

Spatial behaviour of predators on the Predator Free 2050 target list

March 2025

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Manaaki Whenua Contract Report: LC4586

Prepared for: Department of Conservation

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Summary

Project and client

- Predator Free 2050 (PF2050) is a national programme to eradicate ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), kiore/Polynesian rats (*R. exulans*), weasels (*Mustela nivalis*), stoats (*M. erminea*), ferrets (*M. putorius furo*), and brushtail possums (*Trichosurus vulpecula*) from New Zealand by 2050.
- In anticipation of programme roll-out by 2030, the Department of Conservation (DOC) commissioned Manaaki Whenua – Landcare Research to review the spatial behaviour of predators that survive or reinvade eradication areas.

Methods

We used published and unpublished evidence in New Zealand and overseas to address the following questions for each predator species on the target list.

- 1 How do predators use landscapes, particularly when their densities are reduced to very low levels?
- 2 Which microhabitats do they prefer?
- 3 How do predators use landscapes during dispersal and reinvasion?

What are the key knowledge gaps in 1–3, and how can they be addressed?

Review findings

- Home range size varies greatly both within and between predator species. Variation within a species depends on a multitude of factors, including sex, time of year, conspecific density, food availability, habitat type, and the presence of dominant competitors or predators.
- As predator densities decline with elimination attempts, home ranges tend to expand. Survivors are therefore more likely to encounter (although not necessarily interact with) toxic baits, removal devices, or detection devices. Robust mathematical relationships between population density and home range size have been derived only for ship rats and possums.
- Home ranges also tend to be larger in sub-optimal habitats where food is less abundant and conspecific densities are low, and larger where dominant competitors or predators are scarce or absent.
- Predators do not use landscapes randomly but focus their movements on a wide range of landscape features and vegetation types, depending on the predator species. There is some evidence that predators' preference for microhabitats increases with declining conspecific densities and with increasing presence of dominant competitors or predators.
- The maximum dispersal distances that have been recorded for ship rats are 1.5 km; Norway rats, 1.3 km; weasels, 17.4 km; stoats, 65 km; juvenile ferrets, 45 km; and possums, 41 km. The pathways and habitats used by dispersers have rarely been studied.

- While much has been published on the spatial behaviour of most of the predator species reviewed here, there are knowledge gaps that limit the ability to eliminate any of them on the mainland.

Knowledge gaps

- Movements of survivors and reinvaders at near-zero densities, including where survivors aggregate in the landscape.
 - Given the difficulty of researching predator behaviour at very low densities, further experimental releases of telemetered animals into areas with very few – or zero – conspecifics are recommended, either by trapping and collaring survivors, or by capturing animals and releasing them back into their original range after a management operation. Potential reinvaders could be studied by trapping and collaring animals from adjacent areas.
- Detectability of survivors and reinvaders at near-zero densities across a range of devices, lures, and habitat types.
- Reinvasion pathways, including the extent to which certain landscape features block, hinder, or facilitate dispersal.
 - These can be investigated by tracking animals or using genetic kinship techniques.
- Dispersal behaviour in general is poorly understood, especially for Norway rats, kiore, and weasels.
- Efficacy of buffer zones of control in intercepting potential invaders.
 - Test different spatial distributions of traps versus bait stations, including potential non-lethal deterrents.
- Effects of interactions between predator species, such as dominance and competition, on predator detectability and how they use landscapes.
 - For example, subdominant species may expand their movements and be more detectable after the dominant species is removed.
- The ecology of weasels and kiore in New Zealand is largely unknown.
- Distribution of Norway rats, kiore, and weasels in New Zealand.
 - eDNA techniques would be a useful approach.
- Reliable GPS collars/tags for small mammals.
 - Unlike those for possums and cats, there are currently none available with acceptable battery life, accuracy, and cost for mustelids and rodents.

Operational recommendations

- The smallest home ranges for a given species (usually females) should guide the minimum density of toxic baits, removal devices, or detection devices needed to ensure at least one bait or device in every home range.
- Basing the density of kill devices or toxic baits on minimum home range size is expensive, but necessary for elimination purposes. Whilst there may be potential cost savings for predator suppression projects by reducing device or bait density according to the conditions that expand home range size, we advise against this for elimination projects. This is because of other density-dependent behaviours that counter the ability

to remove every animal, such as avoidance by some individuals of lethal devices or baits as population density is reduced.

- Deployment of toxic baits, removal devices, or detection devices should be intensified in the preferred microhabitats identified in this report.
- The width of buffer zones around elimination areas is usually guided by home range size or maximum dispersal distances of the target species. However, the effectiveness of buffer zones is more likely to be a function of the probability of predators interacting with toxic baits or removal devices within the buffer, rather than the width of the buffer. For example, a buffer zone that eliminates every animal does not need to be wide, whereas an inefficient buffer does. A cost-benefit analysis of the acceptable number of incursions into an elimination zone per unit time, and the number of repeated removal treatments, is needed.

A Glossary of common terms is provided at the end of this publication.

1 Introduction

Introduced mammalian predators are highlighted as significant biological pressures in Te Mana o Te Taiao – Aotearoa New Zealand Biodiversity Strategy 2020 (Department of Conservation 2020). Predator Free 2050 (PF2050) is a national programme to eradicate rats, possums, and mustelids from New Zealand, which sits within a group of national programmes intended to advance the goals of the Strategy. However, PF2050 is currently not ready for roll-out and is focusing in the near term on developing new tools and approaches through research and innovation.

During the scoping processes in developing the draft PF2050 Knowledge and Innovation Plan, spacing and movement behaviours of target species were identified as priority research gaps to optimise detection of survivors and invaders. For example, as population densities are reduced, individuals may use space differently by extending their normal home ranges or aggregating in certain habitat patches within a landscape, particularly in variable landscapes such as urban and production environments. Similarly, in the reinvasion context, natural and artificial landscape elements may act as barriers or pathways for dispersal. Understanding how target species use landscapes can inform the optimal distributions and densities of toxic baits, removal devices, and detection devices.

This report reviews the national and international literature, and available unpublished data, to address the following questions:

- 1 How do predators use landscapes, particularly when their densities are reduced to very low levels?
- 2 Which microhabitats do they prefer?
- 3 How do predators use landscapes during dispersal and reinvasion?
- 4 What are the key knowledge gaps in 1–3, and how can they be addressed?

This report will inform a technical workshop planned for early 2025, aimed at developing multi-year research plans to support PF2050's Research Priority 4.2: 'Reduced reinvasion – Increasing the effectiveness of barriers to reinvasion (natural, artificial and combined).' The report also informs Priority 3.1: 'Improved survivor and invader detection.' And, finally, this report also contributes directly to the PF2050 2030 Objective 2: 'We know how to cost-effectively defend boundaries in diverse mainland habitats to prevent the re-establishment of target species.'

2 Methods

We used published and unpublished scientific evidence in New Zealand to address the above questions for each predator species on the current target list (ship rats *Rattus rattus*, Norway rats *R. norvegicus*, kiore/Polynesian rats *R. exulans*, weasels *Mustela nivalis*, stoats *M. erminea*, ferrets *M. putorius furo*, and possums *Trichosurus vulpecula*). We also searched the international literature on the spatial behaviour of *Rattus* spp., *Trichosurus* spp., and species from the Mustelidae family. We used Google Scholar for the international literature search, which has the advantage of revealing records of scientific reports and student theses, as well as papers published in scientific journals. Keywords used for the search included the combination of '*Rattus*' or '*Trichosurus*' or '*Mustela*' and 'space use and population density' or 'microhabitat' or 'dispersal.' The review for *Mustela* yielded 36 articles, which was the highest among the three taxa, followed by 26 for *Rattus* and 21 for *Trichosurus*. Literature on *Trichosurus* spp. outside New Zealand was, naturally, all published in Australia, while those for *Mustela* were mostly from Europe, and for *Rattus* from across the world.

3 Predator species reviews

3.1 Ship rats (*Rattus rattus*)

Home range: Ship rat home range size is inversely related to population density and food supply. In New Zealand, ship rats occur in non-colonial home ranges spread across landscapes, although with 'moderate patchiness' (Watkins et al. 2010). In New Zealand, at typical mainland densities of 2–9 ship rats/ha, males' home ranges are larger (0.1–1 ha, 159–500 m range length) than females' (0.08–0.7 ha, 103–171 m) and females' ranges are exclusive while males overlap with several females and with other males (Innes & Russell 2021). In a low-density population in beech forest in the Eglinton Valley, range lengths were 400–700 m for two males and 200 m for a female. Conversely, on Big South Cape Island where and when densities were very high (up to 36 rats/ha), home ranges were very small (mean 0.06 ha for females; Harper & Rutherford 2016).

At the 3,400-ha pest exclusion fenced area at Sanctuary Mountain Maungatautari in the Waikato, up to 14 pest mammal species were targeted for eradication with aurally distributed brodifacoum, first in two smaller exclosures (of 35 ha and 65 ha) in Sept 2004 and then over the whole mountain in November 2006. Seven ship rats were subsequently tracked and trapped in the resulting low density population during November 2004 to March 2006. Several lines of evidence suggest that these were survivors rather than reinvaders. None had signs of the rhodamine B dye that had been placed outside the reserve; six were females but none had bred. Their home ranges were 10–19.5 ha, which is much larger than those at typical mainland densities. The single male that was caught in January 2005 had a home range of 5 ha, again larger than pre-control range size (Speedy et al. 2007).

Vattiato et al. (2023) reviewed multiple home range studies of ship rats and found an inverse relationship between population density and home range size. Home range size increased c. 11-fold (from 0.61 to 6.79 ha, in summer) as density declined from 25 rats/ha to 1 rat/ha. The upper home range value was highly variable depending on the season.

Microhabitat use: Ship rats are generally abundant in structurally and floristically diverse warm sites in forest interiors; they are less abundant if forests are grazed by ungulates (Harper et al. 2005; Innes et al. 2010; Ruffell et al. 2014). At Pureora Forest Park, traps set on warmer, steeper sites caught most rats while traps set in floristically simple habitats such as roadsides, young radiata pine plantings, and grassland caught fewest (King, Innes et al. 1996). At Ōkārito, Haast, and Moehau, ship rat captures were highest on steeper, east-facing, forest interior sites (Christie et al. 2009). In Mt Aspiring National Park, DOC 150 and DOC 200 traps caught more ship rats near fruiting understorey plants and fewer near large mountain beech (*Fuscospora cliffortioides*) trees (Doyle et al. 2023). At Craigieburn Forest, ship rats were more abundant at low altitude near streams (Harris et al. 2022). They were less abundant in early successional vegetation in an intensively logged part of Puketū forest, in lake margin grassland and shrubland at Lake Waikaremoana and amongst unvegetated volcanic lava on Rangitoto Island (Dowding & Murphy 1994; Blackwell et al. 1998; C.J. Miller unpubl., in Innes & Russell 2021). In the Rakeahua Valley (on Stewart Island / Rakiura), ship rats were the most ubiquitous of the three rat species present, found in subalpine and *Leptospermum* shrublands and were dominant in podocarp-broadleaved forests (Harper et al. 2005).

In urban areas, rats (ship and Norway rats combined) were associated with shrubs and lower canopy vegetation (Miller et al. 2022). Rats were more likely to be detected in residential gardens located closer to forest patches, especially gardens with compost heaps.

The above studies were conducted at sites with moderate to high ship rat densities. We know of no studies that have examined habitat or microhabitat choices of ship rats at very low density (e.g. post-control).

Dispersal/reinvasion: Reinvasion of ship rats into very low-density areas following population control has probably received more study in New Zealand than elsewhere in the world. It is of considerable importance to PF2050 trials but also of historical interest because such movements probably mimic those of the 'first rat ashore' during ship rat colonisations all around the world (Innes et al. 2024).

Surprisingly, three of six male ship rats released experimentally inside pest-free Sanctuary Mountain Maungatautari climbed out over the pest-fence back to their original home ranges within 3 days (Innes et al. 2011). The other three moved 600–1100 m inside the rat-free reserve, which is much further than normal range lengths. They tended to use the same den sites and travel routes for 3–4 days at a time. This behaviour of returning to previously used den sites then making increasingly large movements into surrounding forest is similar to that reported for experimentally released house mice (*Mus musculus*) (Nathan et al. 2013, 2015) and Norway rats (Russell, Beavan et al. 2008; Russell et al. 2010) on islands.

Nathan et al. (2025) examined the mobility of ship rats at very low or zero density inside the Brook Waimārama Sanctuary. Using genetic analysis, they estimated that straight line distances from their putative natal location ranged up to a maximum of 1,510 m but were mostly within 200 m. Rat captures and detections appeared to be concentrated around waterways.

A bio-marked ship rat mother and her litter of seven pups were released into a mainland South Westland study site after aerial 1080 had been applied (Nathan et al. 2020). Only six unmarked individuals were captured during the intensive trapping following the operation, suggesting a low density of survivors. After 12 weeks, final capture locations were up to 675 m from the release point

for the released juveniles, with 796 m between siblings, and the total range length for the mother was > 1.5 km, which were much larger than range lengths at typical mainland densities. Interestingly, all individuals (survivor and released rats) that were finally trapped were in a small 20 ha section of the total 300 ha study area.

A study of ship rat repopulation after an aerial 1080 operation in the Tararua Forest Park showed that rats first increased at the margins of the treatment block 6–12 months after the operation and then increased 4 km into the treatment block after 24–30 months, implying that immigration was a major mechanism of population recovery (Griffiths & Barron 2016). Similarly, a study of ship rats radio-tracked on the edge of another aerial 1080 operation area in Fiordland showed that six radio-tracked individuals moved 70–174 m over the 9-month monitoring period, while four other rats (three females and a male) moved 657–1,516 m into the operational area (Carpenter et al. 2023).

In the Waikato region, ship rats readily invaded forest fragments (fragment mean area 5.3 ha), surrounded by pasture, from 170–380 m away after residents had been eradicated from the forest fragments (King et al. 2011). Genotyping of 493 rats from fragments scattered across 20,000 ha found no differentiation between populations, confirming that rats belonged to one large metapopulation with wide-ranging movements within. Marked rats of both genders moved up to 600 m in a few days (King et al. 2011).

None of these studies looked at pathways in detail, nor at habitat or microhabitat use by the travelling rats. However, they do paint a coherent picture of very flexible movement behaviour, with distances moved inversely related to density. Individuals readily travel hundreds of metres and when density is near zero, they can travel c. 1,500 m in the absence or near-absence of conspecifics (see Glossary).

Ship rats are unwilling swimmers but have apparently swum hundreds of metres to reach offshore islands and so could reinvade landscapes by crossing rivers (Innes & Russell 2021).

3.1.1 Knowledge gaps

Scent trails and how to exploit them

Ship rats are strongly exploratory (Žampachová et al. 2017) and nocturnal; olfaction is their main sense. They scent-mark by rubbing their cheeks and ventral surfaces on objects such as tree branches, and by urinating. Rats can tell individuals apart from such scents, and determine gender, state of oestrous, and dominance (Brown 1985). In one study, male ship rats deposited on average 250 trace-urine marks per hour and females deposited 100 (Mallick 1992).

The hypothesis that scent trails are the main way that ship rats find one another is supported by the accidental discovery by Nathan et al. (2020) that a female rat and litter that they released, moved to the same 20 ha as six other rats that survived the aerial 1080 operation over the 300 ha study site. This suggests that survivors may move considerable distances to aggregate after an aerial 1080 operation. A ‘Judas rat’ released with a tracking device might reveal where survivors aggregate, as suggested previously for rats on islands by Russell, Beavan et al. (2008). Such a study could involve cage-trapping rats at widely spaced locations throughout a forest destined for an aerial 1080 operation, shielding them from the operation, then releasing them back into their home

ranges with tracking devices after the poisoning risk is low. Previous work suggests that their home ranges will expand, and then after some time, they will move to aggregate. Radio-tagged 'stranger rats' of both sexes from a similar forest elsewhere could then be released to see whether they find one another and the aggregated survivor rats.

Scent trails can also be detected by trained dogs, which has the significant advantage of not requiring a rat to interact with a lethal or detection device (Gsell et al. 2010; Shapira et al. 2011; Davis et al. 2023; Glen et al. 2024). In large landscapes with very few ship rats, rats appear to use a travel or search strategy moving along long straight lines (Carpenter et al. 2023). Therefore, a potentially more efficient search strategy by dogs might be along straight lines in order to intercept rat trails, rather the current approach of zig-zag searching or quartering (Zollner & Lima 1999).

Another worthwhile experiment would be to lay scent trails to see if survivor rats could be led to toxic baits, removal devices, or detection devices (from say 100 m away) in very low density (post-control) rat populations. In previous work, live laboratory mice and Norway rats were used to lay rodent walking trails to test rodent detection by dogs (Gsell et al. 2010). In the absence of tame (leadable) ship rats, trails of scent gland or urine extracts of ship rats might suffice. Or perhaps laboratory Norway rats or mice could be used to lay scent trails for ship rats, just as stoats investigate ferret odours (Garvey et al. 2016). Live (laboratory) Norway rats were more effective lures than food lures to catch Norway rats in New Zealand trials (Shapira et al. 2013) but this has not been tested for ship rats. Such 'Delilah rats' were suggested for islands by Russell, Towns et al. (2008).

Habitat and pathway use at very low ship rat densities

The above studies show that ship rats rapidly move large distances (up to c. 1500 m) into areas with extremely low residual rat density after pest control operations, but none of the studies investigated microhabitat selection (e.g. ground vs canopy) or pathway/route use during these travels. However, *Rattus rattus* as a taxon is very generalist in its habitat choices, so it is possible that small differences in understorey or canopy vegetation in New Zealand forests do not greatly influence travel directions or distances or pathways. Fine-scale radio-tracking of ship rats may reveal travel routes in sufficient detail to determine their preferred microhabitats, but observers would need to be very close to the rat to know if it was on the ground or up a tree. Rats are sensitive to being followed at close range at night by noisy humans. Such research is possible, but it is less likely to yield advances for ship rat eradication compared to scent trail research.

3.2 Norway rat (*Rattus norvegicus*)

Home range: Norway rats are much more likely than ship rats to be colonial in New Zealand, and usually occur near food sources and/or water. They may live in quite dense colonies but with large distances between them. This challenges the notion of what a 'low density' population might mean. In a study in indigenous and exotic forests at Pureora Forest Park (central North Island), only 43 Norway rats were caught in 25,864 Fenn trap-nights and 15,552 snap-trap-nights, all in native forest (King, Innes, Flux et al. 1996). Thirty-five of these Norway rats were caught at a single trap site in the Waipapa Ecological Reserve, about a metre from the bank of the Waipapa Stream. In Europe, large 'clans' of rats do not have stable composition but are characterised by arrival and

departure of individuals; in Germany the species is called the 'wanderratte' meaning the 'migrating rat' (Telle 1966). This is consistent with a New Zealand study that found little genetic distance and high genetic relatedness between three populations across c. 30 km in the upper Waitaki Basin and Mackenzie Basin (Doyle 2021).

Like ship rats, Norway rats move further when their density is lower, and males usually move further than females (Russell & Innes 2021). On Motuhoropapa Island, the mean distance between consecutive cage captures was 49 m for females and 113 m for males, with a maximum of 330 m (Moors 1985). Range lengths of seven males radio-tracked on Kapiti Island averaged 439 m (range 218–916 m) and a single female had a range length of 459 m (Bramley 2014). There have been few mainland studies of Norway rat ecology. In the Mackenzie Basin, home ranges were 3.0–5.4 ha and 369–615 m in length, with no significant difference between sexes (Doyle 2021). In urban Hamilton, male Norway rats had range lengths of 108–371 m (mean 273 m, $n = 8$), while the only female tracked had a range length of 239 m (Fitzgerald et al. 2017).

Microhabitat use: In non-commensal situations (see Glossary), Norway rats occur mainly near wet environments such as estuaries, lagoons, lakes, wetlands, rivers and streams (Harper et al. 2005; Russell & Innes 2021) perhaps because they can feed underwater (e.g. on kakahi/freshwater mussels, *Echyridella menziesii*) and they readily dive and swim to avoid predators. Ship rats probably outcompete Norway rats in food-rich, three-dimensional habitats such as forests because ship rats are better climbers (Foster et al. 2011; King et al. 2011; Russell & Innes 2021), however Norway rats have never been shown to increase at sites where ship rats are intensively controlled (in contrast to mice, which do increase). On braided riverbeds – one of the few places where Norway rats are explicitly targeted for control – they favour stable side-streams with some cover and avoid large areas of bare shingle except to prey on eggs and chicks at bird nesting colonies at night. At Lake Waikaremoana, they live mainly around the shoreline and adjacent forest (J. McLennan unpubl. in Russell & Innes 2021). Lister (2022) found no confinement of Norway rats to water in the Te Manahuna Aoraki Project area in the Mackenzie Basin and suggested this was due to the absence of ship rats and lack of subsequent competition, thereby allowing Norway rats to use a wider range of habitats.

In urban areas, rats (Norway rats and ship rats combined) were associated with shrubs and lower canopy vegetation (Miller et al. 2022). Rats were more likely to be detected in residential gardens located closer to forest patches, especially gardens with compost heaps.

Norway rats move mainly along trails (runways) whereas ship rats traverse whole territories (Telle 1966). They can be very competent swimmers and may cross channels up to 2 km wide but such swims depend on currents, water temperature and the life experiences of individuals (Russell, Towns et al. 2008; Russell & Innes 2021). They could therefore readily swim over rivers to colonise new mainland landscapes

Dispersal/reinvasion: Norway rats experimentally released on offshore islands sometimes used forest tracks (Russell et al. 2010). Russell and Innes (2021) noted that single male Norway rats invading islands range widely, probably in search of conspecifics. Home ranges of single adult male Norway rats released on Motuhoropapa Island covered the entire 9.5 ha island (Russell et al. 2010). Initial movements were apparently random, but rats used 'central place foraging' and by the third week had stable den sites from which they made new explorations. Single male Norway rats released onto larger Ulva Island spent 2–3 days around their release site, but then some moved distances up to 1.3 km (Russell, Towns et al. 2008).

No details of Norway rat colonisation or reinvasion pathways are known other than they can swim unaided or from boats or drifting debris, and they can readily cross land, rivers, and estuaries.

3.2.1 Knowledge gaps

Distribution, abundance, and behaviour across mainland New Zealand

More basic studies of Norway rat habitat choice, abundance and behaviour on the New Zealand mainland are needed because the species is widespread but is less targeted for control than ship rats. A better understanding of their distribution could be assisted by citizen scientists reporting rat species counts from the numerous community-based trapping programmes across New Zealand, but rat identification to species is still generally poor, and few lay trappers differentiate between ship rats and Norway rats. Such research would also help train participating observers to have better recognition of different rat species. Rats can be identified to species in about half of camera trap images, therefore, in addition to traps, cameras would be a useful tool for landscape surveys of rat distribution.

Movements

More detailed radio-tracking studies of Norway rat movements are required, including of adults and subadults, males and females, both before and after control. Such a broad approach will determine how Norway rats maintain scattered colonies across New Zealand while rarely seeming to be abundant. Priority study sites are those scheduled for large-scale Norway rat control, such as Stewart Island / Rakiura, the east coast of the South Island, or Mackenzie Basin braided rivers where they are targeted to protect colonial nesting birds. Experimental releases of radio-tagged Norway rats have occurred on New Zealand islands but not in pest-fenced ecosanctuaries or at other post-control mainland sites. In the context of PF2050's objective to achieve large-scale mainland predator control to near-zero abundance, it is important to know whether Norway rats reinvade large areas vacated by ship rats (their competitors) and stoats and cats (their predators). Norway rats were widespread throughout both main islands for decades before the spread of ship rats and stoats caused their distribution to shrink to its present discontinuous pattern. Therefore, Norway rat reinvasion seems possible across most of New Zealand.

Scent trails and how to exploit them

All the scent trail research about ship rats described above also apply to Norway rats. Dogs are likely to be even more efficient detectors of Norway rats because Norway rats climb less than ship rats and therefore leave better ground scents; and Norway rats tend to use specific trails repeatedly. Dogs can be used to locate Norway rat trails to help place devices, or to locate rat dens that may be vulnerable to a rapid management response (such as poisoning or gassing) by the dog handler (Shapira et al. 2011; Glen et al. 2024). Laboratory rats (which are Norway rats) that are accustomed to being handled can be used to lay experimental trails to traps and other devices (Gsell et al. 2010), and as live lures in twin-unit cage traps (Shapira et al. 2013).

3.3 Kiore (*Rattus exulans*)

Home range: Like ship and Norway rats, kiore have variable home ranges; males move further than females and males' ranges increase in the spring when more females are breeding. On Tiritiri Matangi Island, home ranges were 37–60 m across, but highly variable (Nicholas 1982). In the breeding season, adult females strongly avoid each other, and adult males associate with them only for mating. In another Tiritiri Matangi study, four males and three females moved on average 268 m since their last capture (Moller 1977). Kiore populations are irruptive during masting of beech and podocarp trees, and mass seeding of grass (on Tiritiri Matangi). Kiore density fluctuates less on entirely forested islands such as Te Hauturu-o-Toi / Little Barrier Island and Hen Island than on Tiritiri Matangi, and repeated snap-trapping on Kapiti, Stewart Island / Rakiura, and the South Island mainland found low and rather stable kiore numbers there – except after mast events. Their small body size means kiore are vulnerable to interference competition or predation by the larger ship and Norway rats and they may become detectable only after the larger rat species have been greatly reduced (Gronwald & Russell 2020; Wilmshurst & Ruscoe 2021). These features of breeding more when food is abundant and being vulnerable to predation and/or interference competition by the two larger rat species are true also for mice (King 1982; Choquenot & Ruscoe 2000).

We know of no studies of kiore movements at very low population density.

Microhabitat use: Kiore arrived in New Zealand with Polynesian (Māori) immigrants c. 1280 AD and became very widespread in diverse environments, but then disappeared from most of the mainland after Norway and ship rats spread during the 18th to 20th centuries. On Stewart Island / Rakiura, kiore were more abundant in areas with dense ground cover, perhaps reflecting interference by the larger rat species, but on Pearl Island kiore shared forest habitats with ship rats (Harper et al. 2005; Harper 2006).

Kiore are probably at low density in mainland forests (which will always have ship rats, and probably mice) except when there is abundant seed mast, but we know of no studies of microhabitat use in either case. Habitat use is likely to be greatly influenced by interference from the two larger rat species, and perhaps by cats, stoats, and mice.

Dispersal/reinvasion. We know of no studies of kiore natal dispersal (as subadults), or of movements of survivors and reinvaders after control operations.

3.3.1 Knowledge gaps

The same information on movement behaviour at very low densities that is required for other pest species is needed for kiore. Less is known about movements at low density by kiore than ship and Norway rats because kiore are even less targeted on the mainland than Norway rats. Kiore have been eradicated from at least 38 offshore islands larger than 5 ha and 20 smaller ones, and they are targeted alongside ship rats on Great Barrier Island (Aotea Island), but we know of no sustained operations targeting them on the South Island mainland (Ogden & Gilbert 2009; Wilmshurst & Ruscoe 2021). Given that kiore can remain undetected until the dominant larger Norway or ship rats have been heavily trapped first (Harper & Veitch 2006), that rat trapping is scarce, and that identification to species is poor, it is quite possible that kiore still exist but remain undetected on the North Island mainland also.

3.4 Weasel (*Mustela nivalis*)

Home range: There have been few studies on weasel home ranges in New Zealand. Haworth (2018) cites unpublished home range estimates of three male weasels (of 66 ha, 117 ha, 150 ha, respectively), and a female (59 ha) where mice were scarce (E. Murphy & Robins, Department of Conservation, unpubl. data).

Weasel space use and dispersal may be affected by the presence and density of stoats, but this requires further study in most habitats in New Zealand.

Weasel home range and space use have never been studied at very low densities below the carrying capacity of the environment. Whilst weasel incursions have occurred at multiple fenced sanctuaries, their movements and behaviours have not been studied before they were removed.

Microhabitat use: In New Zealand, weasels are widespread but patchy on the two main islands and they have not established on any other islands (King & Murphy 2021). In Pureora Forest Park, weasels were caught only in young plantation pines and along road edges where mice were abundant (King, Innes et al. 1996). In a study in beech forest, weasel captures were associated with forest edge and valley floor habitats (Lough 2006).

Dispersal/reinvasion: The maximum distances over which weasels disperse are poorly studied. In New Zealand, three weasels were recorded on King Billy Island (64 m offshore) and one on each of Quail Island (250 m offshore) and Maud Island (840 m offshore) (Bowie et al. 2011; King 2023). Weasel populations have never established on any island, however. This may indicate they rarely swim these distances, or that given their short life cycle, lack of embryonic diapause, and high mortality rates, if they do swim to islands there are rarely enough individuals that do so simultaneously to succeed in establishing a population. Whether rivers of various sizes or flow rates hinder weasel dispersal requires testing.

Using genetic kinship techniques (see Glossary), Veale and Etherington (2023) measured two long-distance dispersals in Taranaki with a male dispersing 17.4 km, and an individual of unknown sex dispersing 7.1 km. Whether they were juvenile dispersals, transient movements accumulated over time, or roaming behaviour in the mating season, is unknown. The highest altitude weasels have been detected in the Mackenzie Basin of the South Island is 1,696 m.a.s.l. (Foster et al. 2022).

Weasel dispersal has never been studied below the carrying capacity of the environment.

3.4.1 Knowledge gaps

Movement, detectability, and habitat use

Almost nothing is known about weasel movement, invasion, detection, monitoring, and removal. Any study on weasels in any environment in New Zealand will add considerably to our knowledge base.

Multiple studies using GPS or radio-tracking of weasels in different environments in New Zealand are needed. Kaitorete Spit (near Lake Ellesmere / Te Waihora) is an easily accessible site that already has weasel trapping in place, so it is a potential study site. Banks Peninsula, also in the South Island, also has a reasonably large weasel population. Telemetry studies would involve live trapping

animals, attaching devices and monitoring them. Ideally, weasel detection devices (such as CritterPic®; and also the Mostela – see Mos & Hofmeester 2020) and mark-recapture operations would provide more useful data on monitoring efficacy and population dynamics. Landscape genetics could also be considered to understand dispersal, and genetic mark-recapture could be used for home range estimation if scat can be readily found.

Releasing known numbers of weasels with tracking devices into novel areas would provide information on movements at low population density. Including a detection device network at the same location would provide information on the efficacy of the detection devices with animals of known location. Given weasels' reliance on small mammals as prey, the study site would ideally need a moderate to high mouse population density, and low to zero weasel density. There are several candidate areas that could be used for experimental weasel releases. Sanctuary Mountain Maungatautari has previously had weasel incursions, and it has mice and is free from other predators. This would be an ideal location to examine the movement parameters of invading weasels, and given that this occasionally occurs naturally, the information gained has relevance to conservation within the sanctuary. Previously, rats have been released at Sanctuary Mountain Maungatautari to investigate their invasion movements (Innes et al. 2011), so there is a precedent for using this site for weasel research. Alternatively, islands such as Matakana, Rangitoto ki te Tonga / D'Urville Island, and Arapaoa Island have stoat and cat populations, therefore the addition of small numbers of weasels is unlikely to have much effect on biodiversity. Weasels are likely to behave differently when larger carnivores are present so this must be considered when interpreting any results. Releases of weasels on Miramar Peninsula are also an option.

Reliance on rodents for breeding

Many studies have shown local extinctions of weasels following declines in small mammal abundance, with some calculating minimum rodent density thresholds required to support weasel breeding (e.g. Lockie 1966; Erlinge 1974; Tapper 1979). In New Zealand, there is only one small mammal in the size range that could support weasels (and that is mice). Monitoring weasel survival and breeding across varying mouse abundances could provide a threshold that changes weasel population dynamics. This could also be tested in small, fenced sanctuaries.

3.5 Stoat (*Mustela erminea*)

Home range: Like weasels, male stoat home ranges are larger than those of females. Stoats in New Zealand are larger than stoats in much of their native range, and their prey are often sparser. Therefore in general, New Zealand stoats have larger home ranges than in many parts of their native ranges (King et al. 2007). When resource abundance is unusually high, home ranges can shrink dramatically. In a colony of Hutton's shearwaters (*Puffinus huttoni*) monitored during one summer with extremely high prey abundance, male stoat home ranges averaged 16 ha and females' averaged 9 ha (Cuthbert & Sommer 2002). Conversely, in a braided river system where food was less abundant, male home ranges averaged 313 ha in spring, and 185 ha in autumn, while female stoats' home ranges averaged 127 ha in spring and 116 ha in autumn. The larger male home ranges in spring are likely to be related to increased breeding dispersal as they searched for mates. For all stoats, particularly females, home ranges shrink in winter as animals have established territories and boundaries at this point, and females are constructing dens for their litters. However, female stoats are particularly hard to trap from winter to after they have given birth in mid-spring,

therefore this seasonal effect is poorly studied. Stoat home ranges are highly variable even within a single population. In a study at Trounson Park in Northland, the average home range for male stoats was 107 ha, and the average home range for females was 81 ha. However, one male stoat had a home range of only 8 ha, while the largest male home range was 209 ha (Gillies et al. 2007). The average home ranges of stoats in New Zealand can vary by a factor of 35 (9 ha for females in resource abundant situations to 313 ha for males in spring in comparatively resource poor environments) (King & Veale 2021).

Prey resources are not the only determinant of stoat home range size. Other important factors are predation pressure, social structure and behaviour, reproductive strategy, habitat structure, energy expenditure requirements, and competition. Social interactions are probably the most important driver of home range formation for mustelids in New Zealand. Male territories generally border other male territories, while female territories may not border other female territories. When prey density is either extremely high or low, mustelid territoriality may break down (Powell 1994). This was observed on the Otago Peninsula when mice were particularly abundant in the autumn of 1995, causing male stoat home ranges to overlap considerably (Moller & Alterio 1999). The exact scenario that leads to territoriality breaking down is unclear. During a stoat incursion inside the fence at Shakespear Regional Park (Whangaparoa Peninsula) where a female stoat gave birth to a litter, the scat of two male littermates were found in adjacent non-overlapping areas (in January) indicating they were possibly establishing exclusive territories (Ecogene, unpubl. data), despite the likelihood of high prey abundance.

No studies of mustelid movements in New Zealand have been conducted at low population density. Unfortunately, most incursions into stoat-free areas have only been detected when a litter has been born, meaning there are multiple stoats with sightings not linked to individuals. The juvenile male stoat caught on Miramar in 2024 was detected by Predator Free Wellington's camera network and by members of the public. This stoat originated c. 11 km to the west (A. Veale, Manaaki Whenua – Landcare Research, unpubl. data.) and moved widely across the peninsula. While most detections were at the northern end of the peninsula (possibly due to an increase in detection effort there), there were also detections to the south, including to the west of the airport that may have been this same animal. There is a verified photograph at the northern end of the peninsula in February 2024, and another the following day 5 km to the south (D. Henry, Predator Free Miramar, unpubl. data). This shows that male stoats can roam widely with less stable home ranges in situations where other stoats are absent. Female stoats more likely form territories based on habitat quality and prey availability at low population density, while males will roam.

Microhabitat use: There is far more known about stoat behaviour in New Zealand than about weasel behaviour. Stoats are found in almost all habitats in New Zealand, from coastal sand dunes to all forest types, through to the high alpine (King & Veale 2021). However, habitat preferences at any scale are hard to discern and patterns observed in one habitat type can be dramatically different in a different one (Christie et al. 2006; Lough 2006; Martin 2012).

Radio-tagging studies, both in New Zealand and overseas, suggest that to avoid neighbouring open spaces stoats will travel along features that provide cover, such as hedges, habitat edges, and riparian margins (Erlinge 1977; Murphy & Dowding 1994, 1995; Alterio et al. 1998). Linear features such as forest margins, road margins, and waterways also increase the probability of stoat captures (Christie et al. 2006). Similarly, the ecotonal edges of forests are associated with dense ground cover, which provides cover for stoats from predators, and harbours high densities of mice. In the

Hawdon and Poulter valleys, stoats were readily caught along these edges (Lough 2006). The use of edges has been observed in a number of other mammalian predator species, including other mustelid species, and is generally linked to higher abundance of prey species and relative ease of travel through open edge habitat (e.g. Oehler & Litvaitis 1996; Alterio et al. 1998; Ragg & Moller 2000).

However, in Tongariro Forest, tracks and rivers were negatively associated with stoat activity (Martin 2012). This study area was higher, flatter, drier, and further from streams and tracks than other studies. Rodent abundance here was the best predictor of stoat abundance. As for several other studies, ridge tops were also good predictors of stoat catch, and steeper slopes were associated with lower catch rates (Brown 2003; Christie et al. 2006; Smith et al. 2007; Christie et al. 2009; Martin 2012).

All the scat detections and stoat captures after a stoat incursion into the Shakespear Regional Park were in forest and scrub rather than grassland (Ecogene, unpubl. data). Similarly, all the camera trap, scat and captures in Tāwharanui Peninsula, Hauraki Gulf, were in forest, showing a strong preference for areas with cover (M. Maitland, Auckland Council, pers. comm.). In Taranaki, a GPS-tagged stoat was always recorded in scrub and forest patches, showing a preference for this habitat over the open grassland, although it must have moved over open grassland to move between forest patches (Niebuhr & Veale 2020). On Waiheke Island, stoats are mostly caught along the coast and along wetlands and waterways (F. Lepera, Te Korowai o Waiheke, pers. comm.). In mountainous beech forest, stoats appear to remain in either one habitat type or another (beech forest valley floor or alpine grassland) rather than move between habitat types (Smith & Jamieson 2005). This suggests that stoats may develop hunting patterns and habitat preferences when young, which they maintain through adulthood.

Females appear to have more specific habitat choices than males (Linnell et al. 2017). While placing traps near cover, prey runs, prey sources, and along linear features and habitat edges is good practice, there will be atypical stoats in each population that have different preferences for habitat and prey.

Dispersal/reinvasion: Stoats have two main periods of extended movements: 1) juvenile dispersal during summer from November to January; 2) adult male roaming during the breeding season from August to October. Juvenile stoats are largely weaned onto solid food by 5 weeks old, but they stay with their mother in a family group for some time, learning to hunt and explore. Groups of stoats (mother and offspring) have been recorded from October to February in New Zealand, most often in December and January (King et al. 2007). Dispersal generally occurs from around 3 months old, however juveniles whose mothers have died can survive and disperse from a younger age than this. Stoat kits of both sexes are capable of rapid dispersal over long distances before settling down. In New Zealand beech forest, Smith et al. (2007) found considerable site fidelity between years, as in Europe. High mountain ranges above 2,135 m may limit stoat dispersal since this was the highest elevation at which stoats were detected in the Mackenzie Basin (Foster et al. 2022).

King and McMillan (1982) found that female stoats generally travelled smaller distances than males, with one female travelling 5.6 km before returning 3.2 km. In a landscape genetics study in mixed farmland and forest in Taranaki, the maximum distance a female dispersed was 7.2 km (Veale & Etherington 2023). While females appear to disperse less than males, the longest dispersal recorded for a stoat was 65 km (and that occurred in only 24 days) for a female in Fiordland

(Murphy & Dowding 1995). In King and McMillan's study, males dispersed 6–24 km, with one individual travelling a minimum of 20.0 km in 5 days (plus a further 4.4 km in the next 2 days). Murphy and Dowding (1994, 1995) tracked an adult male that moved at least 3.7 km in 3.25 hours. The maximum dispersal distances that are possible are likely to be beyond any of these values and could well be over 65 km in exceptional circumstances. Dispersal is at least partially driven by the need to find a territory that is unoccupied, as juvenile stoats can be killed by resident stoats during their summer dispersal.

The mean distance between close-kin pairs in the Taranaki genetics study was 8 km, the median distance was 3.5 km, and the maximum distance was 39 km (Veale & Etherington 2023). There were five close-kin pairs out of 22 pairs that were separated by over 10 km, and two probable male dispersal events over 35 km were recorded. These statistics will include some close kin that were caught before dispersal, and they indicate how far stoats can disperse before being captured in the trap network in the study area. Additional long-distance dispersals could have occurred, where stoats dispersed outside the trapping network and therefore would not have been recorded.

In a similar landscape genetics study for Capital Kiwi in Wellington, the mean distance between close-kin pairs was 3.4 km, the median distance was 2.4 km, and the maximum distance was 17 km (A. Veale, Manaaki Whenua – Landcare Research, unpubl. data). There were four pairs over 10 km apart, one of which was over 14 km. These results were obtained while this population had been significantly suppressed for several years, unlike the Taranaki results which were obtained earlier in the suppression programme. The lower dispersal distances observed, and the lack of very long-distance dispersals may indicate that when stoat populations are at low density, they do not disperse as far on average, probably because they can find unoccupied territories with less effort.

The stoat population on Waiheke Island is significantly suppressed by a 250 × 250 m trapping grid. Stoats here are usually caught within 1 km of their siblings before dispersal due to the intensive control effort. There is, however, a secondary mode where many stoats are caught between 3 and 4 km from their mother. This suggests that many stoats disperse away from their mothers, changing their behaviour at approximately 3–4 km to establish a territory (if no adjacent stoats are present). Many stoats on Waiheke Island disperse longer distances from their mother than this, with one moving up to 12 km away (on an island only 20 km long). One litter where the mother was trapped when the litter was approximately 8 weeks old had a juvenile male that dispersed across the trapping grid, to be caught 4 months later, 7.3 km from where the mother was caught. Genetic data from Waiheke Island (A. Veale, Manaaki Whenua – Landcare Research, unpubl.) shows that there are males that avoid trapping for multiple years (including ones that are never trapped), roaming the island widely during spring and fathering multiple litters.

Male roaming behaviour is less well understood than juvenile dispersal, but it clearly occurs. Trapping data from Project Janszoon, Abel Tasman National Park, showed an increase in captures on the boundary of the trapping network during spring, occurring to at least c. 3 km into the trapping area (Gormley & Veale 2020). This probably relates to males moving into the national park looking for mates. These roaming movements could be larger, given that these individuals were moving through a trapping grid that would remove many of them before attaining longer distances.

Stoats are extremely able swimmers (Elliott et al. 2010; Veale 2013; King et al. 2014) and have been recorded on almost all islands in New Zealand out to 3 km offshore (Veale et al. 2012). On Rangitoto / Motutapu Islands, at least six individual stoats have swum the 3 km to the islands and

been trapped since the mammal eradication in 2009: five males and one female (Veale et al. 2015). A female gave birth to a litter on Kapiti Island which is 5.2 km offshore, and may have swum there (Prada et al. 2014). This long-distance swim is believed to have been a dispersing juvenile, but stoats are also likely to regularly cross shorter distances as part of their foraging and roaming (King & Moors 1979; Heikkilä et al. 1994). In New Zealand, three radio-collared stoats regularly crossed a fast-flowing river, having a home range on each side, indicating rivers are rarely a barrier to their dispersal (Murphy & Dowding 1994).

In summary, juvenile stoats disperse considerable distances, driven by a need to find an unoccupied home range, with male stoats generally moving further than females. At low population density, dispersal distances probably decrease, but at very low population densities where stoats rarely encounter others, some stoats (particularly males) may roam widely looking for territories containing females.

3.5.1 Knowledge gaps

Movement, detectability, and habitat use (low density)

Little is known about stoat behaviour and movement ecology at low population densities, but addressing this question is considerably harder than for weasels and ferrets because there are likely to be few areas in New Zealand where stoats are either at very low density or absent. The primary reason stoat numbers would be low in any area is because significant control has recently been undertaken. Therefore, releasing stoats into these areas would probably be met with resistance. All stoat-free islands are very unlikely to accept a stoat release, and most are probably too small to provide useful information. The best option is to release GPS-tagged stoats into a large area, recently poisoned with 1080, or into the Perth River valley project run by Zero Invasive Predators (ZIP). The study area must be very large (ideally greater than 20,000 ha) to achieve any meaningful result due to the likelihood of stoats rapidly dispersing out of the area.

Movement and detectability of female stoats in winter-spring

One critical knowledge gap is fine-scale movements of females in winter/spring (July to September) when they are at very low density, ideally in different habitat types. Catching female stoats during this period is extremely challenging, but for elimination (see Glossary) it is vital to be able to remove them before the litters are independent. Females have multiple dens, and they move kits between these dens regularly (King & Powell 2007). Understanding how far apart these dens are and how long they are occupied would also be very useful.

3.6 Ferret (*Mustela putorius furo*)

Home range: Ferret home ranges, like those of other mustelids, are influenced by their nutritional requirements and prey availability, which vary seasonally. Male home ranges are larger than those of females and vary inversely with population density (Efford & Norbury 2005). Male and female home ranges overlap, especially in areas with high rabbit densities – and home ranges are relatively small in these situations – with ferrets keeping in close contact with their neighbours (Ragg 1997; Norbury et al. 1998a; Moller & Alterio 1999). Where prey are scarce, ferrets tend to maintain a typical mustelid intrasexual territoriality system (Powell 1979; Moors & Lavers 1981).

Ferret home ranges increased when food became very scarce after a 99% reduction in rabbit numbers, but not after a 77% reduction (Norbury et al. 1998b). In outdoor enclosures, home range size and overlap in the non-breeding season are determined by food availability, but during the breeding season, access to females became an important resource for dominant males (Medina-Vogel 1998).

Ferret home ranges have been described both when in a steady state environment, and when prey resources have decreased (Norbury et al. 1998b), but they have not been studied when ferret populations are considerably below carrying capacity.

Microhabitat use: Ferrets reach their highest densities in tussock grassland, improved pasture, and scrubland (Marshall 1963; Baker 1989; Middlemiss 1995; Ragg 1997; Alterio et al. 1998). They also occupy dune lands, wetlands (Moors & Lavers 1981; Gillies & Brady 2018), river valleys in forests (Robertson et al. 1984), and ecotones (see Glossary) (King, Innes et al. 1996; Pierce 1996; Gillies et al. 2007). They can also be found along road edges, fence lines, grassy tracks, hedgerows, and waterways (Murphy et al. 1998; Young 1998; Morley 1999; Ragg & Moller 2000). Given that ferrets' preferred prey are usually lagomorphs, their habitat selection is biased towards the presence of rabbits, and hence pasture (Garvey et al. 2022).

In a detailed study of microhabitat preferences in pasture in east Otago, ferrets concentrated their activity in grazed areas, but within these areas they were found more often where herbs, scrub and woody cover were present, and where there was an ecotone between pasture and vegetation cover (Ragg & Moller 2000). The preference for grazed over ungrazed areas was probably related to habitat fragmentation at this site, but grass length was positively correlated with ferret presence overall. Ferrets were also more likely to be present close to fence lines. When denning, ferrets selected areas with cover of all types and avoided open pasture. In pastoral farmland, ferrets particularly favoured man-made structures (sheds, haybarns) (Ragg & Moller 2000). In other studies, ferrets appeared to be attracted into long rank grass where lagomorphs, rodents, and birds were more abundant (Alterio 1994; Moller et al. 1998). In the Mackenzie Basin, Pierce (1987) and Pascoe (1995) found ferrets hunting more frequently in areas with high vegetation cover that supported higher rabbit numbers.

In developed grasslands, ferrets hunt in vegetated gullies (Baker 1989; Ragg & Moller 2000). In thick grass they use small pathways, possibly created by rabbits, hares and stock (Ratz 2000). In large braided river valleys they keep mainly to ecotonal edges and vegetation on river flats (Pascoe 1995; A. Byrom, Manaaki Whenua – Landcare Research, unpubl.). They seldom move onto open river gravel or onto riverine islands while foraging, even when low water flows make shorebird nests accessible, but juvenile ferrets can disperse across river channels and shingle banks (Pierce 1987; Young 1998; Byrom 2002).

Dispersal/reinvasion: Juvenile ferrets of both sexes emerge from natal dens in December–January, and disperse from their natal home range about 6 weeks later (mid-February to mid-March) when c. 3 months old (Byrom 2002). During dispersal they often follow landscape features such as vegetation cover, overgrown stream channels, fence lines, roads, and riverbanks. Published median estimates of straight-line movements of juvenile ferrets are 1.2 km (Caley & Morriss 2001), 5.0 km (Byrom 2002), and 6.35 km (Young 1998). In a landscape genetic study looking at kinship across a ferret population in western Southland, the maximum distance between a close-kin pair was 21.8 km. However, most related ferrets in this system were much closer to each other, with a prediction that 95% of ferrets would be 11.9 km or less from where they were born (Veale et al. 2022),

although this estimate includes some animals caught before dispersal. Maximum dispersals up to 45 km were similar for both sexes (Byrom 2002).

Male and female ferrets are equally likely to disperse, and 50% of juvenile ferrets move more than 2–5 km from their place of birth (Caley & Morriss 2001; Byrom 2002). Most dispersal occurs during late summer (late February and early March), with no sex difference in mean dispersal distance (Caley & Morriss 2001; Byrom 2002; Byrom et al. 2008). Three straight-line dispersal distances of juvenile female ferrets of 12, 20 and 27 km were recorded in the Maniototo district of the Otago region (Ragg 2002).

Caley and Morriss (2001) reported that ferrets dispersed non-directionally across pasture habitat in North Canterbury, with a mean dispersal distance of 2.1 (Standard Error SE, 1.0) km, whereas in the Mackenzie Basin, dispersal has been reported to be directional, following braided riverbed channels. Mean dispersal distances were longer – 6.7 (SE, 1.6) km for males, and 11.8 (SE, 3.4) km for females (Byrom 2002). In a mix of pasture, scrub and riverbed habitat in inland Marlborough, the maximum distances travelled by ferrets of both sexes were 10–27 km (Byrom 2004; Byrom et al. 2008).

The only confirmed record of a wild ferret on an island was on Limestone Island near Whangarei where a male ferret arrived and killed a kiwi before being caught (Curtis 2024). This island is 400 m offshore, and it seems possible that this was natural dispersal via swimming rather than a release. While snow limits the distribution of polecats (*Mustela putorius*) in Europe (Osinga et al. 2023), the amount of snow required to limit their distribution is outside the range encountered in New Zealand. Altitude limits ferret distribution as ferrets are scarce or absent from the subalpine and alpine zones (King et al. 2017), although they have been detected up to 1,731 m.a.s.l. (Foster et al. 2022).

Ferret dispersal into a low density population has not been examined. Byrom (2002) found no link between dispersal probability, or distance, and the density of conspecifics. However, these have not been measured at extremely low population densities.

3.6.1 Knowledge gaps

While much is known about ferret space use and movement in New Zealand, there have been no studies at very low densities that are well below carrying capacity. Trial releases of known numbers of ferrets into novel areas would help address this question. GPS devices for ferrets are easier and more reliable to use given their larger body size than stoats and weasels. Detection dogs and a network of monitoring devices could be trialled simultaneously with these known-location ferrets.

Trial releases of ferrets may have to be conducted outside the range of kiwi, weka, and ground-nesting shore birds, depending on research objectives and the views of stakeholders. Releases in the presence of vulnerable prey would be risky but the results would yield valuable learnings. The far North does not have ferrets and is a possible location for such a trial if conducted beyond the northern limit of kiwi. The Mahia Peninsula is another possible location that does not have ferrets, and it already has significant monitoring infrastructure in place for the PF2050 possum project there. Matakana Island has no ferrets and could be used simultaneously with a weasel release trial. Alternatively, releasing ferrets into an area where recent ferret control has significantly lowered the population is an option. This could be similar to the study by Byrom (2002) but ideally with even

lower ferret population densities, and using GPS collars to monitor both dispersal and home range movement.

3.7 Brushtail possums (*Trichosurus vulpecula*)

Home range: Possum home ranges are affected by habitat, population density, age, female distribution, dominance status, and season. They can vary from 1 to >60 ha (Efford et al. 2000; Harper 2005; Adams et al. 2014; Cowan & Glen 2021), with male home ranges usually being larger than those of females.

Habitat type has a strong effect on possum home ranges. Movement studies in New Zealand report foraging ranges of 250–350 m per night. However, when moving from forest to pasture, which is an important foraging habitat (Gilmore 1967; Harvie 1973), possums move more than 1,000 m per night (Green & Coleman 1981). Foraging ranges up to 1.6 km were found when seasonal food like apples, walnuts, flowering trees, pine pollen cones or new tree leaf growth became available (Jolly 1976; Cowan & Clout 2000). The smallest home ranges of 1–2 ha have been found in forests (Cowan & Glen 2021), but home ranges can be highly variable in shape and size, depending on food abundance in the forest or adjacent habitats (Green & Coleman 1981; Cowan & Clout 2000). Ball et al. (2005) estimated home ranges of 1.75–12.82 ha in a mix of beech forest and farmland. Some individuals denned in the forest and travelled great distances into pasture resulting in larger home ranges. Brockie et al. (1997) also found that possums that live in forest pockets on farmland can move up to 2.6 km when foraging. The largest home ranges of up to 60 ha were found in grassland (Cowan & Glen 2021). Two outlying individual home ranges exceeding 100 ha were found in semi-arid grassland (Rouco et al. 2017).

Whyte et al. (2013) compared possum home range sizes at three sites: two with low population density (1–2 possums/ha) and one with higher density (7 possums/ha). Home ranges at the low-density sites were larger (12 ha and 8.7 ha) than at the high-density site (1.8 ha). However, the habitat also differed significantly, with oaks and sycamores dominant at the high-density site and pine and gorse at the low-density sites. Therefore, the observed differences in home range sizes may be the result of different resource availability. Similarly, possum home ranges in high altitude beech forests where possum density was very low (0.5 possums/ha) were larger than in lowland podocarp forests where possum densities exceeded 7 possums/ha (Cowan & Clout 2000). At Mt. Misery, possum density was lower (0.46 possums/ha) than reported in other studies, and possum movements here averaged c. 1 km (Clout & Gaze 1984). Possum density in urban habitats is generally low, with a reported home range of c. 3.5 ha (Cowan & Glen 2021). In urban Dunedin, however, home range sizes were similar between high- and low-density populations (Harper 2005; Adams et al. 2014). This contradicts findings from non-urban habitats where home range varied inversely with population density (Pech et al. 2010; Whyte et al. 2013). Margetts et al. (2020) reduced the density of possums in forest fragments in Canterbury and found that at the high-density site there was a significant increase in home range from 1.2 ha to 2.4 ha for males, and from 0.7 ha to 1.1 ha for females. This effect was not observed where the possum density was already low before the manipulation.

Vattiato et al. (2023) reviewed multiple home range studies of possums across a variety of habitats in New Zealand and found a significant inverse relationship between population density and home range size. Home range size increased c. 36-fold (from 1.18 to 42.43 ha) as density declined from 15 possums/ha to 0.5 possums/ha. Rouco et al. (2013), Rouco et al. (2017), Efford et al. (2016), and

Anderson et al. (2022) also found similar inverse relationships for possums in New Zealand. Anderson et al.'s (2022) study suggests that when considered together, population density is a far more important determinant of home range size than habitat.

Reproductive status also affects possum movements. In a mixture of open woodland with improved pasture, mixed forest and scrub, home ranges of adult males and females approximately doubled in size during the autumn breeding season (Paterson et al. 1995).

Microhabitat use: Possums are widely distributed across various New Zealand habitats, including forests, shrublands, grasslands, wetlands, and urban and rural areas. The distribution of possums within a habitat can vary with vegetation patchiness, habitat ecotones, edge effects, and social clustering (Efford 2000). Possums are mainly arboreal, with 10%–15% of their activity on the ground (Cowan & Glen 2021).

Possums' movements and use of habitats are largely based on foraging. The diet of possums across a pasture-alpine gradient was affected by sex, season and altitude (Coleman et al. 1985). In forest habitat with adjacent pasture, males foraged twice as much on pasture compared to females, which is reflected in greater home ranges for males. Food availability varies across seasons and depends on the distribution of palatable species, thereby affecting how possums move within their home range. Flowering and fruiting of preferred tree species can increase foraging in these areas leading to aggregations of possums outside their usual home range (Jolly 1976; Ward 1978; Cowan & Clout 2000).

In Hawke's Bay, possum habitats include willows along streams, swamp, and farmland (Brockie et al. 1987). Trap success was highest in the swamp habitat, followed by the willows and was relatively low in open farmland. In podocarp and mixed hardwood forest of the Orongorongo Valley, near Wellington, possums prefer denning in large trees high above the ground (Cowan 1989). Limited availability of preferred denning opportunities sometimes led to aggregation of possums. The availability of suitable denning sites in trees was limited and ground denning was restricted or disturbed by flooding events. Up to five possums shared dens at a time and dens were visited by up to six individuals within a month (Fairweather et al. 1987). The suitability of a tree as a denning site is sometimes a function of its diameter at breast height. Wider trees have a higher chance of having suitable tree holes. The size and depth of the tree hole determines its thermal characteristics. This affects den site selection for possums in Australia, where temperatures in summer can average 30°C (Carthew et al. 2015).

In Central Otago, there appeared to be density-dependence in habitat selection as possums preferred rock and shrub habitats, and avoided grassy areas, at a low density site, but showed no preference for habitat at a high density site (Rouco et al. 2017).

Possum distribution in urban areas is patchy. Even though residential gardens can provide highly nutritious food, occupancy is mostly affected by housing density and availability of forest fragments (Adams et al. 2013). However, individual home ranges can be independent of these forest fragments if the garden vegetation is mature and structurally complex (Harper 2005; Adams et al. 2014). In another urban study, possums were detected most often in forest fragments, and least often in residential gardens, with the probability of possum presence in gardens being higher closer to forest fragments (Miller et al. 2022). Microhabitat features had no significant effect on possum presence in these urban areas.

Dispersal/reinvasion: While adult possums usually occupy an established home range for life (Cowan & Clout 2000), c. 20% of juvenile disperse from their home area (Ward 1985; Brockie et al. 1987; Cowan & Rhodes 1993), although this dispersal rate can be much lower (Byrom et al. 2015). Juvenile dispersal distances can be highly variable. Juveniles moved 0.5–10 km in mixed forest (Clout & Efford 1984; Ward 1985). Dispersal distances were similar in pine plantations (Cowan & Rhodes 1993). A subadult male moved 2.5 km within 3 days down a river valley (Byrom et al. 2015) and dispersals in a South Island dryland ecosystem were up to 5 km (Glen et al. 2012). Brockie et al. (1987) described individuals moving up to 24.5 km when crossing open farmland. The two longest recorded movements (of 32 and 41 km) were both by dispersing females (Cowan & Glen 2021).

In some cases, possum management may affect adjacent uncontrolled populations. Pech et al. (2010) found that dispersal distances into possum-free areas after control increased compared to a control group in an untreated forest. Possums in an area adjacent to the controlled area moved larger distances, had bigger home ranges, and had an increased rate of home range shift. These possums moved up to 350 m in the first 6 months after the control operation, compared to 153 m in the control group. In contrast, in the North Island, an 80% population reduction at an adjacent site did not prompt adult possums to leave their established home range to emigrate to the low density area (Cowan & Rhodes 1993), although juveniles dispersed up to 11.6 km. Rouco et al. (2017) found home ranges increased when individuals dispersed into suitable habitat after possum density was reduced by 65%. However, on the West Coast of the South Island, the direction of movement of possums adjacent to areas where possum density was reduced by a control operation was not biased towards the managed area (Byrom et al. 2015). The number of juvenile possums that dispersed decreased after a control operation killed more than 90% of possums, and the proportion that dispersed and the distance they travelled remained unchanged (Cowan et al. 1997).

Landscape features can affect possum movements. Large rivers can partially restrict travel, promoting movement of possums along valleys (Sarre et al. 2014; Byrom et al. 2015). However, rivers are not impermeable barriers as possums can cross major rivers (Ward 1985; Cowan 2001). Forested ridgelines did not change the movement patterns of possums (Byrom et al. 2015). Altitude can affect possum dispersal (Green & Coleman 1984). In Westland, population density was reduced by trapping to near zero across three altitudinal zones. The main driver of population recovery was dispersal, with recovery being fastest in lowland forest (<400 m a.s.l.) and slowest in alpine forest (>600 m a.s.l.). In the high country of the Mackenzie Basin, an altitude >2,000 m was a significant barrier to possum movements, with the highest detection recorded at 2,079 m (Foster et al. 2021, 2022).

3.7.1 Knowledge gaps

Understanding the movements of possum survivors following elimination attempts can guide post-operational monitoring, mop-up, and biosecurity. Studies analysing the effect of possum control on movement have focused on populations adjacent to managed areas. Adult possums have stable home ranges and do not necessarily move into managed areas. The behaviour of survivors is unknown, but they are likely to be forced to move greater distances or shift their home range to find social contacts (see Sweetapple et al. 2016). Movement patterns, habitat use, and home range can be analysed using GPS collars. One approach is to trap surviving possums after an aerial toxin application and fit GPS collars. Given the difficulty of trapping enough survivors, an alternative approach is to trap possums before an aerial toxin application, fit GPS collars and release them

after the operation at the locations where they were trapped. These possums would not necessarily be true survivors, but this approach allows good sample sizes. They could be desexed, but this would probably remove their primary motivation and subsequent behaviour.

Understanding dispersal rates and distances allows evaluation of invasion risk into possum -free areas and helps with the identification of elimination units that have the highest probability of being defensible from possum invasion in a mainland elimination context. We need more information about possum movements between managed and unmanaged areas, with a focus on elimination and biosecurity. Previous research has shown that a very small percentage of individuals disperse (Pech et al. 2010; Byrom et al. 2015). Therefore, many individuals must be telemetered to gather enough data, which is expensive. The effectiveness of buffers in stopping the spread of bovine TB has been evaluated, but this does not require zero possum dispersal. It is unclear what factors led to different dispersal rates in previous studies. Movement studies in different habitat types and population densities need to be replicated, including tracking movements from source populations into managed areas.

Etherington et al.'s (2014) model of possum dispersal across different landscape features requires validation with real data. Obtaining such data from dispersing possums is difficult as dispersal rates can be very low and unpredictable. Fitting GPS collars to subadult possums (e.g. Byrom et al. 2015) will provide the greatest opportunity for acquiring movement data from dispersing individuals.

4 International studies

4.1 *Rattus* species

Home range: We found six international studies on home ranges of ship rats with three reporting population density estimates in the same studies. These three studies were all conducted on tropical islands. Russell et al. (2011) and Ringler et al. (2014) conducted mark-recapture and spool-and-line experiments on Europa and Juan de Nova Islands in the Mozambique Channel, where they found significantly higher rat densities and smaller home ranges in forests compared to grasslands, regardless of sex and season. Interestingly, home ranges increased on Europa Island but decreased on Juan de Nova Island from summer to winter. The authors suggested that while lower food sources in winter might drive larger home ranges on Europa, the presence of predators, feral cats (*Felis catus*), on Juan de Nova could have driven the reduction in rat home ranges due to a shift in cat diet from seabirds in summer to rats in winter, that increased predation risk and limited rat movements in winter (Ringler et al. 2014). On the other hand, ship rat density in the forests of Puerto Rico was much higher (114.7 ± 201.8 ship rats/ha, $\pm$ SE) than those recorded on Europa and Juan de Nova islands, yet the average home range size of 0.28 ha (range, 0.07 – 0.50 ha) (Berentsen et al. 2018), was similar to that on the two islands.

Apart from resources and predators, rat home ranges are also influenced by sex. On Christmas Island, male ship rats had larger home ranges than females, regardless of habitat type (i.e. coastal forest: females, 0.38 ha; males, 0.54 ha; compared to urban gardens: females, 0.17 ha; males, 0.57 ha) (see Low et al. 2013). Female home ranges were mostly affected by the spatial distribution of food, while male home ranges were determined by the distribution of breeding females, with males expanding their home ranges to maximise the number of females they could access when female

home ranges declined in size. Higgins et al. (2015) observed a similar pattern on San Clemente Island (off California), with males having larger home ranges (2.09 ha) than females (1.53 ha).

Because ship rats and Norway rats are both commensal species, most studies other than those above were conducted in urban environments. Byers et al. (2019) provided a systematic review on these urban studies. Their review indicates that as for natural environments, the size and shape of home ranges of both rat species are influenced by access to food, shelter locations, and mating opportunities. Sex differences in home ranges were also apparent in urban areas, with male Norway and ship rats having home ranges that were 13 and 4 times larger than their female counterparts, respectively.

On Reiono Island in French Polynesia, the home ranges of kiore (0.55–1.94 ha, 95% CI) appeared to be larger in June than December, with females moving longer distances from their home range centres (up to 60 m) than males (up to 40 m), and juveniles moving the least, with distances from home range centres of as little as 10 m (Samaniego et al. 2020). Estimated rat densities here were very high (c. 100 kiore/ha). In a Hawaiian sugarcane field and neighbouring 'wastelands', linear movements of male kiore were longer than those of females, longer in winter than in summer, and longer in young sugarcane than in mature sugarcane (Nass 1977). Kiore with burrows in wastelands moved greater distances than rats with burrows in sugarcane fields. The estimated home range sizes for males (0.18 ha) were larger than those of females (0.06 ha). Similarly, at Kure Atoll in Hawaii, adult male home ranges (0.17 ha, range 0.01–0.73) were larger than those of females (0.08 ha, range 0.01–0.48) (Wirtz 1972).

Microhabitat use: There is overwhelming evidence that ship rats prefer microhabitats with dense vegetation cover. Regardless of the geographic area, rats associate with areas with higher tree density, higher ground vegetation cover, less bare ground, and deeper leaf litter (Shanker 2001; Ringler et al. 2014; Cusack et al. 2015; Madden et al. 2020). Selection for structurally complex understories was apparent for rats living in remnant bush patches in urban areas (Banks & Hughes 2012; Banks & Smith 2015). Clark (1980) reported a positive correlation between densities of ship rats and vegetation biomass, which probably related to availability of food and refuge. He also found that ship rats at low densities had more specific microhabitat requirements, as they were more frequently trapped under shrub or bush than ship rats at higher densities. Similarly, Cox et al. (2000) experimentally enhanced the amount of leaf litter at traps, and found that ship rats were selecting these traps over untreated traps. On farms, ship rats were also observed selecting areas with a higher percentage of horizontal and vertical hollow elements (e.g. wood trunks with hollows, open barrels, and boxes; see Lovera et al. 2019). While ship rats are known to climb trees, Key and Woods (1996) suggested that interspecific interactions could influence arboreality, since they found ship rats were least arboreal where they were the only rat species present.

Only a few studies have investigated microhabitat use by Norway rats. One study was on a farm and the rats selected for sites closer to food sources (livestock feed storage), with abundant vertical solid elements, such as stacked bricks, tree trunks without hollows, posts, and areas with a higher proportion of water bodies (Lovera et al. 2019). In Europe, colonies may have more than 150 individuals that jointly excavate a burrow system that consists of tunnels and chambers that serve as shared nest sites as well as places for food storage. Field colonies are often ephemeral and rats that move between colonies tend to be at or near sexual maturity. Abundance and breeding are greatly influenced by the amount of food available and by season. Where resources are abundant and clumped (like a rubbish dump), Norway rats form multi-male, multi-female groups and defend

a clan territory, but if food is scattered or sparse, male territories may be exclusive and each overlap with the ranges of several females (MacDonald et al. 1999; Schweinfurth 2020).

Dispersal/reinvasion: Dispersal is highly related to the exploratory behaviour of animals. In captive experiments, ship rats displayed different types of exploratory behaviour, with some being 'even explorers' that spent a similar amount of time exploring each part of an unfamiliar environment and some being 'selective explorers' that focused their exploratory activity in a certain part of the environment (Žampachová et al. 2017). Štolhoferová et al. (2024) further showed that these exploratory behaviours have high repeatability, i.e. the rats displayed personalities in their exploratory behaviour that can play an important role in their dispersal and reinvasion strategies.

Hansen et al. (2020) conducted a removal experiment in urban bushland in Sydney Harbour, Australia, in which they bio-marked ship rats with baits and removed ship rats from the core areas of two plots (each measuring 1 ha), followed by removing rats from the entire plots. A delay in reinvasion was evident. During the first 4 weeks, there was no significant influx of new individuals, and the ship rats that were previously radio-tagged did not change their home ranges in response to the removal. The rats that were located at the peripheral areas also did not shift to the core areas. However, during the 3 months after complete rat removal, ship rats reinvaded the core areas of all plots. Interestingly though, invasion rates were similar between treatment plots and control plots where no ship rats were removed, and the authors concluded that ship rats in the area appeared to be highly mobile, resulting in a high degree of population turnover in general.

In Australia, ship rats compete with the native bush rats (*Rattus fuscipes*) for habitats and resources. Ship rats often do not establish where there is a resident native bush rat population, unless there is a sudden boost in ship rat population dynamics, such as an excessive production of young (Banks & Smith 2015). Removal of ship rats could facilitate the establishment of the native bush rats through immigration and an increase in bush rat female residency (Banks & Hughes 2012). It is therefore crucial to consider the presence of other competing species when assessing and minimising reinvasion of ship rats, or any other species of rat.

Most studies on the dispersal of Norway rats were conducted in urban areas (except for two studies on South Georgia and Frégate Island) using genetic analyses to reveal population structures and dispersal barriers. The study on South Georgia Island suggested that Norway rats were able to disperse across fjords and retreated glaciers (Piernéy et al. 2016), while studies in urban areas suggested that while Norway rats disperse along main roads, highways with high traffic volumes could restrict gene flow (Combs et al. 2019; Gatto-Almeida et al. 2022). Resource-poor areas, such as commercial and industrial areas, could also act as dispersal barriers, and Norway rats in resource-rich areas, such as residential areas with abundant food waste resources, are less likely to disperse (Gardner-Santana et al. 2009; Combs, Byers et al. 2018; Combs, Puckett et al. 2018). The distances over which Norway rats were genetically isolated varied among cities, ranging from 250 m to 1.7 km (Gardner-Santana et al. 2009; Combs, Puckett et al. 2018; Combs et al. 2019). Combs et al. (2019) observed less stable genetic clusters within part of one suburb where Norway rats were at lower densities, suggesting that this low-density cluster experienced higher movement and gene flow. On Frégaten Island, Seychelles, which Norway rats colonised in July 1995, most captures were within a 75 × 60 m area for 8 months, then some rats dispersed up to 400 m (Thorsen et al. 2000).

4.2 Mustelidae family

Home range – weasels: In Europe, weasel spacing behaviour and home range size depend on habitat, population density, season, sex, and prey density, and varies considerably within populations (Lockie 1966; Erlinge 1974; King 1975; Delattre 1984). A considerable proportion of weasels do not appear to form stable home ranges, which makes modelling home ranges, movement, and the efficacy of weasel detection networks particularly challenging. In a study in Sweden, Sandell (1986) described three distinct movement patterns for stoats, which also appear to apply to weasels, i.e. stationary, roaming, and transient (see Glossary). Stationary individuals form stable home ranges (for a period) and can form exclusive intrasexual territories. Transient individuals continuously move across the landscape, having no fixed ranges, moving on within a day or even within a few hours to follow prey. Transience appears most common in 1-year-old males, but also occurs in females when not raising litters, and in other age classes. Roaming is the rapid movement over large areas during the mating season, which is most common in larger, older male weasels and stoats (Lockie 1966; Erlinge 1974; Moors 1975; Sandell 1986).

In a study in Scotland in a young plantation overgrown with thick grass full of field voles, ten male weasels had non-overlapping defended territories of 1–5 ha (Lockie 1966). There were also at least 20 transient males that were caught as they passed through the area, with transient movement particularly common in late summer and early spring. In the same area there were three resident females, all with home ranges <1 ha, and there were at least six transient females. For reasons unknown, part way through the study the stable home ranges broke down for all individuals for at least two years, despite high prey availability and reasonable weasel numbers, and the defended territories were not re-established. Similar patterns were observed at Wytham Wood in England, with a mixture of resident and transient weasels, with resident male weasels holding their territory for only c. 7 months on average (King 1980a). This well studied population collapsed and suffered a local extinction due to low prey densities in the late 1970s (Hayward 1983).

In the Kielder Forest in northern England, five of eight radio-tracked male weasels had low site fidelity, moving between different logged forested areas on a daily basis (Brandt & Lambin 2007). For these transient individuals, no home range could be calculated because of their constant movements. The mean overlap between daily home ranges for individual weasels ranged from 1.1% to 35.6%. For resident weasels, distances between daily home range centres were small (147.83 m) compared with longer distances for transient individuals (379.7 m).

For stationary weasels that form territories, males always have much larger home ranges than females (Erlinge 1974; King 1975, 1980a; Delattre 1984), and they change seasonally, with male home ranges expanding nearly 20 times, from the non-breeding season (3.6 ha) to the breeding season (66.3 ha) (King 1975; Sheffield & King 1994; Magrini et al. 2009). Females generally maintain well-defined home ranges during the breeding season (Erlinge 1974; Moors 1975), and these ranges can be surprisingly small (i.e. 0.2–2.1 ha; reported by Nyholm [1959] and 1–2 ha reported by King [1975]). Erlinge (1974) found the same breeding female 29 times within 1.5 ha over 2 months (Henttonen 1987). The weasels hunt their entire range regularly in a rotational manner, thereby minimising the time spent in any one area (King 1980b, 1989).

Resource availability influences weasel density and home range size. Male home ranges increased 7-fold (from 11–37 ha to 117–216 ha) during a year when vole populations crashed at Białowieża National Park, Poland (Jedrzejewski et al. 1995). This corresponded with a reduction in weasel

density from 0.027 individuals/ha to 0.005 individuals/ha in winter, and from 0.102 individuals/ha to 0.019 individuals/ha in summer. Similarly, Sundell et al. (2000) conducted an experiment in large outdoor enclosures to assess the functional response of weasels in response to different densities of prey (East European voles, *Microtus rossiaemeridionalis*) and found that weasel home ranges expanded when prey densities were low. In contrast, Brandt and Lambin (2007) found no effects of vole densities on weasel home ranges, but vole densities were generally lower in their study area. In a study from Finland, weasels travelled further (males 1.4 km, females 1.0 km) when voles were scarce than when they were abundant (660 and 110 m, respectively) (Klemola et al. 1999).

Studies in Europe show that weasels are able but slow swimmers (Stroganov 1962; Svendsen 1982).

Home range – stoats: Unlike weasels, most stoats in Europe appear to form stable home ranges for most of the year, typically exhibiting intrasexual territoriality in which males generally defend non-overlapping home ranges with other males, and females generally defend non-overlapping home ranges with other females, although males and females can overlap (Erlinge 1977; Linnell et al. 2017). Most young female stoats remain close to their place of birth, usually less than 5–6 km away (Erlinge 1977; Debrot & Mermod 1983). Sixteen of the 18 young females observed by Erlinge (1983) in Sweden stayed in the same area for life. King (1983), Debrot and Mermod (1983), Samson and Raymond (1998), and Linnell et al. (2017) reported larger male stoat home ranges (9–51 ha) than those of females (2–16 ha). Female home range sizes were driven by the abundance of prey (with smaller home ranges when prey was abundant); male home range sizes were driven by both food availability and mating opportunities, overlapping with female home ranges (King 1983; Hellstedt & Henttonen 2006; Linnell et al. 2017). In a study in Switzerland, extremely low prey densities resulted in stoat territories breaking down, with male stoats (and potentially female stoats) becoming transient (Debrot & Mermod 1983). Erlinge and Sandell (1986) observed seasonal patterns in male home ranges in response to changes in social structure: males tended to defend small feeding territories during non-breeding seasons but shifted to non-territorial large home ranges that overlapped between different males during the breeding season. Intraguild competition also influenced stoat home ranges: stoats moved greater distances and had larger home ranges in areas with higher levels of intraguild predators (coyotes [*Canis latrans*] and red foxes [*Vulpes vulpes*]), and reduced their use of habitats that were already occupied by competitors of similar size (long-tailed weasel [*Neogale frenata*]) (St-Pierre et al. 2006).

Stoat spacing behaviour and home range size depend on habitat, population density, season, sex, and prey density (Erlinge 1977, 1983; Erlinge & Sandell 1986; Hellstedt & Henttonen 2006; King et al. 2007; Linnell et al. 2017). Stoat abundance in a mountain valley in Switzerland crashed from 6.8 captures/100 trap units in the first year to less than 1 capture/100 trap units in the following 3 years (Debrot & Mermod 1983). These stoats originally had a well-established intrasexual territorial system and were evenly distributed during the high population period, but this system broke down during the population decline, with females becoming restricted to small areas of favourable habitats and males becoming transient and reducing their territoriality. In a study in Sweden, territoriality generally broke down in spring, with some males setting off on long excursions (up to 6 km), others staying in their territory but moved far more actively, and yet others disappearing (Sandell 1986). Large dominant males were more likely to wander widely, whereas small males stayed in their territory. One male stoat covered at least 26 km² during one spring, while other males in the same area employed a stationary pattern, defending a territory of about 2 km² (Sandell 1986).

Stoats, while generally solitary, are social animals. They are keenly interested in the activities of other stoats around them, and they communicate through scent marking along territorial borders (Erlinge 1977; Erlinge et al. 1982). Marking can involve anal dragging, body rubbing, urination or defecation at specific features or on prominent objects (Hutchings & White 2000).

Territorial boundaries are maintained by scent marking and aggressive interactions, which limits the movement of each individual and reduces home range size. However, stoats may potentially expand their range to find neighbouring conspecifics, or for males to ensure there are females within their range.

Both male and female stoats are dominant over weasels. Weasels adapt their behaviour and activity to that of the stoats, and are repeatedly disturbed by stoats even when in a retreat (Erlinge & Sandell 1988). The interactions between stoats and weasels appear to be habitat-specific, and the species do often overlap even at microhabitat scales in some instances (e.g. Aunapuu & Oksanen 2003).

Home range – other mustelid species: Regardless of the species, male mustelids generally have larger home ranges that are mostly double the size of the females' ranges, with clear intrasexual territoriality in which home ranges of the same sex rarely overlap (Hawley & Newby 1957; Gehring & Swihart 2004; Harrington & Macdonald 2008; Peters et al. 2009; Livieri & Anderson 2012). Resource availability also appears to be the main driver of home range size. A meta-analysis of European pine marten (*Martes martes*) home range data from 15 studies across Europe suggested that marten densities were limited by winter severity, while home range sizes were driven by forest cover and rodent abundance, with male home ranges expanding in response to reduction in forest cover and female home ranges reducing in response to greater rodent abundance (Zalewski & Jędrzejewski 2006). Home ranges were also affected by the availability of productive habitats, den, and resting sites (Sasaki & Ono 1994; Zielinski et al. 2004; Melero et al. 2008). Black-footed ferrets (*Mustela nigripes*) consume mostly prairie dogs (*Cynomys* spp.) and use prairie dog burrows as shelters. Ferret home range sizes were inversely correlated with the density of active prairie dog burrows (Jachowski et al. 2010). Effects of mustelid population density on home ranges varied. Molina-Vacas et al. (2009) reported larger home ranges (males, 416 ha; females, 80 ha) for European badgers (*Meles meles*) in an area where population density was low (0.006 badgers/ha) compared to where it was higher (0.019 badgers/ha: male home range, 91 ha; female home range, 56 ha). Herr et al. (2009) reported smaller home ranges of beech marten (*Martes foina*) in urban areas due to greater resources and population density. In contrast, Baghli and Verhagen (2004) reported European polecat (*Mustela putorius*) home ranges that were similar regardless of population density, although their comparison was made between geographic regions with potentially different habitat and food resources.

Microhabitat use – weasels: In Europe, weasels are found in open forests, farmlands and cultivated fields, grassy fields and meadows, riparian woodlands, hedgerows, alpine meadows and forests, scrub, steppe and semi-deserts, prairies, and coastal dunes (Heptner et al. 1967; King, 1989; Nyholm, 1959; Polder, 1968; Svendsen, 1982; King et al. 2007). Weasels are particularly common in areas where small rodents are abundant, such as cut over pine forest (Brandt & Lambin 2007). There are some estimates of the threshold densities of small rodents required to sustain weasel populations. Erlinge (1974) states that a rodent density of at least 10 breeding individuals per ha is necessary. Tapper's (1979) estimate is a little higher (14 individuals/ha), and both studies concerned field voles *Microtus agrestis*. Lockie's (1966) estimate was much higher; he found that weasels

abandoned the area when the density of field voles had declined to 44 animals/ha. A radio telemetry tracking study in Białowieża Forest in northeast Poland found that weasels travelled a mean linear distance of 1.32 ± 0.83 km per day through fields and meadows, riparian margins, sedge meadows, hardwood forests and reed beds (Chappell et al. 2013).

While habitat selection by weasels at landscape scales is strongly dictated by the temporal and spatial variation in small rodent availability, at the microhabitat scale the avoidance of predators becomes the most important factor (Zub et al. 2008). Weasels prefer remnants of natural vegetation in an agricultural landscape, habitats with high grass cover corresponding to high prey (vole) densities in native forests; they also favour dense vegetation and avoidance of areas with high water levels which allow for better thermal regulation in winter (Brandt & Lambin 2007; Zub et al. 2008; Magrini et al. 2009). They therefore avoid areas of open ground such as cultivated agricultural fields, and in farmland environments they have a strong preference for linear habitats including stone walls, fence lines around fields, riparian habitats and edge vegetation (Polder 1968; Moors 1975; Pounds 1981; Sheffield & King 1994; McDonald & Harris 1999; King et al. 2007; Brandt & Lambin 2007; Magrini et al. 2009). In a study of wildlife use of road underpasses, both weasels and stoats strongly favoured underpasses near dense cover (van Vuurde & van der Grift 2005). In a study at Wytham Wood in England, no weasels were recorded more than 5 m from hedges and ditches (MacDonald et al. 2004). Snow presents little obstacle to the distribution, hunting, or movements of weasels (Erlinge 1974; Simms 1979).

Microhabitat use – stoats: Adult female stoats prefer brushwood piles, while juvenile males prefer edges of stream and trails (Samson & Raymond 1998). St-Pierre et al. (2006) suggested that stoats use rodent burrows as refuges from their intraguild competitors.

Microhabitat use – other mustelid species: Habitat studies of other mustelid species show they have a preference for resting sites in hay piles in barns, stables and buildings on farms (Weber 1989; Sasaki & Ono 1994). Self-dug burrows, woodpiles, branches, dry leaves, and dense vegetation such as reed grass are also refuges for mustelids, with nests built from dry grass and moss (Weber 1989; Hajduk 2008; Lodé 2011).

Dispersal/reinvasion – weasels: Whenever weasels move through habitats with little ground cover, they prefer to use road verges, ditches, riverbanks, or fire breaks, which provide some grass cover. However, in one study, a radio-tracked male weasel did cross an area lacking grass cover for at least 300 m (Brandt & Lambin 2007). When crossing unfavourable habitats, the distance weasels cover each time is 4-5 times greater than when they are in a preferred habitat like a clear cut (Brandt & Lambin 2007). Suboptimal habitat of cultivated grassland or built-up areas present moderate barriers to movement, causing some genetic differentiation of populations either side of such areas (McDevitt et al. 2013). Some males crossed c. 1 km of suboptimal habitat (cultivated land), although they may have dispersed around its edges. McDevitt et al. (2013) found that mostly male weasels made long distance dispersals, and that human occupation and development were barriers to their dispersal. When not breeding, all weasels (including females) can cover several km daily (Henttonen 1987).

Dispersal/reinvasion – stoats: Juvenile female stoats generally have a high degree of home range tenure, staying within their natal area where food and shelter are available, and do not undertake long-distance dispersal (Debrot & Mermoud 1983; Erlinge & Sandell 1986). Juvenile male stoats, on the other hand, disperse extensively in spring, and where population densities are high they are sometimes forced by resident males to reside in peripheral areas (Debrot & Mermoud 1983; Erlinge

& Sandell 1986). King (1975) observed a male stoat expanding his range to include 17 new trap sites (approximately 12 ha) within 3 months following the death of another male originally residing at those sites. One male stoat tagged in Alaska most likely travelled further than the 35 km straight distance recorded between capture locations in 6 months (Burns 1964).

Dispersal/reinvasion – other mustelid species: Male-biased dispersal of up to 40 km has been reported for numerous other mustelid species, such as European pine marten, European mink (*Mustela lutreola*), American marten (*Martes americana*), and American mink (*Neogale vison*) (Hawley & Newby 1957; Zalewski et al. 2004; Helyar 2005; Peters et al. 2009; Zalewski et al. 2009). Expansion of home ranges by neighbouring males into the original home ranges of deceased males is also frequently observed, although it is less common for females and can take more than a few months (Hawley & Newby 1957; Molina-Vacas et al. 2009; Peters et al. 2009). Low population density has been suggested as a trigger for dispersal. For example, two male European mink displayed nomadic behaviour and dispersed 40 km away from a low density area (Michaux et al. 2005). Similarly, Peters et al. (2009) observed a juvenile male European mink dispersing into a new area together with its mother, and suggested that the juvenile might have been trying to monopolise its mother as a potential mate given the low population density at the time. One study used DNA analysis of European mink from six European countries and concluded that mink have an isolation-by-distance pattern up to 50 km, i.e. they could be genetically related over distances of up to 50 km. On the other hand, Zalewski et al. (2009) suggested that while mountains are major barriers to gene flow, they are not absolute barriers and only slow down dispersal of American mink.

4.3 *Trichosurus* species

Home range: Of the six home range studies of common brushtail possums in Australia, three were conducted in urban areas or urban edges in Melbourne, Canberra, and Launceston. Home range sizes of females in urban areas were <3 ha, while those of males varied from 1 to 10 ha (Dunnet 1956; Statham & Statham 1997; Adams et al. 2014). However, male home range sizes were often similar to those of females. Small home ranges in urban areas were attributed to the dense distribution of resources. Possum activities were concentrated in the remnant forests in metropolitan Melbourne (Adams et al. 2014). Similar home range sizes for males and females was reported in two studies conducted in more natural areas. Clinchy et al. (2004) found that males were as sedentary as females in a mature eucalyptus forest, and le Mar et al. (2003) reported female home ranges that were unexpectedly large (16.2 ± 3.7 ha, $\pm$ SE) and comparable to those of males (18 ± 5.2 ha, $\pm$ SE) in a mosaic of eucalyptus forest plantation and native rainforest. In contrast, Cruz et al. (2012) described male home ranges of 30.7 ± 19.7 ha, $\pm$ Standard Deviation SD for *Trichosurus vulpecula hypoleucus* (a subspecies of the common brushtail possum) that were larger than those of females (15.5 ± 7.9 ha, $\pm$ SD) in jarrah forest in Western Australia.

Three studies reported the home ranges of the mountain brushtail possum (*Trichosurus cunninghami*), a species that specialises in inhabiting forests environments. All three studies were conducted in the Strathbogie Ranges in north-eastern Victoria, with one study site located within a remnant sclerophyll forest patch (36 ha) and another along linear roadside forests (Martin 2006; Martin et al. 2007; Martin & Martin 2007). There were no sex differences in home ranges within the forest remnant (males, 6.21 ± 0.53 ha, $\pm$ SE; females, 5.59 ± 0.65 ha, $\pm$ SE), but significant differences were apparent between adult (mean 6.0 ± 0.4 ha, $\pm$ SE) and subadult home ranges

(average c. 3.5 ha) (Martin 2006). On roadsides, however, male home ranges (5.1 ± 0.8 ha, $\pm$ SE) were twice the size of female home ranges (2.1 ± 0.3 ha, $\pm$ SE), while the home ranges of females were only one-third the size of female home ranges within the forest remnant (Martin et al. 2007; Martin & Martin 2007).

Martin and Martin (2007) reported an inverse relationship between female home ranges and the density of silver wattle (*Acacia dealbata*), the main food source for the possums, suggesting that female home ranges are resource driven. The influence of food availability on home ranges was also reported for short-eared possums (*Trichosurus caninus*) in eastern Australia (McRae et al. 2022). Possum density was higher (0.46 individuals/ha) and home ranges smaller (10 ha, 95% Confidence Interval CI: 7–14 ha) in a temperate forest with rich food abundance, compared to lower density (0.13 individuals/ha) and larger home ranges (25 ha; 95% CI, 7–85 ha) in a wet sclerophyll forest, where food is scarcer. In the same study, male home ranges (12.5 ha, 95% CI: 8–19 ha) were larger than those of the females (5.5 ha, 95% CI: 3–11 ha).

Microhabitat use: Microhabitat studies on possums all focussed on den use in trees by common brushtail possums, including two subspecies *Trichosurus vulpecula hypoleucus* and *Trichosurus vulpecula fuliginosus*. Possums selected areas with a high availability of trees, especially hollow-bearing trees (Cawthen 2007). On the grounds of a university, possums preferred buildings surrounded by big trees with high canopy cover (Chen et al. 2020). Possums were more likely to occupy certain species of trees and these included: trees that were mature and healthy and provided better buffering against temperature fluctuations; trees with fewer hollows; and trees with hollows 100–300 cm above ground (Isaac et al. 2008; Cruz et al. 2012; Carthew et al. 2015). All possums used multiple den trees (mean 7.2 ± 0.7 trees, $\pm$ SE), with some individuals using as many as 18 trees (How & Hillcox 2000; Martin 2006). Despite their preferences for den trees, possums also denned on the ground in dense vegetation when tree hollows were limited (Martin 2006). However, they remained close to trees while on the ground and shifted to dense cover when predation risks were high (Cruz et al. 2013). These studies all indicate the importance of suitable denning trees in habitat use by possums.

Dispersal/reinvasion: Stow et al. (2006) and Bannister et al. (2019) reported male-biased dispersal in common brushtail possums, with males dispersing further than females from their natal home ranges. Males dispersed 16 times further than females at a distance of 6.45 ± 0.82 km within a national park (Bannister et al. 2019), but in an urban area their dispersal distance was much shorter (<900 m), although still further than that of females (Stow et al. 2006). While young females tend to settle in areas adjacent to their mothers, some non-reproductive females dispersed as far as 700 m (How & Hillcox 2000). Clinchy et al. (2013) conducted a removal experiment at Paddys Land State Forest in Victoria, where they removed 19 female common brushtail possums from the core of their study area and found that 15 other females expanded their home ranges into the removal area. In the 2 years following the removal, these females had taken over the previously occupied dens. The authors discuss the importance of distinguishing between ‘true immigration’, when animals abandon their former home ranges and move into new home ranges, and ‘apparent immigration’, when animals simply expand their original home ranges. They argue that true immigration has the greatest influence on the sustainability of a population.

Male mountain brushtail possums dispersed further than females (Allan et al. 2019). Interestingly, female mountain brushtail possums were more likely to produce male offspring when they

occupied areas with limited resources or were in poor body condition, presumably to maximise dispersal of their offspring and reduce competition (Banks et al. 2008).

5 General patterns of space use

5.1 Home range

One of the basic requirements for achieving animal eradication is a good understanding of home range size. The smallest home ranges described for a given species should guide the minimum density of toxic baits, removal devices, and detection devices needed to ensure at least one device or bait in every home range. Home range size varies greatly for any given population, with female home ranges usually being the smallest.

As predator densities decline with eradication attempts, home ranges expand. They also tend to be larger in suboptimal habitats where food is less abundant and conspecific densities are low; and they are also larger where dominant competitors or predators are scarce or absent.

Basing device or bait density on minimum home range size is expensive, but necessary for elimination purposes, especially if the operation has an initial large-scale 'knock-down' phase. While there may be potential cost savings for predator suppression projects from reducing device or bait density according to the conditions that expand home range size, we advise against this for elimination projects. This is because of other density-dependent behaviours that counter the ability to remove every animal, such as avoidance by some individuals of lethal devices or baits as population density is reduced. Also, some individuals can still maintain small home ranges regardless of the conditions (Anderson et al. 2022). These are the individuals that must be targeted in elimination operations.

5.2 Microhabitat use

Understanding microhabitat use by predators allows a more nuanced and cost-effective approach to deploying toxic baits, removal devices, or detection devices across a landscape. Unfortunately, there are few studies of microhabitat use at very low densities, although some overseas studies suggest that stoats and ship rats that survive eradication attempts tend to aggregate in their preferred microhabitats (Clark 1980; Debrot & Mermoud 1983). Greater preference for certain habitat types at low population density was also observed for possums in New Zealand (Rouco et al. 2017).

Ship rats are very generalist in their habitat choices and prefer vegetation types that are structurally and floristically diverse in warm sites in forest interiors, and dense vegetation with high biomass and fruiting understories. Such microhabitats are likely to be patches rather than linear areas. Norway rats cluster near abundant food sources, including those associated with humans, such as rubbish dumps and livestock feedlots. They prefer margins of wet sites such as estuaries, lakes, streams, and the sea. Kiore prefer vegetation with dense ground cover.

There have been few studies of microhabitat use by weasels in New Zealand. In one study, weasels were caught in young pine plantations and along road edges where mice were abundant; and in a

study in beech forest, they preferred forest edges and valley floors. Most microhabitat studies are from Europe. At landscape scales, weasels are attracted to areas with high availability of small rodents, and at micro scales, they seek habitats that provide safety from predators. Weasels have strong preferences for linear habitats, including stone walls, fence lines around fields, riparian habitats, and vegetation edges. They also prefer natural vegetation remnants on farmland, areas with thick grass (where voles reside), and other dense vegetation types. They also like open forests, farmlands and cultivated fields, farm buildings, grassy fields and meadows, riparian woodlands, hedgerows, alpine meadows and forests, scrub, steppe and semi-deserts, prairies, coastal dunes, sedge meadows, hardwood forests, and reed beds.

Stoats are found across almost all habitats in New Zealand, from coastal sand dunes to all forest types, through to the high alpine. They travel along features that provide cover, such as hedges, habitat edges, and riparian margins, and avoid neighbouring open spaces. Like weasels, they prefer linear features such as forest margins and waterways, roads, farm margins, and ecotonal edges of forests that are associated with dense ground cover. Stoats prefer continuous forest and forest fragments.

Ferrets prefer tussock grassland, improved pasture, and shrublands, biased towards the presence of rabbits. They also occur in dune lands and wetlands. They like river valleys in forest, road edges, fence lines, grassy tracks, hedge rows, and waterways. They den in areas with cover of all types and avoid open pasture. In pastoral farmland, ferrets particularly favour man-made structures (woolsheds, haybarns). In developed grasslands, ferrets hunt in vegetated gullies. In thick grass they use small pathways, possibly created by rabbits, hares and stock. In large, braided river valleys they prefer ecotonal edges and vegetation on river flats. Ferrets are scarce or absent in the thick, wet forests of the west and south of the South Island.

Possums are widely distributed across various habitats in New Zealand, including forests, shrublands, grasslands, wetlands, and urban and rural areas. They frequent willows along streams, swamps, and farmland, wide trees with abundant den sites, shrub and rocky habitats in dryland environments, and urban gardens with mature and structurally complex vegetation.

5.3 Dispersal/reinvasion

Maximum recorded dispersal distances reported for ship rats are 1.5 km, Norway rats, 1.3 km, weasels, 17.4 km, stoats, 65 km, juvenile ferrets, 45 km, and possums, 41 km. Dispersal distances for stoats, ferrets, and possums were measured in moderate to high population densities, and so may not be representative of lower density populations following control. This is because conspecifics with established home ranges usually discourage dispersers from settling in their area. Therefore, dispersal distances are likely to be longer where population densities are high.

Buffer zones of predator control are often established around elimination zones to remove potential immigrants before they invade. The widths of these buffers are usually guided by home range size, or in some cases, by maximum dispersal distances of the target species. However, the effectiveness of buffer zones is more likely to be a function of the probability of predators interacting with toxic baits or removal devices within the buffer, rather than the width of the buffer. For example, there is little point creating a buffer zone based on maximum dispersal distances if predators mostly avoid the baits and devices inside the buffer, such as is the case for stoats on Waiheke Island where most stoats live amongst a trapping network by avoiding traps. Conversely,

there is little point in an overly wide buffer if the baits and devices within it are very effective at removing predators. A buffer zone that eliminates every animal does not need to be wide, whereas an inefficient buffer does. A cost-benefit analysis of the acceptable number of incursions into an elimination zone per unit time, and the number of repeated removal treatments, is required.

The pathways and habitats used by dispersers have rarely been studied. One study showed that juvenile ferrets in dry, open habitat dispersed along linear topographic features and habitat edges such as vegetation cover, overgrown stream channels, fence lines, roads, and riverbanks. It stands to reason that, in general, dispersers will concentrate their movements along the microhabitats outlined above.

Habitats that are usually avoided or used less often (and therefore potential barriers to dispersal in some situations) include high mountain ranges (over 1,700 m for possums and mustelids), high-flow waterways (although not necessarily for Norway rats and stoats, and perhaps for ship rats), open pasture, intense human development, roads with high traffic volume, and commercial and industrial areas.

5.4 Knowledge gaps

It is difficult to frame detailed suggestions for filling knowledge gaps to achieve a predator-free NZ when the tools and tactics for achieving this are so little resolved. Current major pest control regimes include fenced and unfenced ecosanctuaries, aerial 1080, and island eradications (Innes et al. 2024), and priorities for pest mammal research will vary between these. The only project currently advancing large-scale (>10,000 ha) mainland elimination of ship rats, stoats and possums without pest-fences is that in South Westland by ZIP. They use the 'remove and protect' model, primarily with aerial 1080 as the only currently available tool for large-scale initial population reduction on mainland public conservation land. They are experimenting with suitable post-1080 pest detection devices and densities (Bell et al. 2019) but their results are unpublished; the required research is enormous and demands stronger collaboration between agencies, and with ecosanctuary practitioners.

While much is published on the spatial behaviour of most of the predator species reviewed here, there is limited understanding of how they behave at extremely low densities imposed by intensive control. Advancing knowledge of target pest behaviour in low density situations will undoubtedly alter the kinds of toxic baits, removal devices, and detection devices, and how they are used.

Questions such as how far survivors move and if and where they aggregate in the landscape are largely unanswered. Vattiato et al. (2023) noted that detectability and movement of both survivors and reinvaders at near-zero densities remains a critical research need. Our knowledge about dispersal behaviour is particularly poor for Norway rats, kiore, and weasels.

This dearth of information is understandable as capturing enough animals at very low densities is extremely challenging and is usually avoided by students looking for feasible projects. One way to address this problem is to undertake experimental releases of individuals into eradicated areas, such as those of Russell, Beaven et al. (2008), Russell et al. (2010); Innes et al. (2011), and Nathan et al. (2020). All these studies were on ship rats and Norway rats – no such studies exist for kiore, mustelids or possums (although Sweetapple et al. 2016 used the same technique following suppression of possum numbers). Survivors can be simulated by capturing animals in situ before

elimination, attaching telemetry devices, and releasing them back into the site after elimination. Invaders can be simulated by capturing animals from other locations and releasing them into the area after elimination. The risk that these study animals may find mates and breed can be reduced by tracking and removing them immediately after the research is completed, or by releasing only males. We advise against using desexed animals because sexual reproduction and finding mates is usually the main driver of how animals move through a landscape when population density is very low. Discussions of the risks and benefits of such releases are required with stakeholders at each site.

Reinvasion is probably the key factor limiting the feasibility of eradication on the New Zealand mainland because all the pests reviewed here have been eradicated from some islands and pest-fenced ecosanctuaries. Little is known about reinvasion pathways, including the extent to which certain landscape features block, hinder, or facilitate dispersal. The efficacy of 'virtual fences' and buffer zones of control in removing potential invaders is also a critical knowledge gap. Once again, this is difficult work. GPS-collaring as many juvenile predators as possible outside elimination zones will add significantly to this knowledge.

The primary method of studying animal movements is by radio- or GPS-tracking, using collars or tags. Radio-tracking is the conventional technique that is cheaper but labour intensive, require triangulation methods that usually produce approximate locations. GPS-tracking, on the other hand, is more expensive but less labour intensive, and provides fine-scale locations. However, there is a trade-off between the weight of GPS collars/tags, frequency of data collection, and battery life: the lighter the collar or the more frequently it records GPS locations, the shorter the battery life. The precision of GPS data also depends on the location of the study (the more satellites available, the more accurate the data) and the behaviour of the animals (burrowing animals or animals that utilise dense vegetation generally results in less accurate data). To date, there are no GPS tracking devices available for mustelids and rodents with an acceptable battery life and reliable precision.

Any telemetry, or other study, at low density should take advantage of the opportunity to measure detection probabilities at low density, for example, by simultaneous deployment of detection devices such as cameras, chew cards, tracking tunnels, and live capture traps.

We need to better understand the effects of interactions between predator species, such as dominance and competition, on predators' use of landscapes. For example, within the rodent guild, do ship rats displace Norway rats and kiore, and are they more detectable and catchable after ship rats are removed? Within the mustelid guild, do ferrets have the same effect on stoats and weasels, and do stoats dominate weasels? And between guilds, do mustelids have similar effects over rodents? The best research approach will vary with the context of how the various species are removed. Simultaneous removal of all species (e.g. using pre-fed aerial 1080) would, for example, shift the emphasis to interspecific interactions during reinvasion and at very low density.

The ecology of weasels and kiore in New Zealand is severely understudied. Any research on their behaviour, especially at very low density, is sorely needed. The distribution of Norway rats, kiore, and weasels in New Zealand is also poorly understood. A useful way of approaching this knowledge gap is through eDNA techniques.

6 Acknowledgements

We thank Dean Anderson for internal review and Helen O’Leary for editing (both Manaaki Whenua – Landcare Research).

7 References

- Adams A, Recio MR, Robertson B, Dickinson K, Van Heezik Y 2014. Understanding home range behaviour and resource selection of invasive common brushtail possums (*Trichosurus vulpecula*) in urban environments. *Biological Invasions* 16: 1791-1804.
- Adams AL, Dickinson KJ, Robertson BC, van Heezik Y 2013. Predicting summer site occupancy for an invasive species, the common brushtail possum (*Trichosurus vulpecula*), in an urban environment. *PloS One* 8(3): e58422. <https://doi.org/10.1371/journal.pone.0058422>
- Allan BM, Nimmo DG, Arnould JP, Martin JK, Ritchie EG 2019. The secret life of possums: data loggers reveal the movement ecology of an arboreal mammal. *Journal of Mammalogy* 100(1): 158-168.
- Alterio N 1994. Diet and movements of carnivores and the distribution of their prey in grassland around yellow-eyed penguin (*Megadyptes antipodes*) breeding colonies: a thesis submitted for the Degree of Master of Science at the University of Otago, Dunedin, New Zealand. Unpublished thesis, University of Otago.
- Alterio N, Moller H, Ratz H 1998. Movements and habitat use of feral house cats *Felis catus*, stoats, *Mustela erminea*, and ferrets, *Mustela furo*, in grassland surrounding yellow-eyed penguin, *Megadyptes antipodes*, breeding areas in spring. *Biological Conservation* 83(2): 187-194.
- Anderson DP, Rouco C, Latham MC, Warburton B 2022. Understanding spatially explicit capture–recapture parameters for informing invasive animal management. *Ecosphere* 13(11): e4269. <https://doi.org/10.1002/ecs2.4269>
- Aunapuu M, Oksanen T 2003. Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evolutionary Ecology* 17: 371-392.
- Baghli A, Verhagen R 2004. Home ranges and movement patterns in a vulnerable polecat *Mustela putorius* population. *Acta Theriologica* 49: 247-258.
- Baker G 1989. Aspects of mammalian predator ecology co-inhabiting giant skink habitat. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.
- Ball SJ, Ramsey D, Nugent G, Warburton B, Efford M 2005. A method for estimating wildlife detection probabilities in relation to home-range use: insights from a field study on the common brushtail possum (*Trichosurus vulpecula*). *Wildlife Research* 32(3): 217-227.
- Banks PB, Hughes NK 2012. A review of the evidence for potential impacts of black rats (*Rattus rattus*) on wildlife and humans in Australia. *Wildlife Research* 39(1): 78-88.
- Banks PB, Smith HM 2015. The ecological impacts of commensal species: black rats, *Rattus rattus*, at the urban–bushland interface. *Wildlife Research* 42(2): 86-97.

- Banks SC, Knight EJ, Dubach JE, Lindenmayer DB 2008. Microhabitat heterogeneity influences offspring sex allocation and spatial kin structure in possums. *Journal of Animal Ecology* 77(6): 1250-1256.
- Bannister HL, Hodgins P, Moseby KE 2019. Offspring sex and maternal effects influence the development and natal dispersal of an arboreal marsupial. *Journal of Mammalogy* 100(2): 423-434.
- Bell P, Nathan H, Mulgan N 2019. 'Island' eradication within large landscapes: the remove and protect model. In: Veitch CR, Clout MMN, Martin AR, Russell JC, West CJ, eds. *Island invasives: scaling up to meet the challenge*. IUCN SSC Occasional Paper 62. Gland, Switzerland. Pp. 604–610.
- Berentsen AR, Torres-Toledo FB, Rivera-Rodriguez MJ, Davis A, Gilbert AT 2018. Population density and home range estimates of black rat (*Rattus rattus*) populations in southwestern Puerto Rico. *Proceedings of the 28th Vertebrate Pest Conference*. University of California, Davis, pp. 299-303.
- Blackwell GL, Potter MA, McLennan JA, Minot EO 1998. The dynamics and distribution of the small mammal/predator assemblage in mixed forest in the North Island, New Zealand. *Australian Vertebrate Pest Conference* 11: 235-239.
- Bomford M, O'Brien P 1995. Eradication or control for vertebrate pests? *Wildlife Society Bulletin* 23(2): 249-255.
- Bowie M, Kaverman M, Ross J 2011. The Quail Island story – thirteen years of multi-species pest control: successes, failures and lessons learnt. In: Vietch C CM, Towns D eds. *Island invasives: eradication and management*. Gland, Switzerland, IUCN. Pp. 157-161.
- Bramley GN 2014. Home ranges and interactions of kiore (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, New Zealand. *New Zealand Journal of Ecology* 38: 328-334.
- Brandt MJ, Lambin X 2007. Movement patterns of a specialist predator, the weasel *Mustela nivalis* exploiting asynchronous cyclic field vole *Microtus agrestis* populations. *Acta Theriologica* 52: 13-25.
- Brockie R, Ward G, Cowan P 1997. Possums (*Trichosurus vulpecula*) on Hawke's Bay farmland: spatial distribution and population structure before and after a control operation. *Journal of the Royal Society of New Zealand* 27(2): 181-191.
- Brockie R, AAC F, Ward G, Porter, RER 1987. Field biology of Hawke's Bay farmland possums, *Trichosurus vulpecula*. Department of Scientific and Industrial Research, Ecology Division Report 10. 40 p.
- Brown K 2003. Identifying long-term cost-effective approaches to stoat control. Department of Conservation Science Internal Series 137. 26 p.
- Brown RE 1985. The rodents II: suborder Myomorpha. In: Brown RE, MacDonald DW eds. *Social odours in mammals Volume 1*. Oxford, England, Oxford University Press. Pp. 345-457.
- Burns JJ 1964. Movements of a tagged weasel in Alaska. *The Murrelet* 45(1): 10.
- Byers KA, Lee MJ, Patrick DM, Himsworth CG 2019. Rats about town: a systematic review of rat movement in urban ecosystems. *Frontiers in Ecology and Evolution* 7: 13.
<https://doi.org/10.3389/fevo.2019.00013>

- Byrom A 2004. Spread of Tb by ferrets in the northern South Island high country. Landcare Research Contract Report LC0304/146 to the Animal Health Board.
- Byrom A, Nugent G, McKenzie J, Porphyre T, Poutu N, Shepherd J, Whitford J, Yockney I 2008. Animal Health Board Project No. R-80629 Cost-effective control of Tb in the northern South Island high country: identifying the habitats and vector species requiring control. Wellington, TBfree New Zealand.
- Byrom AE 2002. Dispersal and survival of juvenile feral ferrets *Mustela furo* in New Zealand. *Journal of Applied Ecology* 39(1): 67-78.
- Byrom AE, Anderson DP, Coleman M, Thomson C, Cross ML, Pech RP 2015. Assessing movements of brushtail possums (*Trichosurus vulpecula*) in relation to depopulated buffer zones for the management of wildlife tuberculosis in New Zealand. *PloS One* 10(12): e0145636. <https://doi.org/10.1371/journal.pone.0145636>
- Caley P, Morriss G 2001. Summer/autumn movements and mortality rates and density of feral ferrets (*Mustela furo*) at a farmland site in North Canterbury, New Zealand. *New Zealand Journal of Ecology* 25: 53-60.
- Carpenter JK, Monks A, Innes J, Griffiths J 2023. Radio collaring reveals long-distance movements of reinvading ship rats following landscape-scale control. *New Zealand Journal of Ecology* 47(1): 3522. <https://doi.org/10.20417/nzjecol.47.3522>
- Carthew SM, Yáñez B-M, Ruykys L 2015. Straddling the divide: den use by brushtail possums (*Trichosurus vulpecula*) in urban parklands. *Urban Ecosystems* 18: 525-538.
- Cawthen LM 2007. Den use by the common brushtail possum in logged and unlogged dry forest in SE Tasmania. Unpublished Honours thesis, University of Tasmania, Hobart, Australia.
- Chappell MA, Szafrńska PA, Zub K, Konarzewski M 2013. The energy cost of voluntary running in the weasel *Mustela nivalis*. *Journal of Experimental Biology* 216(4): 578-586.
- Chen Y, Doran B, Sinclair-Hannocks S, Mangos J, Gibbons P 2020. Building selection by the common brushtail possum (*Trichosurus vulpecula*). *Wildlife Research* 47(2): 186-195.
- Choquenot D, Ruscoe WA 2000. Mouse population eruptions in New Zealand Forests: the role of population density and seedfall. *Journal of Animal Ecology* 69(6): 1058-1070.
- Christie J, Kemp J, Rickard C, Murphy E 2006. Measuring stoat (*Mustela erminea*) and ship rat (*Rattus rattus*) capture success against micro-habitat factors. *New Zealand Journal of Ecology* 30(1): 43-51.
- Christie JE, Brown DJ, Westbrooke I, Murphy EC 2009. Environmental predictors of stoat (*Mustela erminea*) and ship rat (*Rattus rattus*) capture success. Department of Conservation Research and Development Series 305. 27 p.
- Clark DB 1980. Population ecology of *Rattus rattus* across a desert-montane forest gradient in the Galapagos Islands. *Ecology* 61(6): 1422-1433.
- Clinchy M, Sheriff MJ, Zanette LY 2013. Predator-induced stress and the ecology of fear. *Functional Ecology* 27(1): 56-65.
- Clinchy M, Taylor AC, Zanette LY, Krebs CJ, Jarman PJ 2004. Body size, age and paternity in common brushtail possums (*Trichosurus vulpecula*). *Molecular Ecology* 13(1): 195-202.

- Clout M, Efford M 1984. Sex differences in the dispersal and settlement of brushtail possums (*Trichosurus vulpecula*). The Journal of Animal Ecology: 737-749.
- Clout M, Gaze P 1984. Brushtail possums (*Trichosurus vulpecula* Kerr) in a New Zealand beech (*Nothofagus*) forest. New Zealand Journal of Ecology 7: 147-155.
- Coleman JD, Green W, Polson J 1985. Diet of brushtail possums over a pasture-alpine gradient in Westland, New Zealand. New Zealand Journal of Ecology 8: 21-35.
- Combs M, Byers KA, Ghera BM, Blum MJ, Caccone A, Costa F, Himsworth CG, Richardson JL, Munshi-South J 2018. Urban rat races: spatial population genomics of brown rats (*Rattus norvegicus*) compared across multiple cities. Proceedings of the Royal Society B 285(1880): 20180245. <https://doi.org/10.1098/rspb.2018.0245>
- Combs M, Byers K, Himsworth C, Munshi-South J 2019. Harnessing population genetics for pest management: Theory and application for urban rats. Human–Wildlife Interactions 13(2): 11. <https://doi.org/10.26077/0bcx-v339>
- Combs M, Puckett EE, Richardson J, Mims D, Munshi-South J 2018. Spatial population genomics of the brown rat (*Rattus norvegicus*) in New York City. Molecular Ecology 27(1): 83-98.
- Cowan P 1989. Denning habits of common brushtail possums, *Trichosurus vulpecula*, in New Zealand lowland forest. Wildlife Research 16(1): 63-78.
- Cowan P 2001. Responses of common brushtail possums (*Trichosurus vulpecula*) to translocation on farmland, southern North Island, New Zealand. Wildlife Research 28(3): 277-282.
- Cowan P, Brockie R, Smith R, Hearfield M 1997. Dispersal of juvenile brushtail possums, *Trichosurus vulpecula*, after a control operation. Wildlife Research 24(3): 279-288.
- Cowan P, Clout M 2000. Possums on the move: activity patterns, home ranges, and dispersal. In: Montague TL ed. The brushtail possum: biology, impact and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 24-34.
- Cowan PE, Glen AS 2021. *Trichosurus vulpecula*. In: King CM, Forsyth DM eds. The handbook of New Zealand mammals. 3rd Edition. Melbourne, CSIRO Publishing. Pp. 43-77
- Cowan P, Rhodes D 1993. Electric fences and poison buffers as barriers to movements and dispersal of brushtail possums (*Trichosurus vulpecula*) on farmland. Wildlife Research 20(5): 671-686.
- Cox MP, Cox CRD, G W 2000. Use of habitat by the black rat (*Rattus rattus*) at North Head, New South Wales: an observational and experimental study. Austral Ecology 25(4): 375-385.
- Cruz J, Sutherland DR, Anderson DP, Glen AS, de Tores PJ, Leung LK-P 2013. Antipredator responses of koomal (*Trichosurus vulpecula hypoleucus*) against introduced and native predators. Behavioral Ecology and Sociobiology 67: 1329-1338.
- Cruz J, Sutherland DR, Leung LK-P 2012. Den use, home range and territoriality of the koomal (*Trichosurus vulpecula hypoleucus*) with implications for current forest management strategies. Australian Journal of Zoology 60(3): 141-151.
- Curtis S 2024 Northland loses legendary kiwi Sir Ed to ferret attack. The Northern Advocate. <https://www.nzherald.co.nz/northern-advocate/news/northland-loses-legendary-kiwi-sir-ed/PHHQ4CGGVJCG7BRC7ZALMQNNAE/>

- Cusack JJ, Wearn OR, Bernard H, Ewers RM 2015. Influence of microhabitat structure and disturbance on detection of native and non-native murids in logged and unlogged forests of northern Borneo. *Journal of Tropical Ecology* 31(1): 25-35.
- Cuthbert R, Sommer E 2002. Home range, territorial behaviour and habitat use of stoats (*Mustela erminea*) in a colony of Hutton's shearwater (*Puffinus huttoni*), New Zealand. *New Zealand Journal of Zoology* 29(2): 149-160.
- Davis RA, Seddon PJ, Craig MD, Russell JC 2023. A review of methods for detecting rats at low densities, with implications for surveillance. *Biological Invasions* 25(12): 3773-3791.
- Debrot S, Mermod C 1983. The spatial and temporal distribution pattern of the stoat (*Mustela erminea* L.). *Oecologia* 59: 69-73.
- Delattre P 1984. Influence of the predatory pressure exerted by a weasel population (*Mustela nivalis* L.) upon Microtidae [micromammals, *Microtus arvalis*, *Microtus agrestis*, *Clethrionomys glareolus*, agroecosystem]. *Acta Oecologica Oecologia Generalis (France)* 5(3): 285-300.
- Department of Conservation 2020. Towards a Predator Free New Zealand: Predator Free 2050 Strategy. Department of Conservation, Wellington.
- Dowding JE, Murphy EC 1994. Ecology of ship rats (*Rattus rattus*) in a kauri (*Agathis australis*) forest in Northland. *New Zealand Journal of Ecology* 18: 19-28.
- Doyle P, Seddon PJ, van Heezik Y 2023. The relationship between *Rattus rattus* trap captures and microhabitat in Mt Aspiring National Park. *New Zealand Journal of Ecology* 47: 3560.
<https://doi.org/10.20417/nzj ecol.47.3560>
- Doyle PJ 2021. The spatial ecology, population structure and habitat use of *Rattus* spp. in the South Island, New Zealand. Unpublished MSc Thesis, University of Otago, Dunedin, New Zealand.
- Dunnet G 1956. A live-trapping study of the brush-tailed possum *Trichosurus vulpecula* Kerr (Marsupialia). *CSIRO Wildlife Research* 1(1): 1-18.
- Efford M 2000. Possum density, population structure, and dynamics. In: Montague TL ed. The brushtail possum: biology, impact and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 47-61.
- Efford M, Norbury G 2005. Ferret population assessment: progress and challenges. *Proceedings of the 13th Australasian Vertebrate Pest Conference*. Wellington. 2-6 May 2005. Pp. 75-80.
- Efford M, Warburton B, Spencer N 2000. Home-range changes by brushtail possums in response to control. *Wildlife Research* 27(2): 117-127.
- Efford MG, Dawson DK, Jhala YV, Qureshi Q 2016. Density-dependent home-range size revealed by spatially explicit capture–recapture. *Ecography* 39: 676-688.
- Elliott G, Willans M, Edmonds H, Crouchley D 2010. Stoat invasion, eradication and re-invasion of islands in Fiordland. *New Zealand Journal of Zoology* 37(1): 1-12.
- Erlinge S 1974. Distribution, territoriality and numbers of the weasel *Mustela nivalis* in relation to prey abundance. *Oikos* 25: 308-314.
- Erlinge S 1977. Spacing strategy in stoat *Mustela erminea*. *Oikos* 28: 32-42.
- Erlinge S 1983. Demography and dynamics of a stoat *Mustela erminea* population in a diverse community of vertebrates. *The Journal of Animal Ecology* 52(3): 705-726.

- Erlinge S, Sandell M 1986. Seasonal changes in the social organization of male stoats, *Mustela erminea*. an effect of shifts between two decisive resources. *Oikos* 47(1): 57-62.
- Erlinge S, Sandell M 1988. Coexistence of stoat, *Mustela erminea*, and weasel, *M. nivalis*. social dominance, scent communication, and reciprocal distribution. *Oikos* 53(2): 242-246.
- Erlinge S, Sandell M, Brinck C 1982. Scent-marking and its territorial significance in stoats, *Mustela erminea*. *Animal Behaviour* 30(3): 811-818.
- Etherington TR, Perry GL, Cowan PE, Clout MN 2014. Quantifying the direct transfer costs of common brushtail possum dispersal using least-cost modelling: a combined cost-surface and accumulated-cost dispersal kernel approach. *PLoS One* 9(2): e88293.
DOI:[10.1371/journal.pone.0088293](https://doi.org/10.1371/journal.pone.0088293)
- Fairweather AAC, Brockie RE, Ward GD 1987. Possums (*Trichosurus vulpecula*) sharing dens: a potential infection route for bovine tuberculosis. *New Zealand Veterinary Journal* 35(1-2): 15-16.
- Fitzgerald N, Innes J, Sandoval N 2017. Rat and possum movement in a Hamilton gully. Manaaki Whenua – Landcare Research Contract Report LC2816.
- Foster NJ, Maloney RF, Seddon PJ, Recio MR, Khan MSI, van Heezik Y 2021. Altitudinal distribution of the entire invasive small mammal guild in the eastern dryland zone of New Zealand's Southern Alps. *Biological Invasions* 23(6): 1837-1857.
- Foster NJ, Maloney RF, Seddon PJ, Rodríguez-Recio M, Van Heezik Y 2022. High-elevation landforms limit the movement of invasive small mammal species. *Landscape Ecology* 37(10): 2651-2670.
- Foster S, King C, Patty B, Miller S 2011. Tree-climbing capabilities of Norway and ship rats. *New Zealand Journal of Zoology* 38(4): 285-296.
- Gardner-Santana LC, Norris D, Fornadel C, Hinson E, Klein S, Glass GE 2009. Commensal ecology, urban landscapes, and their influence on the genetic characteristics of city-dwelling Norway rats (*Rattus norvegicus*). *Molecular Ecology* 18(13): 2766-2778.
- Garvey PM, Glen AS, Pech RP 2016. Dominant predator odour triggers caution and eavesdropping behaviour in a mammalian mesopredator. *Behavioral Ecology And Sociobiology* 70(4): 481-492.
- Garvey PM, Glen AS, Clout MN, Nichols M, Pech RP 2022. Niche partitioning in a guild of invasive mammalian predators. *Ecological Applications* 32(4): e2566. <https://doi.org/10.1002/eap.2566>
- Gatto-Almeida F, de Araújo Soares A, Degrandi TM, Tiepolo LM, Pichlmüller F, Hass I 2022. Assessment of dispersal and population structure of Norway rats (*Rattus norvegicus*) in a seaport setting. *Urban Ecosystems* 25(2): 535-544.
- Gehring TM, Swihart RK 2004. Home range and movements of long-tailed weasels in a landscape fragmented by agriculture. *Journal of mammalogy* 85(1): 79-86.
- Gillies C, Brady M 2018. Trialling monitoring methods for feral cats, ferrets and rodents in the Whangamarino wetland. *New Zealand Journal of Zoology* 45: 192-212.
- Gillies CA, Graham PJ, Clout MN 2007. Home range of introduced mammalian carnivores at Trounson Kauri Park, Northland, New Zealand. *New Zealand Journal of Zoology* 34: 317-333.

- Gilmore DP 1967. Foods of the Australian opossum (*Trichosurus vulpecula* Kerr) on Banks Peninsula, Canterbury, and a comparison with other selected areas. *New Zealand Journal of Science* 10: 235-279.
- Glen AS, Byrom AE, Pech RP, Cruz J, Schwab A, Sweetapple PJ, Yockney I, Nugent G, Coleman M, Whitford J 2012. Ecology of brushtail possums in a New Zealand dryland ecosystem. *New Zealand Journal of Ecology* 36(1): 29-37.
- Glen AS, Garvey PM, Innes J, Buchanan F 2024. What can wildlife-detection dogs offer for managing small mammalian predators? *Wildlife Research* 51(1). doi:10.1071/WR23068
- Gormley AM, Veale AJ 2020. The impact of non-target captures on the efficacy of the stoat-trapping network in Project Janszoon. Manaaki Whenua – Landcare Research Contract Report LC3898.
- Green WQ, Coleman JD 1981. A progress report on the movements of possums *Trichosurus vulpecula* between native forest and pasture. Proceedings of the first symposium on marsupials in New Zealand. Pp. 51-62. Victoria University of Wellington, Wellington
- Green W, Coleman JD 1984. Response of a brush-tailed possum population to intensive trapping. *New Zealand journal of Zoology* 11(3): 319-328.
- Griffiths JW, Barron MC 2016. Spatiotemporal changes in relative rat (*Rattus rattus*) abundance following largescale pest control. *New Zealand Journal of Ecology* 40: 371-380.
- Gronwald M, Russell JC 2020. Trappability of low density invasive rats. In: Woods DM ed. Proceedings of the 29th Vertebrate Pest Conference, University of California. Paper No. 36, 8 p.
- Gsell A, Innes J, de Monchy P, Brunton D 2010. The success of using trained dogs to locate sparse rodents in pest-free sanctuaries. *Wildlife Research* 37(1): 39-46.
- Hajduk LI 2008. Space use and habitat selection of long-tailed weasels (*Mustela frenata*) in southern Illinois. Proquest, Umni Dissertation Publishing, Southern Illinois University at Carbondale. 52 p.
- Hansen N, Hughes NK, Byrom AE, Banks PB 2020. Population recovery of alien black rats *Rattus rattus*. A test of reinvasion theory. *Austral Ecology* 45(3): 291-304.
- Harper G, Veitch D 2006. Population ecology of Norway rats (*Rattus norvegicus*) and interference competition with Pacific rats (*R. exulans*) on Raoul Island, New Zealand. *Wildlife Research* 33(7): 539-548.
- Harper GA 2006. Habitat use by three rat species (*Rattus* spp.) on an island without other mammalian predators. *New Zealand Journal of Ecology* 30: 321-333.
- Harper GA, Dickinson KJM, Seddon PJ 2005. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. *New Zealand Journal of Ecology* 29: 251-260.
- Harper GA, Rutherford M 2016. Home range and population density of black rats (*Rattus rattus*) on a seabird island: a case for a marine subsidised effect? *New Zealand Journal of Ecology* 40: 219-228.
- Harper MJ 2005. Home range and den use of common brushtail possums (*Trichosurus vulpecula*) in urban forest remnants. *Wildlife Research* 32(8): 681-687.

- Harrington LA, Macdonald DW 2008. Spatial and temporal relationships between invasive American mink and native European polecats in the southern United Kingdom. *Journal of Mammalogy* 89(4): 991-1000.
- Harris HAL, Kelly D, Innes J, Allen RB 2022. Invasive species and thermal squeeze: distribution of two invasive predators and drivers of ship rat (*Rattus rattus*) invasion in mid-elevation *Fuscospora* forest. *Biological Invasions* 24(8): 2547-2559.
- Harvie AE 1973. Diet of the opossum (*Trichosurus vulpecula* Kerr) on farmland northeast of Waverly, New Zealand. *Proceedings of the New Zealand Ecological Society* 20: 48-52.
- Hawley VD, Newby FE 1957. Marten home ranges and population fluctuations. *Journal of Mammalogy* 38(2): 174-184.
- Haworth D 2018. Weasel (*Mustela nivalis*) dynamics in South Island beech forests of the Maruia Valley. DOC Research and Development Series 355. Department of Conservation, Wellington. 25 p.
- Hayward GF 1983. The bioenergetics of the weasel, *Mustela nivalis*. Unpublished thesis, Oxford University, Oxford, UK.
- Heikkilä J, Below A, Hanski I 1994. Synchronous dynamics of microtine rodent populations on islands in Lake Inari in northern Fennoscandia: evidence for regulation by mustelid predators. *Oikos* 70(2): 245-252.
- Hellstedt P, Henttonen H 2006. Home range, habitat choice and activity of stoats (*Mustela erminea*) in a subarctic area. *Journal of Zoology* 269(2): 205-212.
- Helyar AF 2005. The ecology of American mink (*Mustela vison*): Response to control. Unpublished PhD thesis, University of York, York, UK.
- Henttonen H 1987. The impact of spacing behavior in microtine rodents on the dynamics of least weasels *Mustela nivalis*: a hypothesis. *Oikos* 50(3): 366-370.
- Heptner VG, Naumov NP, Yurgenson PB, Sludskii AA, Chirkova AF, Bannikov AG 1967. Mammals of the Soviet Union: Sea Cows and Carnivores, Vol 2. Vysshaya Shkola, Moscow.
- Herr J, Schley L, Roper T 2009. Socio-spatial organization of urban stone martens. *Journal of Zoology* 277(1): 54-62.
- Higgins TW, Bridges AS, Sanchez JN 2015. Spatial ecology of invasive black rats (*Rattus rattus*) on San Clemente Island, California. *The Southwestern Naturalist* 60(2-3): 186-192.
- How R, Hillcox S 2000. Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* 27(1): 81-89.
- Hutchings MR, White PCL 2000. Mustelid scent-marking in managed ecosystems: implications for population management. *Mammal Review* 30(3-4): 157-169.
- Innes J, Kelly D, Overton JM, Gillies C 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology* 34: 86-114.
- Innes J, Watts C, Fitzgerald N, Thornburrow D, Burns B, MacKay J, Speedy C 2011. Behaviour of invader ship rats experimentally released behind a pest-proof fence, Maungatautari, New Zealand. Island invasives: eradication and management. *Proceedings of the International Conference on Island Invasives*. Gland, Switzerland and Auckland, New Zealand, IUCN (International Union for Conservation of Nature). Pp. 437-440.

- Innes JG, Russell JC 2021. *Rattus rattus*. In: King CM, Forsyth DM eds. The handbook of New Zealand Mammals. 3rd Edition. Melbourne, CSIRO Publishing. Pp. 161-240.
- Innes JG, Norbury G, Samaniego A, Walker S, Wilson DJ 2024. Rodent management in Aotearoa New Zealand: approaches and challenges to landscape-scale control. *Integrative Zoology* 19: 8-26.
- Isaac JL, De Gabriel JL, Goodman BA 2008. Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. *Animal Conservation* 11(4): 281-287.
- Jachowski DS, Millsaugh JJ, Biggins DE, Livieri TM, Matchett MR 2010. Home-range size and spatial organization of black-footed ferrets *Mustela nigripes* in South Dakota, USA. *Wildlife Biology* 16(1): 66-76.
- Jedrzejewski W, Jedrzejewska B, Szymura L 1995. Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. *Ecology* 76(1): 179-195.
- Johnson DH 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61(1): 65-71.
- Jolly JN 1976. Habitat use and movements of the opossum (*Trichosurus vulpecula*) in a pastoral habitat on Banks Peninsula. *Proceedings (New Zealand Ecological Society)*. Pp. 70-78.
- Key GE, Woods RD 1996. Spool-and-line studies on the behavioural ecology of rats (*Rattus* spp.) in the Galapagos Islands. *Canadian Journal of Zoology* 74(4): 733-737.
- King C 2023. Abundance and dynamics of small mammals in New Zealand: Sequential invasions into an Island ecosystem like no other. *Life* 13(1): 156. <https://doi.org/10.3390/life13010156>
- King C, McMillan C 1982. Population structure and dispersal of peak-year cohorts of stoats (*Mustela erminea*) in two New Zealand forests, with especial reference to control. *New Zealand Journal of Ecology* 5: 59-66.
- King CM 1975. The home range of the weasel (*Mustela nivalis*) in an English woodland. *The Journal of Animal Ecology* 44(2): 639-668.
- King CM 1980a. Population biology of the weasel *Mustela nivalis* on British game estates. *Ecography* 3(3): 160-168.
- King CM 1980b. The weasel *Mustela nivalis* and its prey in an English woodland. *The Journal of Animal Ecology* 49(1): 127-159.
- King CM 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*), in relation to seedfall of southern beech. *New Zealand Journal of Zoology* 9(4): 467-480.
- King CM 1983. *Mustela erminea*. *Mammalian Species* (195): 1-8.
- King CM 1989. The advantages and disadvantages of small size to weasels, *Mustela species*. *Carnivore behavior, ecology, and evolution*, Springer. Pp. 302-334.
- King CM, Flux M, Innes J, Fitzgerald B 1996. Population biology of small mammals in Pureora Forest Park: 1. Carnivores (*Mustela erminea*, *M. furo*, *M. nivalis*, and *Felis catus*). *New Zealand Journal of Ecology* 20(2): 241-251.

- King CM, Innes JG, Flux M, Kimberley MO, Leathwick JR, Williams DS 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *New Zealand Journal of Ecology* 20: 215-240.
- King CM, Innes JG, Gleeson D, Fitzgerald N, Winstanley T, O'Brien B, Bridgman L, Cox N 2011. Reinvasion by ship rats (*Rattus rattus*) of forest fragments after eradication. *Biological Invasions* 13(10): 2391-2408.
- King CM, Moors P 1979. On co-existence, foraging strategy and the biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. *Oecologia* 39: 129-150.
- King CM, Murphy EC 2021. *Mustela nivalis vulgaris*. In: King CM, Forsyth DM ed. *The handbook of New Zealand Mammals*. 3rd Edition. Melbourne, CSIRO Publishing. Pp. 285-341. pp. 285-341.
- King CM, Norbury G, Veale AJ 2017. Small mustelids in New Zealand: invasion ecology in a different world In: MacDonald DW, Newman C, Harrington LA eds. *the biology and conservation of musteloids*. Oxford, Oxford University Press. Pp. 257-277.
- King CM, Powell RA, Powell C. 2007. *The natural history of weasels and stoats: ecology, behavior, and management* (2nd edn.). Oxford, Oxford University Press.
- King CM, Veale AJ 2021. *Mustela erminea*. In: King CM, Forsyth DM ed. *The handbook of New Zealand Mammals*. 3rd Edition. Melbourne, CSIRO Publishing. Pp. 285-341.
- King CM, Veale A, Patty B, Hayward L 2014. Swimming capabilities of stoats and the threat to inshore sanctuaries. *Biological Invasions* 16: 987-995.
- Klemola T, Korpimäki E, Norrdahl K, Tanhuanpää M, Koivula M 1999. Mobility and habitat utilization of small mustelids in relation to cyclically fluctuating prey abundances. *Annales Zoologici Fennici* 36:75-82.
- le Mar K, McArthur C, Statham M 2003. Home ranges of sympatric red-necked wallabies, red-bellied pademelons and common brushtail possums in a temperate eucalypt forestry environment. *Australian Mammalogy* 25(2): 183-191.
- Linnell MA, Epps CW, Forsman ED, Zielinski WJ 2017. Space use, movements, and rest site use by short-tailed weasels *Mustela erminea* in managed forests of western Oregon. *Wildlife Biology* 2017(1): 1-9.
- Lister H 2022. Invasive rats and where to find them: Evaluating detection techniques and resource selection by Norway Rats (*Rattus norvegicus*). Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.
- Livieri TM, Anderson EM 2012. Black-footed ferret home ranges in Conata Basin, South Dakota. *Western North American Naturalist* 72(2): 196-205.
- Lockie JD 1966. Territory in small carnivores. *Symposia of the Zoological Society of London* 18: 143-165.
- Lodé T 2011. Habitat selection and mating success in a mustelid. *International Journal of Zoology* 2011(1): 159462. <https://doi.org/10.1155/2011/159462>
- Lough H 2006. Predicting the spatial distribution of stoats, ship rats and weasels in a beech forest setting using GIS. Unpublished MSc Thesis, University of Canterbury, Christchurch, New Zealand.

- Lovera R, Fernández MS, Cavia R 2019. Small rodent species on pig and dairy farms: habitat selection and distribution. *Pest Management Science* 75(5): 1234-1241.
- Low BW, Mills H, Algar D, Hamilton N 2013. Home ranges of introduced rats on Christmas Island: a pilot study. *Ecological Management & Restoration* 14(1): 41-46.
- MacDonald DW, Mathews F, Berdoy M 1999. The behaviour and ecology of *Rattus norvegicus*: from opportunism to kamikaze tendencies. In: Singleton GR, Hinds LA, Leirs H, Zhang Z eds. *Ecologically based management of rodent pests*. ACIAR Monographs 59. Pp 33–48.
- MacDonald DW, Tew TE, Todd IA 2004. The ecology of weasels (*Mustela nivalis*) on mixed farmland in southern England. *Biologia* 59(2): 235-241.
- Madden H, Eggermont E, Verdel K 2020. Micro-and macrohabitat preferences of invasive rodents on St. Eustatius, Caribbean Netherlands. *Caribbean Journal of Science* 50(2): 202-211.
- Magrini C, Manzo E, Zapponi L, Angelici FM, Boitani L, Cento M 2009. Weasel *Mustela nivalis* spatial ranging behaviour and habitat selection in agricultural landscape. *Acta Theriologica* 54: 137-146.
- Mallick S 1992. Urine-marking in three species of *Rattus*. *Wildlife Research* 19(1): 89-93.
- Margetts BI, Ross JG, Buckley HL 2020. Measuring home-range changes following density reduction of Australian brushtail possum. *The Journal of Wildlife Management* 84(1): 185-192.
- Marshall WH 1963. The ecology of mustelids in New Zealand. DSIR Information Series 38. Wellington, DSIR.
- Martin JK 2006. Den-use and home-range characteristics of bobucks, *Trichosurus cunninghami*, resident in a forest patch. *Australian Journal of Zoology* 54(4): 225-234.
- Martin JK, Handasyde KA, Taylor AC 2007. Linear roadside remnants: their influence on den-use, home range and mating system in bobucks (*Trichosurus cunninghami*). *Austral Ecology* 32(6): 686-696.
- Martin JK, Martin AA 2007. Resource distribution influences mating system in the bobuck (*Trichosurus cunninghami*, Marsupialia). *Oecologia* 154: 227-236.
- Martin RD 2012. Geospatial and temporal patterns of stoat (*Mustela erminea*) activity in Tongariro Forest, central North Island, New Zealand. Unpublished MSc thesis, Massey University, Palmerston North, New Zealand.
- McDevitt AD, Oliver MK, Piertney SB, Szafrńska PA, Konarzewski M, Zub K 2013. Individual variation in dispersal associated with phenotype influences fine-scale genetic structure in weasels. *Conservation Genetics* 14: 499-509.
- McDonald RA, Harris S 1999. The use of trapping records to monitor populations of stoats *Mustela erminea* and weasels *M. nivalis*: the importance of trapping effort. *Journal of Applied Ecology* 36(5): 679-688.
- McRae LJ, Griffin AS, Tuckey K, Hayward MW 2022. The population density and trap-revealed home range of short-eared possums (*Trichosurus caninus*) in the Northern Tablelands, New South Wales, Australia. *Australian Mammalogy* 45(1): 71-76.
- Medina-Vogel G 1998. Intrasexual territoriality and the spatial and social behaviour of captive feral ferrets (*Mustela furo* L., Carnivora: Mustelidae). Unpublished PhD thesis, Lincoln University, Lincoln, New Zealand.

- Melero Y, Palazón S, Revilla E, Martelo J, Gosálbez J 2008. Space use and habitat preferences of the invasive American mink (*Mustela vison*) in a Mediterranean area. *European Journal of Wildlife Research* 54: 609-617.
- Michaux J, Hardy OJ, Justy F, Fournier P, Kranz A, Cabria M, Davison A, Rosoux R, Libois R 2005. Conservation genetics and population history of the threatened European mink *Mustela lutreola*, with an emphasis on the west European population. *Molecular Ecology* 14(8): 2373-2388.
- Middlemiss A 1995. Predation of lizards by feral house cats (*Felis catus*) and ferrets (*Mustela furo*) in the tussock grassland of Otago. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.
- Miller KF, Wilson DJ, Hartley S, Innes JG, Fitzgerald NB, Miller P, van Heezik Y 2022. Invasive urban mammalian predators: distribution and multi-scale habitat selection. *Biology* 11(10): 1527. <https://doi.org/10.3390/biology11101527>
- Molina-Vacas G, Bonet-Arboli V, Rt-Plaza ER, Rodríguez-Teijeiro J 2009. Spatial ecology of European badgers (*Meles meles*) in mediterranean habitats of the north-eastern Iberian peninsula. I: home range size, spatial distribution and social organization. *Vie et Milieu/Life & Environment* 59(2a): 223-232.
- Moller H 1977. Ecology of *Rattus exulans* on Tiritiri Matangi Island. Unpublished MSc thesis. University of Auckland, Auckland, New Zealand.
- Moller H, Alterio N 1999. Home range and spatial organisation of stoats (*Mustela erminea*), ferrets (*Mustela furo*) and feral house cats (*Felis catus*) on coastal grasslands, Otago Peninsula, New Zealand: implications for yellow-eyed penguin (*Megadyptes antipodes*) conservation. *New Zealand Journal of Zoology* 26(3): 165-174.
- Moller H, Keedwell R, Ratz H, Bruce L 1998. Lagomorph abundance around yellow-eyed penguin (*Megadyptes antipodes*) colonies, South Island, New Zealand. *New Zealand Journal of Ecology* 22(1): 65-70.
- Moors PJ 1975. The annual energy budget of a weasel (*Mustela nivalis* L.) population in farmland, University of Aberdeen (United Kingdom). Unpublished PhD thesis, University of Aberdeen, Aberdeen, UK.
- Moors PJ 1985. Norway rats (*Rattus norvegicus*) on the Noises and Motukawao Islands, Hauraki Gulf, New Zealand. *New Zealand Journal of Ecology* 8: 37-54.
- Moors PJ, Lavers RB 1981. Movements and home range of ferrets (*Mustela furo*) at Pukepuke Lagoon, New Zealand. *New Zealand Journal of Zoology* 8: 413-423.
- Morley CG 1999. The ecology and behaviour of feral ferrets (*Mustela furo*) in Canterbury farmland, New Zealand. Unpublished PhD thesis, University of Canterbury, Christchurch, New Zealand.
- Mos J, Hofmeester TR 2020. The Mostela: an adjusted camera trapping device as a promising non-invasive tool to study and monitor small mustelids. *Mammal Research* 65(4): 843-853.
- Murphy EC, Clapperton BK, Bradfield PMF, Speed HJ 1998. Effects of rat-poisoning operations on abundance and diet of mustelids in New Zealand podocarp forests. *New Zealand Journal of Zoology* 25: 315-328.
- Murphy EC, Dowding JE 1994. Range and diet of stoats (*Mustela erminea*) in a New Zealand beech forest. *New Zealand Journal of Ecology* 18(1): 11-18.

- Murphy EC, Dowding JE 1995. Ecology of the stoat in *Nothofagus* forest: home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology* 19(2): 97-109.
- Nass RD 1977. Movements and home ranges of Polynesian rats in Hawaiian sugarcane. *Pacific Science* 31: 135-142.
- Nathan H, Agnew T, Mulgan N 2020. Movement behaviour of a translocated female ship rat and her offspring in a low rat density New Zealand forest. *New Zealand Journal of Ecology* 44: 3402. DOI: <https://dx.doi.org/10.20417/nzj ecol.44.8>
- Nathan H, Schadewinkel R, Mulgan N 2025. Spatial distribution of probable ship rat reinvasers in a pest-fenced ecosanctuary. *New Zealand Journal of Ecology* 49(1): 3587. DOI: <https://doi.org/10.20417/nzj ecol.49.3578>
- Nathan HW, Clout MN, MacKay JWB, Murphy EC, Russell JC 2015. Experimental island invasion of house mice. *Population Ecology* 57(2): 363-371.
- Nathan HW, Clout MN, Murphy EC, MacKay JWB 2013. Strategies for detection of house mice on a recently invaded island. *New Zealand Journal of Ecology* 23: 26-32.
- Nicholas M 1982. Spatial organisation of *Rattus exulans* on Tiritiri Matangi Island. Unpublished MSc thesis. University of Auckland, Auckland, New Zealand.
- Niebuhr CN, Veale AJ 2020. Mustelid movement in the Taranaki ring plain: update 2020. Manaaki Whenua – Landcare Research Contract Report LC3821.
- Norbury GL, Norbury DC, Heyward RP 1998a. Space use and denning behaviour of wild ferrets (*Mustela furo*) and cats (*Felis catus*). *New Zealand Journal of Ecology* 22: 149-159.
- Norbury GL, Norbury DC, Heyward RP 1998b. Behavioral responses of two predator species to sudden declines in primary prey. *Journal of Wildlife Management* 62(1): 45-58.
- Nyholm E 1959. Stoats and weasels and their winter habitats. *Suomen Riista* 13: 106-116.
- Oehler JD, Litvaitis JA 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* 74(11): 2070-2079.
- Ogden J, Gilbert J 2009. Prospects for the eradication of rats from a large inhabited island: community based ecosystem studies on Great Barrier Island, New Zealand. *Biological Invasions* 11: 1705-1717.
- Osinga T, Thurfjell H, Hofmeester TR 2023. Snow limits polecat *Mustela putorius* distribution in Sweden. *Wildlife Biology* 2023(1): e01051. <https://doi.org/10.1002/wlb3.01051>
- Pascoe A 1995. The effects of vegetation removal on rabbits (*Oryctolagus cuniculus*) and small mammalian predators in braided riverbeds of the Mackenzie Basin. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.
- Paterson B, Morris R, Weston J, Cowan P 1995. Foraging and denning patterns of brushtail possums, and their possible relationship to contact with cattle and the transmission of bovine tuberculosis. *New Zealand Veterinary Journal* 43(7): 281-288.
- Pech R, Byrom A, Anderson D, Thomson C, Coleman M 2010. The effect of poisoned and notional vaccinated buffers on possum (*Trichosurus vulpecula*) movements: minimising the risk of bovine tuberculosis spread from forest to farmland. *Wildlife Research* 37(4): 283-292.

- Peters E, Brinkmann I, Krüger F, Zwirlein S, Klaumann I 2009. Reintroduction of the European mink *Mustela lutreola* in Saarland, Germany. Preliminary data on the use of space and activity as revealed by radio-tracking and live-trapping. *Endangered Species Research* 10: 305-320.
- Pierce RJ 1987. Predators in the MacKenzie Basin: their diet, population dynamics, and impact on birds in relation to the abundance and availability of their main prey (rabbits). Unpublished report for the Wildlife Service, Department of Internal Affairs. 110 p.
- Pierce RJ 1996. Impacts of ferrets on North Island brown kiwi and brown teal. *Royal Society of New Zealand Miscellaneous Series* 36: 47.
- Piertney SB, Black A, Watt L, Christie D, Poncet S, Collins MA 2016. Resolving patterns of population genetic and phylogeographic structure to inform control and eradication initiatives for brown rats *Rattus norvegicus* on South Georgia. *Journal of Applied Ecology* 53(2): 332-339.
- Polder E 1968. Spotted skunk and weasel populations den and cover usage by northeast Iowa. *Proceedings of the Iowa Academy of Science* 75(1): 142-146.
- Pounds CJ 1981. Niche overlap in sympatric populations of stoats (*Mustela erminea*) and weasels (*M. nivalis*) in north-east Scotland. Unpublished PhD thesis, University of Aberdeen, Aberdeen, UK. 326 pp.
- Powell RA 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Zeitschrift für Tierpsychologie* 50: 153-165.
- Powell RA 1994. Structure and spacing of *Martes* populations. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA, eds. *Martens, sables, and fishers: biology and conservation*. Ithaca, NY, Cornell University Press, Pp. 101-121
- Prada D, Veale A, Duckworth J, Murphy E, Treadgold S, Howitt R, Hunter S, Gleeson D 2014. Unwelcome visitors: employing forensic methodologies to inform the stoat (*Mustela erminea*) incursion response plan on Kapiti Island. *New Zealand Journal of Zoology* 41(1): 1-9.
- Ragg JR 1997. Tuberculosis (*Mycobacterium bovis*) epidemiology and the ecology of ferrets (*Mustela furo*) on New Zealand farmland. Unpublished PhD thesis, University of Otago, Dunedin, New Zealand.
- Ragg JR 2002. Home range, movement and activity patterns of female ferrets: testing hypotheses relating to low trappability in winter and spring. Unpublished report prepared for Animal Health Board, Project No. R-80509.
- Ragg JR, Moller H 2000. Microhabitat selection by feral ferrets (*Mustela furo*) in a pastoral habitat, East Otago, New Zealand. *New Zealand Journal of Ecology* 24: 39-46.
- Ratz H 2000. Movements by stoats (*Mustela erminea*) and ferrets (*M. furo*) through rank grass of yellow-eyed penguin (*Megadyptes antipodes*) breeding areas. *New Zealand Journal of Zoology* 27: 57-69.
- Ringler D, Russell J, Jaeger A, Pinet P, Bastien M, Le Corre M 2014. Invasive rat space use on tropical islands: implications for bait broadcast. *Basic and Applied Ecology* 15(2): 179-186.
- Robertson CJR, Law EH, Wakelin DJ, Courtney SP 1984. Habitat requirements of wetland birds in the Lower Waitaki River catchment New Zealand. *New Zealand Wildlife Service, Occasional Publications* 2(6).

- Rouco C, Norbury GL, Anderson DP 2017. Movements and habitat preferences of pests help to improve population control: the case of common brushtail possums in a New Zealand dryland ecosystem. *Pest Management Science* 73(2): 287-294.
- Rouco C, Norbury G, Smith J, Byrom A, Pech PR 2013. Population density estimates of brushtail possums (*Trichosurus vulpecula*) in dry grassland in New Zealand. *New Zealand Journal of Ecology* 37(1): 12-17.
- Ruffell J, Didham RK, Barrett P, Gorman N, Pike R, Hickey-Elliott A, Sievwright K, Armstrong DP 2014. Discriminating the drivers of edge effects on nest predation: forest edges reduce capture rates of ship rats (*Rattus rattus*), a globally invasive nest predator, by altering vegetation structure. *PloS One* 9(11): e113098. <https://doi.org/10.1371/journal.pone.0113098>
- Russell JC, Beaven BM, MacKay JWB, Towns DR, Clout MN 2008. Testing island biosecurity systems for invasive rats. *Wildlife Research* 35(3): 215-221.
- Russell JC, Innes JG 2021. *Rattus norvegicus*. In: King CM, Forsyth DM eds. The handbook of New Zealand mammals. 3rd Edition. Melbourne. CSIRO Publishing. Pp. 161-240.
- Russell JC, McMorland AJC, MacKay JWB 2010. Exploratory behaviour of colonizing rats in novel environments. *Animal Behaviour* 79(1): 159-164.
- Russell JC, Ringler D, Trombini A, Le Corre M 2011. The island syndrome and population dynamics of introduced rats. *Oecologia* 167(3): 667-676.
- Russell JC, Towns DR, Clout MN 2008. Review of rat reinvasion biology. Science for Conservation 286. Department of Conservation, Wellington, New Zealand.
- Samaniego A, Griffiths R, Gronwald M, Holmes ND, Oppel S, Stevenson BC, Russell JC 2020. Risks posed by rat reproduction and diet to eradications on tropical islands. *Biological Invasions* 22(4): 1365-1378.
- Samson C, Raymond M 1998. Movement and habitat preference of radio tracked stoats, *Mustela erminea*, during summer in southern Quebec. *Mammalia* 62(2): 165-174.
- Sandell M 1986. Movement patterns of male stoats *Mustela erminea* during the mating season: differences in relation to social status. *Oikos* 47(1): 63-70.
- Sarre SD, Aitken N, Adamack AT, MacDonald AJ, Gruber B, Cowan P 2014. Creating new evolutionary pathways through bioinvasion: the population genetics of brushtail possums in New Zealand. *Molecular Ecology* 23(14): 3419-3433.
- Sasaki H, Ono Y 1994. Habitat use and selection of the Siberian weasel *Mustela sibirica coreana* during the non-mating season. *Journal of the Mammalogical Society of Japan* 19(1): 21-32.
- Schweinfurth MK 2020. The social life of Norway rats (*Rattus norvegicus*). *eLife* 9: <https://doi.org/10.7554/eLife.54020>
- Shanker K 2001. The role of competition and habitat in structuring small mammal communities in a tropical montane ecosystem in southern India. *Journal of Zoology* 253(1): 15-24.
- Shapira I, Buchanan F, Brunton D 2011. Detection of caged and free-ranging Norway rats *Rattus norvegicus* by a rodent sniffing dog on Browns Island, Auckland, New Zealand. *Conservation Evidence* 8: 38-42.

- Shapira I, Shanas U, Raubenheimer D, Knapp C, Alberts S, Brunton D 2013. Laboratory rats as conspecific biocontrol agents for invasive Norway rats *R. norvegicus*. *Biological Control* 66(2): 83-91.
- Sheffield SR, King CM 1994. *Mustela nivalis*. *Mammalian species*. Issue 454: 1-10.
- Simms D 1979. North American weasels: resource utilization and distribution. *Canadian Journal of Zoology* 57(3): 504-520.
- Smith DHV, Jamieson IG 2005. Lack of movement of stoats (*Mustela erminea*) between *Nothofagus* valley floors and alpine grasslands, with implications for the conservation of New Zealand's endangered fauna. *New Zealand Journal of Ecology* 29: 45-52.
- Smith DH, Wilson DJ, Moller H, Murphy EC, van Heezik Y 2007. Selection of alpine grasslands over beech forest by stoats (*Mustela erminea*) in montane southern New Zealand. *New Zealand Journal of Ecology* 31: 88-97.
- Speedy C, Day T, Innes J 2007. Pest eradication technology – the critical partner to pest exclusion technology; the Maungatautari experience. In: Witmer GW, Pitt WC, Fagerstone KA, eds. *Managing vertebrate invasive species: Proceedings of an international symposium*. USDA/APHIS/WS; National Wildlife Research Center, Fort Collins, CO, USA. Pp 115–126.
- St-Pierre C, Ouellet JP, Crête M 2006. Do competitive intraguild interactions affect space and habitat use by small carnivores in a forested landscape? *Ecography* 29(4): 487-496.
- Statham M, Statham H 1997. Movements and habits of brushtail possums (*Trichosurus vulpecula* Kerr) in an urban area. *Wildlife Research* 24(6): 715-726.
- Štolhoferová I, Rudolfová V, Skalíková H, Vobrubová B, Frynta D 2024. How to explore a new environment: exploratory tactics of the black rat (*Rattus rattus*). *Current Zoology* 70(11): zoe015. DOI: [10.1093/cz/zoe015](https://doi.org/10.1093/cz/zoe015)
- Stow A, Minarovic N, Eymann J, Cooper D, Webley L 2006. Genetic structure infers generally high philopatry and male-biased dispersal of brushtail possums (*Trichosurus vulpecula*) in urban Australia. *Wildlife Research* 33(5): 409-415.
- Stroganov SU 1962. Carnivorous mammals of Siberia. *Academy of Sciences of the USSR (Israeli Program for Scientific Translations 1969, Siberian branch – Jerusalem, Israel)*. 536 p.
- Sundell J, Norrdahl K, Korpimäki E, Hanski I 2000. Functional response of the least weasel, *Mustela nivalis nivalis*. *Oikos* 90(3): 501-508.
- Svendsen GE 1982. Weasels, *Mustela* sp. In: Chapman JA, Feldhamer GA ed. *Wild mammals of North America: biology, management, and economics*. Baltimore, John Hopkins University Press. Pp. 613-628.
- Sweetapple P, Nugent G, Anderson D, Latham C, Barron MC 2016. Determinants of possum aggregation after control in forest and near-forest farmland (final report). Unpublished Manaaki Whenua – Landcare Research Contract Report LC2573.
- Tapper S 1979. The effect of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland. *The Journal of Animal Ecology* 48: 603-617.
- Telle HJ 1966. Contribution to the knowledge of behavioural patterns in two species of rats, *Rattus norvegicus* and *Rattus rattus*. *Zeitschrift für Angewandte Zoologie* 53: 129–196. National Research Council of Canada Technical Translation 1608. Translated by VN Nekrassoff, Ottawa, 1972.

- Thorsen M, Shorten R, Lucking R, Lucking V 2000. Norway rats (*Rattus norvegicus*) on Frégate Island, Seychelles: the invasion; subsequent eradication attempts and implications for the island's fauna. *Biological Conservation* 96(2): 133-138.
- van Vuurde MR, van der Grift EA 2005. The effects of landscape attributes on the use of small wildlife underpasses by weasel (*Mustela nivalis*) and stoat (*Mustela erminea*). *Lutra* 48(2): 91–108.
- Vattiato G, Binny RN, Davidson SJ, Byrom AE, Anderson DP, Plank MJ, Carpenter JK, James A 2023. Detectability of ten invasive mammal pests in New Zealand: a synthesis of spatial detection parameters. *New Zealand Journal of Ecology* 47: 3552.
- Veale A 2013. Observations of stoats (*Mustela erminea*) swimming. *New Zealand Journal of Zoology* 40(2): 166-169.
- Veale A, Gleeson D, Clout M 2015. Measuring connectivity of invasive stoat populations to inform conservation management. *Wildlife Research* 41(5): 395-406.
- Veale A, Gormley A, Nugent G 2022. Can close kin mark recapture be used to provide population estimates of ferrets and pigs? Manaaki Whenua – Landcare Research Contract Report LC4203.
- Veale AJ, Etherington TR 2023. Assessing mustelid dispersal and the Predator Free Taranaki trapping programme using population genomics. Manaaki Whenua –Landcare Research Contract Report LC4241.
- Veale AJ, Hannaford OD, Russell JC, Clout MN 2012. Modelling the distribution of stoats on New Zealand offshore islands. *New Zealand Journal of Ecology* 36(1): 38-47.
- Ward GD 1978. Habitat use and home range of radio-tagged opossums *Trichosurus vulpecula* (Kerr) in New Zealand lowland forest. In: Montgomery GG ed. *The Ecology of Arboreal Folivores*. Smithsonian Institution Press, Washington, D.C. Pp. 267-287.
- Ward G 1985. The fate of young radiotagged common brushtail possums, *Trichosurus vulpecula*, in New Zealand lowland forest. *Wildlife Research* 12(2): 145-150.
- Watkins AF, McWhirter JL, King CM 2010. Patchiness in distribution of rodents and mustelids in New Zealand forests. *Wildlife Research* 37(1): 13-18.
- Weber D 1989. The ecological significance of resting sites and the seasonal habitat change in polecats (*Mustela putorius*). *Journal of Zoology* 217(4): 629-638.
- Whyte BI, Ross JG, Blackie HM 2013. Differences in brushtail possum home-range characteristics among sites of varying habitat and population density. *Wildlife Research* 40(7): 537-544.
- Wilmshurst JM, Ruscoe WA 2021. *Rattus exulans*. In: King CM, Forsyth DL eds. *The Handbook of New Zealand Mammals*. 3rd Edition. Melbourne, CSIRO Publishing. Pp. 161-240.
- Wirtz WO 1972. Population ecology of the Polynesian rat, *Rattus exulans*, on Kure Atoll, Hawaii. *Pacific Science* 26: 433-464.
- Young JB 1998. Movement patterns of two New Zealand mustelids: Implications for predator pest management. Unpublished MSc thesis, Lincoln University, Lincoln, New Zealand.
- Zalewski A, Jędrzejewski W 2006. Spatial organisation and dynamics of the pine marten *Martes martes* population in Białowieża Forest (E Poland) compared with other European woodlands. *Ecography* 29(1): 31-43.

- Zalewski A, Jedrzejewski W, Jedrzejewski B 2004. Mobility and home range use by pine martens (*Martes martes*) in a Polish primeval forest. *Ecoscience* 11(1): 113-122.
- Zalewski A, Piertney SB, Zalewska H, Lambin X 2009. Landscape barriers reduce gene flow in an invasive carnivore: geographical and local genetic structure of American mink in Scotland. *Molecular Ecology* 18(8): 1601-1615.
- Žampachová B, Kaftanová B, Šimánková H, Landová E, Frynta D 2017. Consistent individual differences in standard exploration tasks in the black rat (*Rattus rattus*). *Journal of Comparative Psychology* 131(2): 150-162.
- Zielinski WJ, Truex RL, Schmidt GA, Schlexer FV, Schmidt KN, Barrett RH 2004. Home range characteristics of fishers in California. *Journal of Mammalogy* 85(4): 649-657.
- Zollner PA, Lima SL 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80(3): 1019-1030.
- Zub K, Sönnichsen L, Szafrńska P 2008. Habitat requirements of weasels *Mustela nivalis* constrain their impact on prey populations in complex ecosystems of the temperate zone. *Oecologia* 157: 571-582.

Appendix 1 – Glossary of terms

Buffer zone – Area of pest control bordering or completely encircling a pest management zone to reduce immigration into the managed area (sometimes referred to as a virtual fence).

Commensal – Relationship between two species (e.g. humans and rats) in which one obtains benefits from the other without harming or benefiting it.

Conspecifics – Animals of the same species.

Detection device – Apparatus that detects the presence of an animal (e.g. chew cards, tracking tunnels, cameras).

Dispersal – Movement of an individual away from its original home range to colonise new habitat and establish a new home range.

Ecotone – A region of transition between two habitats or biological communities

Eradication – Complete removal of every individual of a target species from an area and prevention of immigration into the eradicated area (Bomford & O'Brien 1995).

Elimination – Complete removal of every individual of a target species from an area and successful removal of frequent incursions.

Genetic kinship – Degree of relatedness between individuals based on their shared genes. The spatial extent of relatedness across a landscape reflects the capability of a *population* to disperse through breeding. This is a different metric compared to an *individual's* dispersal behaviour derived by radio- or GPS-tagging animals.

Home range – Area traversed by an individual during its normal activities of food gathering, mating, and caring for young.

Microhabitat – Small-scale habitat (e.g. hedgerow) within a broader vegetation type/land cover (e.g. farmland) which has properties that favour some animal species.

Natal dispersal – Movement of an animal from where it was born to where it will potentially breed.

Predator – Animal that kills and consumes another animal.

Reinvader – Conspecific that moves into and establishes in a control or eradication zone that had been previously occupied by this species.

Removal device – Apparatus that captures or kills an animal (e.g. live traps or kill traps).

Roaming – Animal moving through a landscape with or without a specific purpose.

Sedentary/stationary – Animal whose behaviour is confined to an established home range.

Spatial behaviour – How an animal navigates and uses a landscape. This can be expressed at multiple scales: (1) the distribution of a species at a landscape scale; (2) where an individual

chooses to establish its home range; (3) how an individual selects different resources within its home range; and (4) fine-scale movement patterns within the home range (Johnson 1980).

Suppression – Reduced abundance of a target species to a low level. Suppression requires continuous or repeated use of control tools.

Transient – Animal (e.g. young male) that moves, without settling, over a very large area during a short, defined period. Akin to dispersal.