be due to differences in prey availability, with many of the areas studied sustaining a range of introduced mammalian species that are available to feral cats, in addition, to native species.

There have been very few studies that have assessed seasonal diet in feral cats in New Zealand. On the mainland, Borkin (1999) found that cats preyed upon lagomorphs during peak rabbit breeding season, while Fitzgerald & Karl (1979) found no seasonal difference in diet. Studies on New Zealand offshore islands have not assessed seasonal differences in diet, and have low sample sizes (Table 1). A review on feral cat diets on islands worldwide suggests that feral cats feed on a variety of organisms, and that there are significant differences in diet not only between islands, but also between seasons (Bonnaud et al., 2011). Bonnaud et al. (2011) suggested that the presence of introduced prey species on islands may result in large feral cat populations, leading to higher depredation rates on native species. The synchronised responses in densities between the predator and the main prey can lead to hyper-predation on other species (Chapter 1). For example, Sweitzer et al. (2003) found that there was a corresponding increase in population size of puma (*Puma concolor*) following an increase in mule deer (*Ocodoileus hemionus*), their main prey. A decline in deer numbers led to the puma depredating porcupines (*Erethizon dorsatum*), almost leading to the extinction of porcupines (Sweitzer et al., 2003). This example demonstrates how diet flexibility can lead to unsustainable depredation rates on secondary prey (Sweitzer et al., 2003). Because feral cats can have large impacts on native fauna on islands (Bonnaud et al., 2011; Medina et al., 2011) and seasonality has not been studied before, I investigated whether there was a seasonal difference in feral cat diet on an offshore island in New Zealand where there are native bird species, and high densities of rodents.

Previous studies investigating feral cat diet had communities that included other mammalian predators that could compete with feral cats, thereby reducing the availability of prey species to cats (Fitzgerald & Karl, 1979; Bramley, 1996; King et al., 1996; Alterio & Moller, 1997; Murphy et al., 2004). Competition amongst predators can also lead to resource partitioning with predators coexisting in the same space having dietary separation to reduce interspecific competition (Schoener, 1974; Kitchen et al., 1999). The proposal to remove feral cat competitors (mustelids) from New Zealand with PF2050 would lead to feral cats being the top predator in ecosystems, which may result in a change in diet from reduced competition. Therefore, I wanted to investigate feral cat diets where there were fewer introduced mammalian prey species available, and where feral cats were the top predator.

Feral cats have been the cause of decline for many native bird species in New Zealand, and in at least one case caused the extinction of a species (Stephens Island wren *Traversia lyalli*

(Galbreath & Brown, 2004)). Feathers from the critically endangered kakapo (*Strigops habroptilus*) were found in 5% of feral cat scats collected from Stewart Island (Karl & Best, 1982; IUCN, 2017), and petrels were the most common prey identified in scats and stomachs of feral cats on Herekopare Island (Fitzgerald & Veitch, 1985). Of particular interest in this study is the impact of feral cats on kiwi. The site for this study, Ponui Island, sustains one of the highest densities (1 kiwi/ha) of North Island brown kiwi (*Apteryx mantelli*) in New Zealand (Cunningham et al., 2007). Depredation by introduced mammalian predators is one of the main contributors to the decline in kiwi spp. numbers nation-wide (McLennan et al., 1996). McLennan et al. (1996) found that depredation by stoats and feral cats were the main cause of mortality in brown kiwi chicks. On Ponui Island, 29% of brown kiwi chicks monitored in 2010-12 died from feral cat depredation (Wilson, 2013), a much higher depredation rate than that reported on the mainland (5%) where stoats are present (McLennan et al., 1996).

There is also the possibility that there is a sex bias in the scats that are collected for diet analysis, as demonstrated in jaguars (*Panthera onca*) where significantly more male scats were detected than females (Palomares et al., 2012). A sex bias in scats collected would be particularly interesting if there are sex differences in feral cat diet. Given the sexual dimorphism in body size in felids, I would expect males to be able to kill and eat larger birds. There have been only four studies that have looked at the influence of sex on the diet of feral cats. Pascoe (1995) found that female cats in the McKenzie Basin may prey upon smaller prey, whereas Borkin (1999) and Gillies (1998) found no difference in overall diet between the sexes for feral cat populations in southern (Canterbury, Otago, and Southland) and Northland regions respectively. Middlemiss (1995) found that more “small” prey species were consumed by male feral cats than females in a Central Otago population.

Summarising, the main aim of this study was to determine the diet of feral cats in an area where they are the top mammalian predator, and the available prey includes rodents and a thriving population of brown kiwi, and to use the data to answer the following questions: 1) How many brown kiwi were likely to be consumed by feral cats in the absence of the main mainland predator, the stoat?; 2) Was there a seasonal difference in diet?; 3) Was there a sex bias in the scats that were collected for dietary analysis?; and 4) Were there dietary differences between sexes?

Table 1: Percentage of occurrence of food items of feral cats studied on New Zealand's mainland and offshore islands. *Studies had both gut contents and scat analysis, but only results from gut contents are shown here as sample size of scat analysis was not stated. TR = traces found. Order = frequency of occurrence has been given for each invertebrate order in the study. Refuse and carrion have not been included.

Citation	Location	Sample Size	Gut or scat	Possum	Lagomorph Spp.	Rabbit	Hare	Rodent Spp.	Rat	Mouse	Hedgehog	Mammal Spp.	Stoat	Bird Spp.	Lizard Spp.	Gecko	Skink	Frog	Invert. Spp.	Freshwater crayfish	Eel & fish Spp.
Alterio & Moller (1997)	Coastal Southland & Otago	43	Gut	2	76					26	11			33		2			Order		
Alterio et al. (1996)	Central Otago	83	Scat	3		34			13	80				30							
Baker (1989)	Central Otago	34	Gut*			53				18	3			56	12				44		
Borkin (1999)	Canterbury, Otago & Southland	158	Gut		61				3	5	2			36		3	23	<1	44		
Bramley (1996)	East Cape	9	Gut		56							22		44					44		
Dilks (1979)	Campbell Is.	20	Scat						95					35					60		
Dowding et al. (1999)	Motuihe Is.	61	Scat			90			3	3				20	2				44		
Fitzgerald & Karl (1979)	Orongorongo Valley	677	Scat	19		22			50	43			<1	12	<1				57	3	3
Fitzgerald & Veitch (1985)	Herekopare Is.	30	Gut*											93					47		

Fitzgerald et al. (1991)	Raoul Is.	57	Gut*						86					35					58		
Gibb et al. (1978)	Kourarau	many	Scat			77			Tr	2	Tr		Tr	4		Tr			9		
Gibb et al. (1969)	Te Wharau	68	Scat			68	4		3	29				59		4			10		
Harper (2002)	Stewart Is.	219	Scat	2					83					27	1				Order		
Harper (2010)	Auckland Is.	40	Scat							53				78					5		5 squid
Karl & Best (1982)	Stewart Is.	229	Scat	5					93					44			24		36		
Gillies & Fitzgerald (2005)	Northland	264	Gut	7	30	10			12	22	2	3		19	<1		<1	1	10	<1	2
Gillies & Fitzgerald (2005)	Mackenzie Basin	133	Gut			81			2	4				14			3		8		
King et al. (1996)	King Country	13	Gut	23		23			23	62		8		23					69		
Langham (1990)	Hawke's Bay	361	Scat	5	1				20	50				30					Order		
Marshall (1961)	Little Barrier Is.	94	Scat						39					71					32		
Middlemiss (1995)	Central Otago	25	Gut*		42			15			4			23		8	58		54		
Murphy et al. (2004)	Mackenzie Basin	375	Gut		70				4	9	1			47	30				36		

Pascoe (1995)	Mackenzie Basin	45	Gut*	2	69		2	42	2	13	7	22	42		
Pierce (1987)	Mackenzie Basin	358	Scat		86			3	1	9	<1	13	20		
Ryan (1994)	Mackenzie Basin	57	Scat			88	5	19		7		7	33		2

Methods

Collection

Four hundred and thirty-two scats and casts (regurgitates) were collected opportunistically throughout South Ponui Island from January 2014 - April 2016. For simplicity, the term 'scats' will refer to both scats and casts as they were analysed together. Cat scats were distinguished from farm dog scats by size and shape (Triggs et al., 1984). Seasons were defined as: summer (December – February), autumn (March – May), winter (June – August), and spring (September – November). For each scat the following was recorded on a label that was attached to the bagged sample: date, site, location in the site, habitat type, substrate the scat was found on, approximate age (how fresh it was), and any comments. The location of the scat in relation to a trail (trail location) was also noted as follows: scat was either found on a trail, just off (within one metre of a trail), or off a trail (more than one metre from a trail or there was no trail in the area). All scats were picked up regardless of condition or dryness. Samples were stored at -20^{o}C until analysis.

In addition to scats, cats that were found dead in the study area (n = 2) during the study had their stomach and intestines removed and stored in 99% ethanol for storage until analysis. Due to the small sample sizes from gut content analysis, these samples were included into the scat analysis.

Sorting and ID

Scats: In the lab the samples were defrosted (if frozen) prior to sorting. Samples were washed with hot water into a gradation of sieves (2.0 mm and 250 µm). Material remaining in the sieves after washing was transferred to a petri dish and 75% ethanol was added.

Stomach and intestine: In the lab, a cut was made along the greater curvature of the stomach and along the length of the small and large intestines to remove the contents, which were washed out with water into a gradation of sieves (2.0mm and 250µm). Contents in each sieve were stored in 99% ethanol.

The contents were analysed under an Olympus S740 microscope at 15x magnification. Contents were separated into hair, bone, feather, invertebrates, vegetation, parasites, and extra material, and placed into different containers in 75% ethanol for identification at a later time. Hair was teased out using forceps to ensure no other prey fragments were entangled in it. Endoparasites were opportunistically identified (Appendix C) and will not be dealt with in more detail herein.

Invertebrates were identified using an insect key, modified from Borror et al. (1989), and insect identification books (Crowe (2002) and Grant (1999)). A reference key was also set up using pitfall catches from Ponui Island from Dixon (2015), and a key previously made by Denny (2009). Invertebrates were counted in a conservative manner using body parts which survived the digestion process; e.g. a right and left mandible of similar size belonging to the same family were counted as one individual.

The vertebrate content of the scat was identified to species. When possible, morphological differences were used to identify any bones, hairs or feathers found. To identify birds to species level, distinguishing features were used. These included intact whole feathers, the size of bones, bills, and toe claws. These were identified by experts in ornithology when needed. Identification included a comparison of bones, bills, feathers, and claws to museum specimens, photos of species, and remains of dead specimens collected around the study site when seen. Material from birds that could not be identified to species level or to order level was only noted down as a 'bird'. Feral cat diet was described using the percentage of occurrence of prey items, calculated as the total number of scats with a prey type as a percentage of the total number of scats analysed.

To determine the dry weight of the animal matter in the scats, the material was sorted into different plates. Each plate plus its contents were weighed using electronic scales (Sartorius ED2245) and then they were placed into an oven. The oven was set to 55°C and the weight of each plate measured to 0.1 mg at the same time on consecutive days. The final dry weight was recorded once the weight stayed the same (to 0.1 mg) between consecutive days. Samples were transferred to paper towels, and the plates were weighed to obtain the dry weight of the animal material.

Sexing scats

Felid sex identification was performed using polymerase chain reaction (PCR) targeted to regions in the X and Y chromosome as described by Pilgrim et al. (2005) on the amelogenin region. In domestic cats, the y-chromosome gene has a 20 bp (base pair) deletion absent in the x-chromosome (Pilgrim et al., 2005). Therefore, females were identified as having one band at 214 bp, and males as having one band at 194 bp and another at 214 bp.

To establish the PCR technique, faecal and blood samples were collected from two cats at the Massey University Feline Unit (Massey University Animal Ethics Committee 16/39). These samples were also used as a reference (positive control) for the feral cat samples. One male and one female were placed in individual pens for a maximum of 24 hours to obtain fresh faecal samples. For the blood samples, the jugular area was clipped, and lidocaine gel was applied to the venipuncture site. A blood sample of 3 ml was taken from the jugular vein using a 25 gauge needle and placed into an EDTA tube.

DNA was extracted from 250 µl of colony cat blood collected, using 250 µl of a SDS lysis buffer (20 mM EDTA-$Na_2.2H_2O$, 60 mM Tris HCl, 1% sodium dodecyl sulphate, 1% Triton X-100, pH 8.0), and 0.5 mg/ml Proteinase K (Roche Diagnostics, Switzerland). The mixture was incubated for 30 minutes at 56^oC and equal volumes of phenol:chloroform:iso-amyl alcohol (25:24:1, Sigma, MO, USA) were added. Aqueous and organic phases were separated by centrifugation at 13,400 xg for 15 minutes at 4^oC. The DNA was precipitated using a 10:1 solution of ice-cold 100% ethanol and 3 M sodium acetate (Sigma, MO, USA). The DNA was washed twice with 70% ethanol, allowed to air dry and re-suspended in R40 (40 µg/ml RNase A (Sigma, MO, USA) in TE (10 mM Tris, 1 mM EDTA, pH 8.0)) overnight at 4^oC. Extracted DNA was quantified with a Nanodrop (Thermo Scientific, MA, USA) and stored at -20^oC.

Three hundred and ninety-six of the scat samples collected in the field were used for this part of the study. Selection of samples was based on testing an even spread of location, habitat type, and season. Extraction of DNA from these samples and the reference (colony cats) faecal samples was performed with the ISOLATE Fecal DNA Kit (Bioline, London, UK) using 100 – 150 mg of faeces. Faecal matter was removed from two parts of the scat and weighed using electronic scales (Sartorius ED2245), and placed into a bashing bead lysis tube. It was noted whether the scat was dry, wet, or medium (in between).

PCR primers (Integrated DNA Technologies, Iowa, USA) designed for the amelogenin region of the sex chromosomes in mammals (forward 5'-CGAGGTAATTTTTCTGTTTACT-3', reverse 5'-GAAACTGAGTCAGAGAGGC-3') were used in this study (Pilgrim et al., 2005). The reaction mix was made up of 1 µl DNA, 4 µl of 5x Hot Firepol Blend Master Mix (1x concentration) (Solis Biodyne, Tartu, Estonia), 0.6 µl of each of the forward and reverse primer (0.3 µM concentration), and 13.8 µl of distilled water (to make the reaction mix up to 20 µl). The reaction mix was put into the thermocycler (Applied Biosystems Veriti, Foster City, California, USA) for the following PCR profile: 15 minutes at 94^oC; 45 cycles of 30 seconds at 94^oC, 30 seconds at 54^oC, 30 seconds at 72^oC; followed by 7 minutes at 72^oC; and finishing at 4^oC. The PCR products

(5 µl) were then run through a 2% agarose gel (Bioline, London, UK) for 60 minutes at 60 V with Redsafe dye (iNtRON, Korea). PCR products from the male and the female colony cats' blood were used as positive controls, and a distilled water sample for a negative control. PCR products were visualised using an E-gel Imager (Thermo Scientific, MA, USA).

Determining sex ratio

The sex ratio of the feral cat population on southern Ponui Island was estimated through camera trapping and live-trapping (Chapter 2). Cats that were live-trapped were sexed and marked with reflective tape on their radio collars and ear-notched for individual identification on cameras. Videos collected of cats that had not been trapped were examined to determine sex. Non-resident cats (those cats seen rarely on camera traps) were not used in the sex ratio estimate because this was likely to bias the sex ratio towards male cats. Male felids are more likely to be the dispersers in a population and are often the more transient sex (Croteau et al., 2010; Fattebert et al., 2015). The sex ratio was calculated using the known sex of the resident cats.

Calculating calorie intake

It was assumed that the prey items identified in the scats represent prey that was killed and consumed (except where there were signs that it was scavenged), and simply that a cat did not eat a rat mandible bone found on the forest floor, for example. I calculated that 6.97% of all scats that were produced during the study period were collected, assuming that each of the eight resident cats deposited one scat per day during the 780 days the study took place (Fitzgerald & Karl, 1979; Liberg, 1984). I then estimated the number of each prey species eaten per cat per year. To determine whether I had estimated this realistically, I calculated the calories provided by the calculated total prey eaten per year and compared this to the maintenance requirements for domestic cats (100 kcal x $\text{kgBW}^{0.67}$) (National Research Council, 2006). Because there is no data available for each prey I found, prey types were given general categories to estimate the kilocalories (kcal) as fed for each species. Birds weighing 130 g or more were classed as 'chickens' and those weighing less than 130 g were classed as 'day-old chicks'. For rats, mice, chickens, and day-old chicks, the kcal as fed were provided by Bird & Ho (1976). All insects were classed as 'crickets' due to similar nutrient composition between coleopterans and orthopterans (Rumpold & Schlüter, 2015), and the kcal as fed provided by Wang et al. (2004). The average adult weight was used for each prey, where birds (excluding kiwi and chickens) were from Fitter & Merton (2011), chickens from Havenstein et al. (2003), mice from Ruscoe & Murphy (2005), weta from Griffin (2011), and crickets from Shackleton et al. (2005). Information was available from Shapiro (2005) on the average adult weight of rats caught on Ponui Island. As most of the kiwi were consumed during the breeding season it was assumed that they were chicks and were born in September to estimate age and the corresponding weight (Wilson, 2013) (to use as an average), unless feet were found in the scat that suggested otherwise.

Calculating number of kiwi eaten per year

I assumed that each scat analysed that contained a kiwi represented a kiwi that was depredated by a cat (and not scavenged). Kiwi were mainly identified through feathers, skin, and claws. Often the feet were eaten and sometimes passed through the cat partially intact, allowing an approximate age to be determined.

The timing of brown kiwi chick hatches from September 2013 - January 2016 was obtained from activity data logged in "Chick timer" radio transmitters (KiwiTrack Ltd., Havelock North, NZ) that were collected as part of another study of fifty kiwi on Ponui Island, and provided by I. Castro. Brown kiwi males are usually the sole incubator of eggs and their nocturnal activity reduces as a result of incubation (McLennan, 1988); therefore males' activity pattern allow the hatching dates to be estimated and consequently determine when kiwi chicks were present in the study site.

The number of kiwi estimated to be killed by feral cats per year was calculated using the percentage of scats analysed that contained kiwi chicks. This was compared to the number of kiwi chicks killed per year found by Wilson (2013) for the 2010-11 breeding seasons. The number of chicks produced in a year was calculated using data from Ziesemann (2011) for 2005-07. This included the number of males breeding, the number of clutches per year, the number of eggs per clutch, and the number of chicks hatched per year. The number of chicks preyed upon by feral cats is used as an estimate only because the data collected by Wilson (2013) and Ziesemann (2011) were in different years.

Statistical analysis

All analyses were carried out in R (R Development Core Team, 2008). To identify seasonal differences in diet, a chi-square analysis was calculated to test for differences in the occurrence of each prey type in scats collected during different seasons. An ANOSIM (analysis of similarities) was performed on the percentage of occurrence of prey between seasons. A nMDS (non-metric multidimensional scaling) was created to visualise the variation in diet between seasons. A

Kruskal-Wallis test was used to test for sex differences in weight of all prey types, and the weight of birds eaten between sexes. Chi-square analysis were used to test whether there was a difference between males and females in the location of scats in relation to a trail. A chi-square analysis was also used to determine whether there was a difference in the sex ratio estimated through scats and the known sex ratio determined through camera trap and live-trapping; and also to test for a difference in the prey type found in scats deposited by the two sexes.

Results

Diet composition

Overall, Ponui Island feral cat scats contained more rats (53%) than birds or mice (Figure 1A). Coleoptera were found in more scats than orthopterans. Bird eggs were also found in scats but were not common with only 10% of scats having egg shells present. Two scats collected during lambing season (October) contained wool, suggesting the cats were opportunistically scavenging dead lambs. A range of birds were identified from scats and prey remains (Table 2). Large-sized birds occurred more frequently in scats than small- or medium-sized birds (Figure 1B). The prey with the highest dry weight were rats followed by birds (Figure 1C).

Birds had an occurrence rate of over 40% in scats (Figure 1A). Twenty-two species of birds were identified from cat scats, representing 39% of the bird species found on Ponui Island (Supplementary material: Table S1). Twelve of the 17 species of passerines seen on the island were found in cat scats. Half of the bird species that were identified from scats were native species.

Based on my calculations of the estimated prey eaten by one cat (Table 3), the energy provided by prey was 118,092 kcal per year. This equates to 315.81 kcal per day for each feral cat on Ponui Island. The average weight of all adult cats sampled on Ponui Island (n = 12) was 3.2 kg (Chapter 2). Using the National Research Council (2006) maintenance requirement equation, for 3.2 kg cats the maintenance requirement is 222.6 ± 50% kcal per day. The maintenance requirement calculated for the Ponui Island feral cat population falls within the range of the National Research Council (2006) estimate of 111.3 – 333.9 kcal per day.

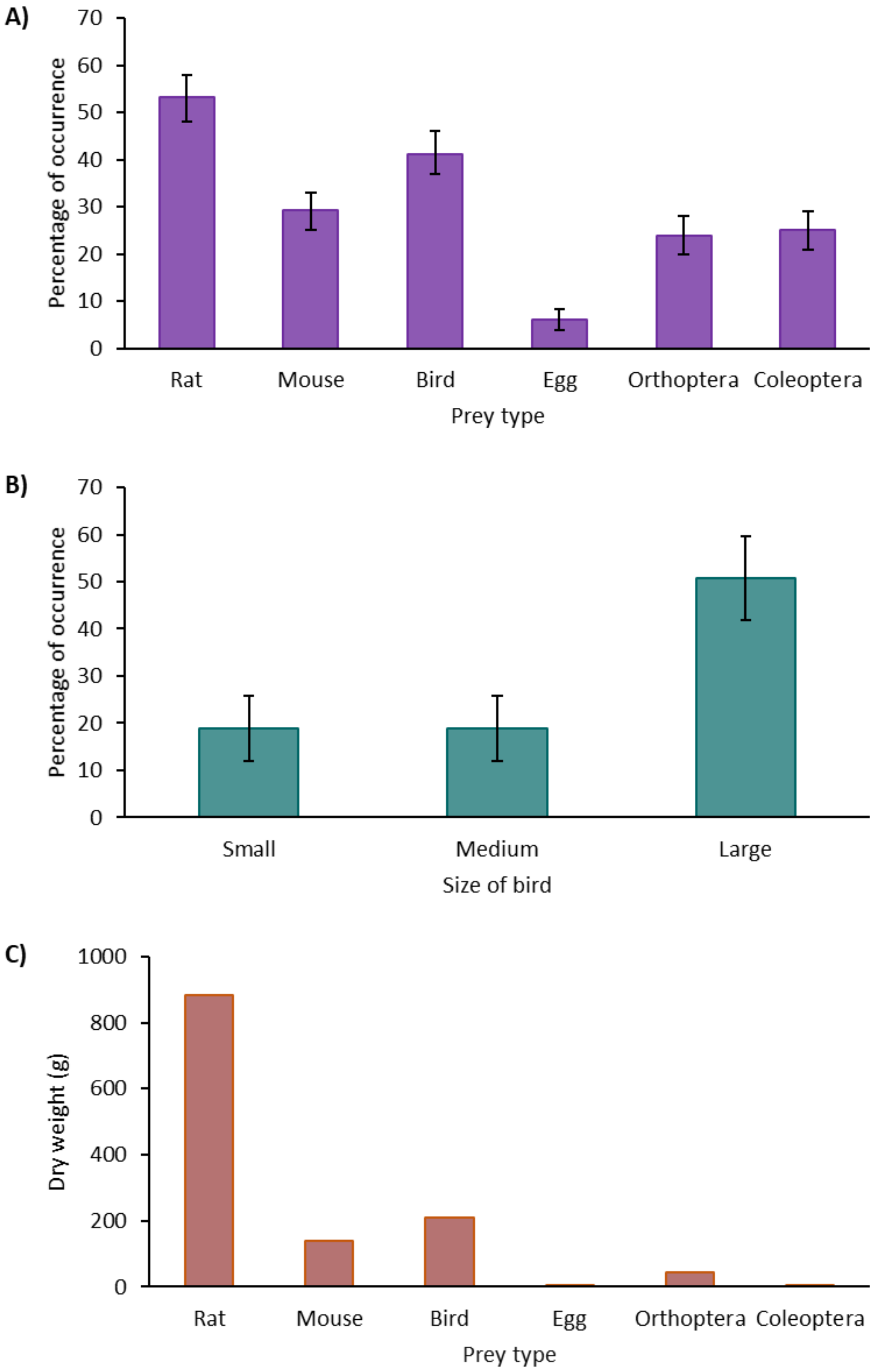

Figure 1: Composition of prey found in feral cat scats. Error bars show the 95% confidence interval. **A)** Percentage of scats analysed (n = 434) that contained the six main prey groups. **B)** Percentage of occurrence of different sized birds in scats that contained identifiable birds (n = 122). Small birds weighed 50 g or less, medium birds weighed between 51-199 g and, large birds are those that weighed 200 g or more. Sizes of birds was based on the average adult body weight. **C)** Dry weight (g) of the six main prey types identified in 434 cat scats.

Table 2: The prey that was identified in feral cat scats, with the total number estimated to have been depredated, and the average weight of the prey animal. The following resources were used for estimating the average prey weight: birds (excluding kiwi and chickens) from Fitter & Merton (2011), Ponui Island brown kiwi chicks from Wilson (2013), chickens from Havenstein et al. (2003), Ponui Island rats from Shapiro (2005), mice from Ruscoe & Murphy (2005), weta from Griffin (2011), and crickets from Shackleton et al. (2005).

Species	**Total number**	**Average weight (g)**	**Species**	**Total number**	**Average weight (g)**
Rat (*Rattus* spp.)	247	134	Weta (Families: Anostostomatidae and Raphidophoroidea)	122	2
Mouse (*Mus musculus*)	123	20.6	Cricket (Family: Gryllidae)	608	0.65
Kereru (*Hemiphaga novaseelandiae*)	9	650	Coleoptera (Order)	202	0.5
Morepork (*Ninox novaseelandiae*)	5	282	Indian myna (*Acridotheres tristis*)	6	127
Sacred kingfisher (*Todiramphus santus*)	3	60	Pukeko (*Porphyrio melanotus*)	7	850
Mallard duck (*Anas platyrhynchos*)	1	1100	North Island brown kiwi (*Apteryx mantelli*)	34	264-2000
Red billed gull (*Larus novaehollandiae*)	1	305	Chaffinch (*Fringilla coelebs*)	1	21
White-faced heron (*Ardea novaehollandiae*)	1	550	House sparrow (*Passer domesticus*)	2	29
Grey warbler (*Geygone igata*)	2	6.5	Australian magpie (*Gymnorhina tibicen*)	3	350
North Island fantail (*Rhipidura fuliginosa*)	9	8	Eastern rosella (*Platycercus eximius*)	1	105
Eurasian blackbird (*Turdus merula*)	4	100	European goldfinch (*Carduelis carduelis*)	1	14
Silvereye (*Zosterops lateralis*)	3	12	Song thrush (*Turdus philomelos*)	1	70
Tui (*Prosthmadera novaseelandiae*)	3	105	Chicken (*Gallus gallus domesticus*)	1	2000
Yellowhammer (*Emberiza citronella*)	1	24	Eel (*Anguilla* spp.)	1	500

Table 3: Estimated number of prey consumed each year by an individual Ponui Island cat, and calorie intake from each prey item per year. Number in scats is the number of prey identified from 434 scats. Weight is the average adult weight of the animal. For the energy density category, species were classed as either chickens (c), day-old chicks (ch), eel (e), egg, insect (i), mouse (m) or rat (r); see methods for further explanation. Prey items are listed in order of total kcal/year/cat.

Prey	Number in scats	Weight (g)	No. per scat	Prey per year	Per individual per year	Total prey weight/cat/year	Energy density category	kcal as fed	Total kcal/year/cat
Rat	247	134	0.568	1658	207	27772	r	1.988	55211
Kiwi	34	400	0.078	228	29	11411	c	1.986	22663
Pukeko	7	850	0.016	47	6	4993	c	1.986	9915
Kereru	9	650	0.021	60	8	4909	c	1.986	9749
Mouse	123	20.6	0.283	826	103	2126	m	2.067	4395
Chicken	1	2000	0.002	7	1	1678	c	1.986	3333
Morepork	5	282	0.011	34	4	1183	c	1.986	2350
Duck	1	1100	0.002	7	1	923	c	1.986	1833
Magpie	3	350	0.007	20	3	881	c	1.986	1750
Unid birds	105	10	0.241	705	88	881	ch	1.620	1427
Myna	6	127	0.014	40	5	639	ch	1.620	1036
Heron	1	550	0.002	7	1	461	c	1.986	917
Blackbird	4	100	0.009	27	3	336	ch	1.620	544
Gull	1	305	0.002	7	1	256	c	1.986	508
Eel	1	500	0.002	7	1	420	e	1.200	503
Tui	3	105	0.007	20	3	264	ch	1.620	428

									Diet
Cricket	608	0.65	1.398	4081	510	332	i	0.920	305
Kingfisher	3	60	0.007	20	3	151	ch	1.620	245
Weta	122	2	0.280	819	102	205	i	0.920	188
Rosella	1	105	0.002	7	1	88	c	1.986	175
Egg	26	3.5	0.060	175	22	76	egg	1.560	119
Fantail	9	8	0.021	60	8	60	ch	1.620	98
Thrush	1	70	0.002	7	1	59	ch	1.620	95
Sparrow	2	29	0.005	13	2	49	ch	1.620	79
Coleoptera	202	0.5	0.464	1356	169	85	i	0.920	78
Silvereye	3	12	0.007	20	3	30	ch	1.620	49
Yellowhammer	1	24	0.002	7	1	20	ch	1.620	33
Chaffinch	1	21	0.002	7	1	18	ch	1.620	29
Goldfinch	1	14	0.002	7	1	12	ch	1.620	19
Grey warbler	2	6.5	0.005	13	2	11	ch	1.620	18

Kiwi

A high number of brown kiwi were found in the scats of the feral cats (34) equating to an overall percentage of occurrence of 7.8%. Kiwi chicks hatched between September - January during the study. All kiwi remains were found in scats that were collected during the kiwi breeding season (September – March) (Figure 2) and the percentage of scats containing kiwi at this time was 13.4%. The highest occurrence of kiwi in cat scats was in December, where 33% of scats analysed had kiwi remains present. One foot was partially intact and was approximated to be from a one-year-old kiwi. At least one kiwi was likely to have been scavenged due to the skin having a "dried and leathery" appearance. Only 16 of the scats that contained kiwi remnants were successfully sexed, with 12 of the scats belonging to male cats and four belonging to females.

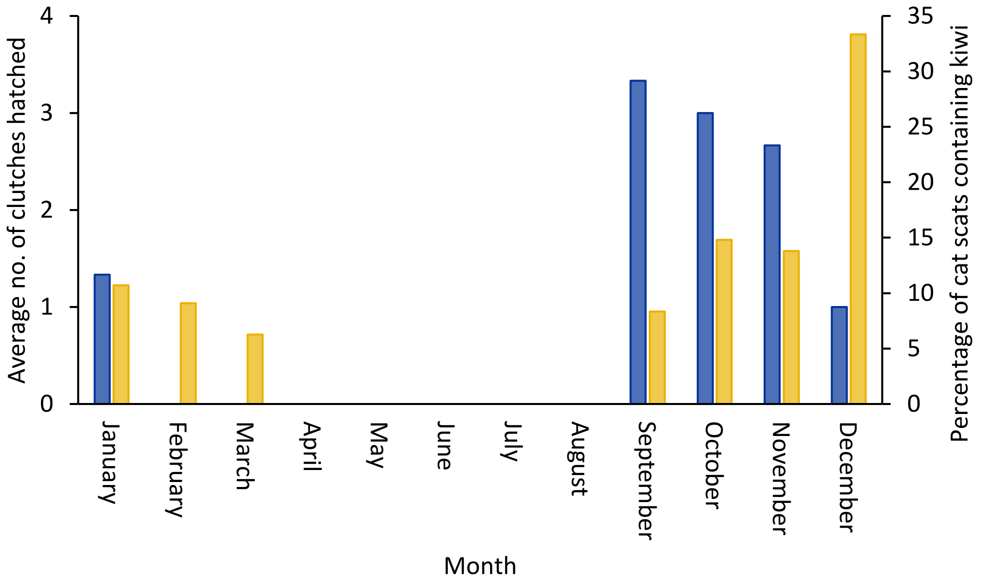

Figure 2: A comparison of the number of brown kiwi clutches that hatched (September 2013 – January 2016) from 16 males (n = 33 clutches) and the percentage of scats analysed from each month (total n = 434) that had kiwi present (n = 34). The blue bars represent the number of clutches hatched, and the yellow bars are the percentage of scats that contained kiwi.

Based on the results from this study, I estimated that 228 kiwi were eaten by feral cats per year in the South and Middle farms of Ponui Island (Table 3). This estimate includes the kiwi that appeared to have been scavenged, and the one-year-old kiwi. Based on previous studies and a 29% depredation rate, the estimation is 65-131 kiwi chicks to die from cat depredation in this site per year (Table 4). Excluding the kiwi that appeared to be scavenged, and the one-year-old kiwi, I assumed that the other kiwi were chicks because they appeared in scats collected during the kiwi breeding season. Therefore, I predict that cats are responsible for 36-72% of kiwi chick mortality on Ponui Island, equating to 215 kiwi chicks per year with a 95% confidence interval of 146-292 kiwi chicks.

Table 4: Estimate of the number of kiwi chicks preyed on by feral cats in the South and Middle farms on Ponui Island using a lower population estimate of 1000 kiwi, an upper population estimate of 2000 kiwi, and a population estimate based on 1 kiwi/ha (Cunningham et al., 2007) across the entire island. Estimates for the calculations are from Ziesemann (2011) and the percentage of chicks killed by cats was used from Wilson (2013).

No. of kiwi	No. of male kiwi[1]	No. breeding males[2]	No. clutches/year[3]	No. eggs/clutch[4]	No. chicks hatched/year[5]	No. chicks depredated by cats[6]
666	333	236	265	344	224	65
1200	600	426	477	620	403	117
1340	670	476	533	693	450	131

[1] Assuming a 50:50 sex ratio.
[2] 71% of monitored males incubated (Ziesemann, 2011).
[3] 12% of incubating males had two clutches per year (Ziesemann, 2011).
[4] There was a mean of 1.3 eggs/clutch (Ziesemann, 2011).
[5] 65% hatching success (Ziesemann, 2011).
[6] 29% of chicks monitored died from cat depredation (Wilson, 2013).

One adult kiwi was confirmed to have been killed by a feral cat on Ponui Island in March 2018 and there was another suspected one in November 2015. The second kiwi died from depredation, but it could not be determined whether the predator was a dog or a cat. Both adult male kiwi had bite wounds on the leg and neck, and in both cases, the animal was not eaten. The wound marks post-mortem changes indicated that in both cases the kiwi died after fleeing from the predator.

Seasonal variations in diet

Rats had a significantly higher percentage of occurrence in the scats collected during the winter (80%) than those collected in the summer (38%) (Figure 3) (Supplementary material: Table S3). Mice were found in scats in similar numbers throughout the seasons but occurred in more scats collected during autumn. There was slight seasonal variation in the occurrence of birds in scats, with the least consumed in autumn, and the most consumed in spring. Eggs were mostly eaten in spring. There was high variation in the occurrence of orthopterans in the diet of feral cats, with a large amount being consumed in summer and autumn. Coleoptera were eaten throughout the year.

There was a difference in the prey items that were found in scats collected in different seasons (ANOSIM, R = 0.77, p-value = 0.001). In winter, feral cats had narrower variation in diet, with rats, Coleoptera, and birds occurring the most (Figure 4). Scats collected during the summer had the widest range of prey items. There was more overlap in the prey found in scats collected in autumn, spring, and summer than there was for winter (Figure 4).

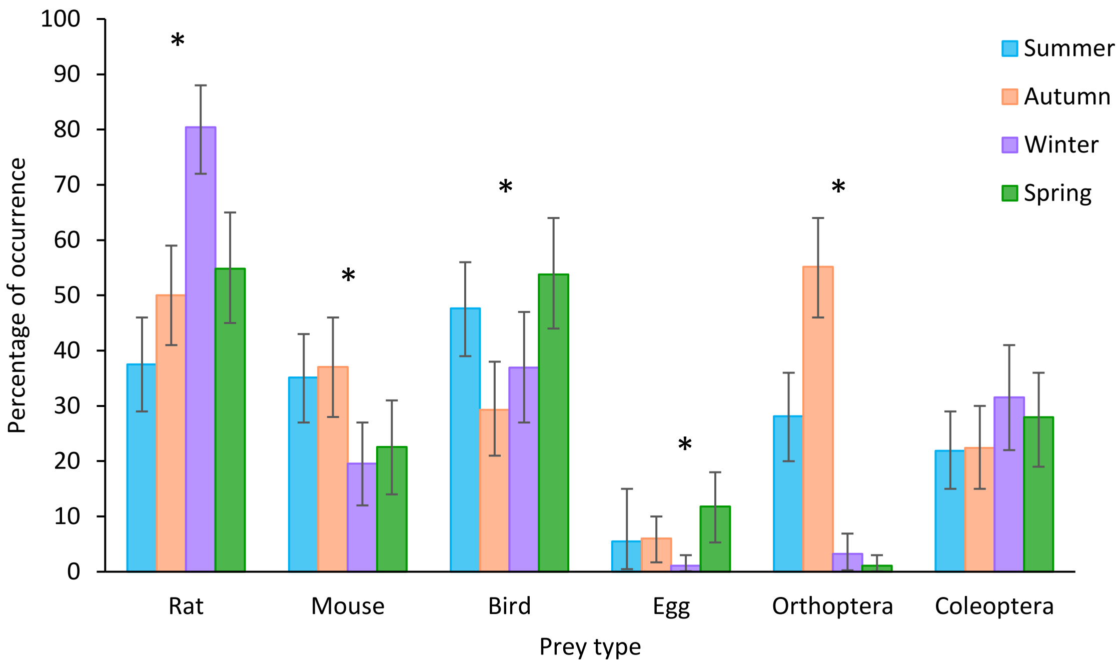

Figure 3: Percentage of scats (n = 434) that contained each of the main prey types across different seasons. Error bars show the 95% confidence interval. *Represents significant differences (p-value < 0.05) in prey type between seasons from chi-square analysis (Supplementary material: Table S3).

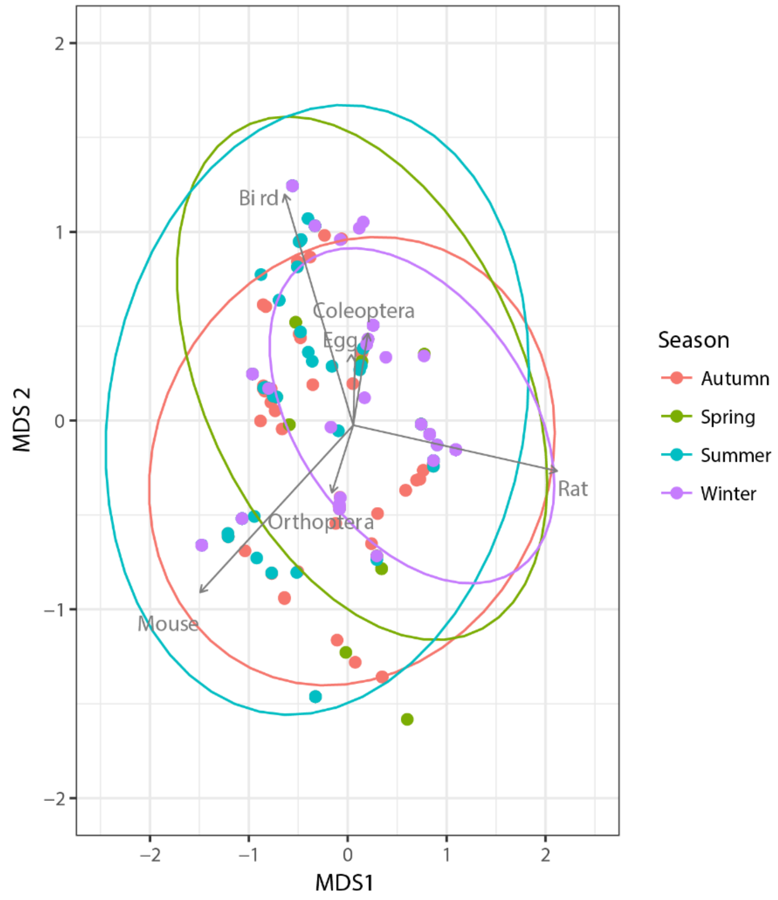

Figure 4: Non-metric MDS ordination of the six prey types found in feral cat scats (n = 434) collected in different seasons. Scats were collected from January 2014 - April 2016.

Sex bias in scats

The moisture content of the scats varied; there were 158 dry scats, 134 medium, and 79 wet. Two hundred and fifty scats were sexed successfully; 73% of dry scats, 57% of medium scats, and 59% of wet scats.

Although the sex ratio of male to female scats was 2.82:1, and the true sex ratio of the cat population estimated by live-trapping and camera traps was 2:1 (male:female), the difference in sex ratio detected by the two techniques (sexed scats and camera trapping/live-trapping) was not significant (chi-square, $x^2 = 0.041$, p-value = 0.839). Two hundred and seventy-five scats were found just off the trail (within one metre of the trail), 54 scats were off the trail (either there was no trail, or more than one metre from the trail), and 142 scats were located on the trail. They were found on a variety of substrates, with 38% found on moss, 30.5% found on grass, and the rest found on dirt, branches, and leaves. Of the 54 scats collected off trails, only 24 scats were sexed successfully, with 42% belonging to female feral cats (Table 5). More scats belonging to males were found on or near a trail (92%) than off the trail. There was no significant difference between the sex of the cat that deposited the scat and the scat's location in relation to a trail (chi-square, $x^2 = 5.47$, p-value = 0.065), although there was a small sample size of scats belonging to females collected.

Table 5: The sex of the cats that deposited the scats and the location (in relation to a trail) where the scats were collected. On = found on a trail, Just off = found within a metre of a trail, Off = found more than one metre from a trail or there was no trail in the proximity.

	Scat location in relation to the trail		
Sex	On	Just off	Off
Female	21	33	10
Male	44	117	14

Dietary differences between sexes

There was a statistically significant difference between the type of prey found in scats deposited by males and females (chi-square, $x^2 = 31.04$, p-value < 0.001). Rats occurred in the same percentage of scats (52%) between males and females (52%) (Figure 5A). Males had more scats (45%) containing birds than females (33%). Coleoptera occurred in a similar percentage of scats between sexes, though Orthoptera occurred more frequently in scats from females (32%) than males (17%). Egg shells and membranes were found in one scat belonging to a female and 14 scats from male cats. There was no significant difference between the average (mean ± SE) weight of prey found in scats belonging to males (49.2 ± 5.5 g) compared to females (26.9 ± 3.8 g) (Mann Whitney U-test; n = 717, df = 1, W = 56136, p-value = 0.298).

While ground birds were found in similar frequencies in scats between the sexes, passerines featured more frequently in scats belonging to females than males (Figure 5B). The birds found in male deposited scats were on average heavier (mean weight = 371 g) than the birds identified in female deposited scats (mean weight = 182 g) (Mann Whitney U-test; n = 38, df = 1, W = 86.5, p-value = 0.047) (Figure 5B). Although male feral cats more commonly had larger sized birds in their scats, the 95% confidence interval overlapped between males and females, most likely due to the small sample size.

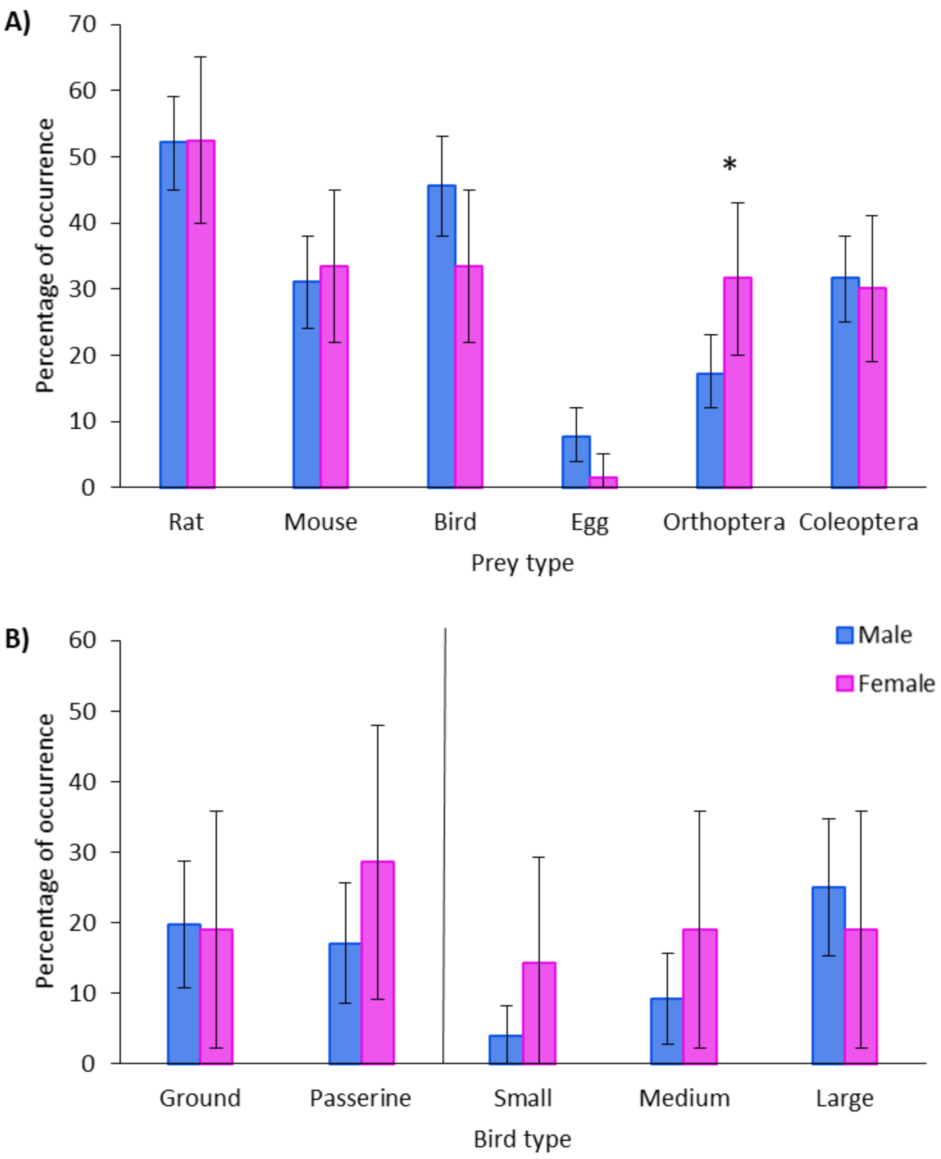

Figure 5: A) Percentage of scats that contained six different prey types in scats belonging to either male-sexed scats (n = 180) or female-sexed scats (n = 63). *Represents significant differences (p-value < 0.05) in prey type between sexes from chi-square analysis (Supplementary material; Table S3). **B)** Percentage of occurrence for different sized birds in male-sexed scats (n = 76) and female-sexed scats (n = 21) that contained birds. The grey vertical line separates different groupings of birds. Ground birds included kiwi, pukeko, and chickens. Passerines are birds under the classification. Large birds are those that weigh 200 g or more, medium birds weigh between 51-199 g and small birds weigh 50 g or less. Error bars represent 95% confidence intervals.

Discussion

The diet of feral cats on Ponui Island resembles, in many ways, the results from studies conducted elsewhere in New Zealand, with small mammals (rats) being the most frequently occurring prey species in scats (Table 1). There was, however, one important difference. Birds feature highly (over 40%) in scats on Ponui Island. This was a surprising result given the high densities that rats reach on Ponui Island (up to 22 rats/ha; 6-11 rats/ha in spring; 6-10 rats/ha in summer) (Shapiro, 2005; Latham, 2006) compared to the mainland (2.9 rats/ha in spring; 7 rats/ha in summer (Dowding & Murphy, 1994; Brown et al., 1996). Only a few studies have found birds to be the most consumed prey type by feral cats, and when they were, this was thought to reflect the absence of either rats (Harper, 2010), or other small mammals (Fitzgerald & Veitch, 1985).

There was no relationship between the percentage of occurrence of mammals and birds in the diets of feral cats in previous studies because there was great variation in diets between populations (Supplementary material: Figure S4). The Ponui Island feral cats were only one of three studies where birds had an occurrence rate of over 40% in scats when rats were the main mammalian prey consumed. There are only two other studies where birds occur in over 40% of analysed scats and rats are the main mammalian prey consumed: a study on Stewart Island (Karl & Best, 1982) and a study on Little Barrier Island (Marshall, 1961). Similar to Ponui Island, feral cats were the top predator on Stewart Island (Karl & Best, 1982), and were the only mammalian predator on Little Barrier Island (Marshall, 1961). The findings from this study, and the similarities between Little Barrier and Stewart Island feral cats, suggest that feral cats may not rely solely on rats as a prey source when they are a top predator, and in areas where there are a large variety of bird species available. This may also suggest that there is some resource partitioning when other predators are also present in the ecosystem. That all three studies were in insular environments may support the conjecture by previous studies that feral cats may have a substantial impact on island populations of birds (Bonnaud et al., 2011; Medina et al., 2011; Doherty et al., 2016).

I found that large birds (weighing 200 g or more) were more frequently eaten than medium or small birds, which is opposite to previous studies that have identified small- and medium-sized birds to be more commonly consumed by cats (Fitzgerald & Karl, 1979; Fitzgerald et al., 1991). Kutt (2012) found feral cats selected prey weighing less than 100 g, suggesting that cats avoided birds weighing more than 100 g. Spencer et al. (2014) found feral cats were more selective of smaller mammals in an area where foxes and dingoes were also present. It is possible that on Ponui Island there are more large bird species available given the lack of mammalian predators and thus these birds become more available for cats. On the other hand, it is also possible that when cats are the top predator they target larger prey. The differences in the average bird size that was preyed upon in this study compared to Australia (Kutt, 2012) may be due to New Zealand birds being easier to catch. Native birds in New Zealand evolved in isolation without mammalian predators, whereas birds in Australia evolved with many native mammalian predators. So the predator naivety displayed by New Zealand birds may make them easier to catch (Holdaway, 1989; Sih et al., 2010).

The large seasonal variation in the occurrence of rats in feral cat scats analysed in this study supports the notion that feral cats are opportunistic and consume prey species based on availability, as opposed to targeting only rat species. I found a significant difference between seasons in the number of scats containing rats, with more rats found in scats collected during the winter, with the least number of rats occurring in scats during the summer. This is likely attributed to the seasonal variation in densities of ship rats on Ponui Island. Latham (2006) and Shapiro (2005) found that rats were at their lowest density during the summer, and their highest in winter. More birds were consumed by feral cats in this study during the spring and summer when egg laying and incubation occur (Cockrem, 1995). Birds are particularly vulnerable to depredation when they are nesting (O'Donnell, 1996; Sanders & Maloney, 2002), and nest depredation was present in this study since an adult and a juvenile fantail were found in one scat, and eggshells were found in 26 scats (one scat belonging to a female, 14 from male cats, and 11 unsexed scats).

Feral cats exhibit diet flexibility, as evident in their change in diet across seasons. With the ability for feral cats to target prey based on availability, it is possible that the reduction in rats and mustelids, from control operations and, in the future, from PF2050, will lead to a temporary increase in bird populations (both native and introduced), and feral cats would start preying more heavily on birds than before. This has been observed in areas where cats are present but not rats, such as Herekopare Island (Fitzgerald & Veitch, 1985), where birds are more frequently consumed compared to other sites with rats. With feral cats remaining largely uncontrolled, Predator Free 2050 may not have the success rate that it could if feral cats were included among the pests to be eradicated.

As the feral cats on Ponui Island are preying on many different species, it is unlikely that the removal of rats would lead to a reduction in feral cat numbers. My findings were in contrast to that found by Harper (2005), who claimed that it was the seasonal low rat abundance that dictated the overall cat density on Stewart Island. Harper (2005) found a high occurrence of rats in scats collected throughout the year, despite large fluctuations in rat densities. When there was low rat abundance, feral cats had higher dispersal and mortality rates (Harper, 2005). There were differences in the occurrence of birds in feral cats diets on Stewart Island between the studies carried out by Harper (2005) and Karl & Best (1982), 30 years apart. More bird species occurred in the diet of feral cats in Karl & Best's study (1982); kakapo, as well as other ground nesters such as penguins (*Eudyptula minor*) and sooty shearwaters (*Ardenna grisea*), were consumed. On the other hand, Harper (2005) found mainly small passerines to be eaten by feral cats. Passerines are smaller than most ground birds found in New Zealand, so may have a smaller calorific payoff once the difficulty of capture is also taken into account. The lower occurrence of birds in the diet of Stewart Island feral cats found by Harper (2005) may be due to the decline in bird populations over the past 50 years (Harper, 2009). The habitat of Stewart Island (a mixture of subalpine and forest habitats) also may not allow feral cats to easily hunt larger ground birds, such as the tokoeka (*Apteryx australis*).

My study found kiwi remains in feral cat scats, with 8% of the scats analysed containing kiwi. Based on the percentage of occurrence of kiwi in feral cat scats, I estimated 146-292 kiwi chicks were being killed by feral cats on Ponui Island each year, which is higher than the estimate based on 29% of kiwi chicks dying from cat depredation (65-131 kiwi chicks) (Wilson, 2013; Alley et al., 2015). My estimates suggest that the percentage of kiwi chicks preyed upon by feral cats may be more than that found by Wilson (2013), and may be as high as 36-72%. The true estimate is most likely to be closer to the lower prediction (36%) as some of the kiwi found in the scats may be one individual kiwi represented many times (eaten over more than one meal), or more kiwi chicks may have been scavenged and this could not be identified. McLennan et al. (1996) found that up to 60% of juvenile mortality in North Island brown kiwi was due to predators, mainly stoats (*Mustela erminea*), with feral cats responsible for only 5%. The removal of stoats from ecosystems may not lead to an increase in kiwi chick survival because feral cats may utilise kiwi chicks as a food source more when there is no interspecific competition for them, or when kiwi chicks become more prevalent from eliminated mustelid depredation.

Kiwi were preyed upon throughout the entire kiwi breeding season when chicks were available. There was evidence of kiwi chicks at different ages being eaten by feral cats in this study based on the foot size of kiwi found in scats. Wilson (2013) found that most of the kiwi chicks that died from cat depredation were between 20-30 days old, however, the youngest was seven days old, and the oldest more than 100 days old. Feral cat scats collected in December had the highest occurrence of kiwi, possibly due to the low density of rats on Ponui Island in December (Shapiro, 2005; Latham, 2006), coupled with low invertebrate biomass (Dixon, 2015) and the increased availability of an alternative food source; kiwi chicks. Wilson (2013) found most of the kiwi that were killed by cats close to the nests, and obtained a video showing a cat observing a kiwi chick before depredating it in front of its nest entrance. Cats have been documented to sit outside rabbit warrens to wait for juvenile rabbits to emerge (Flux, 2007), and Jones (1977) noted one feral cat regularly checking and entering burrows used by nesting petrels. Feral cats may monitor kiwi nests and opportunistically take them. Due to the high depredation rate on young kiwi, and the high number of kiwi remains found in cat scats in this study, even in areas where there are high rat densities, feral cats are likely to be a bigger threat to kiwi than has previously been identified. Further dietary analysis of cat scats during the kiwi breeding season should be carried out in other areas to determine how much feral cats contribute to the continued 2% decline in kiwi numbers annually (Holzapfel et al., 2008).

There were a large number of native bird species identified in the cat scats collected around the study site, which may be due to the majority of bird species on Ponui Island being native (Supplementary material: Table S1). Half of the bird species that were identified were natives, with two species in decline nationally (North Island brown kiwi and red-billed gull (*Larus novaehollandiae*)) (Robertson et al., 2017). Previous studies identified small passerines, seabirds, and ground birds as the most consumed bird type by feral cats (Karl & Best, 1982; Fitzgerald & Veitch, 1985; Harper, 2010). A variety of passerine species were identified in the cat scats in this study, which may be in relation to prey availability. Ponui Island is made up of highly modified habitat with the conversion of forest to farmland, and has a large number of introduced species (Bellingham, 1979; MacLeod et al., 2008). Studies on cats in urban areas have suggested that cats have more of an impact on introduced birds, as those are the bird species most preyed upon and most abundant (Gillies & Clout, 2003; Flux, 2007; van Heezik et al., 2008). Despite the highly modified agricultural landscape, I still identified a large number of native species in the cat scats.

The daily energy intake from prey for a Ponui Island cat calculated in this study was within the range of the daily maintenance energy requirements reported by the National Research Council (2006) for cats of similar weight, though in the upper range of the energy requirement. This is most likely due to the daily energy maintenance requirements for cats being estimated from lab or colony cats living in laboratory thermoneutral conditions (National Research Council, 2006). Although feral cats may have similar maintenance requirements as laboratory cats, they will have higher daily energy requirements than lab cats, due to: thermoregulation, higher activity for hunting prey, reproduction costs, and stress (Burger, 1994). Konecny (1987) also had higher estimations of daily energy provided by prey eaten for feral cats on the Galapagos Islands. Thus, my estimate of the energy intake per day is likely to be close to the daily energy requirement for maintenance, thermoregulation, and higher activity levels of a reproducing feral cat. Therefore, my estimate of the number of prey eaten per year and per day is likely to be close to the true amount eaten by feral cats.

The large number of native birds that are preyed upon by feral cats on Ponui Island when they are a top predator provides support for the control of feral cats. However, control is often sex-biased as males have larger home ranges (Chapter 2) and higher activity levels (Chapter 3), so are more likely to encounter traps than females, and I identified dietary differences between the sexes of feral cats in the type and size of prey that they ate. Females consumed on average smaller prey than males. Female feral cats ate more passerines than males, which were mainly small- and medium-sized passerines, whereas males ate the larger-sized birds, such as pukeko and herons. Male feral cats are on average one and a half times heavier than females (Fitzgerald & Veitch, 1985; Baker, 1989; Fitzgerald, 1990; Mills, 1994; King et al., 1996; Gillies & Fitzgerald, 2005; Recio et al., 2010; Murphy et al., 2011), and this was also the case in the Ponui Island population. Being larger and heavier, it is more likely that the males have the ability to kill larger prey.

More male scats were collected than female scats, and the sex ratio of the scats collected did not reflect the known sex ratio of the feral cat population studied, though the difference was not significant. This was most likely due to the small sample size of scats that could be successfully sexed. Similar to this study, Palomares et al. (2012) found that there was a male jaguar (*Panthera onca*) bias in the scats that were collected in their study. This may be due to felids' scent marking behaviour, where scent-marks may be used to mark territories or attract mates (Bailey, 1974; Smith et al., 1989; Allen et al., 2016). Male feral cats may use scats as a scent mark to other cats, explaining this male bias in collected scats (Palomares et al., 2012).

The dietary differences between sexes coupled with the male bias in scats collected are an important factor to consider in terms of conservation work. If females are eating mainly passerines, and we are not collecting as many of their scats as we do for male cats, then we may be underestimating the effect that feral cats have on passerine populations, and on small- and medium-sized bird populations. The dietary differences between male and female feral cats also need to be taken into account for control programmes. Male feral cats are more likely to be removed during control programmes due to their large home ranges, which could mean that the threat to large bird species is reduced. Control programmes for feral cats may not be as successful in reducing depredation risk to passerines and small native bird species unless female feral cats are also removed (Gillies et al., 2007; Recio & Seddon, 2013).

Rats made up a large proportion of the dry weight of prey from scats, much higher than any other prey type, and dry weight measures did not show similar representation of prey groups in scats as the percentage of occurrence. Measuring the dry weight of prey groups may be misleading because it is a measure of the indigestible material of the prey, and the digestibility of prey varies (Corbett, 1989). Transforming the dry weight in to an estimation of the weight of prey eaten may be a more accurate method for determining the importance of different sized prey in a predator’s diet, but this requires knowledge of the digestibilities of the prey items, which is specific to the predator being studied (Corbett, 1989; Reynolds & Aebischer, 2008). Therefore, a dry weight measure may not be useful in providing information on feral cat diet from scats.

In this study, I have found that in an ecosystem where there are limited mammalian prey species available to feral cats, and no interspecific competition, feral cats prey on a variety of species and are not solely relying on rats as a main food source. I identified a large seasonal variation in diet and this is likely due to the seasonal prey availability, particularly kiwi chicks. Male cats tended to eat larger prey than females, and scats belonging to males were more likely to be collected, posing the problem that the impacts of female feral cats could be underestimated. This study highlights how the proposal of PF2050 to remove mustelids and rats and not feral cats may not lead to high recoveries of native species, because feral cats also have detrimental effects on native species, and in some populations, the density of feral cats is not dependent on rat density alone.

This chapter highlighted the impact feral cats have on native bird populations on Ponui Island, and that they are unlikely to be controlling rats. Therefore, the feral cat population may be able to be removed without having detrimental indirect effects on native bird populations, such as through the mesopredator release of rats, as described in Chapter 1. In the next chapter, I integrate the different aspects of feral cat ecology studied throughout this thesis on the Ponui Island population, and how this knowledge can be used to create effective control and eradication programmes.

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Supplementary material

Table S1: Species of birds seen on Ponui Island during the study (2014-2017). This is based on the birds identified from Bellingham (1979) and information was supplemented by past students working on the islands as well as the Chamberlin family who own the farm on Ponui Island.

Type	Common name	Scientific name	Type	Common name	Scientific name
Seabird	Australian gannet	*Sula bassana serrator*	Gamefowl	Brown quail	*Synoicus ypsilophorus*
	Black fronted tern	*Chlidonias albostriatus*		Indian peafowl	*Pavo cristatus*
	Caspian tern	*Hydroprogne caspia*		Turkey	*Meleagris gallopavo*
	White-fronted tern	*Sterna striata*		Chicken	*Gallus gallus domesticus*
	Variable oystercatcher	*Haematopus unicolor*	Kiwi	North Island brown kiwi	*Apteryx mantelli*
	New Zealand dotterel	*Charadrius obscurus*	Rail	Pukeko	*Porphyrio melanotus*
	Common tern	*Sterna hirundo*	Pigeon	Kereru	*Hemiphaga novaseelandiae*
Gull	Black-backed gull	*Larus dominicanus*		Spotted dove	*Streptopelia chinensis*
	Red-billed gull	*Larus novaehollandiae*	Plover	Spur winged plover	*Vanellus miles*
	Black billed gull	*Larus bulleri*	Cuckoo	Shining cuckoo	*Chrsococcyx lucidus*
Shag	Pied shag	*Phalacrocorax varius*		Long tailed cuckoo	*Eudynamys taitensis*
	Little shag	*Phalacrocorax melanoleucos*	Kingfisher	Sacred kingfisher	*Todiramphus santus*
	Black shag	*Phalacrocorax carbo*	Passerine	Grey warbler	*Geygone igata*
Heron	Reef heron	*Egretta sacra*		Yellowhammer	*Emberiza citronella*
	White-faced heron	*Ardea novaehollandiae*		Greenfinch	*Carduelis chloris*

Waterfowl	Grey duck	*Anas superciliosa*
	Mallard duck	*Anas platyrhynchos*
	Paradise shelduck	*Tadorna variegata*
	Canada goose	*Branta canadensis*
Penguin	Little blue penguin	*Eudyptula minor*
Swamp	Australasian bittern	*Botaurus poiciloptilus*
	Pied stilt	*Himantopus himantopus*
Raptor	Harrier	*Circus approximans*
	Barn owl	*Tyto alba*
	Morepork	*Ninox novaseelandiae*
Parrot	Kaka	*Nestor meridionalis*
	Galah	*Eolophus roseicapilla*
	Eastern rosella	*Platycercus eximius*
	Silvereye	*Zosterops lateralis*
	North Island fantail	*Rhipidura fuliginosa*
	European goldfinch	*Carduelis carduelis*
	Chaffinch	*Fringilla coelebs*
Passerine	House sparrow	*Passer domesticus*
	Song thrush	*Turdus philomelos*
	Skylark	*Alauda arvensis*
	Welcome swallow	*Hirundo tahitica*
	New Zealand pipit	*Anthus novaseelandiae*
	Eurasian blackbird	*Turdus merula*
	Tui	*Prosthmadera novaseelandiae*
	Common starling	*Sturnus vulgaris*
	Indian myna	*Acridotheres tristis*
	Australian magpie	*Gymnorhina tibicen*

Table S2: Results of chi-square analysis, including statistical outputs of the test for the occurrence of each prey type in scats collected in each season, df = 3, n = 434.

Prey type	x^2 value	p-value
Rat	39.895	<0.001
Mouse	11.709	0.008
Bird	15.478	0.001
Egg	9.487	0.023
Orthoptera	110.6	<0.001
Coleoptera	3.456	0.326

Table S3: Results of chi-square analysis, including statistical outputs of the test for the occurrence of each prey type in scats deposited by each sex, df = 1, n = 243.

Prey type	x^2 value	p-value
Rat	6.64×10^{-31}	1
Mouse	0.028	0.866
Bird	2.376	0.123
Egg	2.111	0.146
Orthoptera	5.093	0.024
Coleoptera	0.004	0.949

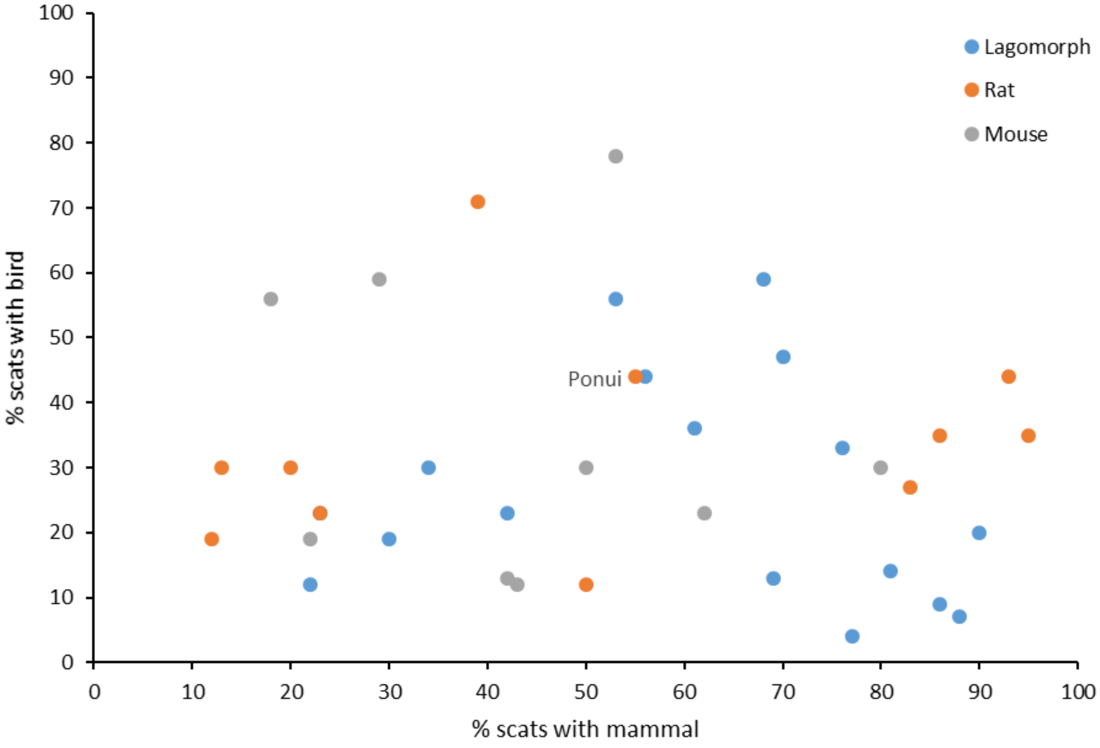

Figure S4: The percentage of occurrence of birds in relation to the percentage of occurrence of different mammal types (lagomorph, rat, and mice) in scats from Table 1. Ponui data from this study has been added and labelled.

Chapter 7 – Major findings and integrating aspects of feral cat ecology into effective control

Plate 7: Still from camera trap showing an encounter between an adult brown kiwi and a feral cat (Patches).

Synthesis

This thesis presents the most comprehensive study of feral cat ecology in New Zealand and provides information and knowledge of how the ecology of invasive species can be used to develop management strategies. I tested the home range versus population density relationship by using two male removals to detect changes in home range sizes of the remaining resident cats in response to these decreases in density. The first removal resulted in an increase in home range size of the resident cats, whereas the second resulted in four unmarked males immigrating into the population within three months of the male cat removal. I have shown that there is a high correlation ($R^2 > 0.9$) in activity patterns described using camera trap and collar-mounted accelerometry devices. Camera traps can be used to describe feral cat activity, provided there is enough data; 600 or more videos were needed where one camera was placed every 25 ha to study a feral cat density of 1.17 cats/km^2. I studied reproductive patterns of feral cats and found that females have on average two litters per year, and 3-4 kittens per litter. However, recruitment is low, with only 3-4% of kittens surviving to one-year-old. Two kittens died from infanticide and one was still born or died soon after birth. Kittens were moved between different dens as they developed; kittens were born in tight, enclosed areas, then moved to scrub areas when they were between 2-4 weeks old. Queens moved shorter distances when they had young kittens (less than seven-weeks-old), compared to when they were pregnant or had older kittens. Population genetics analysis suggests the Ponui Island feral cat population is genetically isolated and that there have been no recent introductions. Parentage analysis revealed that only a few males fathered kittens within the study site, and this was biased in favour of the heaviest males and those that overlapped the most with the queen. Dietary analysis using scats revealed the feral cats were consuming rats when the rats were at their highest density (winter), and consumed alternative prey at higher frequencies when rats were at their lowest density (summer). There were sex differences in diet with males consuming large-sized birds (>200g) more frequently than females, and females consuming more small-sized birds (<50 g) such as passerines.

Here, I outline a control programme for feral cats on Ponui Island to show how feral cat ecology can be used to develop control protocols.

Types of control for feral cats, and past eradications

There have been at least 102 successful and 17 unsuccessful eradications targeting feral cats on islands worldwide, with the remaining 27 eradications either planned, incomplete, or in progress (DIISE, 2015). Feral cat populations have been eradicated by employing several methods such as: poison baits, trapping, hunting/shooting, introducing viral diseases, and in one case, cats were run down and killed by hitting them with sticks (Nogales et al., 2004; Campbell et al., 2011). Most of the successful eradication operations used a toxin or a virus to reduce the feral cat population, and then used other techniques such as cage and leg-hold traps, and shooting to remove the final-remaining individuals. An initial knockdown with a toxin or virus is, however, feasible only on islands that are uninhabited by people (Nogales et al., 2004), or in mainland populations that are far from urban or built-up areas, due to the risk to house cats. The risk of pet cats contracting viruses can be reduced through the use of vaccines (e.g. feline panleucopenia (FPL)), however.

Past eradication attempts have failed because of insufficient effort or support, or methods were used that did not target all cats (Campbell et al., 2011). The removal of feral cats tended to be easier on small islands (<200 ha), however that does not mean that eradication of feral cats on small islands is always successful. More than 50% of the unsuccessful eradication operations were on small islands (Campbell et al., 2011).

Using knowledge of feral cat ecology to develop an eradication protocol for the population drastically increases the likelihood of successful eradication. For example, there were two eradications carried out on Tasman Island (Australia); one in the 1970s and another in 2010 (Campbell et al., 2011; Robinson et al., 2015). The first attempted eradication failed due to a lower rate of ingestion of 1080 (sodium monoflouroacetate) meat-baits than expected, most likely caused by the lack of knowledge of the seasonal diet of the cats on the island (Robinson et al., 2015). The cats could not be removed faster than they were reproducing, and after 3-4 years the attempted eradication attempt was placed on hold (Campbell et al., 2011). In 2009, the eradication of feral cats on Tasman Island was reconsidered. This time they carried out an eradication feasibility study that included assessing seasonal prey availability. They timed the aerial baiting to seasons of low prey availability when feral cats were more likely to have higher ingestion rates of bait (Christensen et al., 2013; Robinson et al., 2015). In 2010, PAPP (para-aminopropiophenone) meat-baits were used to primarily target feral cats, followed by trapping feral cats that did not die from poisoning (Robinson et al., 2015). This resulted in cats being successfully eradicated in just two weeks (Robinson et al., 2015). While Tasman Island is only 120 ha, feral cats were also eradicated from the much larger Faure Island (5,800 ha) using similar methods (meat-baits and trapping) and eradication was achieved in less than a month (Algar et al., 2010).

The eradication of feral cats from Tasman Island and Faure Island, as well as the unsuccessful eradication attempts, demonstrate how knowledge of feral cat ecology should be used to develop eradication procedures for the targeted population (Algar et al., 2010; Campbell et al., 2011; Robinson et al., 2015). A tailored eradication programme can reduce the associated costs and time, as well as increasing the chances of successful eradication.

How representative are Ponui Island feral cats of other populations?

The feral cat population on Ponui Island is similar to other feral cat populations in many aspects. I found that the density of feral cats on Ponui Island was 1.17 cats/km^2 (Chapter 2), which is similar to other populations in New Zealand, such as those studied in Orongorongo Valley (Fitzgerald & Karl, 1986), and Central Otago and the Mackenzie Basin (Norbury et al., 1998). The Ponui Island feral cats had similar home range sizes to those reported in previous studies (100% MCP, median ± IQR) of 428 ± 154 ha for males and 203 ± 75 ha for females (Molsher et al., 2005; Gillies et al., 2007), and also followed the home range versus density relationship (Chapter 2) (Liberg et al., 2000), suggesting that the Ponui Island population has similar constraints to other populations. Additionally, the male and female feral cats on Ponui Island were similar in body weight to those in other feral cat populations throughout New Zealand (Chapter 2).

One of the main differences between the Ponui Island population and mainland populations is the limited migration caused by its insular environment. I found that the Ponui Island population has unlikely had any new introductions in recent years (Chapter 5) compared with the continual gene-flow between neighbouring mainland populations (Cross, 2016); this level of genetic isolation was similar to that reported for other island populations (Pontier et al., 2005; Koch et al., 2014). Working with an insular population might have limited my ability to test the home range versus density relationship using the male removals. Increased immigration can result from removing individuals in a population and creating unoccupied areas, which is a response observed in mainland populations that have high connectivity with peripheral populations

(Keedwell & Brown, 2001). For these removals, my study site was the southern part of the island, which allowed me to study the immigration of cats from the northern part of the island.

Ponui Island differs from many other locations throughout New Zealand in being mustelid-free. Mustelids have a widespread distribution throughout mainland New Zealand but did not establish on as many offshore islands as feral cats (Clapperton & Byrom, 2005; Gillies & Fitzgerald, 2005; King, 2005; King & Murphy, 2005). Ponui Island is comparable to Stewart Island in that it also has no mustelids (Karl & Best, 1982). However, Stewart Island is much larger in landmass, and has a permanent urban human population. There is greater immigration potential for the feral cat population on Stewart Island since there is a larger population of house cats, which may increase the number of abandoned cats that could immigrate into the feral cat population (Aguilar et al., 2015). The targeted removal of mustelids from many areas (Parkes & Murphy, 2003) may result in more of New Zealand's ecosystems resembling that of Ponui Island. Mustelid removal would increase native bird populations, such as kiwi spp. (McLennan et al., 1996; Holzapfel et al., 2008), but removes inter-specific competition for feral cats. The removal of mustelids, but not feral cats, from many areas may result in ecosystems similar to Ponui Island. Thus, the Ponui Island feral cat population may be more representative of other feral cat populations that have mustelids removed in the future.

An integration of ecology and control

Control operations can have unforeseen cascading ecological effects (Chapter 1) as a result of the removal of a pest species from an ecosystem, and there are calls for more research before deciding to control or eradicate a species from an area (Doherty & Ritchie, 2017). There are three components that I argue are needed for successful feral cat control operations. For each step I will outline how knowledge of the ecology of the feral cat can be used, and will integrate results from the studies within this thesis as examples. These components are: 1) deciding to control a feral cat population; 2) implementing a control programme; and 3) predicting the recovery and reinvasion of a population.

Deciding to control a feral cat population

Impact on prey species

Diet studies can inform on the impact that feral cats are having on native species and whether they are controlling other mesopredators or invasive pests. Before eradication, there must be careful consideration of the predator-prey dynamics between feral cats and other invasive species, accompanied by modelling the effects of removing the depredation pressure imposed by feral cats on any invasive prey in the area. This will allow recognition of areas where the removal of cats could lead to mesopredator release, leading to higher depredation rates on native species. For example, the cat eradication on Ile Amsterdam was abandoned after the mesopredator release of rats and mice (Holdgate & Wace, 1961). However, diet studies prior to the cat eradication attempt would have been able to predict this trophic cascade.

On Ponui Island, I found that there was seasonal variation in the feral cats' diet that appears to be based on the availability of prey, as feral cats mainly consumed rats when these were at their highest density, and consumed more birds and alternative prey during seasons of low rat abundance (Chapter 6). The removal of rats on Ponui Island would certainly result in increased depredation pressures on native bird species. Feral cats preyed on a range of native bird species, eating almost 40% of the bird species that were available to them, two of which are declining nationally (Chapter 6). I also identified that feral cats were killing a large number of kiwi (estimated 228) each year. Both of these findings suggest feral cats are having a detrimental effect on native fauna. Considering the overall diet of feral cats on Ponui Island, only 53% of the scats contained rats, which was lower than that identified in other studies (Dilks, 1979; Karl & Best, 1982; Fitzgerald et al., 1991; Harper, 2002; Harper, 2005). The seasonal differences of prey items found in scats showed that feral cats mainly consumed rats while they were at their highest density. These results suggest that the eradication of rats from Ponui Island would not reduce the density of the feral cats through coupled predator-prey responses. Whereas, for example, an eradication of rats from Stewart Island may reduce the density of feral cats due to their higher reliance on rats as a main prey source (Harper, 2005). Harper (2005) found that feral cats had higher mortality and dispersal during times of low rat abundance. This difference between the responses by the feral cats on Stewart Island and Ponui Island to rat eradication may be due to Ponui Island having higher alternative prey availability, such as ground birds. Although Stewart Island has some similar bird species, the habitat type (mixed subalpine and forest habitat) may not allow feral cats to easily hunt the large bird species.

Eradication should not be solely based on past diet studies. In the 30 year period between the studies by Karl & Best (1982) and Harper (2005) on Stewart Island, birds and reptiles became less important in the feral cat diet, perhaps reflecting a change in vertebrate communities over the past fifty years, as noted by Harper (2009). This reinforces the need for up-to-date data on the diet of feral cats in each population before attempting eradication.

Diet studies can also identify the impacts that feral cats are having on native species. Studies that span different seasons can identify prey switching in feral cats. There are two important things to consider; the effect that removal of rats will have on feral cat populations (from Predator Free 2050), and how removal of feral cats will affect prey populations, such as rats. For example, Bonnaud et al. (2007) found that rats occurred in 70% of feral cat scats from Port-Cros Island, in the Mediterranean sea, and cats were also having negative impacts on seabirds. Although feral cats had high depredation rates on rats, there was no significant increase in rat activity following the removal of feral cats on the island (Bonnaud et al., 2010). This is most likely because that rat population was controlled by bottom-up processes (Bonnaud et al., 2010), and mesopredator release occurs in top-down regulated systems (Russell et al., 2009). Since the eradication of feral cats, the seabird population on Port-Cros Island is expected to increase because the eradication removed the depredation pressure on the seabirds without increasing the invasive mesopredator. An understanding of the predator-prey dynamics that were outlined in Chapter 1 allows for the prediction of how these eradications can affect other species in the ecosystem.

Secondly, if rats are not controlled before or concurrent with feral cat control, this poses the question; how will the removal of feral cats affect the densities of the main prey? Rats compete with kiwi chicks for food (Shapiro, 2005), and on Ponui Island, Wilson (2013) found that starvation was a main cause of mortality for kiwi chicks, signifying that food is a limiting resource for kiwi survival. Mesopredator release of rats through the removal of feral cats could have significant cascading effects; cat removal could increase rat densities, adding to higher invertebrate intake by rats, more competition for food between rats and kiwi, and potentially increased starvation of kiwi chicks. Mesopredator release occurs in systems that are top-down regulated (Russell et al., 2009), therefore, information on the factors (depredation pressure or food abundance) regulating the rat abundance would be needed to predict how the removal of feral cats could affect rat densities.

Feral cats are unlikely to be significantly reducing rat densities on Ponui Island, because they consume them based on their seasonal availability. Using data from Chapter 6, I estimated the number of rats that are likely to be consumed by the feral cat population in South Ponui Island. I used previous density calculations from Ponui Island to estimate the number of rats in the area in different seasons and coupled this with data on seasonal changes in the diet of the cats to estimate the number of rats eaten each season (Table 1 & 2). I estimated the number of female rats and how many young they would have produced, and added these numbers into the calculation to estimate the number and density of rats on South Ponui Island if there was no feral cat depredation on rats (Table 2). This showed that based on the seasonal variation in rat density, and the seasonal variation of consumption of rats by cats, feral cats are unlikely to have a large effect on the densities that rats reach in this study site. Therefore, the removal of feral cats is unlikely to result in mesopredator release of rats on Ponui Island, and will decrease the depredation of native species.

Dietary studies on the feral cats on Ponui Island reveal that this population is having a detrimental effect on many native species, particularly brown kiwi. This population should be eradicated because they are unlikely to be controlling the rat densities, and feral cat eradication would reduce the depredation pressures on native bird species.

Table 1: Number of rats depredated per season each year on Ponui Island by the feral cat population. This is based on the differences in the percentage of occurrence in feral cat scats between seasons, from Chapter 6. Note – there have been no estimates of rat density during autumn on Ponui Island.

	No. scats deposited per season	No. scats analysed	Percentage of scats analysed	No. rats eaten	No. rats per scat	No. rats eaten each year
Summer	720	128	0.075	48	0.38	270
Winter	736	92	0.063	74	0.80	592
Spring	728	93	0.064	51	0.55	399

Table 2: Number of rats on Ponui Island and estimated rat density with no feral cat depredation.

						With cat depredation		Without cat depredation	
	No. rats eaten each year	No. females eaten[1]	No. females that would be reproducing[2]	No. pups produced[2]	No. adults and pups surviving cat depredation	Rat density[3]	No. rats on island[4]	No. rats on island[5]	Rat density[6]
Summer	270	135	59.6	331	601	8.56	15151.2	15753	8.90
Winter	592	296	18.6	103	695	19.31	34178.7	34874	19.70
Spring	399	200	53.0	295	694	8.96	15859.2	16553	9.35

[1] Based on a 50:50 sex ratio.

[2] Estimated from average breeding parameters of ship rats in New Zealand forests (Daniel, 1972; Best, 1973; Innes, 1977; King & Moller, 1997; Innes et al., 2001; Efford et al., 2006).

[3] Average rat density for each season calculated from Shapiro (2005) and Latham (2006).

[4] Calculated from the average rat density (Shapiro, 2005; Latham, 2006) and the total island area (1770 ha).

[5] Calculated from the number of rats on the island with the additional adults that would not be depredated by feral cats, as well as the pups that would be produced.

[6] Calculated from the number of rats on the island if there was no cat depredation by the total island area (1770 ha).

Genetic isolation of the population

Population genetics allows the study of gene-flow and new introductions into the population (Ficetola et al., 2008). Assuming that island populations are genetically isolated is misleading. Abdelkrim et al. (2005) showed that there was gene-flow between populations of Norway rats (*Rattus norvegicus*) from different islands, leading to a concept of treating areas as eradication units as opposed to single island populations. This is an important concept to consider for proposed control or eradication programmes, because their long-term success will depend on the connectivity between the controlled and neighbouring populations. Genetically isolated island populations are ideal candidates for eradication due to their lack of immigration into the population (Bomford & O'Brien, 1995).

I investigated the genetics of feral cats on Ponui Island to determine whether the population was likely to be isolated, and found that there have likely been few or no new introductions of cats to the island in recent times (Chapter 5). On Ponui Island, an eradication of feral cats is likely to have long-term success because of the apparently low likelihood of reinvasion. My results are similar to the findings by Koch et al. (2014) who also found isolation of the Dirk Hartog Island (Australia) feral cat population from the mainland population. The high cost of eradicating cats from areas (Campbell et al., 2011), coupled with the lack of resources available for conservation work and pest control, means the identification of genetically isolated populations will increase the effectiveness of control programmes. Eradication programmes could focus on populations with the highest predicted success.

Although islands may be geographically isolated with low gene-flow, there is still the chance of reinvasion that is human-mediated. Feral cats were eradicated from Motuihe Island, also in the Hauraki Gulf, but were later reintroduced, most likely by people (Dowding et al., 1999). Releasing or leaving unwanted pet animals anywhere in New Zealand is illegal under the Animal Welfare Act (New Zealand Government, 1999), but this practice still occurs. This can lead to cats being reintroduced into newly eradicated areas. As this behaviour has continued, there is a need to further educate people about the risks of leaving unwanted cats to establish feral cat populations, and to educate pet owners about the importance of neutering their pets.

Once it has been decided that the removal of the feral cat population will not have negative cascading effects throughout the ecosystem, and that the area is unlikely to be recolonized by neighbouring cats, then a control programme can be implemented.

Implementing a control programme

Trapping and targeted poisoning as control methods

Feral cat populations that do not depredate rats, or where the rat population is not being eradicated, should be controlled using traps, targeted poisons (primary poisoning with laced meat-baits), or both. The primary poison that is most commonly used for feral cat control is 1080 (Nogales et al., 2004), and a mainland Australian feral cat population was reduced significantly through 1080 poisoning with laced meat baits (Short et al., 1997). There has been the recent development of a new toxin (PAPP or para-aminopropiophenone) that could be used in future eradication operations (Johnston et al., 2011; Eason et al., 2014). Primary poisoning of feral cats using meat-baits, though a common control method used in Australia (Glen et al., 2007), is not currently used in New Zealand, although this could be used in the future.

Trapping and targeted poisoning should coincide with low prey abundance and food shortage for feral cats because they are more likely to uptake poisoned baits or enter traps to eat bait during these times. An eradication attempt on Serrurier Island, that had only a single cat, failed because the two baiting attempts were carried out during the seabird breeding season when the feral cat was eating seabird chicks (Campbell et al., 2011), demonstrating that timing of baiting is important. Feral cats were successfully eradicated from Faure Island in three weeks most likely because aerial baits were spread on to the island during a period of predicted low prey availability (Algar et al., 2010). For a feral cat eradication on Stewart Island, baits targeting feral cats and trapping should be carried out when rats are at their lowest density (summer to autumn), because feral cats are predicted to have higher bait uptake due to low prey availability (Harper, 2005). However, bait uptake by feral cats is more difficult to predict on Ponui Island. Feral cats consumed alternative prey in higher frequencies during seasons when rat density was low, and did not have higher mortality or dispersal rates during these seasons, unlike Stewart Island feral cats (Harper, 2005). These findings suggest that on Ponui Island, there may not be an ideal season (when primary and alternative prey are low) to deliver targeted meat-baits for cats, and that bait uptake would most likely be constant throughout the year. It cannot be predicted whether this would result in a high enough bait uptake to be effective for this population.

Feral cats are commonly trapped during control programmes. For a demographically young population, Short et al. (2002) recommends that traps should to be set in the first half of the year to target recently weaned sub-adults. This technique could be useful for populations with high recruitment rates such as those on Marion Island, Dassen Island, and in Shark Bay (Western Australia) (Apps, 1983; van Aarde, 1983; Short et al., 2002). Targeting the large number of kittens and sub-adults that survive to independence and are weaned has the potential to reduce the recruitment rate and the population size. However, this would not be productive for stable populations with low kitten survival and recruitment, such as the Ponui Island population, which had only 29% of the kittens weaned (at 14-16 weeks old) surviving to one-year-old (Chapter 4). This is because the majority of kittens (76%) die naturally before they reach two-weeks-old. Therefore, it would be more productive to target trapping towards adult cats.

Knowledge of the home range size and overlap in the feral cat population can be used to determine the optimal spacing of traps for control programmes (Bengsen et al., 2012). Bengsen et al. (2012) found that feral cats on Kangaroo Island (Australia) had an average home range size of 480 ha (range = 287-818) for females and 780 ha (range = 194-1922) for males. Bengsen et al. (2012) suggested 770 m as the minimum spacing between traps for the Kangaroo Island population, based on the radius of the smallest home range in the study. Applying the method used by Bengsen et al. (2012), the smallest home range radius was 400 m for the Ponui Island feral cats, which would be the optimal trap spacing for this population. This logic could also be applied to other feral cat populations. I found a strong correlation (R^2 >0.75) between the density of the feral cat population and the home range size of the residents in both mainland and island studies (Chapter 2). This means that if the density of the cat population is known, then the home range of the resident cats could be estimated from the home range versus density relationship, and the estimate could be used to determine ideal trap spacing for the population.

On Ponui Island, the male feral cats had a significantly larger home range size (100% MCP) of 428 ± 154 ha (median ± IQR) than the females who had an average of 203 ± 75 ha (Chapter 2). Males overlapped in home range more than females, and my results for home range size and overlap were similar to previous studies (Turner & Mertens, 1986; Biró et al., 2004; Gillies et al., 2007). Female feral cats have more exclusive home ranges than males, and also have smaller home ranges, therefore trap placement should be based on female home range size rather than that of the males. More males are caught in live-trapping studies (Appendix B) than females (2:1, male:female), despite the sex ratio of feral cat populations being typically 1:1 (Appendix D). If traps are set too far apart, then this is likely to exacerbate male bias in trapping, because male feral cats have larger home ranges (Chapter 2) and higher activity levels (Chapter 3) than females.

Biased removal of male feral cats should be avoided for two reasons; 1) Removing males will alleviate some of the depredation pressure on large-sized prey, but not on passerines or other small birds that are depredated more frequently by female feral cats (Chapter 6). 2) The removal of mainly males will reduce intra-specific competition between males for mating opportunities. This could lead to lower incidences of infanticide, increasing the number of kittens that survive and are recruited into the population (Chapter 4), potentially increasing the population size.

The initial population reduction (or “knockdown”) for control programmes should be done as quickly as possible to reduce the immigration of cats into the newly vacated areas (Parkes et al., 2014). The removal of two male cats on Ponui Island (Chapter 2) resulted in new cats moving into the newly unoccupied area within a month of the second resident cat being removed. Thus, my results suggest that the knockdown phase should happen within a month.

Parkes et al. (2014) also recommended that the knockdown phase should be fast to limit recruitment into the population. Females on Ponui Island had a seasonal pattern to reproduction, with the majority of pregnancies occurring from September - April (Chapter 4). Females moved shorter distances when they had young kittens (less than seven-weeks-old) than when they were pregnant or had older kittens. I recommend that trapping for feral cat control on Ponui Island is carried out between June and August. This would increase the chances of females encountering traps, and would remove females before the breeding season.

Traps and baits should be placed in areas that feral cats frequent the most. Bengsen et al. (2012) found that the feral cats on Kangaroo Island preferentially used woodland habitats and avoided open pasture, suggesting that feral cat control should be targeted towards woodland habitats for that population. On Ponui Island, the home ranges of feral cats contained all three habitat types: forest, scrub, and pasture (Chapter 2). I found habitat type, location (gully or ridge), and trail width were habitat features that had a significant influence on cat activity at camera traps (Chapter 3). These results could be used to target certain locations for trapping, such as those on ridges, in scrub and forest habitats, and on wide trails (<3 m) (Chapter 3).

Feral cats are most active between sunset and sunrise, and visited traps during these times (Chapter 3). Traps should be set at these times to increase trapping efficiency, and reduce bycatch of non-targeted species. House cats are more active during the day than feral cats (Lincoln, 2016) so, the chances of capturing a house cat during the day are high. In human habited areas, to reduce the chances of capturing house cats rather than feral cats, live-traps should be set between 16:00-07:00 h. I also recommend that house cats in areas with active feral cat control should be locked in the house while the traps are set.

Secondary poisoning as a control method:

Targeting both feral cats and rats concurrently could be an option for control if rats are a large component of the feral cats' diets. Secondary poisoning of cats is dependent on feral cats consuming poisoned rats. The dietary studies undertaken to decide that the feral cat population should be controlled can be used to determine the best time for poison drops. Secondary poisoning of feral cats should not be the only method used to eradicate cats. This method can have unpredictable results (Campbell et al., 2011). Secondary poisoning mainly reduces cat numbers, and has only led to one successful eradication, which was on Tuhua through secondarily poisoning cats through rats (Campbell et al., 2011).

Secondary poisoning of feral cats with brodifacoum is not recommended as a control method due to the low secondary mortality of feral cats and high rates of secondary poisoning of non-target native species (Dowding et al., 1999; Gillies & Pierce, 1999; Eason et al., 2002). Secondary poisoning of cats with brodifacoum does not cause very high mortality rates in cats (Alterio, 1996), and has lower mortality rates than secondary poisoning with 1080 (Gillies & Pierce, 1999; Heyward & Norbury, 1999). Feral cats do not often eat carrion, so secondary poisoning is dependent on cats eating rats that are dying from poisoning. Brodifacoum takes a long time to kill rats (approximately one week), which increases the chances of the cats consuming poisoned rats (Eason & Wickstrom, 2001). However, feral cats need to consume a large number of poisoned rats to obtain a lethal dose of brodifacoum, since the LD50 (lethal dose to kill 50% of the population) for rats is 0.36-0.56 mg/kg body weight and 25 mg/kg body weight for cats (Rattner & Mastrota, 2018). While 1080 kills rats faster (6-48 hours) than brodifacoum, feral cats are more sensitive to 1080, and do not need a large dose to die from it; 1.2 mg/kg LD50 for rats, 0.3 mg/kg LD50 for cats (Eason & Wickstrom, 2001; Eason et al., 2011).

Secondary poisoning may only be successful if the feral cats depend heavily on rats as a main prey source. For example, Dowding et al. (1999) found that only 21% of the monitored feral cats on Motuihe Island died from secondary brodifacoum poisoning, which may have been due to the high densities of rabbits on the island. Dowding et al. (1999) concluded that feral cats may have been eating mainly the muscle of rabbits rather than the internal organs, so were unlikely to obtain a lethal dose of brodifacoum from rabbits. Poison drops targeting the main mammalian prey of the feral cats should be timed so the baits are dropped when the cats are likely to have the highest consumption of the poisoned prey. On Ponui Island, poisons targeting rats should be aerially-dropped during or just before winter. This is because 80% of the feral cat scats collected in winter contained rats.

The most effective control method for the Ponui Island population would most likely be trapping. This is because there are an estimated 20-30 individuals on the island, and this is likely to be the most cost-effective method. The feral cats on Ponui Island have a higher consumption of alternative prey during seasons of low rat availability, therefore, it is difficult to predict the bait uptake by the cats. Secondary poisoning would not be recommended unless the rats are also being eradicated, and 1080 would be recommended rather than brodifacoum, due to its higher mortality rate in feral cats.

Predicting the recovery and reinvasion of a population

The last step of a control programme is monitoring the area to determine the programme's success, and estimate the rate of recovery of the population in the case of eradication failure. Knowledge on the reproduction of invasive species can be used to estimate the recovery of a population (Byrom, 2002).

One of the key factors identified by Bomford & O'Brien (1995) for control or eradication of pests is that the rate of removal must be higher than the rate of replacement. Feral cats generally have two litters per year, and in the stable Ponui Island population, only 3-4% of the kittens survived to recruitment (one-year-old) (Chapter 4). My results were contrary to the feral cat populations studied on Marion Island and Dassen Island, where half of the population was less than one-year-old (Apps, 1983; van Aarde, 1983). The Dassen Island population was increasing at the time of that study following a large culling effort (Apps, 1983), suggesting that the control of a population leads to higher survival of juveniles and increased recruitment, leading to rapid recovery of the population after control measures. This means that feral cat populations have the ability to increase rapidly in size following control programmes.

I found infanticide to be a cause of mortality in the Ponui Island feral cat population (Chapter 4), and potential multiple paternity within the population (often used as a counterstrategy to infanticide) (Chapter 5) indicates that infanticide may be a reproductive tactic in this feral cat population (Wolff & Macdonald, 2004). The removal of cats, particularly males, through control programmes, reduces the competition between males for mating opportunities, and may reduce infanticide, leading to more kittens surviving. Therefore, feral cat populations need to be reduced quickly (rapid knockdown) and eradicated, otherwise there will be a need for ongoing control. For example, the attempted eradication of feral cats from Tasman Island during 1977-79 was unsuccessful due to a lack of concentrated effort meaning that the cats were reproducing faster than they were being removed from the population (Campbell et al., 2011).

The removal results from Chapter 2 also lend further support that feral cat populations should be reduced in size as quickly as possible, due to the uncertainty of movements of resident cats to the change in population density. Feral cats may increase their home range size in response to the reduction in density, or there could be reinvasion by peripheral cats. Immigration into a population would mean that there would always be a need for continued monitoring and control of the population, and eradication would not be possible (Bomford & O'Brien, 1995).

To summarise, the method that would be the most appropriate for the Ponui Island feral cat population is trapping. Trapping should occur from June to August, and traps should be placed at a minimum distance of 400 m apart to ensure every cat encounters a trap. Traps should be set between 16:00-07:00 h, and placed on ridges, in forest and scrub habitat, and on wide trails, considering these habitat features were associated with higher cat activity. If primary poisoning using meat-baits is adopted as a control method in New Zealand, then this method could be used. However, bait uptake is predicted to be consistent throughout the seasons due to the feral cats consuming alternative prey at higher frequencies during seasons when rat densities are low, making it difficult to predict when the baits should be applied to the island, and whether it would be successful. Secondary poisoning would only be recommended if the rats on the island are also being eradicated. 1080 rather than brodifacoum should be used due to the higher mortality of feral cats by secondary 1080 poisoning than secondary brodifacoum poisoning. Cereal-baits containing 1080 should be dropped on the island during winter when the feral cats have the highest consumption of rats. Due to the unpredictability of secondary poisoning, trapping should be carried out at the same time as the poisoning.

Future research and challenges arising from this thesis

The main challenge that I faced during this thesis was the size of the Ponui Island feral cat population. I had small sample sizes for most of my studies despite trapping the majority of the cat population in the southern end. The small sample size presented many statistical challenges and made inferences from the data difficult. This was especially true for the work in the feral cat reproduction chapter, where I was limited to the three resident females in the study area and only one that was successful at raising kittens to weaning age (14-16 weeks old). I had a small number of kittens to monitor and measure, and the high juvenile mortality rate created further difficulties in obtaining data for kittens aged five weeks or older. Despite this, the small dataset that was collected on kitten growth has raised some interesting questions in relation to the difference in growth rates between young wild- and captive-raised individuals. This difference seems not to have been reported before. Surprisingly, feral kittens aged between 1-5 weeks-old weighed more, on average, than the colony kittens. This should be investigated further to determine if this is common in other feral cat populations, and to investigate the mechanisms that are driving this difference.

Another challenge was that I could only remove one cat and rely on the natural death of another to study the home range versus density relationship, due to the small size of the feral cat population. I had interesting results from the removals that could be used in managing feral cat populations, and the relationship between home range versus density should be explored further. I only studied the removal of male cats but it would be interesting to investigate what effect removal of a female has on the home range sizes of other resident females or males, and on the immigration rate of other cats into the study population. Future studies should repeat similar removals with a larger cat population to determine how many cats need to be removed to achieve this vacuum effect.

Unfortunately, I was unable to manipulate the rat density to investigate prey switching in these feral cats because the endangered North Island brown kiwi (*Apteryx mantelli*) inhabits Ponui Island. Before this study, it was not known how the removal of cats could have affected the rat population, and whether it would lead to an increase in depredation pressure on kiwi as well as other native species. Instead, to test the level of prey switching occurring, I measured seasonal changes in diet. Due to time constraints, I could not measure the seasonal prey density, nor how this change was reflected in feral cat diet, and instead relied on previous studies on Ponui Island.

Concurrent monitoring of kiwi chicks with the feral cats would have allowed for a better estimate of the impact feral cats have on kiwi. Given the large number of feral cat scats that had kiwi remains in them during the kiwi breeding season, I recommend the need for further studies on feral cat diets during the kiwi breeding season in other populations where both species coexist, particularly in areas where there are no mustelids such as on Stewart Island.

Concluding remarks

Feral cat ecology needs to be incorporated into control protocols using similar methodology to that used for the Ponui Island population. The impacts of feral cats on native species should not be underestimated. Although there is difficulty with gaining support from the public for feral cat control, as conservationists we cannot ignore these findings that feral cats are having devastating impacts on our native fauna, and they need to be targeted for control and eradication. We need more stringent laws with house cat ownership, and targeted control towards feral cats, before we lose more species to feral cat depredation.

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Appendix A: List of conference presentations and other works from this thesis.

2018

- Society of Conservation Biology (Oceania) (Wellington) – *Capturing the purr-petrator: Feral cats and predation on native birdlife.*
- Ornithological Society New Zealand (Waitangi) – *Rats, kiwi, and native birds: What's really in a feral cat's diet?*

2017

- Australasian Wildlife Management Society Conference (Sydney) – *A test of the home range and density relationship in feral cats.*
- Australasian Wildlife Management Society Conference (Sydney) – *Who's your daddy? A confirmation of parentage for an infanticide case in feral cats.*
- Massey University Institute of Agriculture & Environment Symposium (Palmerston North) – *Infanticide and juvenile survival in feral cats.*
- International Mammalogical Congress (Perth) – *Feral cat activity, home range, and density: What happened when cats are removed?*
- Massey University Wildbase Symposium (Palmerston North) – *Reproduction in an island population of feral cats.*

2016

- Wildlife Rehabilitators Network New Zealand Conference (Palmerston North) – *Activity patterns of feral cats: Implications for kiwi.*
- Australasian Wildlife Management Society Conference (Auckland) – *The activity of feral cats: A comparison of camera traps and accelerometers.*
- Wildlife Society of New Zealand Veterinary Association Conference (Christchurch) – *The sordid lives of Ponui Island cats.*
- Massey University Wildbase Symposium (Palmerston North) – *The feral cat: A deadly predator.*

2015

- New Zealand kiwi hui (Whangarei) – *Kiwi and cats after dark: Camera trapping for behaviour and interactions.*
- Camera trap footage of North Island brown kiwi used in BBC documentary: *Attenborough's Big Birds.*

2014

- Wildlife Society of New Zealand Veterinary Association Conference (Wanaka) – *What kiwi and cats get up to after dark: A pilot study using trail cameras.*

Appendix B: Information on previous studies collaring feral cats

Summary of studies on methods used to collar domestic cats worldwide, with a focus on feral cats. - Not stated in study. Information includes the type of anaesthetic used and any reversing agent. For studies that used GPS devices on collars, the fix rate (number of location fixes) is stated. For VHF studies, the method used to locate the cats is stated.

Citation	Location	Cats	Collar Type	Sedation	Reversing Sedation	Trapping	Bait	TX Weight	Location Detection	No. of Cats	No. Males	No. Females	Length of Study	Fix rate
Algar et al. (2010)	Dirk Hartog Is. Australia	feral	GPS and VHF	4mg/kg Zoletil 100	-	Soft catch leg hold traps	Cat faeces and urine	105g	GPS	15	13	8	March-May 2009	10, 40 & 80 mins
Apps (1986)	Dassen Is., South Africa	feral	VHF	10 mg/kg ketamine hydrochloride or a mix of 10mg/kg ketamine hydrochloride and 5 mg/kg xylazine	-	Cage traps	Fresh rabbit	-	Location and sightings	8	5	3	Mar 1979 – Jun 1980	Once daily
Bengsen et al. (2012)	Kangaroo Is., Australia	feral	GPS	150 µg kg^{-1} medetomidine hydrochloride (Domitor)	Atipamezole hydrochloride (Antisedan)	Live cage traps	Chicken wings or tinned fish	137-154g	GPS	16	9	4	Apr-Oct 2010	2 or 5 hours

Biró et al. (2004)	Godollo, Hungary	feral	VHF	Xilazin HCl: Ketamin HCl = 2:5 0.1ml/kg	-	-	-	-	Triangulation with tower antennae, and direct tracking	3	1	2	8-11 months in 1990-93	-
Burrows et al. (2003)	Gibson Desert, WA, Aus	feral	VHF	-	-	Padded jaw leghold traps and treddle snares	-	-	Triangulation from vehicle, and following on foot		2	1	6 days tracking	From every 2 hours to twice a day
Edwards et al. (2001)	Northern Territory, Aus	feral	VHF	Ketamine or Xylazine at 0.1ml per kg of body mass	-	Hook cage traps and Victor 1 Soft Catch traps	Kangaroo meat or commercial cat food	115g	Honing in	19	8	2	Jul 94 – Dec 97	Once every 2 weeks
Fitzgerald & Karl (1986)	Wellington, NZ	feral	VHF	Ketamine 10mg per 1kg	-	Drop-door cage traps	Fish heads	25g	Honing in to within 10m	9	4	5	Apr 81 – May 83	Morning and afternoon fixes
Gillies et al. (2007)	Trounson Kauri Park, Northland, NZ	feral	VHF	Ketamine (100mg/ml)	-	Drop door cage traps	Rabbit and hare meat	-	Triangulation	45	14	7	Jan 96 – May 00	Once per day
Harper (2007)	Rakeahua Valley, Stewart Is. NZ	feral	VHF	Domitor (0.23 mL/kg)	Antisedan	Victor 1.5 soft catch traps	Thawed frozen fish	33g and 45g	Triangulation	22	16	9	Feb 00 – Jun 01	Once or twice per day for 4 weeks per season
Hilmer et al. (2010)	Dirk Hartog Is. Australia	feral	GPS and VHF	Zoletil 100	-	Padded leg hold traps	Cat faeces and urine	105g	GPS	8	5	3	3 weeks	10 min

Horn et al. (2011)	Champaign-Urbana, Illinois, USA	House and feral	VHF	0.08mg/kg Domitor or 1-2.2mg/kg Anased	0.2mg/kg Antisedan	Tomahawk live traps	Sardines	<3% body weight	Triangulation	42 (24 feral, 18 house)	6	10	Jan 07 – May 08	2x week
Johnston et al. (2011)	French Is., Dirk Hartog Is., Christmas Is.	feral	VHF and GPS	4mg/kg Zoletil 100	-	Victor soft catch leg hold traps	Cat faeces and urine, and Felid attracting phonic (FAP)	130g	Antenna attached to vehicle	33	6	4	Feb 08-Jul 08, Mar 09 – May 09	-
Jones & Coman (1982)	Vic, Aus	feral	VHF	Ketamine	-	Cage traps and padded-jaw rabbit leghold traps, also used dogs	-	-	Honing in and visualisation	6	4	2	8-21 months	Once a week or fortnight, some for 5 consecutive days for 8 weeks
Konecny (1987)	Galapagos Is	feral	VHF	Ketamine	-	Tomahawk double-end, live traps	Tuna	-	Honing in and visualisation	14	10	4	Cats followed for 2 weeks to 6 months	Every hour for 6 hour bouts
Martin et al. (2013)	Kerguelen archipelago, Sub Antarctic Islands	feral	GPS and VHF	15mg/kg Ketamine and 0.5mg/kg Acepromazine (Vetranquil)	-	Double-door cages	Fresh rabbit meat	165g	GPS	3	3	0	Dec 09 – Jan 10	5 mins

Metsers et al. (2010)	Otago and Canterbury	house	GPS	-	-	-	-	125-130g	GPS	38			10 days	15 mins
Moller & Alterio (1999)	Otago Peninsula, NZ	feral	VHF	-	-	Collapsible wire-mesh cages and soft-catch Victor traps	Lagomorph meat	-	Triangulation	11	7	3	Jun-Oct 1992) and (Apr-May 1995)	1-2 locations each night or day
Molsher et al. (2005)	NSW, Australia	feral	VHF	Ketamine and Rompun (xylazine HCl) 0.1mg/kg or Domitor on small cats	Antisedan when Domitor used	Wire mesh cages and Victor soft catch leg-hold traps	Rabbit flesh	42g	Triangulation and direct sighting	21	15	6	May-Aug 1995	
Moseby et al. (2009)	South Australia	feral	GPS and VHF	Ketamine and Domitor	Antisedan	Victor Soft-Catch rubber jawed leg-hold traps	Cat urine and FAP (felid attracting phonics)	135g	Aeroplane and aerial to get general location and mortality signal	13	10	3	Apr-Aug 2006	4 hours
Norbury et al. (1998)	Central Otago and Mackenzie Basin	feral	VHF	0.5-1.0 ml Ketamine and Xylazine	1 ml yohimbine hydrochloride	Cage traps	Rabbit meat	48g	helicopter	28	11	14	Mar 94-Mar 96	Once every 7-34 days
Recio et al. (2014)	Godley Valley, SI, NZ	feral	GPS and VHF	0.23-0.38ml Ketamine (100mg ml^{-1}) and 0.24-0.40ml	0.12-0.20ml Antisedan	Collapsible live animal traps and soft catch leg holds	Rabbit meat and dry/wet commercial cat food	125g (used cats > 2.5kg)	GPS	21 (34 trapped)	19	15	1 year	15 minutes (for 15 days)

				Domitor (1mg ml^{-1})										
Recio et al. (2010)	Tasman Valley, NZ	feral	GPS	0.23-0.38ml Ketamine (100mg ml^{-1}) and 0.24-0.40ml Domitor (1mg ml^{-1})	0.12-0.20ml Antisedan	Collapsible live animal traps and soft catch leg holds	Rabbit meat and dry/wet commercial cat food	125g	GPS	5 (one tracked twice)	4	1	May-Aug 2005	15 mins

References for Appendix B:

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Appendix C: Endoparasites identified in scats and gut contents from Ponui Island feral cats.

Endoparasites (such as nematodes) that were found in scat samples and in the gastrointestinal tract of dead cats were placed into separate containers with 70% ethanol for identification. *Toxocara* species were identified by their cephalic alae (Fisher, 2003; Mikaeili et al., 2013). All other species were taken to parasitologists for identification using morphological features.

Parasitic nematodes and cestodes were found in 22% of the total scats analysed (n = 432); only 66% of the total number of the parasites could be identified as the rest were partially broken up and unidentifiable. *Toxocara cati* represented 95% of the nematodes that could be identified. Two stomachs from dead cats also had *T. cati* present, with one containing 52 individuals. Seventeen *T. cati* were found in one scat. Two nematodes in one scat were identified as belonging to the genus *Mastophorus*. Two parasitic worms were cestodes, with one identified to species level: *Taenia taeniaeformis.*

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Appendix D: Sex ratio of feral cat populations

Table 1: Sex ratios of feral cat populations from eradications. The sex ratio of feral cat populations was calculated from eradication programmes where the cats were either shot or trapped, and the sex ratio was reported. The eradications that were examined were from the reviews on feral cat eradications by Nogales et al. (2004) and Campbell et al. (2011), as well as feral cat eradications reported on the Database of Island Invasive Species Eradications (DIISE, 2015).

Study	Location	Males	Females	Sex ratio (males : females)	Comments
Fitzgerald & Veitch (1985)	Herekopare Island	20	13	1.54:1	
Veitch (2001)	Little Barrier Island	21	45	0.47:1	Disease released, so not all of population and 4 cats might have been poisoned
Hayde (1992)	Great Dog Island	95	93	1.02:1	
Domm & Messersmith (1990)	North West Island	46	34	1.35:1	
Beaver & Mougal (2009)	Cousine Island	33	40	0.82:1	
Rauzon et al. (2008)	Wake Islet (Wake Atoll)	46	51	0.90:1	Some unknown sex
Rauzon et al. (2008)	Wilkes Islet (Wake Atoll)	12	7	1.71:1	Some unknown sex
Rauzon et al. (2008)	Peale Islet (Wake Atoll)	10	12	0.83:1	Some unknown sex
Robinson & Copson (2014)	Macquarie Island	358	378	0.95:1	
Rauzon (1985)	Jarvis Island	52	56	0.93:1	Maximum of 41% cats on island died from released disease. Rest hunted

References for Appendix D:

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