Enhancing conservation outcomes for New Zealand's coastal ecosystems through knowledge of hedgehog (*Erinaceus europaeus*) spatial ecology.

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Thesis Abstract

Aotearoa New Zealand has experienced significant biodiversity loss from the impacts of invasive species. This thesis has applied spatial ecology principles to conservation biology, focusing on invasive hedgehogs (*Erinaceus europaeus*) in a duneland ecosystem in northern New Zealand. Due to its generally milder climate compared to Europe and the absence of natural predators that hedgehogs face in their native habitats, hedgehogs have thrived as an invasive species in numerous ecosystems across New Zealand. Reliable estimates of home range sizes for hedgehogs in duneland ecosystems are critical as less than 30 percent of New Zealand's natural duneland systems remain for native species such as the New Zealand dotterel (*Charadrius obscurus aquilonius*) and the critically endangered New Zealand fairy tern (*Sternula nereis*). My research aimed to quantify and understand hedgehog spatial ecology and habitat use in Northland's duneland coastal ecosystems and provide insights that can guide more effective control measures of hedgehogs.

My study was conducted at Tara Iti Ecological Sanctuary (Tara Iti), located in Mangawhai, Northland, New Zealand, from Spring 2022 to late Autumn 2023. Eleven hedgehogs (four males and five females during November 2022 and two males during May 2023) were live captured and fitted with Lotek Pinpoint VHF-75 tags for a maximum of seven days. GPS data were used to estimate the home range and nightly distances travelled by hedgehogs. Trail camera sampling was carried out to indicate the presence of pest species and six years of hedgehog trapping data from the study areas were analysed.

Hedgehogs occupy a small core area of their home range intensively while covering its entirety over several foraging nights. Home ranges overlap significantly between individuals of either sex, but core ranges are more independent. The overall mean home range size was 7.1 ha ± 1.6 ha. The average home range was higher for males (8.1 ± 2.3 ha) than for females (5.6 ± 2.1 ha), but the difference was not statistically significant due to small sample sizes and high variation between individuals. The mean nightly home range was similar for males (3.4 ha) and females (3.6 ha). The average nightly distance travelled by female hedgehogs (2054 m ± 580 m) was higher than male hedgehogs (1632 m ± 237 m). One female hedgehog travelled over 4 km in one sampling night, this is the highest distance that has ever been recorded by a European hedgehog in a single night. It is suspected that this was a dispersal event given the linearity of the trip. This hedgehog covered the full width of Tara Iti from the neighbouring farmland to the edge of the golf course, indicating that hedgehogs can travel from the neighbouring farmland to shorebird nesting areas in one night of activity.

I found a strong seasonal trend in the hedgehog trapping data, with peaks in January, February (austral summer), and May (austral autumn) and a low in July (austral winter). Based on my results, DOC250 are more effective traps for targeting hedgehogs and roads and habitat edges should be utilized. To control hedgehogs in vulnerable areas, a trap density of 100 m by 100 m, with one DOC250 trap per hectare, should be used. An intensive trapping program, primarily in early spring and summer, should target hedgehogs to impact the adult population and protect breeding shorebirds. Secondary intensive control should be undertaken in late autumn to primarily target females and juvenile hedgehogs while they are preparing for hibernation.

My findings support the need for specific home range estimates for vulnerable ecosystems due to variability and plasticity in hedgehog behaviour based on habitat and climate factors. Trapping regimes should consider home range estimates, average nightly distances travelled, recorded dispersal distances, and habitat preferences when planning hedgehog control programs.

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Table of Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 6

List of Tables

Chapter 2

Chapter 3

Chapter 6

Chapter 1: Introduction

1.1 Spatial ecology and invasive species

Invasive species significantly threaten biodiversity and ecosystem functioning worldwide (Simberloff et al., 2013). Therefore, understanding the spatial dynamics of invasive species and their interactions with native ecosystems is crucial for effective conservation management. My research applies spatial ecology principles to conservation biology, focusing on invasive hedgehogs (*Erinaceus europaeus*) in duneland ecosystems in northern New Zealand. Spatial ecology, the study of spatial patterns and processes in ecological systems, offers valuable insights into understanding the spread and potential impacts of invasive species (Collinge, 2010). In the context of invasive hedgehogs in New Zealand, spatial ecology can be used to understand how landscape features, habitat suitability, and dispersal mechanisms influence the invasion process.

1.1.1 Invasive species in New Zealand

New Zealand has experienced significant biodiversity loss from the impacts of invasive species (Clout, 1999; Goldson et al., 2015). This island archipelago is particularly vulnerable to invasive species because of its high levels of endemism, unique island ecosystems, and geographical isolation (Macinnis-Ng et al., 2021). Less than half of New Zealand's indigenous vegetative land cover remains, with 811 species classified as threatened and 2416 at risk (DOC, 2020). Current conservation practices are dominated by controlling or eradicating existing populations of invasive species (Clout, 1999; Goldson et al., 2015; Carter et al., 2016). Anthropogenic impacts such as habitat loss and fragmentation have exacerbated the decline of native species, while invasive species have increased due to human manipulation (Craig et al., 2000). Introduced brush-tailed possums (*Trichosurus vulpecula*) are a well-known example, introduced in the nineteenth century to start a fur trade, and have since had a detrimental impact on native bird populations and forest ecosystems (Richardson et al., 2017). Efforts to conserve native species have been undertaken in various ways, such as creating a predator-proof island, mainland sanctuaries, and pest management programs (Clout, 1999). The impact of invasive species on New Zealand's ecosystems are diverse and not always well understood (Goldson et al., 2015). Hedgehogs are a lesser-known invasive species, and more research is needed to determine the specific impacts on native species populations, such as invertebrates and lizards (Jones et al., 2005; Spitzen – van der Sluijs et al., 2009; Blackburn et al., 2014; Nottingham et al., 2019).

1.1.2 Spatial ecology

Spatial ecology investigates spatial patterns and processes in nature and their ecological consequences (Collinge, 2010). Fletcher and Fortin (2018) broadly define spatial ecology as the study and modelling of the role of space on ecological processes, such as population dynamics, species interactions and dispersal, and how they affect ecological patterns, such as species abundance and distribution. They also describe the spatial subdisciplines derived from ecological disciplines, such as animal movement and plant dispersal modelling, landscape genetics, metapopulations, and spatial epidemiology (Fletcher & Fortin, 2018). The combined effects of endogenous processes, such as movement, dispersal, and migration, and exogenous processes, such as the response to climate and local habitat features, result in the spatial patterns observed in organisms (Fletcher & Fortin, 2018). Spatial ecology theory is based on the concept that organisms are not distributed uniformly or randomly, and that spatial distribution and abundance are primarily based on resource availability and competition (Tilman et al., 1997; Laguna et al., 2021; Wang et al., 2021).

Spatial ecology provides a powerful framework for understanding the spatial dynamics of ecosystems and biodiversity, thereby informing conservation strategies and management practices. By integrating spatial principles into conservation biology, we can enhance the effectiveness and sustainability of conservation efforts. Knowledge of the spatial ecology of animals under free-ranging conditions is crucial to understanding their habitat requirements, population dynamics, and life-history strategies (Barthel et al., 2018). Kays et al. described movement as a defining characteristic of animals - animals move to find resources and mates and avoid predators. High-resolution location data reveals detailed information about animal movement beyond home range size and habitat preferences, which has implications in conservation biology (Kays et al., 2015). For example, high-resolution spatial data on movement and dispersal in wolves (*Canis lupus*) in both North America and Europe has helped to reduce human-wildlife conflicts by showing evidence of consistent avoidance of anthropogenic features in the landscape (Treves et al., 2009; Carricondo-Sanchez et al., 2020). This detailed information also allows scientists to consider the behavioural and ecological mechanisms that underlie animal movements, such as life history, ecosystem services, social behaviour, and physiology (Kays et al., 2015).

1.1.3 GPS technology

Wildlife spatial data provides essential information on animal behaviour, habitat preferences, movement patterns, activity levels, and spatial distribution (Allan et al., 2013; Stevenson et al., 2013; Kays et al., 2015). These empirical data are collected using techniques such as GPS tracking, camera traps, radio telemetry, and satellite imagery (Fattebert et al., 2013; Bartoszek et al., 2021; Gracanin & Mikac, 2022). Many spatial ecology studies have utilised radio telemetry to collect animal location data (Berry, 1999; Haigh, 2011; Rautio et al., 2013; Bartoszek et al., 2021). For example, radio telemetry was used to quantify the movements and habitat use of an invasive population of Burmese python (*Python bivittatus*) in southern Florida, which has contributed to the decline of native wildlife across the Greater Everglades ecosystem (Bartoszek et al., 2021). However, radio telemetry is a labour-intensive method of collecting location data and observer presence is known to influence animal behaviour (Kays et al., 2015). It is also not cost-effective to use radiotelemetry for many animals and environments (McShea & Madison, 1992).

Within the last twenty years, global positioning system (GPS) technology has become more readily available for use in wildlife research. However, the cost of GPS units has been a limiting factor (Thomas et al., 2011). Over the last ten years, GPS technology has advanced significantly, becoming less expensive and more lightweight (Kays et al., 2015). This has led to the ability of researchers to use GPS trackers more widely on smaller animals, such as birds and small mammals (Recio et al., 2011; Glasby & Yarnell, 2013; Stevenson et al., 2013; Kays et al., 2015). For example, GPS tags were used to identify spatial and temporal aspects of the foraging behaviour at sea of Hutton's shearwaters in New Zealand, which were previously unknown (Bennet et al., 2019).

Compared to radio-tracking, GPS has the benefit of collecting a high number of location fixes, with minimised disturbance to animal behaviour, and requires less effort from researchers (Urbano et al., 2010; Recio et al., 2011). However, the limitations of low-cost GPS units are battery life and the requirement to be paired with a VHF unit to facilitate recovery (Recio et al., 2011; Foster et al., 2020). Another consideration is that GPS units require signal transfer with satellites, and they do not perform as well in dense canopy cover and may not be able to record location fixes when animals are underground (Glasby & Yarnell, 2013; Forrest et al., 2022).

1.1.4 Relevance to conservation

Spatial ecology is applied in conservation biology to deliver more effective biodiversity conservation and management (Fletcher & Fortin, 2018). Global climate change and anthropogenic impacts are causing an alarming rate of biodiversity loss (Vačkář et al., 2012; Habibullah et al., 2022). Urbanisation and agriculture have led to fragmented landscapes in which populations of organisms have shifted significantly (Collinge, 2010). Studying the spatial ecology of a species can inform researchers how habitat loss and fragmentation affect species and ecosystems (Collinge, 2010).

Knowledge of the spatial ecology of invasive species helps to answer key ecological and management questions (Stevenson et al., 2013). The spatial ecology of an invasive species must be understood to implement an effective management plan (Bartoszek et al., 2021). GPS tracking of tagged animals can also document how climate change affects species distribution and ecological function (Kays et al., 2015). This is particularly relevant to pest animal species where climate change may be exacerbating the negative impacts and allowing range expansion into new and vulnerable areas (Hellmann et al., 2008; Walther et al., 2009; Humes, 2017; Macinnis-Ng et al., 2021). For example, the range expansion further south of the introduced cane toad (*Rhinella marina*) in Australia has been facilitated by warming temperatures (Macgregor et al., 2021). Another example in marine environments is the European green crab (*Carcinus maenas*), which has invaded parts of North America and expanded its range because of warming sea temperatures and changing ocean currents (Compton et al., 2010). Understanding the underlying causes and patterns of animal movement is key to managing and restoring landscapes and the spread of introduced pest species (Nathan et al., 2008).

Research into spatial ecology also helps to identify dispersal corridors between populations, which has implications for species conservation and invasive species management by indicating where human-wildlife conflict may arise and barriers to dispersal occur (Ciucci et al., 2009; Fattebert et al., 2013; Kays et al., 2015). An advantage of GPS tags is their ability to track dispersal movements of study animals beyond the typical home range size and document range expansion of a species (Kays et al., 2015). For example, the long-distance dispersal of a subadult male leopard was tracked over three countries in southern Africa, indicating the possibility of meta-populations (Fattebert et al., 2013). Whereas the long-distance dispersal of a rescued wolf was also documented across a human-dominated landscape from the northern Apennines in Italy to the western Alps in France (Ciucci et al., 2009).

1.2 Hedgehogs

There are 17 known species of hedgehogs in five genera (*Atelerix, Erinaceus, Hemiechinus, Mesechinus,* and *Paraechinus*) present in various regions of Europe, Asia, Africa, and the Middle East (He et al., 2012; Ai et al., 2018; Velo-Antón et al., 2019; Zolotareva et al., 2021). The genus *Erinaceus* contains four species: the Amur hedgehog (*Erinaceus amurensis*), southern white-breasted hedgehog (*Erinaceus concolor*), western European hedgehog (*Erinaceus europaeus*), and northern white-breasted hedgehog (*Erinaceus roumanicus*) (Zolotareva et al., 2021). Hedgehogs inhabit a variety of habitats, from deserts to tropical forests (He et al., 2012). Many of these species are declining due to habitat loss and fragmentation due to urbanisation in their native regions (Hof & Bright, 2009; Abu Baker et al., 2017; Berger et al., 2020; Araguas et al., 2022).

1.3 Western European hedgehogs (Erinaceus europaeus) in their native range

Western European hedgehogs (*Erinaceus europaeus*) have been widely researched in their native environment in Europe, where they are a species of conservation focus (Gurnell et al., 2015; Marco-Tresserres & López-Iborra, 2022). There has been a decline in the number of hedgehogs in Europe due to habitat loss and fragmentation caused by urbanisation and intensification of agriculture (Hof & Bright, 2009; Haigh, 2011; Berger et al., 2020; Taucher et al., 2020). Hedgehogs have a wide geographic distribution, tolerating a wide range of climatic conditions (Rautio et al., 2013). Their natural range extends west from England to Finland, at the northern limits, to Spain, in the south (Haigh, 2011). They have been introduced to New Zealand and Scotland (Jackson., 2006; Jones, 2021).

1.3.1 General behaviour and ecology

Hedgehogs are small solitary mammals that are nocturnal (Reeve, 1994). Their body is covered in sharp spines, which are modified hairs made of keratin (Jones, 2021). When hedgehogs feel threatened, they curl up in a tight ball and present their spines as a protection against predators (Jones, 2021). A combination of two separate muscles allows hedgehogs to roll up, and they cannot be easily uncurled. Natural enemies of European hedgehogs include badgers, foxes, and dogs (Hof & Bright, 2009; Hof et al., 2019). In the United Kingdom, hedgehogs are less likely to be found where badgers are present (Hof et al., 2019). When hedgehogs are unstressed, their spines flatten black, enabling them to move through dense vegetation. They have been recorded swimming across open water three metres wide and are good climbers (Reeve, 1994). Hedgehogs are non-territorial, and their ranges often overlap with both sexes (Riber, 2006; Rautio et al., 2013). Hedgehogs have a strong sense of smell and depend on olfactory cues when foraging for food (Reeve, 1994). They will concentrate their feeding on locally abundant food and alter their foraging behaviour to revisit food-rich areas, such as artificial feeding stations (Cassini & Krebs, 1994). Despite their solitary behaviour, hedgehogs have been known to congregate locally at a rich food source (Cassini & Krebs, 1994). During these instances, access to food may depend on a social hierarchy favouring heavier female hedgehogs (Cassini & Föger, 1995).

1.3.3 Diet

Hedgehogs primarily consume invertebrates, with their natural diet including beetles (Coleoptera), caterpillars (Lepidoptera), and earthworms (Clitellata) (Reeve, 1994; Rautio et al., 2016). They will consume various other food items, such as eggs and nestlings of ground-nesting birds, mice and frogs, fruits, and food offered by humans (Morris, 1985; Reeve, 1994).

1.3.4 Dens

As hedgehogs are only active at night, they need somewhere to shelter and sleep during the daytime, so they construct dens. They also require a safe place during winter hibernation to survive the long cold periods. Reeve (1994) classified three types of hedgehog dens: daytime nests for use during the spring and summer, breeding nests for female hedgehogs and their litters, and hibernation nests over winter. Within the northern extent of their distribution, hedgehogs also construct pre-hibernation dens (Rautio et al., 2014). Hedgehogs require dry, well-drained habitats to construct dens, often at the base of bushes, tussocks, or fallen logs (Reeve, 1994). Hibernation nests are larger and are constructed with more insulation materials (Rautio et al., 2014). Multiple nests are constructed throughout a hedgehog's home range (Rautio et al., 2014).

1.3.5 Hibernation & torpor

Hedgehogs experience periods of torpor to conserve energy while inactive during the daytime and winter (Ruf & Geiser, 2015). During daily torpor, the metabolic rate drops to approximately 30 percent of the normal rate and body temperature is maintained above 30 degrees Celsius (Ruf & Geiser, 2015). Hedgehogs enter hibernal torpor when ground temperatures fall below 11 degrees Celsius (Dmi'el & Schwarz, 1984). This allows hedgehogs to survive long cold temperatures over winter when little food is available. Their body temperature drops to within a few degrees of ambient temperature, and their metabolic rate falls to about 5 percent of the normal metabolic rate (Ruf & Geiser, 2015). Hedgehogs may hibernate for several months during winter (Haigh et al., 2012b). In Finland, the northern limit of their distribution, hedgehogs spend over 200 days hibernating (Rautio et al., 2014).

1.3.6 Breeding biology

In Europe, the life expectancy for female hedgehogs is 2.1 years and 2.6 years for male hedgehogs (Rasmussen et al., 2023). Juvenile hedgehogs usually reach sexual maturity around one year of age (Jackson, 2006; Reeve, 1994). During the breeding season, male hedgehogs search actively for female hedgehogs to mate with (Haigh, 2012a). Hedgehogs have a promiscuous mating system where males and females mate with multiple individuals (Haigh, 2012a; Jones, 2021). Males exhibit distinctive courtship behaviour, known as “cartwheeling”, where they circle female hedgehogs for long periods and attempt to bite their feet (Haigh et al., 2012a). There is no pair bonding, and males play no part in raising young (Jones, 2021). Throughout the breeding season, female hedgehogs have a succession of oestrus cycles and do not experience post-partum oestrus (Deanesly, 1934). The gestation period for hedgehogs is short and only lasts 31-35 days (Deanesley, 1934).

1.4 Ecology of hedgehogs in New Zealand

In New Zealand, introduced hedgehogs are a pest species, and research has focused on understanding the impacts of hedgehogs on native species. Most research has been undertaken in pastoral habitats where hedgehogs are abundant, and few studies have focussed on hedgehogs in coastal habitats. Significant research has been undertaken in the South Island of New Zealand in braided river systems where hedgehogs are a nest predator of native ground-nesting birds (Sanders & Maloney, 2002).

1.4.1 General behaviour and ecology

The general behaviour of introduced hedgehogs in New Zealand is similar to that of wild hedgehogs in Europe, with some differences due to an absence of natural predators and a different climate (Reeve, 1994; Jones, 2021). Hedgehogs are active from dusk until dawn, with some studies finding them most active 2-3 hours after sunset (Brockie, 1974). Hedgehogs seen during the day are generally in poor health (Jones, 2021). Estimates in New Zealand of a hedgehog’s average life span (2-3 years) are similar to estimates from Europe (Brockie, 1974; Parkes, 1975). The introduction of hedgehogs to New Zealand has resulted in their release from natural enemies, such as badgers and foxes. Hedgehogs are occasionally predated by feral pigs, ferrets, feral cats, and dogs, but not to the degree that density is limited (Smith et al., 1995). With no natural predators to keep hedgehog numbers under control, density dependence may become the only natural limiter of population growth (Jackson, 2006).

1.4.2 Diet

Hedgehogs in New Zealand have a relatively broad omnivorous diet, consisting of insects and other invertebrates, as well as lizards, frogs, mice, and the eggs and chicks of ground-nesting birds (Jones et al., 2005; Nottingham et al., 2019). They predominantly feed on beetles and larvae, earwigs, spiders, millipedes, earthworms, and slugs, but it does depend on what is locally available (Berry, 1999; Campbell, 1973; Jones et al., 2005; Nottingham et al., 2019). In lesser amounts, hedgehogs may feed on native wētā, giant centipedes, lizards, and birds' eggs (Nottingham et al., 2019). Hedgehogs are known to scavenge on other animal carcasses and have been described as "opportunistic insectivores" as they mainly feed on insects but eat other animal matter when available (Jones & Norbury, 2006; Moss & Sanders, 2001).

1.4.3 Dens

Dens are typically ellipsoidal chambers in loose detritus or vegetation with a well-concealed entry hole (Moss & Sanders, 2001; Jones, 2021). Hedgehogs have also been observed to nest in rock crevasses and old rabbit burrows (Moss & Sanders, 2001). Den construction in New Zealand is similar to what is described in Europe, except in warmer regions, dens tend to be smaller and contain less insulation material (Parkes, 1975; Moors, 1979).

1.4.4 Hibernation & torpor

In the South Island of New Zealand, hedgehogs usually hibernate from mid-April to early September (Moss, 1999). Hibernation begins later, in June or July, further north in Wellington and Hawkes Bay (Brockie, 1974; Parkes, 1975). Brockie (1974) found that hedgehogs in Wellington lost an average of 10% of their body weight over winter hibernation. Juvenile hedgehogs must reach at least 300 grams of weight to have enough energy stores to survive hibernation (Brockie, 1974). Hedgehogs exhibit partial arousal during hibernation and may leave the nest for short periods to go foraging (Dmi'el & Schwarz, 1984; Reeve, 1994; South et al., 2020; Walhovd, 1979). This explains why a small number of hedgehogs are still trapped during winter in New Zealand (King et al., 1996; Reeve, 1994). There are sex differences in the timing of hibernation for hedgehogs, with females beginning and emerging from hibernation a few weeks later than males (Parkes & Brockie, 1977).

1.4.5 Breeding biology

In New Zealand, both sexes of hedgehogs have typically left hibernation by mid-September (Parkes & Brockie, 1977; Moss, 1999). The hedgehog breeding season begins as soon as they leave hibernation

(Jones, 2021). This indicates that the earliest litters of hedgehogs could be born around mid to late October. In the South Island, pregnant females were captured from early November to January, which is likely later than the North Island hedgehogs (Jones, 2021). The average litter size of hedgehogs in the North Island is 2.7 (Brockie, 1974). Juvenile hedgehogs will first leave the nest to go foraging with their mother at three to four weeks of age and become independent by six to seven weeks (Jones, 2021). Juvenile dispersal could occur as early as January in warmer regions.

1.4.6 Further research needed to understand hedgehog ecology in New Zealand

An in-depth investigation into the timing and duration of both hibernation and the breeding season is necessary to fill knowledge gaps in hedgehog ecology in New Zealand. The duration of the hibernating period of European hedgehogs is variable depending on latitude and climate (Brockie, 1974; Parkes, 1975; Moss, 1999; Haigh et al., 2012; Rautio et al., 2014). In warmer areas of New Zealand, such as Northland, few hedgehogs are thought to hibernate, and only for short periods (Brockie, 1974; Moors, 1979). Moors (1979) found that some hedgehogs in coastal Manawatu, North Island, did not hibernate, and others only had short periods of torpor. Brockie (1974) found a similar pattern in hedgehogs in Wellington that fluctuated with the severity of climatic conditions. A shorter hibernation period for northern hedgehogs would mean they would need to build fewer energy reserves to survive hibernation, and there would be a lower winter mortality rate (South et al., 2020).

Due to a milder climate than in Europe, the hedgehog breeding season is likely extended, especially in warmer regions in the North Island. For example, heavily pregnant female hedgehogs have been found during August in Kaitaia (Jones, 2021). This indicates that the local climate influences the length of the hedgehog breeding season. Jackson (2006) discovered that most female hedgehogs resumed sexual activity after the birth of an early litter of hoglets. In Europe, late litters of hedgehogs are considered common and are likely a second attempt at breeding for females that failed to rear an early litter of young (Reeve, 1994). However, Jackson (2006) confirmed that hedgehogs would attempt to have multiple litters in favourable conditions on the Scottish Island Uist, where they were introduced. There is insufficient evidence to confirm that hedgehogs will have second litters during one breeding season in New Zealand (Jones, 2021).

1.5 Implications for conservation in New Zealand

1.5.1 Introduction and distribution

Hedgehogs were introduced to New Zealand in 1870 by European colonisers to remind them of home and as a way of controlling garden pests, such as snails and slugs (Kriechbaum et al., 2018; Jones, 2021). The extent to which hedgehogs effectively control introduced slugs and snails has never been demonstrated (Jones, 2021). Hedgehogs are abundant and widespread in New Zealand (Nottingham et al., 2019). The success of hedgehogs in New Zealand can be attributed to plentiful food, few competitors and predators, and a climate with mild winters (Jones, 2021). Hedgehogs are present throughout lowland districts of New Zealand and some offshore islands, including Chatham, Waiheke, and Rakiura Islands (Brockie, 1974). Surveys in Waikato farmland found hedgehogs to be widely distributed, and hedgehogs were the most frequently detected small mammal (Tempero et al., 2007). There are fewer hedgehogs in areas where there are more than 250 frost days per year, such as alpine habitats, and areas with greater than 2500 mm of rain per year, such as Fiordland on the southwest corner of the South Island (Brockie, 1974; Jones, 2021). However, some still survive in these areas; as Foster et al. (2021) demonstrated, female hedgehogs do inhabit and enter hibernation in the high alpine zones of the Southern Alps.

1.5.2 Pest status

Hedgehogs are regarded as a less serious threat to native wildlife than other mammalian predators, such as mustelids, cats, and rats (Glen et al., 2019). Public perception of hedgehogs is a hindrance to conservation efforts, with several hedgehog rescues actively rehabilitating sick hedgehogs and releasing them. Rats, mustelids, and possums have been targeted by a nationwide "Predator Free 2050" plan that aims to eradicate these introduced mammalian predators from the mainland of New Zealand by the year 2050. While considerable evidence implicates hedgehogs as a serious threat to native invertebrates and ground-nesting birds, this mammalian predator has been left off the target list at a national level. Hedgehogs are also not classified as "unwanted organisms" under the Biosecurity Act 1993, meaning they are not managed by the Ministry for Primary Industries (MPI) national pest program.

However, hedgehogs are classified as pests under regional pest management plans. In Auckland, hedgehogs are regionally under "sustained control" to reduce their spread and impact (Auckland Council, 2020). In the Hauraki Gulf Controlled Area of the Auckland Region, hedgehogs are under "site-led" control (Auckland Council, 2020). The "site-led" approach aims to manage existing populations of hedgehogs on offshore islands in the Hauraki Gulf and prevent them from spreading to pest-free islands. For example, Rangitoto and Motutapu Islands (close to mainland Auckland) successfully eradicated mammalian predators, including hedgehogs, and now the focus is to prevent reintroductions (Griffiths et al., 2015; Auckland Council, 2020).

Greater Wellington Regional Council (Greater Wellington) and Otago Regional Council also have a site-led approach to hedgehog control. Whereby, if hedgehogs can cause damage to an area, they should be excluded or eradicated or "contained, reduced or controlled within the area to an extent that protects the values of that place" (Greater Wellington, 2020). Wellington has designated exclusion zones where "no person shall possess and/or release any hedgehog" without risking prosecution under the Biosecurity Act 1993 (Greater Wellington, 2020). Under Otago Regional Council's pest management plan, hedgehogs are only considered pests in site-led programmes in Otago Peninsula, West Harbour/Mt Cargill, Quarantine Island and Goat Island (Otago Regional Council, 2019). The pest status of hedgehogs is relevant at a national and regional level as it allows for penalties against the intentional release of unwanted animals in vulnerable areas and provides strategic direction for areas to undertake control programs.

1.5.3 Threats from hedgehogs

Invasive hedgehogs in New Zealand have been implicated in the decline of native fauna, particularly ground-nesting birds, and invertebrates. Hedgehogs are a threat to native biodiversity through direct and indirect predation of native wildlife (Berry, 1999; Jackson & Green, 2000; Jones et al., 2005; Jones & Norbury, 2010; Spitzen – van der Sluijs et al., 2009; Nottingham et al., 2019). Berry (1999) described the possible implications of hedgehogs to ecological restoration as the removal of large quantities of invertebrates, competition with native insectivores, and predation of native vertebrate species. Hedgehogs are also vectors of several diseases that can be transmitted to livestock and humans (Jones, 2021). They are a spillover host of bovine tuberculosis (bTB), a disease of concern to the agricultural industry in New Zealand (Lugton et al., 1995; Gorton, 1998; Jones, 2021). This has prevented the export of hedgehogs from New Zealand back to the United Kingdom to boost their population numbers (Lugton et al., 1995; Jones, 2021). New Zealand Hedgehogs also carry strains of *Staphylococcus*, *Salmonella*, ringworm fungus, and *Sarcoptes scabiei* and *Caparinia tripilis* mite infestations causing “mange” (Gorton, 1998; Kriechbaum et al., 2018; Jones, 2021). These zoonotic diseases can all be transmitted to humans by handling infected hedgehogs without hygiene measures (Kriechbaum et al., 2018; Ruszkowski et al., 2021).

Impacts on invertebrates

Hedgehogs are important predators of small native invertebrates in New Zealand (Jones et al., 2013). Dietary analysis studies have found evidence of hedgehogs predating rare native beetles, wētā, and giant centipedes (Jones et al., 2005; Spitzen – van der Sluijs et al., 2009; Jones & Norbury, 2010; Jones et al., 2013). The diet of hedgehogs varies with the prey types available in their local environment (Jones et al., 2005; Jones & Norbury, 2011; Nottingham et al., 2019). Beetles and their larvae (*Coleoptera*) were consumed in the highest volumes by hedgehogs in urban forest fragments of Auckland, with introduced slugs (*Lixmax maximus)* and earthworms (*Oligochaeta*) following (Nottingham et al., 2019). Giant centipedes (*Cormocephalus rubriceps*) were present in 5% and wētā in 14% of hedgehog guts (Nottingham et al., 2019). In the Upper Waitaki Basin, hedgehogs consumed beetles, moths (*Lepidoptera*), earwigs (*Dermaptera*), Hymenoptera, and Orthoptera in the highest quantities (Jones et al., 2005). Hedgehogs also consumed wētā, found in 22% of guts, with a single hedgehog containing 283 wētā legs, indicating they can be preyed on in high quantities (Jones et al., 2005). Jones and Norbury (2011) also found that beetles and earwigs were consumed in large volumes in the dryland habitat of the South Island. Hedgehogs predated two rare species of beetles, the sand scarab (*Pericoptus frontalis*) and the Alexandra chafer beetle (*Prodontia modesta*) (Jones & Norbury, 2011).

Using enclosure-based experimental manipulation, Jones et al. (2013) demonstrated that the number of ground wētā decreased significantly with increasing hedgehog density. More research is needed to quantify the effects of hedgehogs on native invertebrate populations. They can consume large volumes of prey, with some estimates as high as 160 grams per day (Wroot, 1984). This is a significant amount of food, given that the average weight of a hedgehog in the wild is around 680 grams (Brockie, 1974). Invertebrates contribute to ecosystem functioning, and their reduction can negatively impact trophic pathways (Nottingham et al., 2019). Whether the reduction of invertebrates by hedgehogs has ecosystem effects through loss of functions carried out by those invertebrates is yet to be determined (Blackburn et al., 2014; Nottingham et al., 2019).

Impacts on lizards

Evidence of native skink and gecko predation has been found during several dietary analyses of hedgehogs (Jones et al., 2005; Spitzen – van der Sluijs et al., 2009; Jones & Norbury, 2010). Skinks are vulnerable to hedgehog predation as they are torpid during the night when hedgehogs are foraging, meaning they cannot actively avoid predation (Jones et al., 2013). Both skink and gecko remains were found in 9% of hedgehog guts collected from the Mackenzie Basin (Moss, 1999). Skink remains were also found in 21% of hedgehog guts from Macraes Flat in Otago, 14% from dryland habitat in the South Island, and 6% from the Upper Waitaki Basin (Jones et al., 2005; Spitzen – van der Sluijs et al., 2009; Jones & Norbury, 2011). Jones et al. (2013) also showed juvenile McCann's skinks to significantly decrease with increasing hedgehog density through enclosure-based experimental manipulation. Lizards were found in 2% of hedgehog guts examined in urban Auckland (Nottingham et al., 2019). High densities of introduced plague skinks (*Lampropholis delicata*) exist in the Auckland Region, which likely constitutes the majority of skink predation by hedgehogs in urban forest fragments (Nottingham et al., 2019). It is suspected that high numbers of hedgehogs can have a significant impact on native lizards, but the extent to which hedgehogs impact the survival of native lizard populations is unknown (Jones et al., 2005; Spitzen – van der Sluijs et al., 2009).

Impacts on birds

Evidence of the impact of hedgehogs on ground-nesting birds in New Zealand has been collected in the form of video footage of nest predation and dietary analysis (Berry, 1999; Hendra, 1999; Moss, 1999; Sanders & Maloney, 2002; Nottingham et al., 2019). Hedgehog dietary analyses have found evidence of bird predation in varying quantities (Berry, 1999; Nottingham et al., 2019). Moss (1999) found bird remains (eggshells and feathers) in 15% of hedgehogs examined from the Mackenzie Basin in spring and summer. Bird remains were found in 7% of hedgehogs examined in urban forest fragments in Auckland (Nottingham et al., 2019). Hendra (1999) found bird feathers in 8% of hedgehogs collected throughout a year from Trounson Kauri Park in Northland. Dietary analysis of hedgehogs at Boundary Stream by Berry (1999) found the taxonomic composition overlapped with North Island brown kiwi (*Apteryx mantelli*) by 70%-80%, indicating kiwi likely compete with hedgehogs for the same prey items.

There is substantial evidence of nest predation to native ground-nesting birds by hedgehogs at several sites (Dowding, 1998; Jackson & Green, 2000; Dowding & Murphy, 2001; Sanders & Maloney, 2002). At Tāwharanui Regional Park, hedgehogs predated NZ dotterel nests before there was a pest-proof fence and were responsible for two of every three nest failures (Dowding, 1998). In the South Island, hedgehogs are a predator of birds nesting in braided riverbeds, including banded dotterel (*Charadrius bicinctus*), black stilts (*Himantopus novaezelandiae*), black-fronted terns (*Chlidonias albostriatus*), wrybills (*Anarhynchus frontalis*), and South Island pied oystercatchers (*Haematopus finschi*) (Sanders & Maloney, 2002). Sanders and Maloney (2002) found hedgehogs responsible for 20% of recorded nest predation events at 172 monitored banded dotterel, black stilt, and pied oystercatcher nests in the Upper Waitaki Basin. Prior to this study, hedgehogs were only treated as by-catch by trapping programs in braided river systems, and this highlighted the need for targeted control of hedgehogs (Sanders & Maloney, 2002).

Introduced hedgehogs have also been a problem for ground-nesting birds in Scotland. A study on an internationally significant population of wader birds (*Charadrii*) on the Island of South Uist in Scotland found introduced hedgehogs to be threatening them with regional extinction (Jackson & Green, 2000). Hedgehogs were introduced in the 1970s and caused the decline in six species of ground-nesting wading birds and their nest success (Jackson & Green, 2000). The average hedgehog density was 57 hedgehogs km^{-2}, which is high compared to their natural range (Jackson & Green, 2000). Jackson and Green (2000) found the risk of nest predation by hedgehogs to be proportional to hedgehog population density. There is evidence that hedgehogs do not seek out bird nests but instead come across them incidentally during foraging trips (Jackson, 2006).

1.5 Duneland systems and hedgehogs

Coastal duneland systems are widespread along various parts of New Zealand's extensive coastline, such as Ninety Mile Beach, Farewell Spit, and Te Paki (Hilton et al., 2000). Duneland systems are coastal ecosystems found along the shores of oceans and large lakes, created by natural processes of wind and waves depositing sand and forming dunes (Gadgil & Ede, 1998). Dunes are dynamic environments that constantly undergo reshaping from wind and wave action (Hesp, 2000). In active foredunes, natural vegetation is dominated by grasses, sedges, and herbs (Hilton et al., 2000). There are diverse flora and fauna that have adapted to low moisture conditions, high salinity, and wind exposure

(Elser, 1970; Jamieson, 2010). Stable backdunes can include a range of native trees and shrubs such as flax (*Phormium tenax*), *Griselinia,* cabbage tree (*Cordyline australis*), and thick-leaved mahoe (*Melicytus crassifolius*) (Stephenson, 1999; Dahm et al., 2005; Jamieson, 2010). Many threatened species are found in New Zealand's coastal dunelands, such as rare species of plants, lizards, and shorebirds (Milne & Sawyer, 2002; Jamieson, 2010). For example, the Muriwai Gecko (*Woodworthia aff. maculata*), katipō spiders (*Latrodectus katipo*), fairy tern (*Sternula nereis*), and New Zealand dotterel (*Charadrius obscurus*) (Costall, 2006; Jamieson, 2010; Brooks et al., 2011; Melzer et al., 2022).

In New Zealand, dune areas have been heavily modified by human impacts and development (Hesp, 2001). The total area of active duneland in New Zealand has reduced by 70% since the early 1900s (Hilton et al., 2000). They are classified as endangered ecosystems (Hilton, 2006). The leading causes of duneland decline and degradation include stabilisation and afforestation, and on a smaller scale, sand mining, agricultural development, urbanisation, waste disposal, human recreation, and military activities (Gadgil & Ede, 1998; Hilton et al., 2000; Hilton, 2006; Jamieson, 2010). For example, the widespread loss of native vegetation cover due to stock grazing has resulted in unstable dunes and shifting sand (Gadgil & Ede, 1998; Hilton et al., 2000; Hilton, 2006). As a result, exotic pine plantation (*Pinus* radiata) and marram grass (*Ammophilia arenaria*) were commonly used for dune stabilisation and afforestation (Gadgil & Ede, 1998; Hilton et al., 2000; Hilton, 2006). Duneland systems in New Zealand are vulnerable to the spread of invasive species, climate change, and rising sea levels (Jamieson, 2010). Exotic species of plants and trees have contributed to the widespread degradation of active dunelands, such as gorse (*Ulex europaeus*), lupin (*Lupin arboreus*), bone seed (*Chrysanthemoides monilifera*) and acacia trees (*Acacia sophorae*) (Hilton et al., 2000; Jamieson, 2010). Due to intensive farming practices, most native vegetation sequences are limited to remnants on foredunes (Jamieson, 2010).

There is limited research on the effects of hedgehogs on coastal duneland systems. Hedgehogs are abundant in coastal duneland ecosystems of the North Island (Jeffries, 2011; Jones, 2021). High densities of hedgehogs are found in coastal farmland and dunelands in Northland, where the weather is mild, and frosts are rare (Jones, 2021). In coastal farmland with long pastures, invertebrate prey of hedgehogs is abundant (Jones, 2021). Nest availability is also high in the dry soils of duneland systems. Many rare species of endemic invertebrates inhabit sand dunes, which are vulnerable to hedgehog predation (Brockie, 1957; Patrick & Dugdale, 2000).

Spatial ecology approaches, such as habitat suitability modelling and spatial analysis of predation risk, can help quantify the extent of hedgehog impacts on native species and identify priority areas for conservation intervention (Kliskey & Byrom, 2004). Taxa with limited refugia or specialised habitat requirements, such as ground-nesting shorebirds in an endangered coastal duneland ecosystem, may be at greater risk than species with broad habitat tolerance. For example, the New Zealand fairy tern is critically endangered, with only 40 birds nesting in northern coastal dunelands (Brooks et al., 2011). Although there are no documented cases of hedgehog predation on fairy tern, the risk is high, and the potential impact is severe if hedgehogs were to get into the breeding area.

1.6 Thesis structure and objectives

Compared to other mammalian predators, such as possums (*Trichosurus vulpecula*) and stoats (*Mustela erminea*), hedgehogs are relatively understudied in New Zealand (Nottingham et al., 2019). The existing knowledge gaps in the spatial ecology and impacts of European hedgehogs in the northern coastal ecosystems of New Zealand highlight the need for additional scientific research. To implement effective management actions, the nature and severity of impacts must be understood (Nottingham et al., 2019). These areas provide essential breeding habitat for many ground-nesting birds, including the critically endangered New Zealand fairy terns (Tara-iti) and New Zealand dotterels. We lack information on the home range size for hedgehogs in coastal habitats or how it varies with age, sex, and time of year. This knowledge gap is important as there is evidence that hedgehogs pose a significant threat to our biodiversity, but there is a lack of quantitative knowledge of how they use these habitats. Without this crucial information, conservation managers cannot implement effective control measures in areas with breeding native shorebirds. My research aims to quantify and understand hedgehog spatial ecology and habitat use in Northland's duneland coastal ecosystems and provide insights that can guide more effective control measures of hedgehogs.

1.6.1 Chapter 1: Introduction

This chapter introduces spatial ecology theory, invasive species, and their relevance to conservation worldwide and in New Zealand. The ecology of European hedgehogs is described in both the native range in Europe and the introduced range in New Zealand. The implications of invasive hedgehogs to conservation in New Zealand are discussed, and specific threats to native invertebrates, lizards, and birds are described. Duneland ecosystems and the potential impacts of hedgehogs on these threatened landscapes are described. Finally, an overview of the thesis structure and objectives for each chapter are outlined.

1.6.2 Chapter 2: Methodology

This chapter describes the study site and provides background information about the study. The methodology for data collection and data analysis are provided in detail for Chapter 3 and Chapter 4. This includes the process of searching the study site, attachment of transmitters, and recapture and release of hedgehogs. The process of data collection of pest animal trapping and camera trapping data are also described in detail.

1.6.3 Chapter 3: Hedgehog spatial ecology in northern coastal ecosystems of New Zealand

In this chapter, I provide evidence to expand knowledge of the spatial ecology of hedgehogs in northern New Zealand. I present information on their behavioural ecology, habitat preferences, movement patterns, activity levels, and spatial distribution. The evidence I provide aims to support pest control operations by highlighting the importance of trap density, informed by home range estimates, and the need for large buffer zones to account for dispersal based on the recorded travel distances. Furthermore, I discuss factors that affect the home range size and distance travelled by male and female hedgehogs, including habitat quality, breeding behaviour, and seasonality.

Objectives:

(1) Estimate the size of the home range and average distances travelled by male and female hedgehogs in a northern coastal ecosystem.
(2) Expand current knowledge of the movement patterns, habitat preferences, and spatial distribution of hedgehogs using GPS location data.

1.6.4 Chapter 4: Hedgehog control

In this chapter, I analyse pest trapping data to reveal trends in seasonality and habitat preferences of hedgehogs in northern coastal ecosystems. Spatial hot spot analysis of trapping data provides evidence of optimal trap locations and trap types. I compare trapping data from two different study sites, using different trap densities and trap types, and discuss the effectiveness of current hedgehog control. I also aim to help fill knowledge gaps in the general ecology, behaviour, and home range variability of hedgehogs in a diverse duneland ecosystem (pasture, wetlands, scrub, and dune grassland).

Objectives:

(1) Provide evidence of seasonal trends in hedgehog activity to inform optimal timing of control efforts.
(2) Provide support for pest control operations by providing evidence of habitat preferences, effective trap types, and trap density for controlling hedgehogs.
(3) Help fill knowledge gaps in the general ecology, behaviour, and home range variability of hedgehogs in a diverse duneland ecosystem.

1.6.5 Chapter 5: Thesis conclusions and recommendations

In this chapter, I summarise the key findings of my research, from the analysis of hedgehog spatial and trapping data, and provide recommendations for best-practice hedgehog control. The implications of my findings within the context of invasive species management and conservation are discussed. I also discuss how my research can contribute to the advancement of knowledge in the conservation of hedgehogs in their native range in Europe. The limitations of my research are outlined and areas for further investigation are suggested.

Footnote: Impacts of extreme weather

The data collection in my study was impacted by multiple severe flooding events in Northland, New Zealand, during January and February 2023. It was intended that the hedgehog population density in the Tara Iti Ecological Sanctuary would be estimated using mark-recapture. However, not enough hedgehogs were captured after the flooding events in January and February to estimate the hedgehog population density accurately. The total rainfall in January and February was extraordinarily high, and they were two of the wettest months ever recorded in Northland (NRC, 2023). Two significant storm events during January 2023 led to an average total monthly rainfall of 366 mm across Northland, 485% of the expected January rainfall. The worst flooding occurred in Mangawhai during Cyclone Gabrielle (12th-15th February 2023). Mangawhai recorded a maximum February rainfall of 653mm, 976% of the expected February rainfall (NRC, 2023). The rainfall for April and May 2023 also remained higher than average, receiving 177% and 217% of the expected monthly rainfall, respectively (NRC, 2023). These weather events impacted the ability of fieldwork to be carried out due to extensive surface flooding and road closures. More importantly, the surface flooding covered significant areas on the periphery of wetlands and low-lying areas at the study site, modifying the hedgehog habitat. In some low-lying areas, the floodwaters remained for months took a long time to recede (see also Figures 1.1 & 3.12).

Figure 1.1 An area of the golf course after the February 2023 cyclone. Low-lying areas of the golf course remained flooded for an extended period, and wind-thrown trees can be seen in the distance.

Chapter 2: Methods

2.1 Study site

My study was conducted at Tara Iti Ecological Sanctuary (Tara Iti) located in Mangawhai, Northland, New Zealand (-36.1346,174.62058) from September 2022 to May 2023. The 622 ha ecosanctuary is comprised of the Tara Iti golf course, Auckland Council Regional Parkland, and the coastal margin managed by the Department of Conservation (DOC). Tara Iti is an eastern coastal margin dune system that has been modified by various human activities over the last 20 years. Previously, the land was covered in exotic pine plantations, and extensive landscaping and re-vegetation were undertaken to return it to a more natural dune-like environment. Currently, a golf course covers 20% of the sanctuary with native dune grassland interspersed for dune stabilisation. The remainder of the sanctuary is covered by exotic pine plantations, regenerating native vegetation, and wetlands. Ecological restoration of the sanctuary is primarily led by Tara Iti Golf Course in partnership with Auckland Council, DOC, Massey University, and The Shorebird Trust. Tara Iti Ecological Sanctuary is a breeding site for the critically endangered fairy tern (*Sternula nereis*), as well as other endemic shorebirds, such as the New Zealand dotterel (*Charadrius obscurus*). To help protect these species, the site has undergone intensive trapping and monitoring programs for the last six years, which have removed over 2,500 pest animal species. A summary of Tara Iti's trapping history can be found in the appendices (section 6.1). The Tara Iti golf course is also undertaking a pest control program in the Black Swamp Predator Control Zone (Black Swamp; Figure 2.1), 1303 ha of private farmland to the west of Tara Iti, to provide a buffer zone for the threatened species breeding in Tara Iti. The Black Swamp Predator Control Zone is a partnership between private landowners, Tara Iti Golf Course, the Shorebird Trust, and Auckland Council.

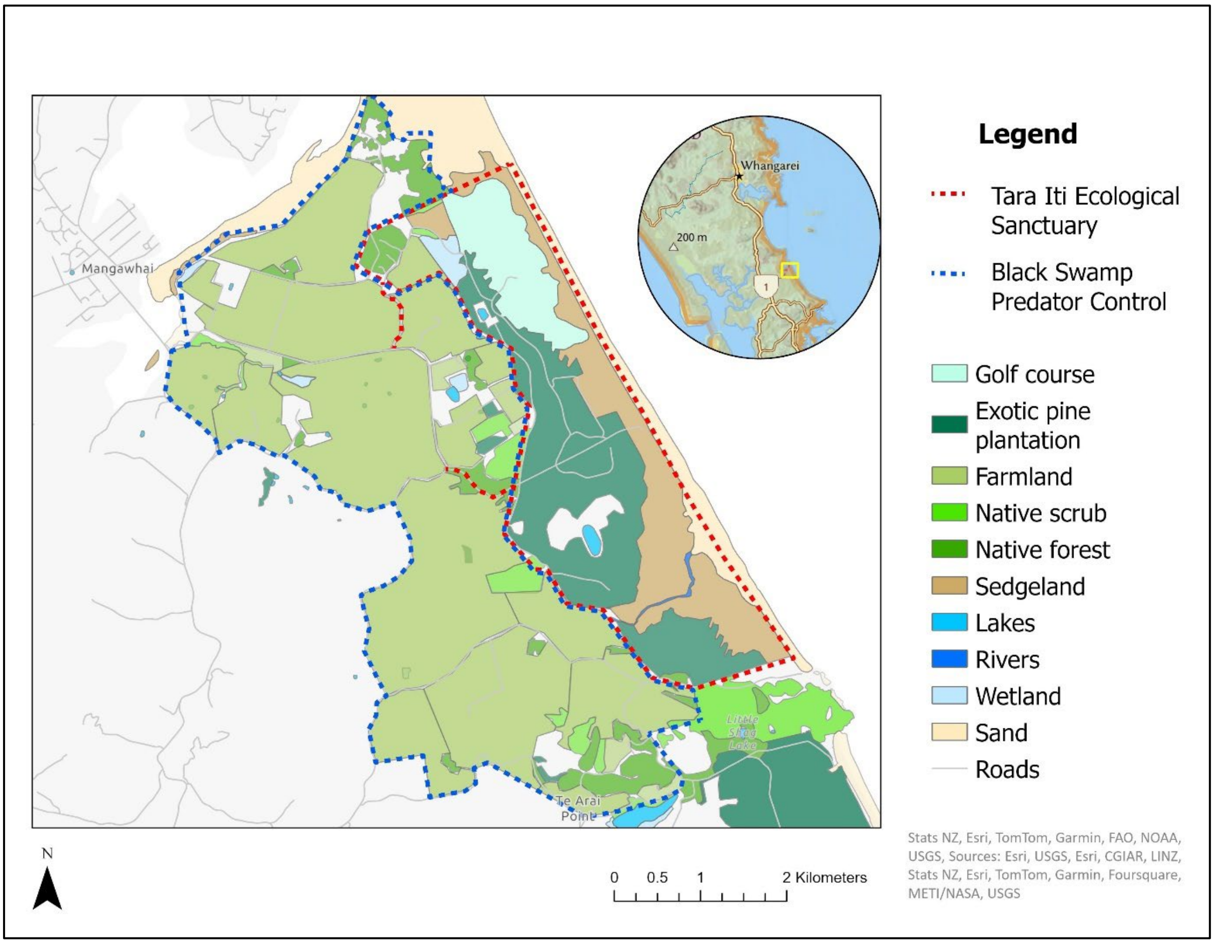

Figure 2.1 Map indicating study site boundaries and habitat types for Tara Iti and Black Swamp. Red lines indicate Rako Drive and Black Swamp Drive, which are included in the control area.

Figure 2.2 The study site, Tara Iti Golf Course, with the foredunes and the edge of the golf course visible.

2.2 Data collection

2.2.1 Sampling design

Multiple severe weather events during January and February 2023 impacted the sampling design, affecting both the habitat in the study area and the researchers' ability to get to the study site and carry out fieldwork. Consequently, the original sampling design had to be modified. The main difference was the seasonal comparisons, which could not be completed due to a lack of site access and low hedgehog captures.

Table 2.1 Initial sampling design vs modified sampling design.

	Initial design	*Modified design*
1)	Estimation of hedgehog population size through mark-recapture. Four recapture surveys were to be undertaken throughout one year.	Estimation of the home range and nightly home range size of 11 hedgehogs for the Spring-Autumn period.
2)	Estimation of the seasonal home range size of hedgehogs throughout one year using GPS tags. Aimed to capture at least 10 hedgehogs every 3 months, in each season of one year.	Trail camera sampling to indicate the presence of pest species and analysis of hedgehog trapping data from Tara Iti and Black Swamp study areas.

2.2.3 Searching

The study area was searched for 4-6 hours after sunset, using 2-4 researchers. A table detailing dates, search effort, and weather conditions can be found in the appendices (Table 6.1). Approximately 57.5 search hours were completed in spring 2022 during a weeklong sampling period in early November using 3-4 researchers. In summer 2023, 42.5 search hours were carried out during three weekends in February using 2-4 researchers. In autumn 2023, 42 search hours were carried out by three researchers during two weekends in March and May. Handheld spotlights were used to search for hedgehogs, and a thermal imaging scope was used for approximately 28.5 search hours toward the end of the sampling period once it became available.

Researchers worked on different transects but stayed within calling distance. Because of severe weather, the sampling was less systematic than planned, as set transects were not able to be repeatedly searched due to changing habitat conditions. However, we attempted to evenly split the search time between different habitat types found in the study area, such as the golf course, farmland, and pine forest. The approximate area searched over the sampling period is displayed in the appendices (Figure 6.4). Terrain and vegetation affected search efforts due to visibility and health and safety considerations. After storm events, there were many windthrown trees throughout the pine habitat, which had to be avoided to prioritise health and safety. Search efforts in the pine habitat were primarily focused on blocks where the undergrowth was cleared, making it safer to search and provided greater visibility to observe hedgehogs. The area searched each night was also partly determined by the local weather conditions, such as wind strength and direction. For example, the golf course was exposed to strong winds, so search efforts there were primarily focused during calm conditions. Some low-lying areas were not able to be searched after the weather events during January-March 2023 when flood waters remained for extended periods of time. Areas where hedgehogs had been captured on trail-cameras and in previous sampling, such as paddocks and road edges next to farmland, were often searched multiple times a night.

2.2.4 Processing and attachment of transmitters

Once spotted, hedgehogs were live captured by hand and held for approximately 10-15 minutes while they were measured and then fitted with GPS/VHF transmitters. Each hedgehog was inspected for general physical condition, sexed, and weighed. The hedgehogs were marked using 10mm lengths of 1.6mm coloured plastic sleeving (heat-shrink polyolefin), glued to six spines using household superglue, following the method recommended by Reeve et al. (2019). This enabled the short-term identification of individual hedgehogs. A household epoxy adhesive (Araldite 90 seconds) was used to glue the tags to the dorsal spines of the hedgehog (Jones & Norbury, 2006; Recio et al., 2011). The sharp tips of the spines were trimmed in a small area (1.5 cm by 1.5 cm) using a small pair of wire cutter pliers to maximise adhesive to the tags. The hedgehogs were kept under observation for a short period to ensure the glue had set and were then released near the point of capture. All animal handling and transmitter attachment and removal methods were approved by the Massey University Animal Ethics Committee (reference number: AEC 22/50).

Figure 2.3 A study hedgehog after marking and transmitter attachment.

2.2.5 Equipment

Household kitchen scales (*Avanti*; precision estimate ±1 g) were used to record the weight of the hedgehogs on capture and release. If two hedgehogs were captured in the same location, a plastic cat carry cage was used to temporarily hold one. The thermal imaging scope used (Sytong, RM03-35LRF) was designed for use with a rifle and has a detection range of greater than 1000 m.

Figure 2.4 The thermal imaging scope used in this study. Sytong RM03-35LRF.

The GPS loggers used were 9 PinPoint VHF-75 tags manufactured by Lotek (Lotek NZ Ltd). These tags contain both a GPS logger and a VHF transmitter. The battery life of the GPS loggers was approximately 7 days. The PinPoint tags incorporate the 'Swift Fix' firmware, enabling rapid fixes for more frequent location recordings and improved battery-saving optimisation. The tags are designed for use with birds and weigh approximately 6g - well below the limit of 6.6% of a tagged hedgehog's body mass, a guideline Recio et al. (2011) deemed appropriate for hedgehogs. This method allows natural movement, defensive curling, and minimised snagging in burrows. During November 2022, the GPS units were scheduled to log nightly positions at 5-minute intervals for 10 hours (20:00 h–06:00 h) for a maximum of 4 nights. During May 2023, the GPS units were scheduled to log nightly positions at 15-minute intervals for 13 hours (18:00 h– 07:00 h) for a maximum of 6 nights. The schedule aimed to capture hedgehog activity while conserving battery life during periods of inactivity. Static tests estimated a mean locational error of 3.31 m in open areas and 14.04 m under canopy cover, which is considered an acceptable locational error for recording hedgehog movements (Foster et al., 2021; Reeve et al., 2021). The fix success rate (FSR) was 99.4% in both open and moderate canopy cover.

2.2.6 Recapture and release

Once sampling sessions were complete, the PinPoint tags were scheduled to emit a signal for tracking using VHF radio telemetry. A Yagi aerial and VHF receiver were used to track the signal to the daytime dens of the hedgehogs. The tags were removed by cutting the tips of the dorsal spines to which they were glued, a process that took approximately 10 minutes of handling time. The point locations of the hedgehog dens were recorded using a handheld Garmin GPS device (eTrex 32x). Once the tag was removed, the hedgehogs were inspected, weighed, and then released back to their daytime dens. Care was taken to try to minimise disturbance to the dens.

2.3 Data analysis

2.3.1 Basic hedgehog data

Basic data on the hedgehogs was recorded in an Excel spreadsheet (see Table 6.2 and Table 6.3). The weight of each hedgehog on initial capture, and recapture and release were recorded in grams. The sex, date and time of capture and recapture, number of sampling nights, location of capture, location of the den, colour marker, and total number of fixes were recorded. The point location coordinates for the capture location and recapture (den) locations were also recorded. Measurements of the front and hind feet of the hedgehogs were initially recorded, but it was abandoned as it caused handling time to be too long, and not all the hedgehogs would uncurl enough to be able to take an accurate measurement.

2.3.2 Data processing

Once the tags were removed from the hedgehogs, they were attached to the Lotek DLC interface for data download. The Swift Fix location data from the tags had to be processed in the PinPoint Host to get a text file. The text files were converted to a ‘CSV’ file and then processed in Excel. The location fixes were recorded in Universal Standard Time (UMT) and were converted to New Zealand Standard Time (NZST). The number of failed fixes for each tag were noted, and a fix success rate (FSR) was calculated for each hedgehog dataset and each sampling night. The datasets for each hedgehog were split up into sampling nights. A sampling night was defined as one night of activity for a hedgehog, from the first location fix (taken after sunset) to the last location fix at sunrise. The Excel spreadsheets containing the location data were then imported into ArcGIS Pro (Esri, version 3.1.2) using the table-to-feature class tool. The feature classes were added to a map and plotted using the Plot XY function. The location data were cleaned in ArcGIS Pro by removing outlier data points that appeared to be caused by high locational error (e.g., location fixes in the sea).

2.3.3 Statistical analysis

GPS location data from the tagged hedgehogs were plotted and analysed using ArcGIS Pro to calculate the seasonal home range, nightly home range, and average distance travelled. The seasonal home range is defined as the estimated home range size during the period sampled in this study. The nightly home range is defined in this study as the area utilised by a hedgehog in a single sampling night. Incremental analysis was performed on the two most extensive hedgehog datasets to determine the minimum number of sampling nights and locational fixes needed to reach a horizontal asymptote and estimate the seasonal home range. The capture points and known den locations were overlaid from GPS point locations taken during hedgehog capture and recapture. The Kernel Density Estimation (KDE) tool, using the Natural Breaks Classification with 10 classes, was utilised to produce a density raster from point data for each hedgehog dataset, indicating the core area of the home range. The 100% minimum convex polygons (100% MCP) were calculated using the Minimum Bounding Geometry tool to estimate the area of the seasonal home range and the nightly home range. Sampling nights were colour-coded to distinguish them from one another. The Points-To-Line feature was utilised to visualise the sequence of travel over each sampling night and allowed for the nightly distance travelled to be calculated. The nightly distance travelled was determined by summing the straight-line distances between each location fix. This value was then averaged over the total number of sampling nights for each hedgehog dataset to calculate the average distance travelled. The Count Overlapping Features tool calculated the home range overlap between hedgehogs. All figures containing habitat and home range layers were made in ArcGIS Pro.

RStudio (Build 524, Posit Software) and Minitab (version 21.4.1) were used to perform all statistical analyses. Linear regression models were created to test the effects of sex, weight, and distance travelled on overall home range size. Additionally, the effects of sex, weight, and seasonal home range size on the average distance travelled were tested using a linear regression model. The Spearman Rank test was performed to assess the correlation between the weight of the hedgehogs and the seasonal home range and nightly home range. Descriptive statistics for the seasonal home range and nightly home range, including 95% confidence intervals and standard error for the mean home range for male and female hedgehogs, were calculated using RStudio. The variance in the mean seasonal home range and nightly home range for male and female hedgehogs were calculated, and Levene's Test for Homogeneity of Variance was performed in RStudio. Minitab was utilised to generate box and whisker plots for the nightly home range and nightly distance travelled for each hedgehog.

2.4 Animal trapping data

2.4.1 Data collection

Trapping data from Tara Iti Ecological Sanctuary (Tara Iti) and the Black Swamp Predator Control Zone (Black Swamp) from 2016 to 2023 were recorded on *Trap.NZ* and were available for analysis (Groundtruth Ltd., 2023). *Trap.NZ* is a free online data management service where community trapping programs can be uploaded onto a mapping system, and pest control data can be stored and viewed (Groundtruth Ltd, 2023). All pest animal catch data and trap information for Tara Iti and Black Swamp were downloaded from *Trap.NZ*. Tara Iti's pest control program aims to protect native wildlife and enhance the biodiversity of the ecosystem by controlling mammalian predators (Flavell-Johnson, 2022). The goal of the Black Swamp is to provide a buffer zone to manage mammalian predators at low densities, reducing the likelihood of pest animals reaching ecologically sensitive along the coast where fairy tern (tara iti) and other native shorebirds breed (Flavell-Johnson, 2022).

2.4.2 Control devices

Tara Iti uses predominantly DOC250 traps, as well as live capture cage traps, Trapinators, Steve Allen (SA2), and DOC200 traps. Double-set DOC200 traps (containing two traps side by side) are used in areas close to fairy tern breeding sites. The Black Swamp Predator Control Zone primarily contains DOC200 traps, with only a small number of DOC250s, Trapinators, and Timms traps. In the Black Swamp project area, traps are provided to private landowners free of charge by Auckland Council. Both DOC250 and DOC200 traps are enclosed in a wooden box with two mesh baffles to exclude non-target animals (see Figures 6.1 and 6.2 in the appendices). DOC250 traps are designed primarily for ferrets (*Mustela furo*) with a standard baffle aperture size of 80 mm by 80 mm (Garvey & Byrom, 2021). DOC200 traps target stoats (*Mustela erminea*) and weasels (*Mustela nivalis vulgaris*) with a smaller baffle aperture of 60 mm by 60 mm (Warburton et al., 2008). Trapinators and Timms traps are designed to target brush-tailed possums (*Trichosurus vulpecula*). Steve Allen (SA2) traps target feral cats and possums. Although there is no trap specifically designed for hedgehogs, both DOC 200 and 250 traps have met the National Animal Welfare Advisory Committee (NAWAC) criteria for kill traps targeting hedgehogs (Jones et al., 2021).

Table 2.2 The number of traps used in the study sites.

Trap type	***Black Swamp (1330.01 ha)***	***Tara Iti (621.9 ha)***	***Marginal Strip (175 ha)***
DOC200	183	30	244
DOC250	8	110	1
Trapinator	31	37	
SA2	0	31	21
Cage Trap	0	15	3
Timms	4	0	
BT200			2
BT250			1
Leg hold			8
Total	**226**	**223**	**280**

2.4.3 Trapping Regime

Tara Iti

Mustelids (stoats, weasels, and ferrets), possums, rats, and feral cats are all targeted by Tara Iti's pest control program. Hedgehogs are treated as bycatch and are not specifically targeted, although they constitute a high proportion of the total trap catch. Trap lines in Tara Iti follow transect lines with a spacing of approximately 200 m for DOC250 and DOC200 traps (Figure 4.3). Live capture cages are spaced 500 m apart, and possum traps are approximately 200 m to 500 m apart. In Tara Iti, the DOC200 traps are mostly located in and around the golf course. Traps are typically checked fortnightly year-round (with some variability) by the conservation managers for Tara Iti. Rats are targeted through a 50 m by 50 m network of bait stations used to distribute rodenticide. All data from the trap checks are recorded in *Trap.NZ*, allowing ongoing monitoring of progress. Pest monitoring is also conducted using "run-through" tracking tunnels to index rodent and mustelid abundance. There were two months (April 2020 and September 2021) when traps could not be serviced due to COVID-19 lockdowns, and no data were recorded.

Coastal Marginal Strip

The coastal marginal strip in Tara Iti Ecological Sanctuary has a higher level of pest control due to its proximity to fairy tern breeding sites and is managed by the Department of Conservation (DOC). This includes the trapline running along the beach and the surrounding area near the river mouth on the southern end of Tara Iti. These traps are checked weekly during the shorebird breeding season (August to February). The highest level of control is implemented, involving a high-density trap network with a 50 m spacing of double-set DOC200 traps, live capture traps every 200 m, and rat poison bait stations on a 50 m by 50 m grid (Figure 4.3).

Black Swamp

Mustelids are specifically targeted by the Black Swamp trapping regime, but rat, possum, and hedgehog numbers are also reduced by the trapping program. The minimum control level is one DOC200 trap per six hectares of land, but some areas have a higher trap density. There are larger distances between traps, but the network covers twice the size of the Tara Iti area. In Black Swamp, traps are checked monthly during the winter months (March to July) and once every fortnight over the summer months (August to February). This is to target pest control efforts during both the native bird breeding season and the mustelid breeding season. Approximately half the traps in the Black Swamp Control area are maintained by private landowners, and the rest are maintained by the conservation managers for Tara Iti.

2.4.4 Data analysis

Processing

The animal trapping data from 2016 to September 2023 were exported from *Trap.NZ* as CSV files and imported into Excel to be processed. All trap information and location data were exported from *Trap.NZ* and converted to CSV files that could be imported to ArcGIS Pro. Hedgehog capture data by month and year were combined with the trap location coordinates. Habitat layers for Mangawhai were exported from the Land Information New Zealand Data Service (LINZ, 2023).

Statistical Analysis

A bar chart of the hedgehog catches per year from 2018 to 2023 was created in Microsoft Excel to show the drop in hedgehog catches in 2023. Excel was also used to generate a chart of the seasonality trends in hedgehog catch from monthly catch data exported from *Trap.NZ*. The Excel forecast function was used to predict the expected hedgehog catch for 2023 based on the previous six years of data. The forecast function predicts future values by using linear regression and creates a line of best fit for future data based on historical data. Trap locations were mapped using ArcGIS Pro and overlaid with habitat layers and a heat map of the number of hedgehogs caught at each trap location from 2020 to 2023, revealing hot spots in hedgehog catches (LINZ, 2023). Additionally, a map of the trap locations within the seasonal home range of the study hedgehogs was created in ArcGIS Pro to indicate the gaps in the trap network. The hedgehog catches from 2020 to 2023 for Black Swamp and Tara Iti were plotted in Excel to demonstrate differences in the numbers of hedgehogs caught between the sites.

2.5 Camera trapping data collection

A network of baited trail cameras was initially set up to indicate hedgehog presence to assist live capture fieldwork. These trail cameras collected pest animal footage from Tara Iti from November 2022 to May 2023. Hedgehogs were targeted, but the cameras also captured the presence of other pest animals. The trail camera data were analysed alongside the animal pest trapping data.

2.4.1 Equipment

Two types of Bushnell trail cameras (Trophy Cam E3 essential and Core S-4K No Glow) were used to collect pest animal footage. These cameras have infrared LED night vision flash to ensure clear footage can be recorded during the night. They were programmed to capture three pictures when activated by motion and have a trigger speed of 0.3 seconds. The passive infrared sensor (PIR) is motion-activated up to approximately 30 metres.

2.4.2 Placement

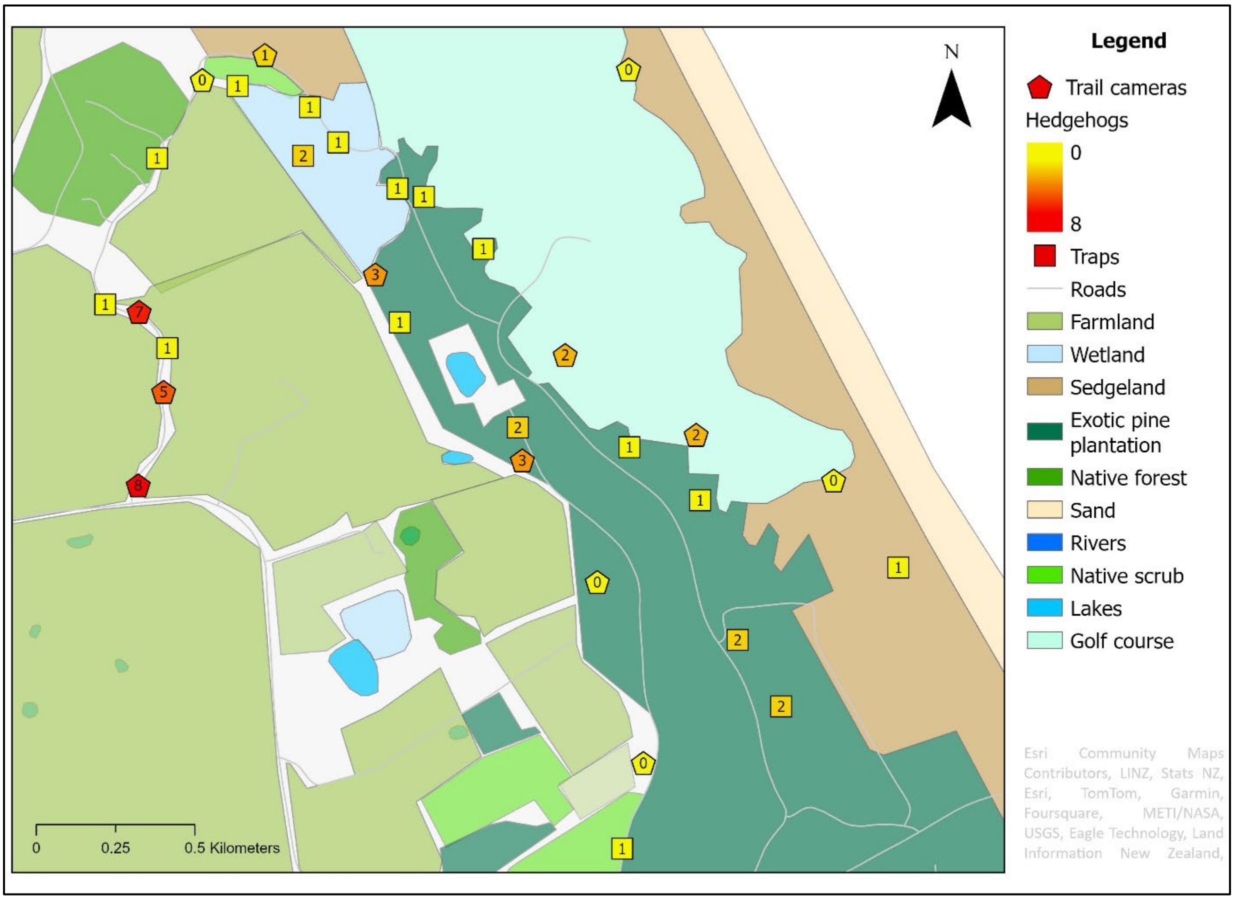

Figure 2.5 Map of the 13 trail camera locations with the number of hedgehogs recorded and the trap locations where hedgehogs had been trapped during the same period (March–May 2023). November 2022 data was excluded as many traps were disabled during this period.

Camera sites were set up in different habitats where live capture sampling was conducted, such as pine forest, golf course, wetland, and edges of farmland and roadsides. A total of thirteen camera sites were used during sampling (Figure 2.5). The camera locations were chosen non-randomly along linear features (such as fence lines and tracks) where animals could be caught moving through the area. The cameras were attached to trees where possible, or stakes and fence posts in open areas, approximately 20 cm off the ground. A dry or tinned cat food was placed approximately 1 m to 1.5 m on the ground in front of the camera. Vegetation, such as long grass, was cleared in front of the cameras so it would not block the cameras from taking a clear image.

2.4.3 Experimental design

Trail camera footage was collected for approximately a week during the months of November 2022, March 2023, April 2023, and May 2023 (Table 2.3). Not all thirteen camera sites were utilised for the full duration of sampling. Following the November 2022 sampling, four new camera sites were added around the golf course to indicate hedgehog presence. However, two of the camera sites on the golf course were excluded during April and May 2023 due to golfing activities restricting researchers' access. The trail cameras were baited daily with tinned cat food ("Fancy Feast") during November 2022. From March to May 2023, the cameras were baited weekly with either tinned or dry cat food (Whisker's cat biscuits). The SD cards and batteries were also checked weekly when the bait was refreshed. The trail cameras were set to record during the night only (sunset to sunrise) and were activated by motion detection.

Table 2.3 Sampling effort of trail camera footage.

Camera sites	*Month*	*Sampling nights*	*Camera nights*
9	November 2022	5	45
13	March 2023	9	117
11	April 2023	8	88
11	May 2023	6	66

2.4.4 Data analysis

The animal trail camera footage was downloaded from camera SD cards, and pictures were processed manually. Trail camera data were recorded in a Microsoft Excel spreadsheet (Table 6.4) The timing of visits (by hour of night) of hedgehogs to baited cameras was plotted in Excel to determine which hours of the night they were most likely to visit. The proportion of camera recordings by species was compared between the different sampling periods, and bar charts were plotted using Minitab software. A map of the camera locations, including nearby trap locations, and a heatmap of hedgehog camera recordings and trap catch for the same time period were generated in ArcGIS Pro (Figure 2.5).

Chapter 3: Hedgehog spatial ecology in northern coastal ecosystems of New Zealand

3.1 Introduction

3.1.1 Home range

Home range refers to the area that an animal occupies and within which they confine the majority of their essential activities such as foraging, den construction, reproduction, and rearing young (Burt, 1943; South, 1999; Börger et al., 2008; Heathcote at al., 2023). A territory is distinguished from a home range in that it is actively defended by an individual from other competitors, usually conspecifics (Burt, 1943; Börger et al., 2008). Not all species are territorial and actively defend their home range (Burt, 1943). In the context of spatial ecology, the home range represents the spatial extent over which an animal carries out its daily and seasonal activities (Börger et al., 2008). Home range is a core concept in spatial ecology, and quantifying home range size is a basic step towards understanding the ecological requirements of a species (Börger et al., 2008). Studying the home range of a species can provide insight into several aspects of ecology, such as resource utilisation, movement patterns, population dynamics, behavioural ecology, and conservation management (Ofstad et al., 2019; Butler et al., 2020; Olejarz et al., 2022). For example, Olejarz et al. (2022) found there to be kin-related home range overlap when studying the spatial ecology of female brown bears (*Ursus arctos*) in Finland. Animals confining their activities to a discrete home range is thought to reflect the fitness benefits that come with obtaining a spatial knowledge of the landscape (Heathcote et al., 2023). It allows an animal to learn the location and exploit patchily distributed resources such as food and shelter (Heathcote et al., 2023). For example, Heathcote et al. (2023) showed the mortality risk of pheasants from predators to be highest at the outer edge of the home range, where individuals had less spatial information.

Variability in home range size within many mammal species is driven by demographic characteristics such as age class, sex, and reproductive state (Devillard et al., 2008; Abu Baker et al., 2017). Home range size often differs between males and females within a species, and in many cases, males have larger average home ranges than females (Rautio et al., 2013; Abu Baker et al., 2017). This has been observed in mammalian species such as moose (Cederlund & Sand, 1994), racoons (Gehrt & Frttzell, 1997), bats (Safi et al., 2007), and hedgehogs (Rautio et al., 2013; Abu Baker et al., 2017). However, age class and reproductive state can also affect the home range size (Cederlund & Sand, 1994; Devillard et al., 2008). For example, European rabbits (*Oryctolagus cuniculus*) have larger home ranges during the reproductive season for both sexes, and juveniles have larger home ranges than adults (Devillard et al., 2008). If variability in home range exists within a species due to demographic characteristics, it is important to have separate estimates for juveniles, males, and females within a species to assist in both invasive species management and conservation of endangered species (Safi et al., 2007; Devillard et al., 2008; Abu Baker et al., 2017).

3.1.2 Relevance to invasive species management

Home range is an important ecological concept that can also help guide the spatial management of invasive species (Smith et al., 2015; Hradsky et al., 2019). In many cases, invasive species exhibit higher biological success in their introduced range than in their natural range (Parker et al., 2013). Quantifying home range estimates and habitat preferences can optimize targeted control of elusive animals (Bartoszek et al., 2021). For example, Rodríguez-Recio et al. (2022) studied the home range behaviour and resource selection of introduced feral cats (*Felis catus*) on the remote subantarctic Auckland Islands of New Zealand to assist in the eradication of this pest species. They found the average home range size to be larger than estimates from other offshore islands and the mainland of New Zealand (Rodríguez-Recio et al., 2022). Smith et al. (2015) demonstrated how home range data can be used to optimise control of invasive stoats (*Mustela erminea*) by employing a modelling approach to advise on the line spacing of control devices (such as traps). If conservation managers can ensure a trap is within the estimated home range size of individuals within a population, then they increase the probability of those individuals interacting with the traps (Smith et al., 2015).

3.1.3 Knowledge gaps and rationale

There are currently no studies estimating hedgehog home range size using GPS technology in the northern coastal ecosystems of New Zealand. Jefferies (2011) previously estimated the home range size of hedgehogs in the coastal dunelands of Auckland using radio telemetry. Overall, home range estimates used to guide pest control measures of hedgehogs in the North Island of New Zealand are limited and based on field techniques and radio telemetry only (Brockie, 1974; Parkes, 1974; Gorton, 1997; Berry, 1999). Duneland coastal ecosystems are distinct, diverse, and threatened landscapes (Hilton, 2006) that provide refuge to many endangered species (Costall, 2006; Jamieson, 2010; Brooks et al., 2011; Melzer et al., 2022). The nature of duneland systems means that the nesting birds that use dunelands are often ground nesters, making them vulnerable to predation by hedgehogs. Likewise, reptile species in duneland systems also tend to be ground-based. Hedgehogs are hypothesized to have a detrimental effect on these ecosystems and native species but there is a lack of quantitative evidence on their specific impacts on duneland systems. Previous research estimating home range size in hedgehogs in both Europe and New Zealand shows high variability in estimates based on the environment and climate (Brockie, 1974; Parkes, 1975; Haigh, 2011; Rautio et al., 2013; Rodríguez-Recio et al., 2013; Gago et al., 2022). This indicates the critical need for specific estimates of hedgehog home range in a coastal duneland system to help guide best practice control of hedgehogs in this environment.

3.1.4 Objectives

In this chapter, I address two key objectives (1) to provide estimates of the home range size and average distances travelled by male and female hedgehogs in a northern coastal ecosystem and (2) to expand current knowledge of the movement patterns, habitat preferences, and spatial distribution of hedgehogs using GPS location data.

3.2 Results

3.2.1 Search effort

A total search time of 142 hours was carried out in variable weather conditions from September 2022 to May 2023 (Fig. 3.1). Eleven hedgehogs (four males and five females during November 2022 and two males during May 2023) were live captured and fitted with Lotek Pinpoint VHF-75 tags for a maximum of seven days. The average fix success rate was 92% for the GPS tags, which is considered high for hedgehogs (Reeve et al., 2021). On three occasions, the tag detached from the hedgehog before the end of sampling. All 11 hedgehogs captured visually appeared healthy during the initial capture. The weights of the hedgehogs ranged from 466 g to 834 g. The heaviest tagged female (834g) was nursing 4 hoglets weighing 66 g each. Upon recapture, Hedgehog 2 was found curled outside, not in a den, and had lost 42 g of weight. This hedgehog could have been suffering from disease, although, hedgehogs have been known to sleep in the open or under minimal cover in warm weather (Moss, 1999; Barthel et al., 2018). The average weight of the female hedgehogs sampled (728 g) was heavier than the male hedgehogs sampled (590 g). A group of three female hedgehogs were located by researchers because they were heard making vocalisations (snorting). It was uncertain what the context was for these vocalisations, such as aggressive or social behaviour. However, other hedgehog studies have noted loud rasping and snorting noises during aggressive encounters as well as during courtship (Haigh et al., 2012).

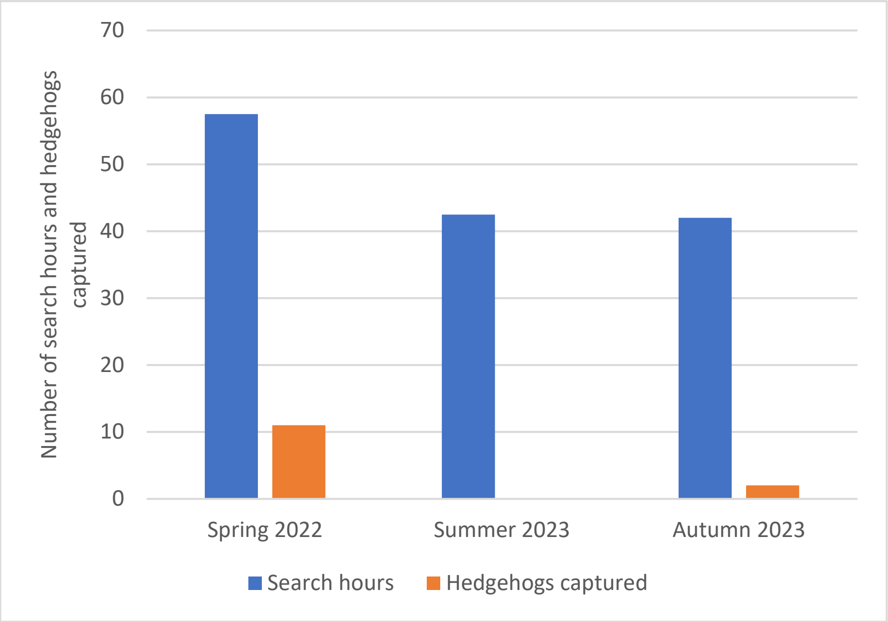

Figure 3.1 Search effort vs hedgehogs caught during each season where sampling occurred. 58 search hours were carried out in Spring 2022 and 11 hedgehogs were live captured (9 GPS tagged). No hedgehogs were caught during Summer after 43 search hours. 2 hedgehogs were captured after 42 search hours in Autumn 2023.

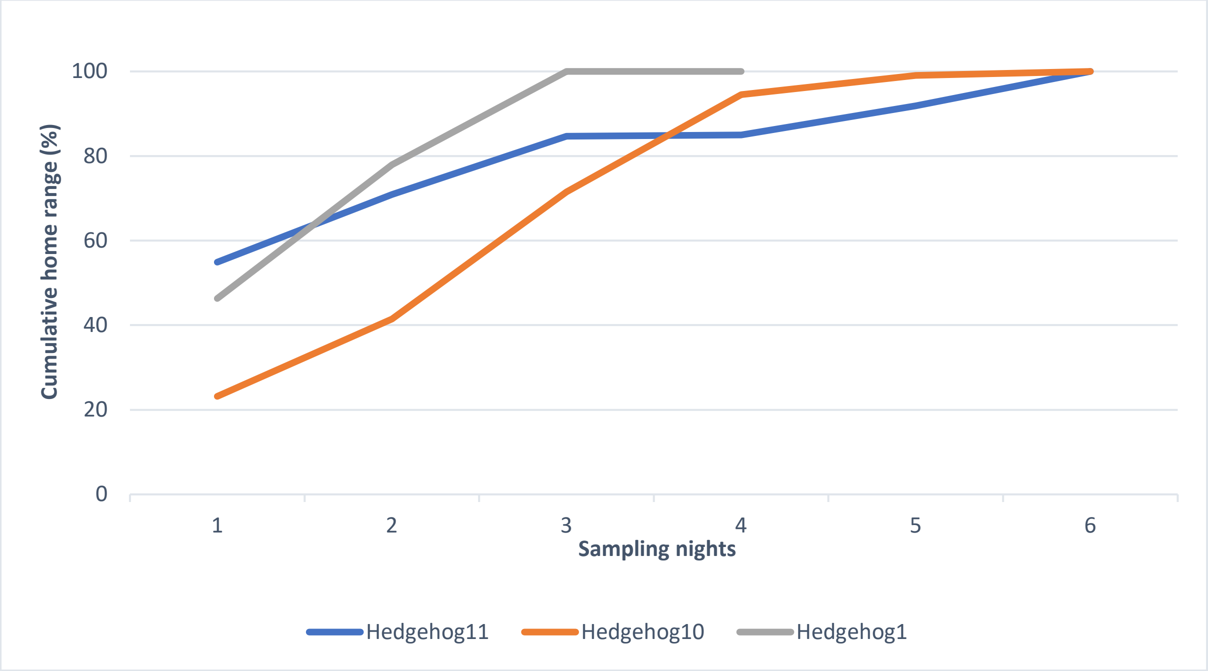

Figure 3.2 The cumulative seasonal home range for Hedgehogs 1 (M), 10 (M), and 11 (M).

Hedgehogs do not cover their entire home range in one night but instead cover an increasing area of the seasonal home range over three or more days. Incremental analysis of the home range of three hedgehog datasets indicates that a minimum of three sampling nights is required to estimate over 80% of the home range of a hedgehog. During the first sampling night, Hedgehog 10 only covered approximately 20% of its overall home range. Whereas Hedgehogs 1 and 11 covered closer to 50% of their home range during the first sampling night. Hedgehog 1 covered 100% of their home range after three sampling nights, whereas Hedgehog 10 took five nights, and Hedgehog 11's home range was still increasing, so it could not be determined.

3.2.2 Seasonal home range

The seasonal home range varied in size and shape between individual hedgehogs and sexes. The mean home range (± standard error) for all hedgehogs was 7.1 ± 1.61 ha (95% CI 3.5, 10.7). The average seasonal home range was higher for males, 8.06 ± 2.34 ha (n= 6), than for females, 5.62 ± 2.13 ha (n= 4) based on 100% MCP, but this difference was not statistically significant ($p > 0.05$). The seasonal home range for male hedgehogs ranged from 4.14 ha to 19.2 ha and female hedgehogs ranged from 1.84 ha to 11.3 ha. The variance for males (32.72) was higher than for females (18.20) but this was not statistically significant (Levene's Test for Homogeneity of Variance, F-value=0.014, $p > 0.05$). The lack of statistical significance may have been due to the small sample size (n=10).

Hedgehog 8 had the largest home range (11.29 ha) out of the female hedgehogs sampled. Her home range covered predominantly exotic pine forest whereas Hedgehogs 4 and 5 were in pasture and had much smaller home ranges (1.84 ha and 2.89 ha). Not enough data were collected for Hedgehog 7 (female) to determine the home range size. Hedgehog 1 (male) had the largest home range out of all the hedgehogs sampled (19.21 ha) which was mainly in farmland habitat with some small fragments of hedgerows and native bush where the den was located.

Linear regression using the variables sex, weight, and average distance travelled showed only distance travelled to be a significant predictor of the overall home range size ($R^2 = 0.569$; $p < 0.05$). The Spearman Rank Correlation test did not find a significant correlation between the weight of the hedgehogs and the seasonal home range ($\rho = -0.17$, $p > 0.05$).

Hedgehogs do not use the area of their home range equally—core areas are occupied more intensively (Figure 3.4). Kernel density estimation (100%) based on location point data defined the core and edge habitat of each study hedgehog's home range. The core habitat used by the hedgehogs was a significantly smaller area compared to the 100% MCP. The core area ranged from 0.86 ha to 3.77 ha (n=7).

Table 3.1 Data collected from 11 tagged hedgehogs.

ID	Sex	Season	Seasonal home range (ha)	Average distance travelled per night (m)	Sampling nights	Weight (g)	FSR (%)
7	F	Spring	*	4,071	1	572	99.1
4	F	Spring	1.84	1,140	3	672	99.4
5	F	Spring	2.89	1,326	3	785	92.6
9	M	Spring	4.96	1,454	1	672	95.1
3	M	Spring	4.14	1,749	3	691	98.7
11	M	Autumn	4.41	799	6	484	70.3
6	F	Spring	6.47	2,680	1.5	622	99.1
2	M	Spring	7.16	2,093	3	555	91.3
10	M	Autumn	8.48	1,282	6	466	79.3
8	F	Spring	11.29	3,586	2	834	96.4
1	M	Spring	19.21	2,418	4	672	90.7

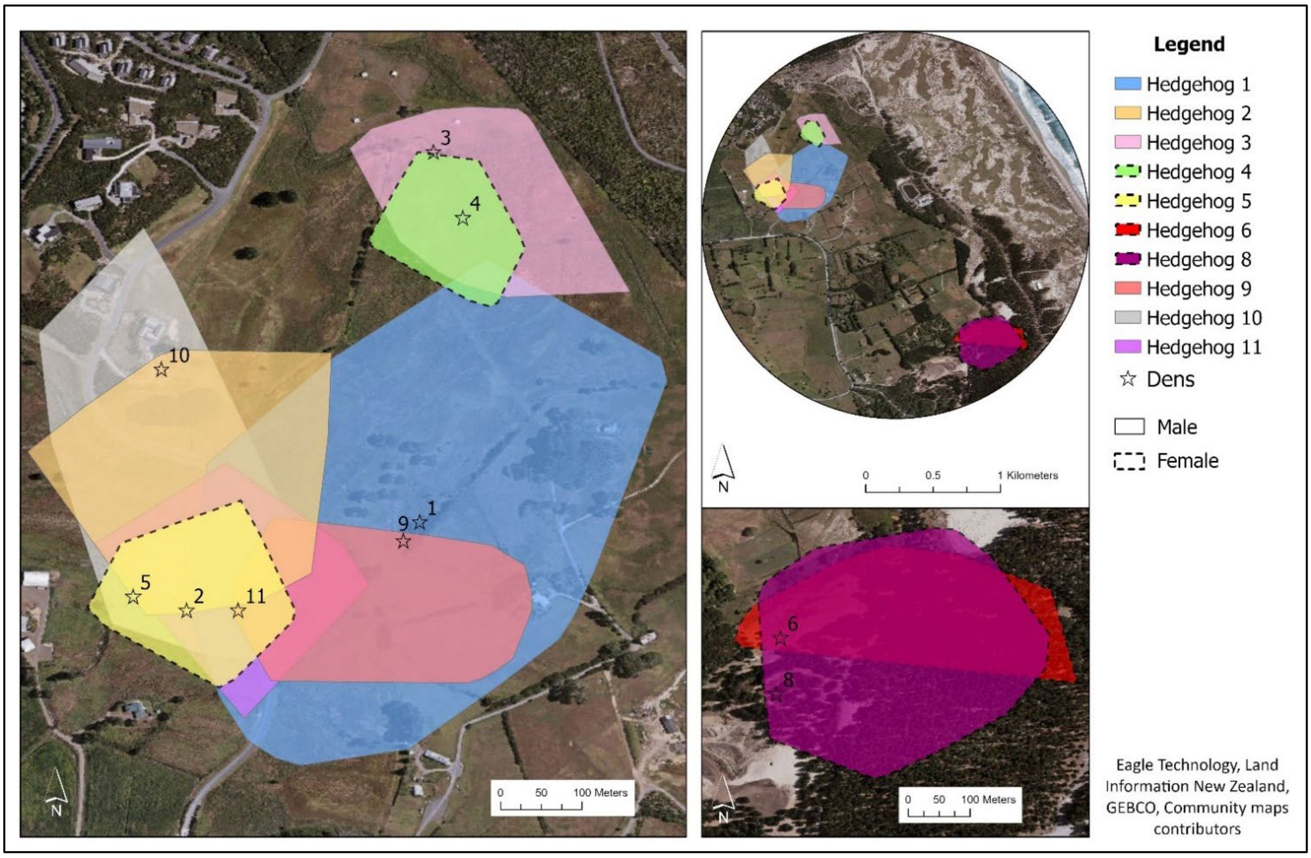

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Figure 3.3 The seasonal home range of 11 hedgehogs as 100% minimum convex polygons.

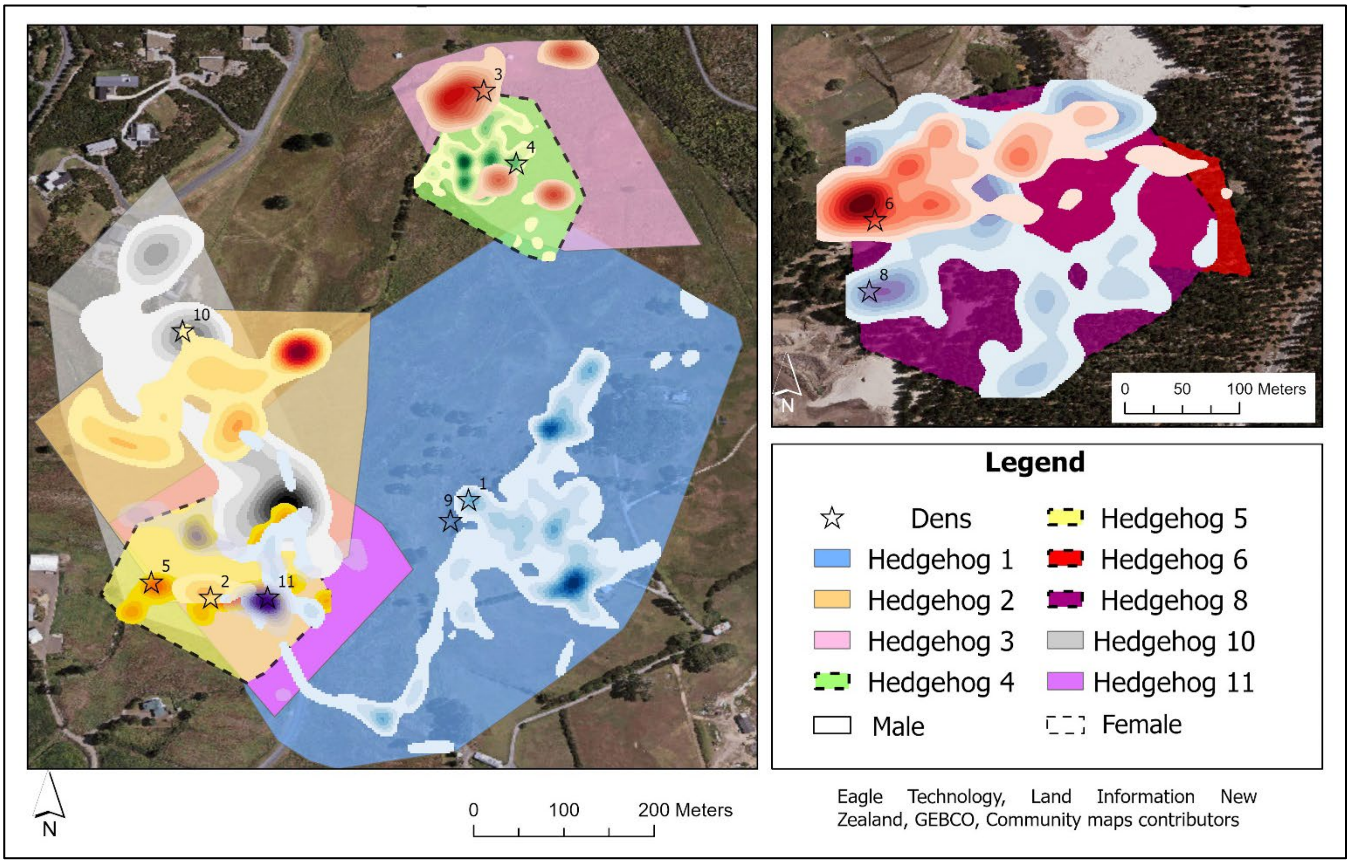

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Figure 3.4 Kernel density estimation (KDE) of the seasonal home range. Hedgehogs 7 and 9 were excluded as there was insufficient data to calculate a core range.

3.2.3 Nightly home range

The nightly home range size and shape varied over different nights and between individuals (Figure 3.6). In some cases, the hedgehogs foraged in different areas of the seasonal home range over consecutive nights. The area foraged over the sampling nights often overlapped, especially over roads and nesting areas (Figure 3.6). The mean area foraged each night (the nightly home range) was 3.46 ha with a standard deviation of 3.26.

The nightly home range for males ranged from 0.5 ha to 13.7 ha. The nightly home range for females ranged from 0.6 ha to 10.9 ha. The mean nightly home range was similar for males (3.4 ha; n=23) and females (3.6 ha; n=9). However, the median nightly home range was higher for males (2.6 ha) than females (1.4 ha). The variance in the nightly range was higher for female hedgehogs than male hedgehogs but this was not statistically significant ($p > 0.05$). The Spearman Rank Correlation test indicated a mild positive correlation between the hedgehog weight and nightly home range, but this was not significant ($\rho = 0.22$, $p > 0.05$).

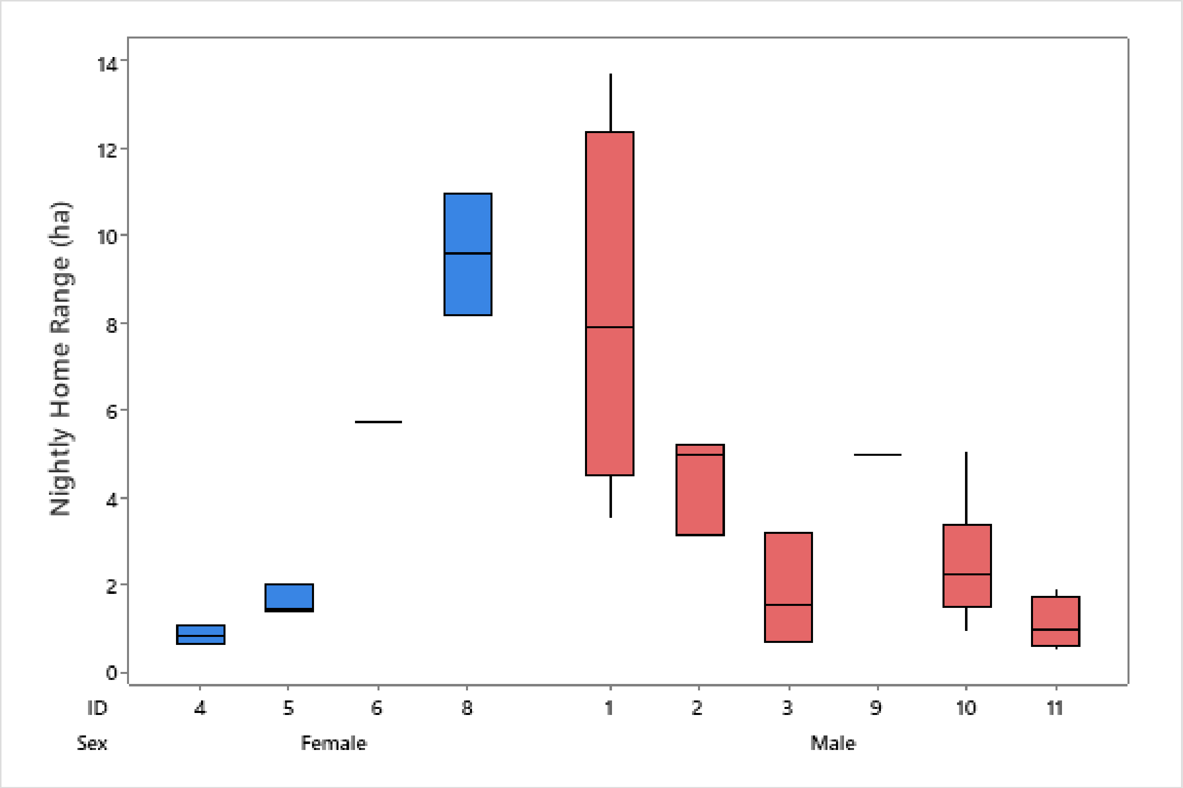

Figure 3.5 Box and whisker plot of the nightly home range data from each hedgehog. Female hedgehogs in blue and male hedgehogs in red. Only 1 sampling night was gathered from hedgehogs 6 and 9.

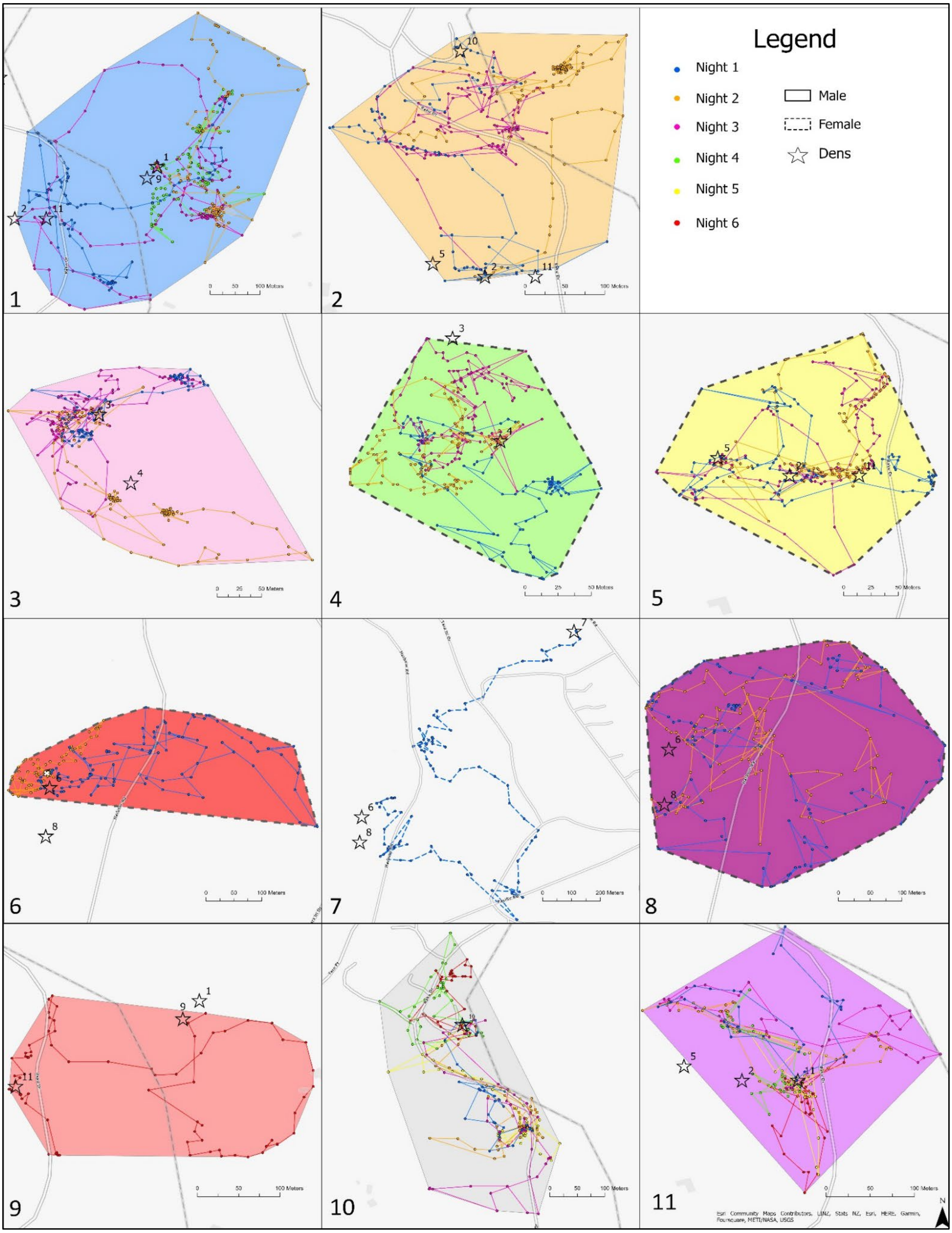

Figure 3.6 Nightly activity of each tagged hedgehog with colour-coded sampling nights.

3.2.4 Distance travelled

The average distance travelled per night (± standard error) was 1853 m ± 267 m (95% CI 1245 m, 2459 m). The male hedgehogs ranged from 799 m to 2417 m, with an average of 1632 m ± 237 m. The female hedgehogs ranged from 1140 m to 4071 m, with an average of 2054 m ± 580 m travelled per night. The average distance travelled by females was higher than males, but this was not statistically significant ($p > 0.05$). The highest distance travelled in one sampling night (4071 m) was completed by Hedgehog 7 (female) and appeared to be a dispersal trip. This hedgehog covered the full width of Tara Iti from the neighbouring farmland to the edge of the golf course, indicating that hedgehogs can travel from the neighbouring farmland to shorebird nesting areas in one night of activity. Linear Regression using the variables sex and weight showed neither to be a significant predictor of the average distance travelled. The Spearman Rank Correlation test indicated a moderate positive correlation between the hedgehogs' weight and nightly distance travelled that was significant ($\rho = 0.403$, $p < 0.05$). The variance in the nightly distance travelled was higher for female hedgehogs than males but was not statistically significant ($p > 0.05$).

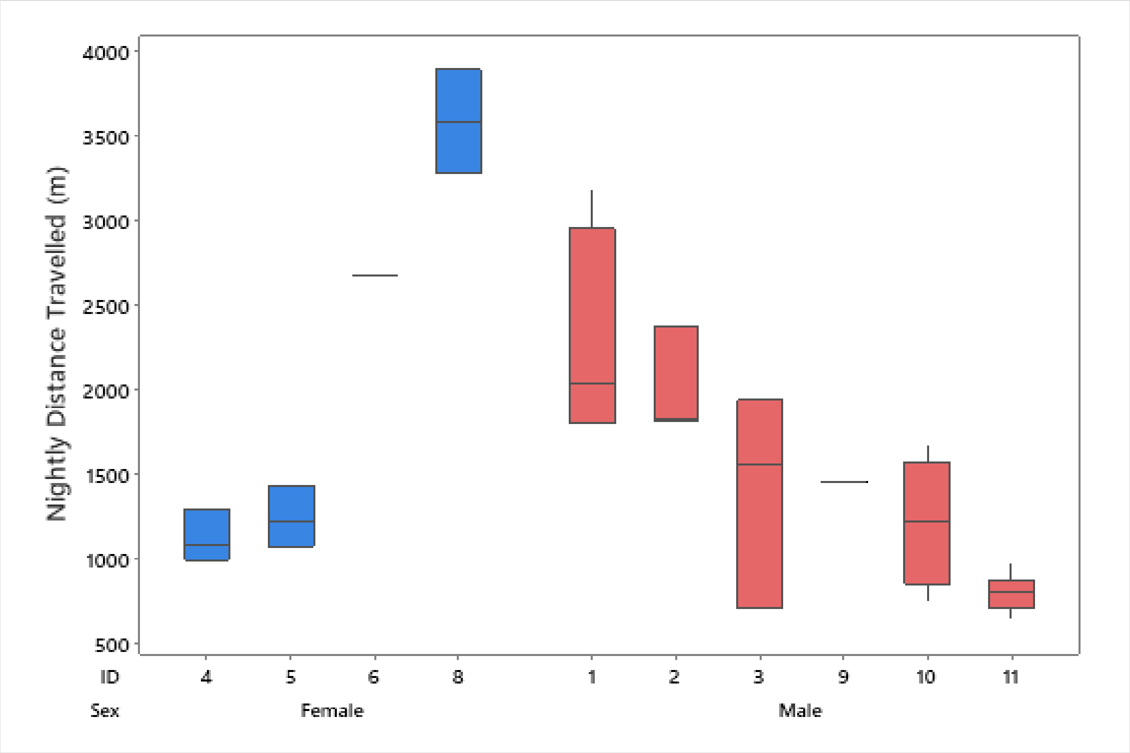

Figure 3.7 Box and whisker plot of the nightly distance travelled (m) by each hedgehog. Female hedgehogs are in blue, and male hedgehogs are in red. Only one sampling night was gathered from hedgehogs 6 and 9. Hedgehog 7 was considered an outlier and excluded from this plot.

3.2.5 Home range overlap

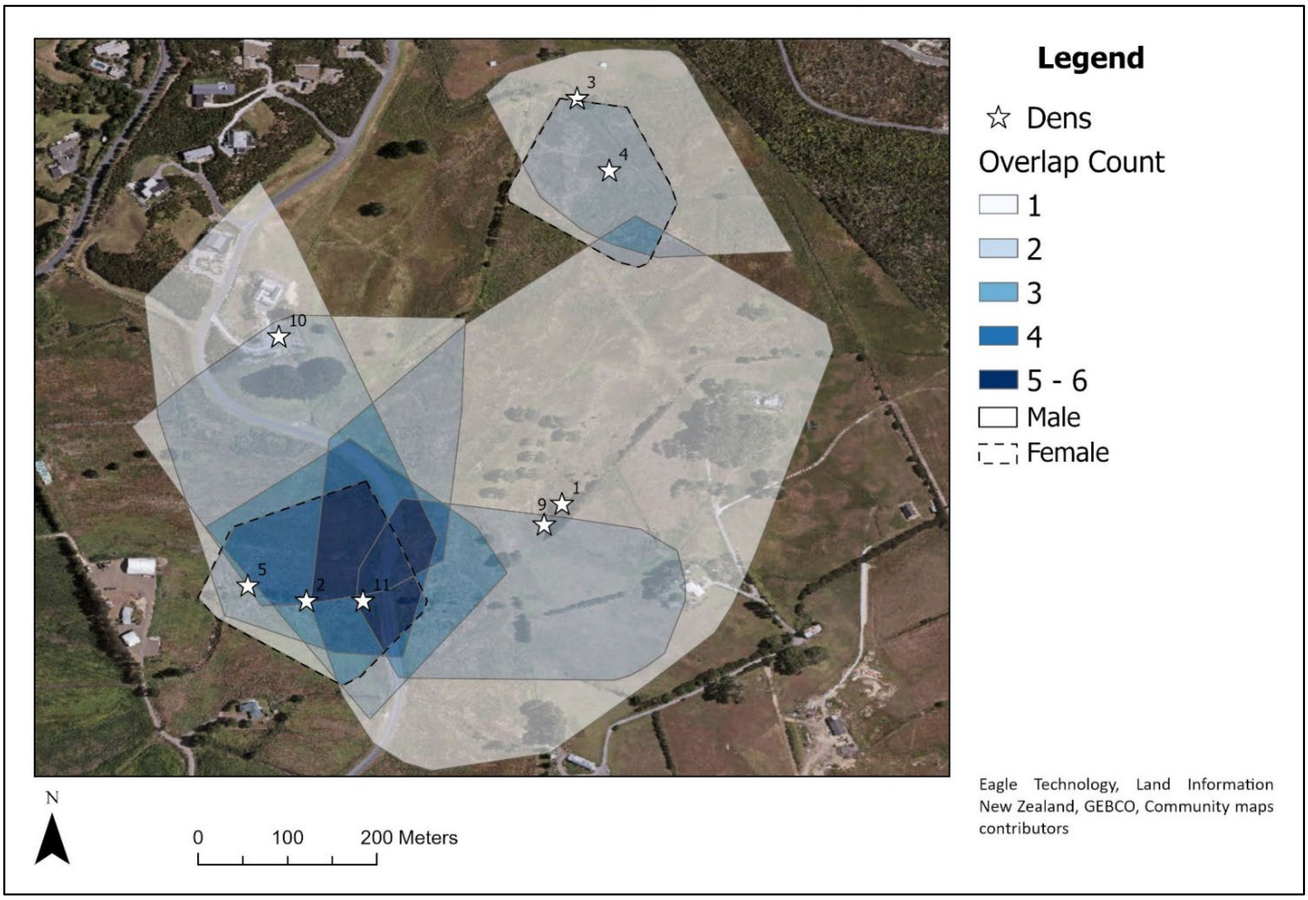

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Figure 3.8 The seasonal home range overlap between hedgehogs 1-5 and 9-11. The overlap count is indicated by colour intensity, the darker the colour, the higher the overlap count. Dens are indicated by a star symbol with a hedgehog ID number.

Of the 11 study hedgehogs, all the seasonal home ranges overlapped with at least one other hedgehog of either sex. There was an area of 0.53 ha where 6 home ranges overlapped over a road (Rako Drive), and an area of 1.37 ha where 5 or more home ranges overlapped. The foraging areas of some hedgehogs overlapped significantly. However, there is less overlap in the kernel density estimated core range of hedgehogs (Figure 3.4) compared to the seasonal home range estimated by 100% MCP. Some of the hedgehog den sites were located close together. Two of the hedgehog dens (1 and 9) were located only 28 m apart. Hedgehogs 5, 2 and 11 all had dens in the same hedgerow, approximately 50 m apart, and there was overlap in activity of these areas between hedgehogs (Figure 3.4).

3.2.6 Hedgehog dens

Table 3.2 Hedgehog den descriptions.

Hedgehog ID	Sex	Weight (g)	Den Description
1	Male	672	Ball of dried grass beneath fern undergrowth.
2	Male	555	Found in curled up by a gorse bush, not in a den.
3	Male	691	Ball of dried grass in overgrown pasture by large pampas grass.
4	Male	672	Ball of dried grass in overgrown pasture.
5	Female	785	Under a log covered by overgrown Kikuyu grass.
6	Female	622	Under a dump pile of dead vegetation.
7	Female	572	Nest dug in the side of a sand dune, covered by dead tussock grass (Figure 3.9).
8	Female	834	Nest dug into the sandy soil on a hill covered by leaf litter and dead vegetation. *Breeding den with four hoglets.*
9	Male	672	Dense ball of dead grass in a small fragment of native trees and fern undergrowth.
10	Male	466	Hole at the base of toetoe grass, covered by dried grass (Figure 3.10).
11	Male	485	The base of a dead gorse bush, covered by dried grass and vegetation (Figure 3.11).

Figure 3.9 Uncovered den of Hedgehog 7.

Figure 3.10 Uncovered den of Hedgehog 10.

Figure 3.11 Uncovered entry to den of Hedgehog 11, hedgehog inside.

3.3 Discussion

3.3.1 Home range

Overall, I observed that hedgehogs occupy a small core area of their home range intensively while covering its entirety over several foraging nights. This finding is consistent with previous hedgehog research from England (Morris, 1988) and the South Island, New Zealand (Moss, 1999). Morris (1988), also found that the nightly range used by hedgehogs varied and increased cumulatively with the number of sampling nights, reaching an asymptote after six to seven nights. Moss (1999) also found that hedgehogs occupied a core area that was a fraction of their total home range. However, the core range reported by Moss (1999) using radio-tracking data was higher than my estimates that used GPS location data and kernel density analysis.

Previous research on the home range of European hedgehogs shows estimates to be highly variable depending on the habitat and environmental conditions in both their introduced range in New Zealand and their native range in Europe (Moss, 1999; Rautio et al., 2013; Rodriguez Recio et al., 2013; Gago et al., 2022; Table 3.3). In my study, the overall mean home range size was 7.1 ha ± 1.6 ha. The average seasonal home range was higher for males (8.1 ± 2.3 ha) than for females (5.6 ± 2.1 ha), but the difference was not statistically significant due to small sample sizes and high variation between individuals. Male hedgehogs ranged from 4.1 to 19.2 ha and female hedgehogs ranged from 1.8 to 11.3 ha. Few studies investigating home range have been completed in non-pastoral habitats (Table 3.3). My estimates fit most closely with Jeffries' (2011) study in coastal dunelands in Auckland and Gorton's (1998) study in a mixture of pastoral farmland and native bush in Lake Wairarapa in the North Island of New Zealand; both study's findings fall within my estimated range for male and female hedgehogs. Reliable estimates of home range sizes for hedgehogs in duneland ecosystems are critical as less than 30 percent of New Zealand's natural duneland systems remain for native species such as the endangered New Zealand dotterel (*Charadrius obscurus aquilonius*; Dowding, 2020) and the critically endangered New Zealand fairy tern (*Sternula nereis*; Hilton et al., 2000; Brooks et al., 2011).

Overall, the home range estimates in northern New Zealand (Parkes, 1975; Gorton, 1998; Jeffries, 2011) are smaller than estimates in the native range of hedgehogs in Europe (Reeve, 1982; Riber, 2006; Haigh, 2011; Rautio et al., 2013), except for some urban areas (Korslund et al., 2023). Home range estimates from hedgehogs in the colder climate of the South Island of New Zealand (Moss, 1999; Rodriguez Recio et al., 2013) are more similar in size to estimates from hedgehogs in Europe than to hedgehogs in northern New Zealand. The main reasons for differences between these studies, and my own, likely include habitat and the latitudinal effects on climate conditions (Rautio et al., 2013; Gago et al., 2022). Home range estimates for hedgehogs in milder parts of their European native range, such as Spain, are similar to my estimates (Gago et al., 2022; Marco-Tresserres &

López-Iborra, 2022). This further supports the idea that climate conditions underpin the variability of the home range sizes in European hedgehogs (Moss, 1999; Rautio et al., 2013; Rodriguez Recio et al., 2013; Gago et al., 2022).

Hedgehogs in Europe are on average heavier (Morris, 1984; Dowding et al., 2010; Gurnell et al., 2015; Marco-Tresserres & López-Iborra, 2022) than hedgehogs in New Zealand by 50 to 200 grams (Brockie, 1974; van Heezik et al., 2023). This indicates that Bergmann's rule could partly explain the difference in home range size between hedgehogs in New Zealand and Europe. Bergmann's rule states that mammals in a cooler climate tend to be larger than those within the same species inhabiting a warmer climate (Meiri & Dayan, 2003). Hedgehogs in Europe will require larger body fat reserves to survive a colder and longer hibernation period, and they must concentrate their activity on building up these reserves during a shorter period before winter. Larger animals produce more metabolic heat and experience less heat loss than small animals (Meiri & Dayan, 2003). Smaller hedgehogs have a greater surface-to-volume ratio and lose more heat in cold conditions, and thus would experience higher mortality over winter conditions in Europe.

This in part explains the differences in home range size, but other factors, such as habitat quality and natural predators are likely to influence the home range of hedgehogs in their natural range in Europe (Dowding et al., 2010). The reported differences in home range size between New Zealand and Europe are also likely linked to higher food availability due to warmer temperatures, a longer active season, and a shorter hibernation period in New Zealand (Jones, 2021).

Nightly differences in home range

The size of the home range and distances travelled varied between individual hedgehogs and over different sampling nights for individual hedgehogs. The mean nightly home range was similar for males (3.4 ha; n=23) and females (3.6 ha; n=9). The range was wide for both males (ranging from 0.5 ha to 13.7 ha) and females (ranging from 0.6 ha to 10.9 ha). Hedgehogs foraged in different areas of their home range over consecutive nights, potentially seeking fresh foraging areas where food resources have not been depleted or seeking out new nesting areas. In their natural range, Gurnell et al. (2015) found hedgehogs in The Regent's Park in London to have a nightly home range of 1.5 ha for males and 2.2 ha for female hedgehogs. Dowding et al. (2010) estimated a nightly home range of 2.87 ha for male hedgehogs and 0.77 ha for female hedgehogs in the United Kingdom. Although I detected no significant sex-based difference in the nightly home range, individual variability in the nightly ranging behaviour of hedgehogs from night to night and between the sexes in their native range in England was reported by Morris (1988). Morris (1988) estimated the mean nightly home range to be 5.15 ha and ranged from 1.54-12.54 ha for hedgehogs inhabiting pastoral farmland in England and concluded that it is difficult to make generalizations about the nightly activity of hedgehogs due to the variability in hedgehog behaviour from night to night.

Factors such as weather and temperature likely play a part in regulating the nightly activity of hedgehogs. Hedgehogs likely spend more time in dens during bad weather such as high wind and heavy rain based on observations during my study. Only one small juvenile hedgehog was found during searching on nights with poor weather conditions (high winds and rain). In contrast, Dowding et al. (2010) found hedgehog ranging behaviour and activity were not significantly affected by rainfall. Whereas temperature, in combination with other variables such as sex and time of night, significantly affected hedgehog movement patterns (Dowding et al., 2010). Increased nightly temperature is associated with an increase in the abundance of invertebrate prey items and an increase in hedgehog activity (Dowding et al. 2010). Conversely, it is expected that low temperatures, associated with low invertebrate abundance, result in lower hedgehog nightly activity.

Home range overlap

The high degree of overlap in the home range among hedgehogs provides evidence that hedgehogs are not territorial. These findings align with results from other studies in New Zealand that have all demonstrated overlapping home ranges in hedgehogs (Campbell, 1973; Parkes, 1975; Gorton, 1997; Moss, 1999). Moss (1999) found hedgehog home ranges to overlap by 26 to 39 percent. In my study, several hedgehogs had home ranges that almost entirely overlapped (100% MCP). However, the core areas used frequently by individual hedgehogs within their home range, such as their den sites, tend to overlap less with those of other hedgehogs in comparison to the foraging areas (< 30% versus >80%). Patterns of overlapping home ranges have been observed in other small mammal populations (Wauters & Dhondt, 1992; Koskela et al., 1997; Steinmann et al., 2005). In red squirrels (*Sciurus vulgaris*), there is extensive range overlap between both sexes, however, core ranges overlap between individuals of different sexes more and dominant females defend their core range from other females (Wauters & Dhondt, 1992). Home ranges overlap in bank voles (*Clethrionomys glareolus*) but the range overlap between females decreases when they are pregnant and raising young (Koskela et al., 1997). Similar observations were also found in corn mice, with home range overlap higher between males and females (Steinmann et al., 2005). These studies conclude that a likely cause of home range overlap is the need for social contact between males and females for breeding. The home range overlap observed in hedgehogs is consistent with a promiscuous mating system where both males and females will mate with multiple individuals (Rautio et al., 2013). Both promiscuity and mixed paternity have been confirmed in hedgehogs in previous research (Jackson, 2006; Moran et al., 2009). Six of the tagged hedgehogs had home ranges that overlapped over a portion of the road (Fig. 3.8). The implication of a high degree of overlap is that common travel routes for hedgehogs, such as road edges, can be exploited to increase the chance of encounter between traps and multiple individual hedgehogs.

Core range

In my study, the core range of hedgehogs was estimated at between 0.86 ha to 3.77 ha. The core range represents the area within the home range that hedgehogs utilise most intensively and is typically much smaller in size compared to the 100% MCP (Minimum Convex Polygon) home range (Wauters et al., 2007). Hedgehogs in my study exhibited multiple hot spots of activity, which included known den and other likely but unconfirmed den sites. Hedgehogs are known to use more than one den and do not occupy the same den every night (Jones, 2021). Other small mammal species such as red squirrels (*Sciurus vulgaris*) have been shown to intensively use a core area, smaller than their total range (Wauters & Dhondt, 1992). Sugar gliders (*Petaurus breviceps*), an Australian small mammal species, used an average core home range (50% KDE) of 1.55 ha (Gracanin & Mikac, 2022). The conservation implication of hedgehogs having a core range is that it indicates the density of traps needed to result in a high chance of hedgehogs encountering traps. For example, in vulnerable shorebird breeding habitat, the density of traps should be based on the core range of a hedgehog. A similar recommendation of a trap density of one trap per hectare has been suggested by Moss (1999) based on the core range estimate of hedgehogs.

Table 3.3 Previous home range estimates for hedgehogs organised by latitude.

Location	*Latitude*	*Species*	*Habitat*	*Season*	*Sex*	*Mean home range ±SE (ha)*	*Range (ha)*	*Method*	*n*	*Citation*
New Zealand										
Northland	-35° 34'	European hedgehogs (*E. europaeus*)	Pastoral farmland, arable land, pine forest, and scrubland in a coastal duneland system.	Spring-Autumn	Both sexes Males Females	7.1 ± 1.61 8.06 ± 2.34 5.62 ± 2.13	1.8-19.2 4.1-19.2 1.8-11.3	GPS tracking, 100% MCP	10 6 4	Present study.
Auckland Region	-36° 51'	European hedgehogs (*E. europaeus*)	Coastal dunelands.	Summer	Males Females	16.7 6.7		Radio-tracking.		Jeffries, 2011.
Hawkes Bay	-39º 19’	European hedgehogs (*E. europaeus*)	Mixed forest, grassland, and scrubland.	Summer-Autumn	Males	29.3	9.4-46.9	Radio-tracking, 95% MCP	7	Berry, 1999.
Manawatu	-39º 36’	European hedgehogs (*E. europaeus*)	Pastoral farmland and pine plantation.	All seasons for 18 months	Males Females	2.5 3.6	0.8-4.8 1.0-6.5	Mark-recapture, convex polygons	4 10	Parkes, 1975.
Wellington	-41º 17’	European hedgehogs (*E. europaeus*)	Suburban area, with amenity grassland.	All seasons for 2 years.	Both sexes	18.7	5.1-25.9	100% MCP	10	Brockie, 1974.
Lake Wairarapa	-41º 12’	European hedgehogs (*E. europaeus*)	Pastoral farmland and native bush.	Spring-Autumn	Males Females	9.6 4.2	7.4-12.7 3.0-5.1	Radio-tracking, 95% MCP	3 3	Gorton, 1998.
Canterbury	-43º 36’	European hedgehogs (*E. europaeus*)	Pastoral farmland.	Summers over 2.5 years	Males Females	2.4 2.8		Mark-recapture, convex polygon	7 7	Campbell, 1973.

Mackenzie Basin	-43° 52'	European hedgehogs (*E. europaeus*)	Grassland and scrubland within a braided river floodplain.	Summer	Males	45.3 ± 5.88		GPS tracking, k-LoCoH	13	Rodriguez Recio et al., 2013.
					Females	12.7 ± 0.4			2	
				Autumn	Both sexes	23.5 ± 3.51			15	
Mackenzie Basin	-43° 52'	European hedgehogs *E. europaeus*)	Scrub, willow, and grassland near braided rivers.	Spring-summer	Males	94.0	16.6-196.9 (males)	Radio-tracking, 100% convex polygons	11	Moss, 1999.
					Females	43.6			3	
				Late summer-autumn	Males	37.9	5.6-73.6 (females)		4	
					Females	11.4			4	
Europe										
Finland	64º 54’	European hedgehogs (*E. europaeus*)	Urban area.	Spring-autumn	Males	97.9 ± 6.1	88.3-111.2	Radio-tracking, 100% MCP	4	Rautio et al., 2013.
					Females	55.2 ± 17.1	23.6-82.2		3	
Kristiansand, Southern Norway	58°2′	European hedgehogs (*E. europaeus*)	Urban area.	Late summer-autumn	Males	10.2		Radio-tracking, 100% MCP	3	Korslund et al., 2023.
					Females	9.5			3	
Denmark	56° 00’	European hedgehogs (*E. europaeus*)	Deciduous forest, arable land, and grassland.	Summer	Males	96 ± 4.9		Radio-tracking, 100% MCP	24	Riber, 2006.
					Females	26 ± 5.7			7	
Rural Ireland	53°19'	European hedgehogs (*E. europaeus*)	Pasture, scrub, woodlot, and arable land.	Spring-autumn	Males	56 ± 0.67		Radio-tracking, 100% MCP	4	Haigh, 2011.
					Females	16.5 ± 0.49			3	
West London, England	51°30′	European hedgehogs (*E. europaeus*)	Suburban area with amenity grassland, and patches of deciduous forest.	Over 3 years.	Males	32 ± 3.6	15.5–41.5	Radio-tracking, minimum area method	6	Reeve, 1982.
					Females	10 ± 0.83	5.5–12		7	

Valencia City, Spain	39º 28’	European hedgehogs (*E. europaeus*)	Suburban area with patches of pine forest, scrub, and crops.	One year, all seasons	Males	9.93		Radio-tracking, 100% MCP	14	Gago et al., 2022.
Southern Spain	37° 29’	European hedgehogs (*E. europaeus*)	Urban area.	Spring and early summer	Males Females	27.7 ± 11.1 5.5 ± 1.96	11.3-48.9 3.4-9.4	Radio-tracking, 100% MCP	3 3	Marco-Tresserres & López-Iborra, 2022.
Other hedgehog species										
Israel	31°30'	Southern white-breasted hedgehog (E. europaeus concolor)	Suburban area.	Over 3 years.	Males Females	1.56 ± 0.41 1.58 ± 0.72		Radio-tracking.	4 3	Schoenfeld & Yom-Tov, 1985.
Israel	31°30'	Long-eared hedgehog (*H. auritus aegyptius*)	Suburban area.	Over 3 years.	Males Females	4.97 ± 1.49 2.85 ± 0.57		Radio-tracking.	5 6	Schoenfeld & Yom-Tov, 1985.
Valencia City, Spain	39º 28’	Algerian hedgehog (*Atelerix algirus*)	Suburban area with patches of pine forest, scrub, and crops.	One year, all seasons	Males	7.83		Radio-tracking, 100% MCP	17	Gago et al., 2022.
Qatar, Middle East	25° 19’	Ethiopian hedgehogs (*P. aethiopicus*)	Natural desert habitat Irrigated farmland	Spring-early summer for 2 years.	Males Females Males Females	231.2 ± 9.57 150.6 ± 8.51 103.4 ± 4.94 42.0 ± 3.32	61-515 (both sexes) 9.3-249 (both sexes)	GPS tracking, 100% MCP	12 10 12 12	Abu Baker et al., 2017.

3.3.3 Nightly distance travelled

The average distance travelled per night by hedgehogs in my study was 1853 ± 268 m. Notably, the average distance travelled by female hedgehogs (2054 m ± 580 m) was higher than male hedgehogs (1632 m ± 237 m). The estimated nightly distance travelled by males is generally consistent with other reported distances in New Zealand (Gorton, 1997; Berry, 1999). However, my estimate for female hedgehogs was higher than what has been previously reported (Gorton, 1997). This finding was unexpected, as most previous studies have indicated that males tend to travel greater distances than females (Riber, 2006; Gurnell et al., 2015; Marco-Tresserres & López-Iborra, 2022). In their native range, Gurnell et al. (2015) reported that male hedgehogs, on average, moved 892 m per night and travelled as far as 2 km, while females moved an average of 821 m per night and travelled as far as 1300 m. Marco-Tresserres and López-Iborra (2022) found male hedgehogs covered twice the distance (1,077 ± 251 m) that females travelled per night (504 ± 156 m). Morris (1988) found that radio-tracked hedgehogs in England travelled on average 1000 m – 2000 m, and one male travelled up to 3.1 km in one night. Riber (2006) found the average distance travelled per night for male hedgehogs in rural Denmark to be 2042 m and 1187 m for females. The longest recorded distance by Riber (2006) was 3.2 km by a male hedgehog.

In my study, the female hedgehog with the largest home range and the highest average distance travelled was discovered nursing four hoglets in her den in early November, during late spring. Female hedgehogs may have a larger home range and travel greater distances when they are raising their young. Lactation in female hedgehogs demands a greater daily energy expenditure and a substantial time investment in foraging (Pettett et al., 2017). Marco-Tresserres and López-Iborra (2022) found that female hedgehogs in southern Spain spent significantly more time foraging than male hedgehogs and visited artificial feeders more often but did not travel further. However, the foraging behaviour of females in their study was likely affected by the presence of artificial feeders, which could explain the low average travel distance of female hedgehogs. Cassini and Föger (1995) found female hedgehogs foraged more in areas of open meadow that contained a higher density of earthworms, a prey item, compared to males. Two dietary analysis studies in New Zealand found that female hedgehogs consumed 3-4 times more native lizards compared to male hedgehogs (Jones et al., 2005; Spitzen-van der Slujis et al., 2009). It was suggested by Jones et al. (2005) that lizards may be a significant source of lipids and proteins for females with higher energy demands while raising young. In my study, there was a significant positive correlation observed between the hedgehog's weight and distance travelled per night, and females were on average heavier than males. While Marco-Tresserres & López-Iborra (2022) also reported a positive interaction between weight and distance travelled, this interaction was not statistically significant.

Two female hedgehogs in my study had home ranges in predominantly exotic pine habitat and the rest were found to roam mostly in pastoral farmland. Habitat quality also likely influences the average distances travelled by foraging female hedgehogs. The highest average distances travelled by females were those found in pine habitat. At my study site, the pine habitat had lower diversity and abundance of invertebrates compared to scrubland, sedgeland, and dune grassland habitats. Invertebrate sampling has not been undertaken in pastoral farmland at my study site for comparison. However, in New Zealand pastures hedgehogs consume large numbers of invertebrates such as grass grubs (*Costelytra zealandica*), beetles (Order Coleoptera) and porina moth (*Wiseana cervinta*) larvae (Campbell, 1973). Research into hedgehog foraging behaviour in the braided river systems of the South Island of New Zealand found that hedgehogs preferred grassland habitats where prey items were most abundant (Jones & Norbury, 2006). A combination of factors such as habitat quality and reproductive state could explain the high average distance travelled by female hedgehogs in my study.

Dispersal

In my study, one female hedgehog travelled over 4 km in one sampling night (Figure 3.6, ID 7). This is the highest distance that has ever been recorded by a European hedgehog in a single night. It is suspected that this was a dispersal event rather than a regular foraging night given the linearity of the trip. Doncaster et al. (2001) found evidence that dispersing hedgehogs preferred habitat edges, which acted as corridors. In their natural range, dispersals between populations up to 4 km apart are rare events (Doncaster et al., 2001). This hedgehog in my study weighed 572 grams during late Spring. Anecdotal evidence from Berthoud (1978) and Reeve (1994) suggests juvenile hedgehogs disperse during their first year, before winter hibernation. So, if it is a true dispersal event then it appears to have occurred after winter hibernation. The implications of this are significant as it indicates the need for a larger buffer control area for vulnerable breeding shorebirds.

3.3.4 Dens

The hedgehog dens (also referred to as nests in literature) were found at the base of vegetation varying from overgrown pasture grass, toetoe (*Austroderia spp.*), native ferns (Order Polypodiales), and gorse (*Ulex europaeus*). The dens observed during my study were similar to what has been described in previous studies in New Zealand (Parkes 1975; Moors, 1979; Moss 1999; Moss & Sanders, 2001; Jones, 2021). The hedgehogs in my study typically constructed ellipsoidal chambers in loose detritus or vegetation with a well-concealed entry hole and under the cover of another bush or tussock. As my study was carried out from spring to autumn, most of the nests observed (except one confirmed breeding den) were likely daytime nests as opposed to hibernation nests (Reeve, 1994). Dense bushes with low branches, leaf litter, and dense tussock grasses are utilized by hedgehogs for den construction (Moors, 1979; Moss, 1999; Marco-Tresserras & López-Iborra, 2023).

Three of the hedgehogs had dens relatively close to one another in the same hedgerow within open pastureland. In areas where the land is regularly disturbed, such as agricultural fields, there may be limited areas available for suitable den sites. This may explain why hedgehogs 2, 5 and 11 had dens nearby in the same hedgerow because adjacent paddocks are cultivated for maize using machinery. On arable farms in Britain, dense hedgerows and field margins were shown to be utilised intensively by hedgehogs, likely due to higher food and nest site availability (Hof & Bright, 2010; Haigh et al., 2012b).

The two male hedgehogs captured during May 2023 (autumn) had a lower average location fix success rate (FSR), around 70 percent compared to 90 percent during spring sampling. GPS tags require communication with satellites to record location fixes and do not perform as well when animals are underground (Glasby & Yarnell, 2013; Forrest et al., 2022). The lower FSR appears to be partially due to these hedgehogs returning to their dens earlier in the morning (before 6 am) than hypothesised (7 am sunrise). This could be temperature-driven as the coldest period of the night is typically before dawn. However, these hedgehogs also had periods of failed fixes through the middle of the night on multiple sampling nights. Portions of lost time in failed fixes are near their den sites, which is supported by the locations before and after the lost data. This indicates that hedgehogs are less active during the night in autumn compared to spring and may spend more time resting. Another possibility is that the hedgehogs were constructing hibernation dens. In autumn hedgehogs are preparing hibernation dens before the onset of winter (Rautio et al., 2014). Rautio et al. (2014) also noted there was a transition period during autumn in Finland before winter hibernation when hedgehogs reduced foraging, constructed new nests, and spent more time in their dens.

In Europe, the northern climate is harsh and winter mortality in hedgehogs is high (Rautio et al., 2014). Hedgehog hibernation dens must be well constructed with thick insulation materials to protect them during extended periods of cold weather (Reeve, 1994; Rautio et al., 2014). Hedgehogs were not tagged during winter in my study, so I was not able to compare winter hibernation nests in New Zealand compared to that in Europe. However, previous research provides evidence of plasticity in hedgehog behaviour and ecology in the construction of dens in response to different climate conditions (Rautio et al., 2014; Marco-Tresserras & López-Iborra, 2023). For example, hedgehog nests in Spain, at the southern limits of their range, were looser and smaller compared to those described further north in Finland (Rautio et al., 2014), and were mostly constructed from leaves and grass (Marco-Tresserras & López-Iborra, 2023). Similar observations have been made in New Zealand by Parkes (1975) and Moors (1979) about the construction of dens in a warmer climate compared to Europe.

3.3.5 Factors affecting the home range size of hedgehogs

Weight

Hedgehog weight did not show a significant correlation with either nightly home range or seasonal home range. However, previous research on hedgehogs in Europe and other small mammals has found weight to have a significant effect on home range. Marco-Tresserres & López-Iborra (2022) found a significant positive interaction between weight and the MCP100 home range. The relationship between weight and home range size was stronger for male hedgehogs than females (Marco-Tresserres & López-Iborra, 2022). Gago et al. (2023), also found a significant positive correlation between home range size and weight in European hedgehogs. The body weight of male red squirrels is positively correlated with home range size (Wauters & Dhondt, 1992). Hedgehog body weight did not have a significant influence on the home range size of Ethiopian hedgehogs (*Paraechinus aethiopicus*) (Abu Baker et al., 2017).

Sex

The sex of the hedgehog did not have a significant effect on the home range size in my study. This result contrasts with previous New Zealand studies that have found male hedgehogs do have a larger home range and travel further than females (Moss, 1999; Jones & Norbury, 2006; Shanahan et al., 2007; Rodriguez Recio et al., 2013). Rodriguez Recio et al. (2013) tracked 27 hedgehogs in the Mackenzie Basin, South Island, New Zealand, and found that the home range of male hedgehogs in summer was nearly four times the size of the female hedgehogs' home range (Rodriguez Recio et al., 2013). Moss (1999) also found the average home range for male hedgehogs in the dryland habitat of the central South Island of New Zealand to be significantly larger than that of female hedgehogs. The effects of habitat and a larger sample size could explain why the studies by Moss (1999) and Rodriguez Recio et al. (2013) revealed significant sex differences in home range size. It is suspected that achieving a larger sample size in my study may have revealed a significant difference between the home range size of male and female hedgehogs. However, Moss (1999) found a significant difference between males and females in the autumn home range size with a smaller sample size. It is also noted that there was a male-biased sex ratio (13 males and 2 females) in the study by Rodriguez Recio et al. (2013).

In Europe, Rautio et al. (2013) found that male European hedgehogs in Finland had a larger home range than females for all seasons except pre-hibernation when females had a larger home range. Male hedgehogs also had a larger home range than females in rural Denmark (Riber, 2006), rural Ireland (Haigh, 2011), and southern Spain (Marco-Tresserres & López-Iborra, 2022). Male Ethiopian hedgehogs (*Paraechinus aethiopicus*) have larger home ranges than females and roam greater distances (Abu Baker et al., 2017). The sex differences in home range size in hedgehogs are likely a reflection of their promiscuous reproductive strategy where males roam large distances in search of females (Riber, 2006; Abu Baker et al., 2017; Marco-Tresserres & López-Iborra, 2022). Hedgehog populations are declining in Europe (Taucher et al., 2020), so a possible explanation for the sex differences in home ranges could be that males have to travel further during the breeding season to find female hedgehogs for mating.

Habitat quality

The quality of foraging habitat has been shown to affect the home range sizes of small mammals (Wauters & Dhondt, 1992; Abu Baker et al., 2017). For example, in red squirrels, home range size of females was inversely correlated with food abundance (Wauters & Dhondt, 1992). Abu Baker et al. (2017) studied the effects of land use and sex on the home range size and movement of Ethiopian hedgehogs (*Paraechinus aethiopicus*) in the Middle East. Ethiopian hedgehogs inhabiting resource-poor desert environments had significantly larger home ranges and travelled longer distances compared to those inhabiting resource-rich irrigated farmland. As food availability increases, the home range size is expected to decrease and in heterogeneous environments, the spatial distribution of small mammals will vary with an uneven distribution of resources.

Within their natural home range of England, the spatial distribution of hedgehogs is influenced by the distribution of predators and food resources (Doncaster et al., 2008). In New Zealand, due to the absence of natural predators, hedgehog spatial distribution is based on the availability of food and nesting resources alone (Jones & Norbury, 2006; Dowding et al., 2010). The quality of the foraging habitat will affect the spatial distribution and home range size of hedgehogs (Micol et al. 1994; Cassini & Föger, 1995; Jones & Norbury, 2006). The presence of suitable nesting sites is also linked to hedgehog spatial distribution (Shanahan et al., 2007). As hedgehogs have a promiscuous mating system, the home range of female hedgehogs is most influenced by the availability of food and shelter availability, whereas the home range of male hedgehogs is most influenced by female distribution (Rautio et al., 2013; Abu Baker et al., 2017).

The quality of foraging habitat for hedgehogs can be estimated by invertebrate sampling to estimate food availability (Campbell, 1973; Jones & Norbury, 2006). Jones and Norbury (2006) found hedgehogs preferred foraging in scrub habitat which had the highest invertebrate abundance compared to other habitats. Whereas Cassini and Föger (1995) found that the relative density of hedgehogs in an open meadow habitat increased with the relative abundance of earthworms. Shanahan et al. (2007) found hedgehogs tended to remain in dense grassland, likely because of its suitability for nesting sites. Invertebrate sampling was carried out at my study site in May 2022 using pitfall traps in four habitat types, dune grassland, sedgeland, pine forest, and scrubland (W. Ji, personal communication, March 1, 2024). Scrubland habitat had the highest diversity of invertebrates and the highest Shannon index, indicating better evenness of species abundance. The community structure differed between the habitat types, but a similar number of orders and families were found in dune grassland, pine forest, and sedgeland. The dune grassland had the highest abundance of invertebrates but was heavily dominated by one species (family Tylidae in order Isopoda). Terrestrial crustaceans (order Isopoda) have not been shown to be an important prey item of hedgehogs in relation to their abundance in dunelands (Brockie,1959; Reeves, 1994; Jeffries, 2011). Further investigating the food abundance in pastoral farmland near my study site would be a useful comparison to help explain the apparent habitat preferences of hedgehogs.

Latitude

Rautio et al. (2013) found that European hedgehogs inhabiting northern latitudes have larger home ranges than those in more southern latitudes. In the northernmost reach of the European hedgehogs' home range, there are longer winters, and hedgehogs spend more time in hibernation (Rautio et al., 2013). Seasonality correlates strongly with latitude, with southern Europe and northern New Zealand experiencing milder temperatures in winter and hotter summers. This pattern has been observed in New Zealand where hedgehogs in the South Island have a larger home range and spend more time in hibernation than those in the North Island (Moss, 1999; Rodriguez Recio et al., 2013; Foster et al., 2020). New Zealand is within the Southern Hemisphere temperate zone and spans 1,600 kilometres through latitudes 34 to 47 degrees south (Macara, 2018). Whereas the United Kingdom spans a length of 1000 kilometres between 49 and 59 degrees north. The effects of climate and environmental conditions on hedgehog ecology support the need for local home range estimates when managing invasive hedgehog populations. Winters are mild in most of New Zealand compared to Europe. This means that hedgehogs have a shorter hibernation period, lower winter mortality, and a longer breeding season (Brockie, 1974; Jones, 2021).

It is important to note that the effects of sex, weight, habitat quality, and latitude are all likely to covary and influence the observed patterns. For example, a warmer climate is linked to higher food availability for hedgehogs (Dowding et al., 2010; Jones, 2021). The real influence of the environment on hedgehog spatial ecology will be multifactorial and this should be considered when studying the home range of hedgehogs.

3.3.6 Constraints and limitations

Based on previous literature, there is evidence that seasonality has a strong effect on the home range and activity of hedgehogs (Fig. 4.2) (Brockie, 1974; Parkes, 1975; Moss, 1999; Rautio et al., 2013). The effects of seasonality are also likely to correlate strongly with the effects of latitude. Due to the impacts of multiple flooding events at the study site during January and February 2023, no hedgehogs were captured during the summer season. Large areas of the site remained flooded with water for weeks, as the water table was so high, and there was no natural drainage. As a result, the effects of seasonality on the home range could not be compared across different seasons. It is suspected that the flooding events resulted in a high mortality rate of hedgehogs due to the amount of habitat submerged in water, likely drowning dens. The occurrence of hedgehogs during nightly spotlighting was too low to estimate the population density through mark-recapture accurately.

Future hedgehog research should focus on gathering more information on the ecology of hedgehogs in vulnerable habitats, such as duneland systems. Further investigation into the effects of seasonality on hedgehog spatial ecology would be beneficial in estimating how the home range size changes with the season, to further optimise control measures. Tracking hedgehogs through the winter period could also provide insight into the nature of their hibernation in a warmer climate. Further study with larger sample sizes may reveal more significant sex differences in the home range size of hedgehogs. Continued research on hedgehogs in the northern climate of New Zealand could provide further guidance on best practice control and assist in better understanding the potential impacts of hedgehogs in duneland ecosystems.

Figure 3.12 Examples of areas within the study site that had been flooded.

3.3.7 Conclusions

I have advanced the understanding of hedgehog spatial ecology by providing home range estimates and average nightly distances travelled in a northern duneland ecosystem, as well as expanding current knowledge of the movement patterns, habitat preferences, and spatial distribution of hedgehogs. In summary, hedgehogs occupy a small core area of their home range intensively while covering its entirety over several foraging nights. Home ranges overlap significantly between individuals of either sex, but core ranges are more independent. My findings highlight the need for local home range estimates in vulnerable ecosystems due to variability and plasticity in hedgehog behaviour based on habitat and climate factors. Trapping regimes should consider home range estimates, average nightly distances travelled, recorded dispersal distances, and habitat preferences when planning hedgehog control programs.

Chapter 4: Hedgehog control

4.1 Introduction

4.1.1 Invasive species control

Invasive species management is a complex and global challenge that requires significant financial investment, effort, innovation, and collaboration (Green & Grosholz, 2021). Population control is the most common strategy used to manage the ecological and economic impacts of invasive species (Clout, 1999; Goldson et al., 2015; Carter et al., 2016; Green & Grosholz, 2021). The reported economic damage and management costs from biological invasions in New Zealand have been estimated at approximately 97 billion dollars over the last 50 years (Bodey et al., 2022). Invasive weeds and pest animals such as possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*), rats (*Rattus rattus*), and fire ants (*Solenopsis invicta*) cost New Zealand around 170 million per year (Bodey et al., 2022). Invasive species control is essential in the ecological restoration of native habitats and the protection of biodiversity in New Zealand (Pech & Maitland, 2016). The removal of mammalian predators such as stoats, weasels, ferrets, rats, and possums is a necessary conservation focus to facilitate the recovery of native species and ecosystem function (Clout, 1999; Goldson et al., 2015; Carter et al., 2016; Glen et al., 2019). Knowledge of the spatial ecology of an invasive species is crucial to implementing effective control measures (Smith et al., 2015; Rodríguez-Recio et al., 2022). Research and monitoring are essential to understanding the impacts of invasive species, as well as the effectiveness of pest control measures (Pech & Maitland, 2016). Removing invasive predators is costly and time-consuming (Glen et al., 2015; Goldson et al., 2015; Bodey et al., 2022), especially in remote environments (Russell et al., 2015). Understanding the effectiveness of control measures is a crucial step in managing the impacts of an invasive species (Goldson et al., 2015; Russell et al., 2015). Furthermore, control methods must be cost-effective; hence, developing low-cost methods of removing invasive species is a key component of our ability to deliver practical pest management at a scale large enough to achieve New Zealand's Predator-Free vision (Goldson et al., 2015; Russel et al., 2015).

4.1.2 Factors that can affect the effectiveness of control measures

Control of invasive mammalian predators in New Zealand generally involves a combination of vertebrate toxic agents such as sodium fluoroacetate (1080), humane kill-traps, and barriers (predator-proof fences) to exclude pest animals from protected areas (Warburton et al., 2008; Goldson et al., 2015; Russel et al., 2015). Several factors, such as trap design and spacing of control devices can influence the effectiveness of control measures for certain invasive species (Smith et al., 2015; Jones et al., 2021). For example, Jones et al. (2021), found that the standard wire baffle size on DOC200 traps excluded large hedgehogs from entering traps. Furthermore, the spacing and density of traps in the landscape can affect the probability that an animal encounters that trap in their daily activities (Smith et al., 2015). The higher the density of traps in an area, the more likely the animal is to encounter it; however, this is not always practical in terms of costs and time (Goldson et al., 2015; Russel et al., 2015). Trap placement density also assumes that invasive animals use all habitats in their home range equally, which is not always the case. For example, Glen et al. (2019) found detections of stoats, rats, and possums in tracking tunnels highest in bush habitats compared to edge or pasture habitats. Whereas feral cat detections were higher in the edge habitat compared to the bush or pasture habitats (Glen et al., 2019). Trap placement and other invasive species control methods make assumptions about animal movement, bait attractiveness, and habitat use based primarily on current knowledge of the target species. In many cases, detailed knowledge only exists for invasive species in their native range rather than the invasion area, so a key assumption is that this behaviour and ecology remain largely unchanged. However, successful invasive species, by definition, often have broad ecological requirements and plasticity in their behaviours (Parker et al., 2013). This is where knowledge of the spatial ecology of invasive animals is crucial in implementing efficient control measures (Smith et al., 2015; Rodríguez-Recio et al., 2022).

Seasonality and demographic dynamics can also affect the effectiveness of control measures of invasive species (Jackson, 2006; Wells et al., 2016). It is well-known that seasonality affects the activity and reproductive behaviour of many small mammals (Everts et al., 2004; Caravaggi et al., 2018; Jones, 2021), which in turn can affect the effectiveness of control measures during different times of year (Moss, 1999; Wells et al., 2016). Demographic dynamics such as age class and how it affects fecundity can also determine the effectiveness of control measures when not all age classes are being targeted (Jackson, 2006; Wells et al., 2016). For example, seasonally timed efforts of removal (after the breeding season) and targeting individuals with the highest reproductive value in invasive rabbits (*Oryctolagus cuniculus*) have the greatest impact on population size (Wells et al., 2016). In species with high reproductive rates and fluctuations in population numbers, control methods during the periods when they are at their lowest may be an efficient control option.

4.1.3 Hedgehog control in New Zealand

The Department of Conservation (DOC) is the government agency responsible for the protection of Aotearoa New Zealand's natural and historical heritage (Towns et al., 2019). DOC has managed to successfully eradicate hedgehogs as part of wider mammalian predator eradication programs on island and mainland sanctuaries targeting stoats (*Mustela erminea*), cats (*Felis catus*), hedgehogs (*Erinaceus europaeus*), rabbits (*Oryctolagus cuniculus*), mice (*Mus musculus*) and three species of rat (*Rattus norvegicus, R. rattus* and *R. exulans*). For example, Rangitoto and Motutapu Islands and Zealandia ecosanctuary have successfully eradicated all mammalian predators (Burns et al., 2011; Griffiths et al., 2015). Hedgehogs have been trapped in high numbers in conservation areas across the country but are not specifically targeted by many trapping programs (Spitzen–van der Sluijs et al., 2009; Glen et al., 2019). For example, during a 3-year period, over 1300 hedgehogs were trapped as by-catch in Macraes Flat in Otago, New Zealand (Spitzen – van der Sluijs et al., 2009). The total yearly catch remained relatively constant over the 3 years, around 400-450 hedgehogs (Spitzen–van der Sluijs et al., 2009). Predator control in a 6000-ha pastoral landscape in Hawkes Bay resulted in the removal of 748 hedgehogs as bycatch over 4 years (Glen et al., 2019). This trapping program resulted in lower detection of both cats and hedgehogs in the treatment sites (that had undergone trapping) compared to the non-treatment sites and had apparent benefits for some native species such as cockroaches and skinks (Glen et al., 2019).

Although hedgehogs often represent a large proportion of trap catches (Glen et al., 2019) and can be controlled effectively (Griffiths et al., 2015), there are still knowledge gaps in the specific impacts of hedgehogs on ecosystems and limited information on the ecology of introduced hedgehogs in New Zealand. However, experts do hypothesise that grassland and duneland habitats, such as Macraes Flat in Otago and Tara iti ecosanctuary, are refuges for reptiles, ground-nesting birds, and invertebrates, and are particularly vulnerable to invasive hedgehogs (Sanders & Maloney, 2002; Spitzen – van der Sluijs et al., 2009; Jones & Norbury, 2010; Jones et al., 2013).

4.1.4 Knowledge gaps and rationale

With many trapping programs treating hedgehogs as non-target animals (Russell et al., 2015; Glen et al., 2019) there is a lack of quantitative data on the impacts of hedgehogs and how to effectively control populations. Although hedgehogs make up a large proportion of Tara Iti's total pest catch, they have previously been treated as bycatch rather than a target species. The current trapping program at Tara Iti has resulted in target species, such as stoats, possums, and rats, now being detected at low numbers (A. Flavell-Johnson, personal communication, September 2, 2022). As New Zealand dotterel nests are still being predated, with hedgehogs being a suspect, there has been interest by conservation managers in better controlling the hedgehog population. The main aim of this chapter is to inform better control of invasive hedgehogs in general based on analysis of past trapping data and provide specific recommendations to improve the trapping regime at my study site. To inform best practice control, it is essential to understand how factors such as seasonality, trap type, density of control devices, and habitat types might affect the effectiveness of hedgehog control. I also aim to help fill knowledge gaps in the general ecology, behaviour, and home range variability of hedgehogs in a diverse duneland ecosystem (pasture, wetlands, scrub, and dune grassland).

4.1.5 Objectives

In this chapter I address three key objectives (1) to provide evidence of seasonal trends in hedgehog activity to inform optimal timing of control efforts, (2) to provide support for pest control operations by providing evidence of habitat preferences, effective trap types and trap density for control of hedgehogs, and (3) help fill knowledge gaps in the general ecology, behaviour, and home range variability of hedgehogs in a diverse duneland ecosystem.

4.2 Results

4.2.1 Trapping data

Tara Iti trapped a total of 1,364 hedgehogs from 2016-2023 and hedgehogs made up over 50% of Tara Iti's total pest catch. Until 2023, Tara Iti was consistently trapping over 200 hedgehogs per year, with only a mild decreasing trend. There is a strong seasonal trend in the hedgehog catch at Tara Iti with peaks in January-February and April-May, and lows in July (Figure 4.2). Over 50 hedgehogs were trapped in one month during January 2018, May 2020, and February 2022. From July 2022 to June 2023, Tara Iti trapped an unusually low number of hedgehogs, only 40% of the 2021-2022 catch (Figure 4.1). There is an absence of a seasonal trend in the 2023 trap catch data, with no peak in January and only a mild peak in May (Figure 4.2). The decline in hedgehog trap catches during 2023 coincided with multiple severe weather events that hit the Northland of New Zealand during January and February 2023.

Forest margins and roadsides have the highest hedgehog catch at Tara Iti (Figure 4.3). The coastal margin and golf course have the lowest hedgehog trap catch (Figure 4.3). Individual DOC250 traps have caught as many as 13 hedgehogs over the last three years. Many of the high-catch DOC250 traps are located near a road. The DOC250 traps along the roadside have a high hedgehog catch compared to the DOC200 traps in similar locations. The golf course traps are mostly DOC200 traps and have caught very few hedgehogs.

There is more than one trap in all the study hedgehogs' home ranges except for Hedgehogs 4 and 5 which overlap with no traps (Figure 4.4). There are gaps in the trap network where hedgehogs may not encounter any kill traps based on my home range estimates from Chapter 3. During May 2023 a marked hedgehog from November 2022 was found killed in a DOC250 trap on Rako Drive. This hedgehog was likely Hedgehog 1 or Hedgehog 9.

Tara Iti has a higher hedgehog trap catch compared to Black Swamp. From November 2020 to June 2023, 154 hedgehogs were trapped at Black Swamp, compared to 486 at Tara Iti (Figure 4.5). There is a mild seasonal trend in the Black Swamp trap catch data, with the highest catch during January and February. Given the Black Swamp project area is over twice the size of Tara Iti and has more active traps (excluding the marginal strip project area), it would be expected to have a higher hedgehog catch than Tara Iti.

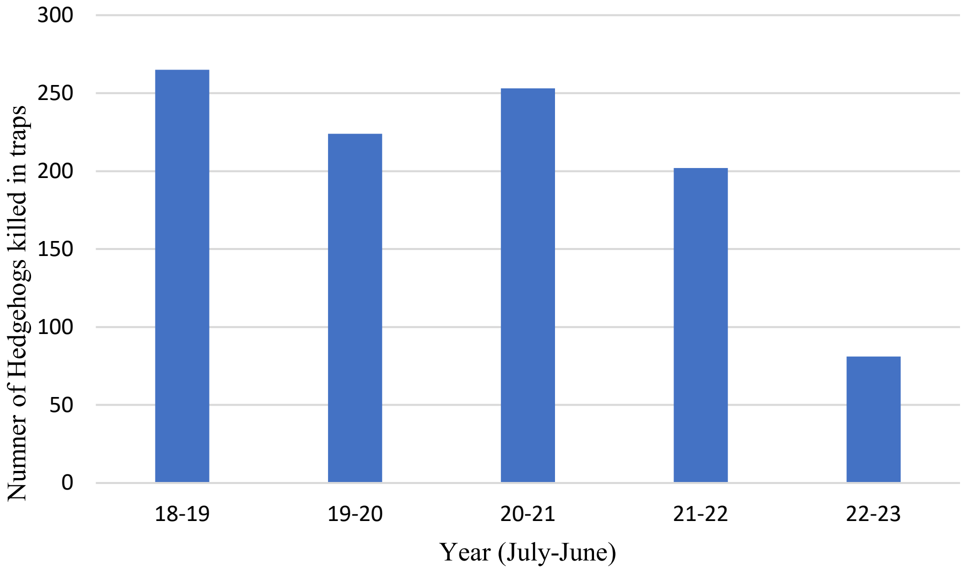


Figure 4.1 The total number of hedgehogs trapped over the last 5 years at Tara Iti. There is an unusually low 2022-2023 hedgehog catch. The total number of traps maintained is similar throughout the 5 years.

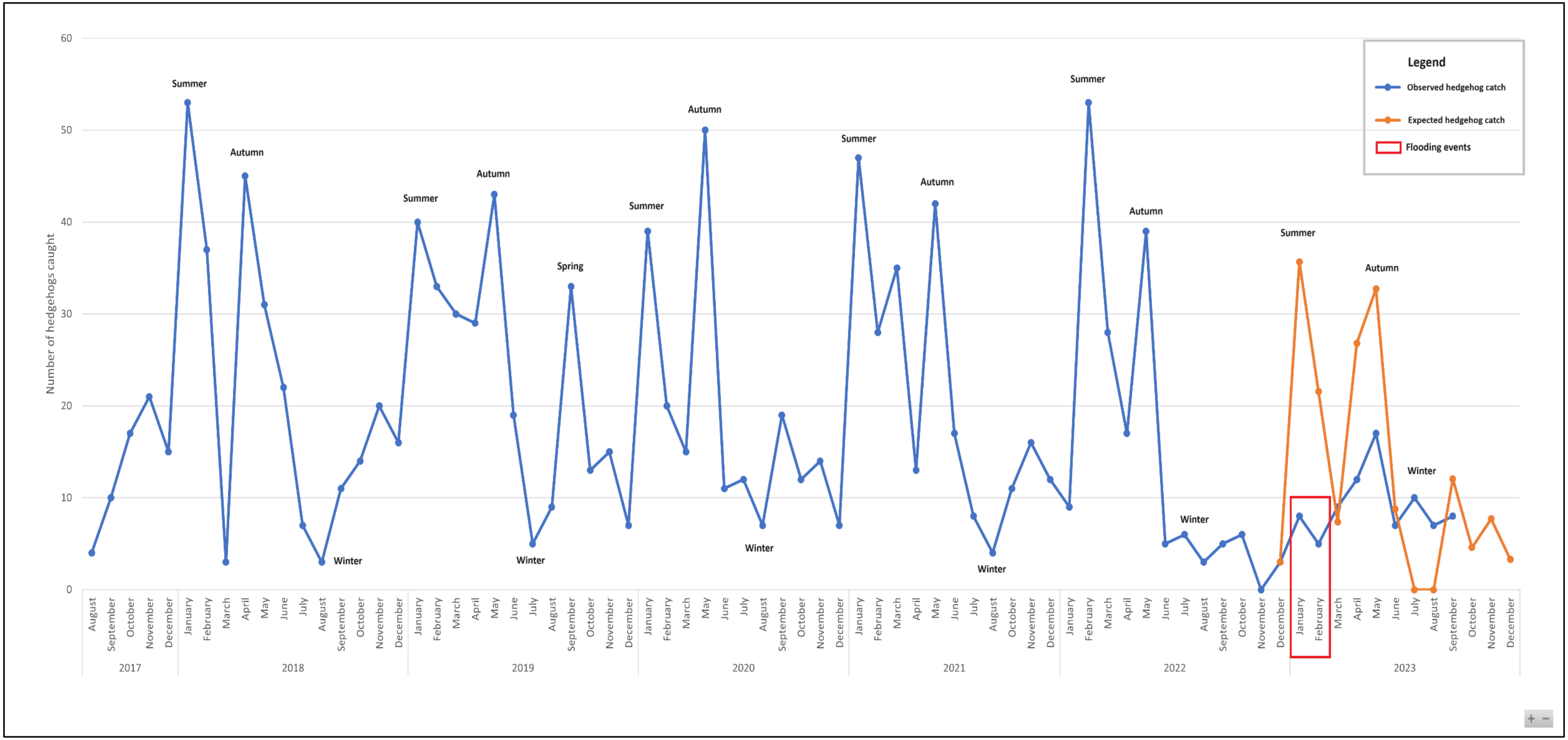
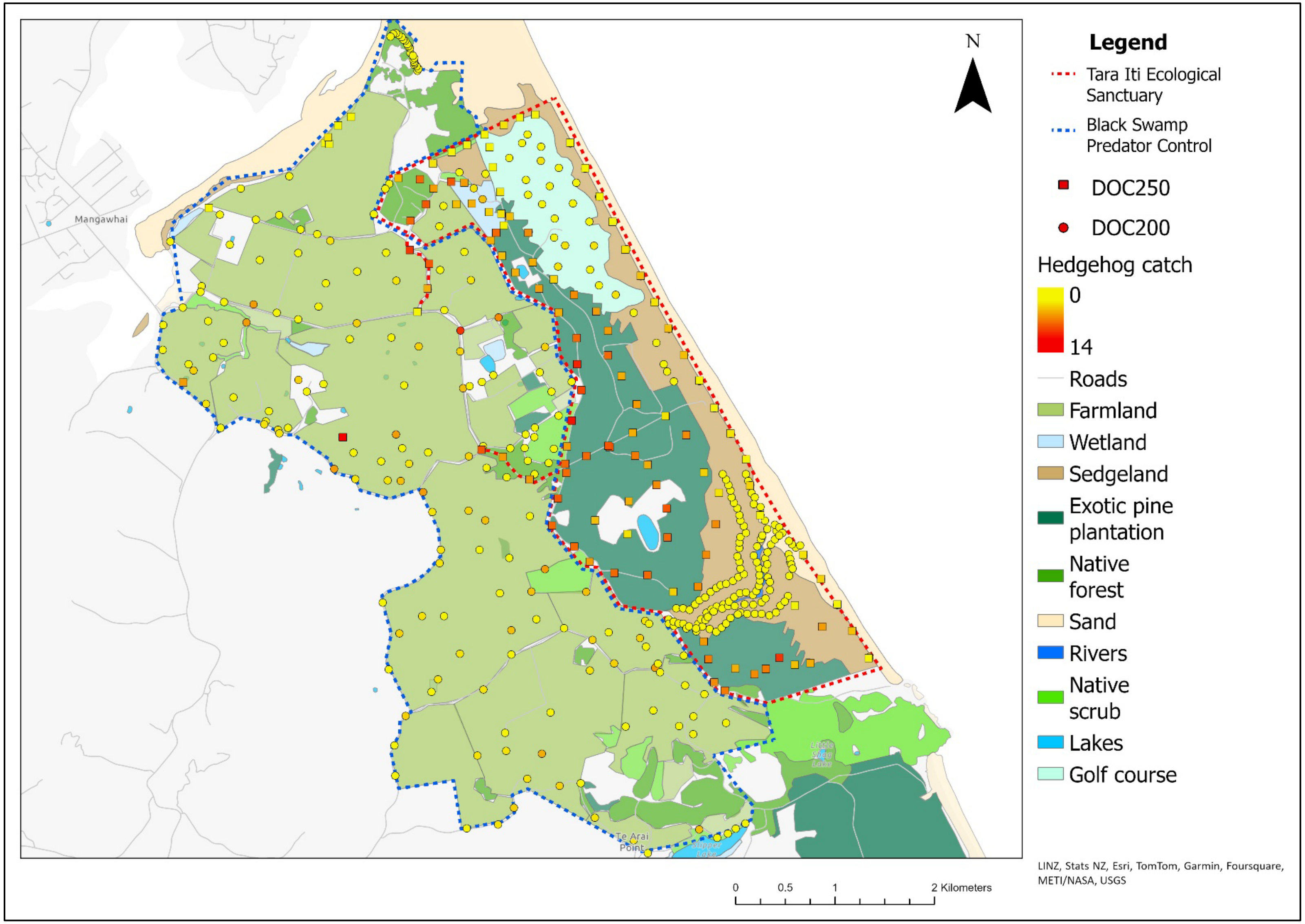


Figure 4.2 The seasonal trend in hedgehog trap catch data from Tara Iti from August 2017 to December 2023. The blue line is the observed hedgehog catch and the orange line is the expected (forecasted) hedgehog catch based on previous years data. The observed hedgehog catch during 2023 was significantly lower than expected due to severe flooding events in Northland, New Zealand (indicated by red box).



LINZ, Stats NZ, Esri, TomTom, Garmin, Foursquare, METI/NASA, USGS

Figure 4.3 Map of trap catch data from 2020 to 2023 with habitat layers.

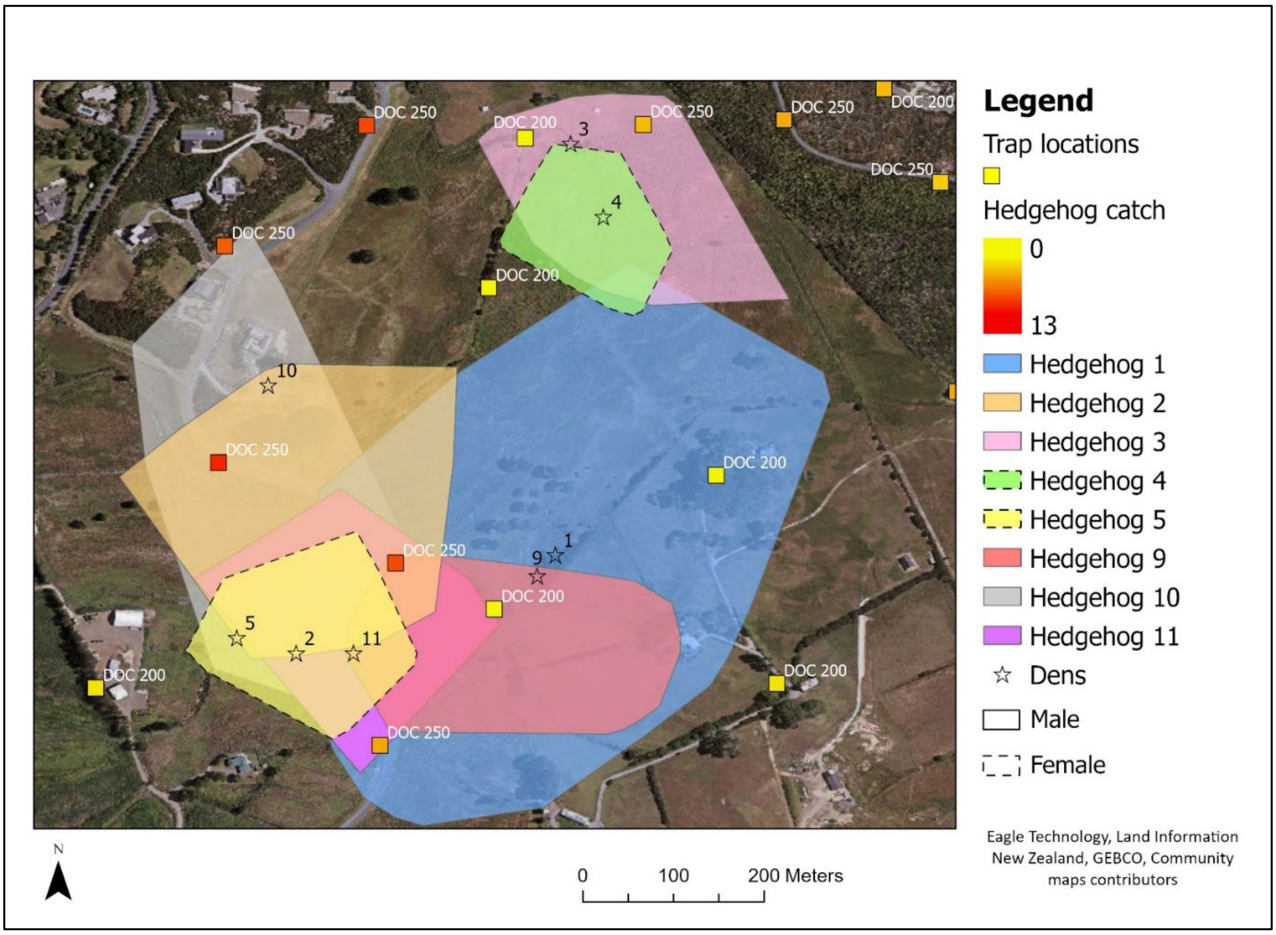


Figure 4.4 Map of the traps located within the seasonal home range of the study hedgehogs.

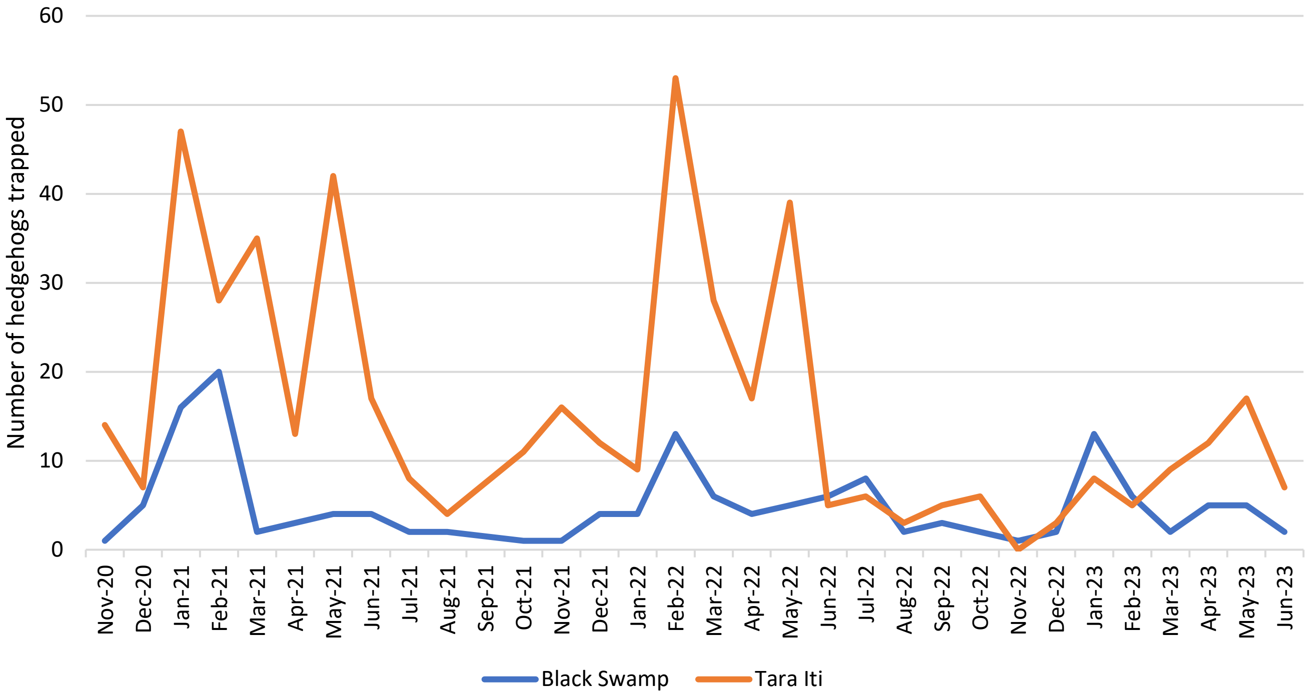


Figure 4.5 The number of hedgehogs trapped by month at Tara Iti (orange) and the Black Swamp control area (blue) between 2020 to 2023. The hedgehog catch at Black Swamp is significantly lower than Tara Iti despite a higher number of control devices (listed in Table 2.2). The DOC-managed Marginal Strip hedgehog catch is excluded from this figure.

4.2.2 Trail camera data

I collected hedgehog and other pest presence data over 316 camera nights during November 2022, March, April, and May 2023. There were 133 pests recorded, with the highest recorded species being cats (n=62) and hedgehogs (n=47). The highest number of pests (n=53) was recorded during April 2023. The highest ratio of hedgehog recordings to camera nights, reaching 0.38, occurred in November 2022, followed by April 2023 (0.25). The lowest ratio (0.03) of hedgehog recordings to camera nights was during March 2023; this was not long after the study site experienced severe flooding. May 2023 also had a low ratio of hedgehog recordings to camera nights (0.06).

The camera data exhibited a similar pattern to the trap catch data in that the highest recordings of hedgehogs occurred on trail cameras near roads (Figure 2.5). Specifically, the three trail cameras located on the Rako Drive roadside recorded the highest number of hedgehogs, and this is also where over half of the hedgehogs were live captured. There were hedgehogs trapped close to cameras that recorded hedgehogs during March-May sampling. It is possible that the number of recordings on cameras positioned on the Rako Drive roadside was inflated due to individual hedgehogs revisiting on consecutive nights once they learned that the cameras were baited with food. Hedgehogs were recorded every hour between 6:00 p.m. and 5:00 a.m. There was a relatively even distribution in the timing of visits to cameras by hedgehogs, with visits during all hours of the night. The lowest number of hedgehog recordings was at 2:00 a.m.

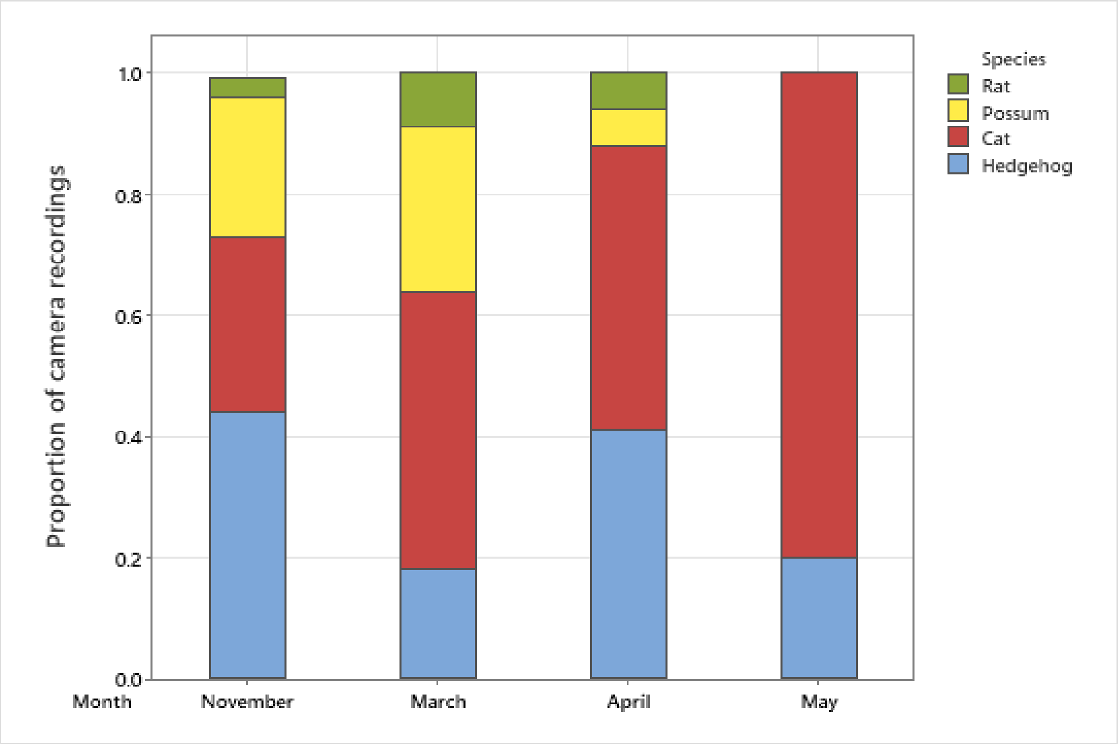


Figure 4.6 The proportion of camera recordings by species during sampling in November 2022 and March to May 2023.

4.3 Discussion

4.3.1 Seasonality and timing of current pest control efforts

Overall, the population of hedgehogs at Tara Iti appears to be large and stable despite the ongoing intensive trapping regime. Although unusually low numbers of hedgehogs were trapped in 2023 following the extreme flooding events, the number of hedgehogs trapped has now rebounded. I found a strong seasonal trend in the hedgehog trapping data, with peaks in January, February (austral summer), and May (austral autumn) and a low in July (austral winter). Hendra (1999) observed a similar seasonal pattern of abundance in hedgehogs over three years of trapping data from Trounson Kauri Park in Northland, with peaks in late summer and autumn and lows in winter. These findings support the recommendation that the level of trapping effort should vary with the season so as to correlate with these peaks.

Seasonality is known to affect the population dynamics and movements of small mammals (Briese, 1974; O'Connell, 1989; Merritt et al., 2001). Small mammal populations often vary with both seasonal and yearly variations in climate and habitat conditions (O'Connell, 1989). These species use different strategies to avoid cold winter temperatures, such as changing from nocturnal to diurnal behaviour (Guiden & Orrock, 2020) and hibernation and torpor (Jones, 2021). Plasticity in the timing of activity is a means of conserving energy during periods where metabolic costs are high, such as winter (Guiden & Orrock, 2020). In terms of invasive species management, the seasonal variations in populations of small mammals can be used to help guide more efficient trapping programs (King, 1994; Moss, 1999; Foster, 2023). For example, introduced stoats (*Mustela erminea*) also have a predictable variation in numbers trapped over the year. Generally, the capture rate is low in winter and spring but increases suddenly in summer and then declines slowly over late summer and autumn (King, 1994). The abundance of stoats is closely related to the availability of their main prey, such as rabbits, which also follow seasonal patterns (King, 1994). Foster (2023) found seasonal changes in the spatial ecology of pest species such as introduced brushtail possums (*Trichosurus vulpecula*) and feral cats (*Felis catus*) in alpine zones of the South Island of New Zealand. Knowledge of the changes in the seasonal distribution of these pest species allows for spatially and temporally optimised control throughout the year (Foster, 2023).

The clear seasonal trend in the capture of hedgehogs as part of pest control at Tara Iti provides an opportunity to refine current pest control measures for hedgehogs. The peak hedgehog catch at Tara Iti in January and February likely coincides with juvenile dispersal (Moss, 1999; Jackson, 2006). The second peak in May could be an increase in foraging activity pre-hibernation or the dispersal of late litter or second litters of juvenile hedgehogs. Seasonality affects the activity and behaviour of hedgehogs (Moss, 1999; Jones, 2021). Hedgehog activity increases during both the breeding season and pre-hibernation (Moss, 1999). Previous studies have shown hedgehog activity and home range sizes to decrease in autumn in a pre-hibernation "transition phase" (Rautio et al., 2014). This indicates that the second peak in hedgehog catch during late autumn is most likely the dispersal of late litters or second litters of juvenile hedgehogs. Most introduced female hedgehogs attempt second litters in Scotland (Jackson, 2006), but second litters have not been confirmed in New Zealand (Jones, 2021).

Males actively search for female hedgehogs for mating as soon as they leave hibernation and most adult female hedgehogs become pregnant within two weeks of emerging from hibernation (Jackson, 1999; Haigh, 2012). Hedgehogs increase foraging activity to increase fat reserves to prepare for hibernation (Jones, 2021). They are relatively inactive over winter when they are hibernating (Moss, 1999; Jones, 2021). Those periods of higher activity are likely to coincide with greater prey abundance and/or more extensive foraging ranges; both predictions have implications for trap placement.

Moss (1999) also recommended that trapping should consider seasonal changes in hedgehog behaviour and activity. Trapping efforts could be reduced over winter hibernation while hedgehog activity is low. However, hedgehogs do leave hibernation temporarily for short periods (Walhovd, 1979; Dmi'el & Schwarz, 1984; South et al., 2020), as is supported by Tara Iti's trapping data. Low numbers of hedgehogs are still trapped over the winter months. Trapping should be intensified before the bird breeding season (typically August-September; Gorton, 1997; Moss, 1999). This provides maximum protection to ground-nesting birds and is timed with increasing activity of hedgehogs post-hibernation and when they are actively searching for mates (Moss, 1999; Jackson, 2006).

4.3.2 Demographic dynamics

Many researchers (Brockie, 1958; Campbell, 1973; Parkes, 1975; Gorton, 1997; Moss, 1999) have suggested that if hedgehogs are to be specifically targeted, trapping would best be undertaken primarily in late summer-autumn and secondarily in early spring-summer. Juvenile hedgehogs likely contribute towards a large proportion of hedgehog catch in late summer-autumn as this is when dispersal is occurring (Moss, 1999; Jackson, 2006). Jackson (2006) found that the average productivity per year of adult female hedgehogs (4.04 young), was nearly five times greater than the average productivity of sub-adult females (0.82 young). Therefore, to control a population of hedgehogs, it will be more effective to target adult females rather than juveniles (Jackson, 2006). This could be achieved by targeting female hedgehogs as they come out of hibernation (in September and early October) and before litters of young are produced. This finding is supported by Wells et al. (2016) who studied population control of invasive rabbits in Australia. They found there will be greater reductions in the population size of invasive rabbits if individuals with the highest reproductive values are selected for removal (Wells et al., 2016).

Previous research suggests that the opportunity exists to target specific age or gender groups of hedgehogs (Parkes & Brockie, 1977; Moss, 1999). Male hedgehogs are known to leave hibernation up to six weeks before females, therefore trapping in late August to early September would likely target predominantly male hedgehogs (Parkes & Brockie, 1977; Moss, 1999). Conversely, Jackson (2006) suggests that reducing the male density of hedgehogs would have little impact on pregnancy rates and females are promiscuous and thus have mating opportunities with multiple males. Adult female hedgehogs enter hibernation later than males, which provides an opportunity to target females only during late Autumn (Moss, 1999). A similar difference in the onset of hibernation is observed for juvenile hedgehogs. Juveniles must reach a weight of at least 300g to survive winter hibernation (Brockie, 1974). Hence, juvenile hedgehogs must achieve maximum weight gain before going into hibernation and so enter hibernation later than adult hedgehogs (Moss, 1999). Trapping late in the season would also target this cohort.

4.3.3 Trap type

DOC250 traps captured the majority of hedgehogs at Tara Iti, with DOC200 traps having a low hedgehog catch in comparison. My findings provide evidence that DOC250 traps are more effective at catching hedgehogs than DOC200 traps. Tara Iti is controlling a higher number of hedgehogs compared to Black Swamp, despite having a smaller control area and a lower number of traps (excluding the marginal strip). The Black Swamp uses predominantly DOC200 traps which do not appear to be controlling hedgehogs well in the buffer area surrounding Tara Iti. This could partly explain why there is such a high hedgehog catch along the boundary of Tara Iti, as most adult hedgehogs are dispersing through the Black Swamp Predator Control Zone without being caught in traps. This finding is supported by research undertaken by Manaaki Whenua (Landcare Research New Zealand). Manaaki Whenua performed trap aperture trials with adult European hedgehogs to test their ability to fit through apertures in the mesh as used in standard trap sets (Jones et al., 2021). They found no hedgehogs could fit through the smallest aperture trialled, 60 x 60 mm, equivalent to that used on standard DOC200 and 150 trap sets (Jones et al., 2021). All hedgehogs, apart from one large male (weighing 1.53 kg), were able to fit through the 80 × 80 mm apertures, equivalent to a DOC250 trap set (Jones et al., 2021; see Figure 6.2). It is important to note that they did not do trials with juvenile hedgehogs weighing less than 400g and used only large adult hedgehogs. Small adult hedgehogs and juveniles in the wild appear to fit through the mesh apertures of standard DOC200 trap sets.

On Rangitoto and Motutapu Islands in the Hauraki Gulf hedgehogs were eradicated using a combination of Mk VI Fenn^{TM} and DOC200 or DOC150 traps with enlarged baffle openings from 60 mm by 60 mm to 90 mm (wide) by 110 mm (high), hunting with spotlights, and indicator dogs (Griffiths et al., 2015). Enlarging the baffle holes on a standard DOC200 has risks of catching non-target animals, such as feral cats, inhumanely if employed on the mainland. This method would also not be acceptable in areas with kiwi (*Apteryx mantelli*) or weka (*Gallirallus australis*) due to a high risk of bycatch. Fenn traps are not NAWAC tested for hedgehogs and cannot be guaranteed to meet the standards to be designated as a humane kill trap. An application of the rodenticide brodifacoum preceded trapping efforts on Rangitoto and Motutapu (Griffiths et al., 2015). Although hedgehogs are susceptible to brodifacoum poisoning, they can however tolerate high, sublethal levels (Alterio, 1996). For example, brodifacoum did not kill any of the 37 radio-tagged hedgehogs at Boundary Stream over four months, despite it being present in bait stations throughout the whole period (Berry, 1999). A variety of methods were employed to complete the eradication from Rangitoto and Motutapu Islands such as intensification of the trapping grip, repositioning of traps, and using different trap types and lures (Griffiths et al., 2015).

4.3.4 Trap density

Many trapping programs targeting invasive mammalian predators employ a trapping grid design based on home range and population density estimates (Smith et al., 2015; van Heezik et al., 2023). The current spacing of control devices at Tara Iti (excluding the marginal strip where trapping is intensified) that can kill hedgehogs is around 200 m apart. However, there are gaps in the trap network (Fig. 4.4) where hedgehogs may not encounter any kill traps based on my home range estimates from Chapter 3. Hedgehogs with home range estimates on the lower end of the range, around 1-2 ha, may not encounter any traps during their normal ranging activity. On Rangitoto and Motutapu Islands, the trapping grid was intensified from 100 m by 400 m to a 100 m by 100 m grid in ungrazed pasture, ungrazed regenerating forest and open pasture to help eradicate the remaining hedgehogs on the island (Griffiths et al., 2015). Moss (1999) also recommended using a minimum trap spacing of 100 m, with a density of one trap per hectare in braided river habitats of the South Island with vulnerable ground-nesting birds. However, a recent population density estimation of hedgehogs in exotic pastures in Otago during late February/early March was 0.46 hedgehogs per ha (van Heezik et al., 2023). This estimate was lower than previous estimates from Parkes (1975) and Gorton (1997) and indicates that one trap per two hectares is appropriate. This suggests the critical need to establish a robust population density estimation at my study site to help guide an effective trapping grid design.

4.3.5 Trap placement, travel pathways, and habitat preferences

Traps located near roads and forest margins had the highest hedgehog catch, whereas traps located on the golf course and coastal margin had the lowest catch. The trail cameras with the highest number of hedgehog recordings were also located near roadsides. Road use by hedgehogs as a travel path is common and hedgehogs are frequently killed on roads in both New Zealand and Europe (Moore et al., 2020; Jones, 2021). The use of forest margins could reflect food abundance or ease of movement for dispersing individuals. Riber (2006) found hedgehogs in a Danish rural area preferred forested areas and edge habitat to open areas. Male hedgehogs commonly made use of habitat boundaries for movement in the Waitaki Basin in the South Island of New Zealand (Shanahan et al., 2007). However, Glen et al. (2019) found hedgehog detections using large tracking tunnels to be similar for bush, edge, and pasture habitats in New Zealand. Favourable foraging habitat for hedgehogs may depend on how food resources are depleted by conspecifics (Doncaster et al., 2008). Competition for food with other hedgehogs could be the driver for hedgehogs dispersing out of the neighbouring farmland and into Tara Iti if the population density of hedgehogs is higher in the Black Swamp due to ineffective control measures.

4.3.6 Camera trapping

Based on camera trap recordings, the activity levels appeared relatively consistent throughout the night. There was no time of night when hedgehogs were captured on camera more often. This suggests that hedgehogs at this site likely spend most of the night foraging. Glen et al. (2014) found that capture rates for cats and hedgehogs were higher with camera traps than kill traps. This makes camera trapping suitable for use in estimating relative hedgehog abundance (Glen et al., 2014). It is important to note that the camera trapping in this study was not designed in a way that is a reliable measure of hedgehog abundance, rather it was employed as an indication of hedgehog presence. However, the camera data does indicate trap placement along roads and habitat edges may encounter common travel routes for hedgehogs and increase kill trap success.

4.3.7 Constraints and limitations

We do not know the level of hedgehog control needed to achieve optimal benefits for native wildlife (Jones, 2021) but it will vary with habitat type, community composition, and time of year. To determine how well current trapping regimes reduce the density of hedgehogs, there needs to be an estimation of pre-control and post-control population density (Jones, 2021; van Heezik et al., 2023). In the original project proposal, I intended to carry out a mark-recapture experiment to determine the population density of hedgehogs at Tara Iti. Due to the effects of Cyclone Gabrielle on fieldwork, this was not possible. Further research is required to estimate the population density of hedgehogs at this site.

Researchers have investigated hedgehog density and the effects of predator control on native fauna in parts of New Zealand (Glen et al., 2019; van Heezik et al., 2023). Van Heezik et al. (2023) provided a robust population density estimate of 0.46 hedgehogs per hectare in pasture habitat on the Otago

Peninsula, South Island, New Zealand, using a spatially explicit capture-recapture (SECR) live-trapping experiment. Previous studies estimated hedgehog density using mark-recapture experiments in pastoral farmland in New Zealand (Campbell, 1973; Parkes, 1975; Gorton, 1997). Spatially explicit capture-recapture experiments differ from traditional mark-recapture experiments by incorporating spatial information, and estimating the density and parameters needed to predict capture rates of potential trapping regimes (Anderson et al., 2022). SECR model parameters account for variability in the detectability of animals in relation to trap placement, making estimates more robust (van Heezik et al., 2023). Glen et al. (2019) investigated the effects of predator control across 6000 ha of pastoral landscape in Hawke's Bay, North Island, New Zealand, by monitoring the effects of control on predators and native prey against a non-treatment area (with no predator control). Hedgehogs were not specifically targeted by the trapping regime but were monitored at significantly lower site occupancy in the predator removal area compared to the non-treatment area (Glen et al., 2019). Monitoring the effects that hedgehog control has on native wildlife, such as invertebrate abundance and shorebird nesting success, would be useful in quantifying the impacts of hedgehogs and the benefits of targeted predator control.

4.3.8 Implications for best practise control of hedgehogs

Following the seasonal trends in hedgehog behaviour and activity could allow for a more efficient and cost-effective trapping program. Based on the analysis of trapping data in my study, I would recommend an alternative time to target trapping efforts on hedgehogs to Brockie (1958), Campbell (1973), Parkes (1975), Gorton (1997), and Moss (1999). Targeting adult hedgehogs coming out of hibernation in early spring (September) with the highest reproductive value before they begin producing young will provide the greatest protection to ground-nesting birds during the breeding season (Jackson, 2006). Therefore, hedgehogs should be targeted by an intensive trapping program primarily in early spring-summer. Secondary control would be recommended during summer to late autumn to intensify trapping efforts while hedgehogs are actively preparing for hibernation.

A high-density network of traps should be utilised and serviced regularly to make the most impact on the hedgehog population. The trap density, spacing, and placement should be guided by knowledge of home range estimates and habitat preferences. Based on my results, DOC250 are more effective traps for targeting hedgehogs and roads and habitat edges should be utilized. When planning optimal trap placement, it is important to consider the level of human disturbance in the surrounding area, as well as the availability of suitable nesting sites. For instance, where paddocks are grazed by livestock, hedgehogs are likely to seek out hedgerows or scrub with more cover for constructing their dens (Hof & Bright, 2010). A trap density of 100 m by 100 m, with one DOC250 trap per hectare is recommended for areas where intensive hedgehog control is desired (Moss, 1999; Griffiths et al., 2015).

- DOC250 traps should be used to target hedgehogs.
- To control hedgehogs in vulnerable areas, a trap density of 100 m by 100 m, with one DOC250 trap per hectare, should be used.
- An intensive trapping program, primarily in early spring and summer, should target hedgehogs to impact the adult population and protect breeding shorebirds.
- Adult female hedgehogs with the highest reproductive value should be targeted to impact the population effectively.
- Secondary intensive control should be undertaken in late autumn to primarily target females and juvenile hedgehogs while they are preparing for hibernation.
- The level of trapping effort should vary with the season to correspond with the times of year with the highest activity of hedgehogs. Control efforts could be reduced during winter.
- Road edges and habitat edges should be utilised for trap placement.

Chapter 5: Thesis conclusions and recommendations

5.1 Thesis conclusions

Invasive species threaten biodiversity and ecosystem functioning worldwide, and their impacts on native fauna are diverse and not always well understood (Simberloff et al., 2013). Understanding the spatial dynamics of invasive species and their interactions with native ecosystems is crucial for effective conservation management. Aotearoa, New Zealand, is said to be a world leader in invasive species management. My research has applied spatial ecology principles to conservation biology, focusing on the case of invasive hedgehogs (*Erinaceus europaeus*) in a duneland ecosystem in northern New Zealand. Duneland ecosystems are threatened landscapes, vulnerable to the impacts of invasive species, and provide essential breeding habitat for the critically endangered New Zealand fairy terns (Tara iti). Given the warmer climate and fewer natural enemies, hedgehogs have been demonstrated to be successful invaders of New Zealand. This is the first study to use GPS technology to investigate hedgehog spatial ecology in the northern region of New Zealand and provide home range estimates in a northern coastal duneland ecosystem.

Home range is a core concept in spatial ecology, and quantifying home range size is an essential step towards understanding the ecological requirements of an invasive species (Börger et al., 2008; Smith et al., 2015; Hradsky et al., 2019). In many cases, invasive species exhibit higher biological success in their introduced range compared to their natural range in their native region (Parker et al., 2013).

Quantifying home range estimates and habitat preferences can optimise targeted control of elusive animals and increase the probability of encountering control devices (Smith et al., 2015; Bartoszek et al., 2021). I have advanced the understanding of hedgehog spatial ecology by providing home range estimates, average nightly distances travelled, and expanding current knowledge of the movement patterns, habitat preferences, and spatial distribution of hedgehogs in a northern duneland ecosystem. In summary, hedgehogs occupy a small core area of their home range intensively while covering its entirety over several foraging nights. Home ranges overlap significantly between individuals of either sex, but core ranges are more independent.

Overall, the estimated home range size from my study and other estimates from northern New Zealand (Parkes, 1975; Gorton, 1998; Jeffries, 2011) are smaller than estimates in the native range of hedgehogs in Europe (Reeve, 1982; Riber, 2006; Haigh, 2011; Rautio et al., 2013), and the South Island, New Zealand (Moss, 1999; Rodriguez Recio et al., 2013). The main reasons for differences between my study and estimates from Europe and the South Island, New Zealand, likely include habitat quality and the latitudinal effects on climate conditions (Rautio et al., 2013; Gago et al., 2022). Hedgehogs in Europe are, on average, heavier (Morris, 1984; Dowding et al., 2010; Gurnell et al., 2015; Marco-Tresserres & López-Iborra, 2022) than hedgehogs in New Zealand by 50 to 200 grams (Brockie, 1974; van Heezik et al., 2023). This indicates that Bergmann's rule could partly explain the difference in home range size between New Zealand and European hedgehogs.

I found that the average distance travelled by female hedgehogs was higher than that of male hedgehogs. My estimate for female hedgehogs was higher than previously reported in New Zealand and Europe (Gorton, 1997; Gurnell et al., 2015; Riber, 2006; Marco-Tresserres & López-Iborra, 2022). A combination of factors such as habitat quality and reproductive state could explain the high average distance travelled by female hedgehogs in my study. I observed the longest recorded nightly distance travelled by a female hedgehog, over four kilometres in one night of activity. Trapping regimes should consider home range estimates, average nightly distances travelled, recorded dispersal distances, and habitat preferences when planning hedgehog control programs.

With many trapping programs treating hedgehogs as non-target animals (Russell et al., 2015; Glen et al., 2019), there is a lack of quantitative data on the impacts of hedgehogs and how to control populations effectively. Overall, the population of hedgehogs at Tara Iti appears to be large and stable despite the ongoing intensive trapping regime. I found a strong seasonal trend in the hedgehog trapping data, with peaks in January, February (austral summer), and May (austral autumn) and a low in July (austral winter). The seasonal trend provides an opportunity to refine current pest control measures for hedgehogs at Tara Iti. The peak hedgehog catch at Tara Iti in January and February likely coincides with juvenile dispersal (Moss, 1999; Jackson, 2006). The second peak in May could be an increase in foraging activity pre-hibernation, the dispersal of late litter, or second litters of juvenile hedgehogs. Juvenile hedgehogs likely contribute towards a large proportion of hedgehog catch in late summer-autumn as this is when dispersal occurs. To control the population of hedgehogs, it will be more effective to target adult females rather than juveniles due to their higher reproductive value. Adult hedgehogs should be targeted to provide maximum protection to breeding shorebirds as they emerge from hibernation (from late August) and before litters of young are produced. Adult female hedgehogs enter hibernation later than males, which provides an opportunity to target this cohort during late Autumn (Moss, 1999).

Based on my home range estimates from Chapter 3, there are gaps in the trap network at my study site where hedgehogs may not encounter any kill traps. Hedgehogs with home range estimates on the lower end of the range, around 1-2 ha, may not encounter any traps during their normal ranging activity. Moss (1999) also recommended targeting core areas when trapping hedgehogs and suggested having at least one trap per core area and every 100 metres. A trap spacing of 100 m by 100 m was also used to aid in eradicating the remaining hedgehogs from Rangitoto and Motutapu Islands (Griffiths et al., 2015). Based on the core range of hedgehogs in this study, I recommend a trap spacing of 100 m and a trap density of 1 trap per 1 ha.

Analysis of trapping data, trail camera footage, and GPS location revealed habitat preferences for roads and forest edges. My findings also provide evidence that DOC250 traps are superior to DOC200 traps for controlling hedgehogs. The Black Swamp uses predominantly DOC200 traps that do not appear to control hedgehogs in the buffer area surrounding Tara Iti adequately. This could partly explain why there is such a high hedgehog catch along the boundary of Tara Iti, as most adult hedgehogs are likely dispersing through the Black Swamp Predator Control Zone without being caught in traps. I recommend using the larger DOC250 traps in areas to target hedgehogs rather than increasing the baffle holes on the smaller DOC200 traps to prevent non-target kills of native birds and feral cats.

Protection of hedgehogs in Europe

Western European hedgehogs (*Erinaceus europaeus*) are a species of conservation focus in their native range in Europe (Gurnell et al., 2015; Marco-Tresserres & López-Iborra, 2022). The number of hedgehogs in Europe has declined significantly due to habitat loss and fragmentation caused by urbanisation and intensification of agriculture (Hof & Bright, 2009; Haigh, 2011; Berger et al., 2020; Taucher et al., 2020). The findings from my research on introduced hedgehogs in New Zealand may assist researchers aiming to fill knowledge gaps in hedgehog general ecology, behaviour, and home range variability in Europe. Insights into hedgehog home range, nightly distances travelled, spatial distribution, and habitat preferences in New Zealand coastal habitats may apply to similar habitats in Europe.

Aspects of research to be expanded

My findings highlight the need for local home range estimates in vulnerable ecosystems due to variability and plasticity in hedgehog behaviour based on habitat and climate factors. Seasonality strongly affects hedgehogs' home range and activity (Brockie, 1974; Parkes, 1975; Moss, 1999; Rautio et al., 2013). The effects of seasonality are also likely to correlate strongly with the effects of latitude. Further investigation into the effects of seasonality on hedgehog spatial ecology would be beneficial in estimating how the home range size changes with the season to optimise control measures further. Tracking hedgehogs through the winter period could provide information on hibernation and winter mortality in a warmer climate, whether all hedgehogs hibernate, and for how long. If hibernation is shortened in northern New Zealand, then hedgehogs have a prolonged breeding season. Confirming whether hedgehogs in northern New Zealand can produce more than one litter in a single breeding season would also be valuable information for informing control measures.

Due to the impacts of multiple flooding events on the study site, the occurrence of hedgehogs during nightly spotlighting was too low to accurately estimate the population density through mark-recapture. Establishing a robust population density estimation at my study site is critical to helping guide an effective trapping grid design and support recommendations for minimum trap spacing. An estimation of pre-control and post-control population density would be beneficial in determining how well current trapping regimes reduce the density of hedgehogs.

Moss (1999) found hedgehogs to roam most widely during spring and summer but were less likely to encounter live capture traps. They speculated this was because the hedgehogs were interested in seeking members of the opposite sex rather than taking food from baited traps (Moss, 1999). To increase the effectiveness of trapping, trialling conspecific scents in traps could be effective when hedgehogs are actively searching for the opposite sex to mate with. Conspecific scents as a luring method are effective with other invasive species, such as house mice (*Mus musculus*) (Shapira et al., 2013).

5.2 Recommendations for best practice hedgehog control

Based on the findings of this study and previous literature on the European hedgehog, we can provide recommendations for best practice control. The general recommendations for improving hedgehog control that emerged from spatial data analysis are as follows:

1. Intensify trap density and frequency of trap servicing during critical periods (early spring and late autumn). An intensive trapping program, primarily in early spring and summer, should target hedgehogs to impact the adult population and protect breeding shorebirds.
2. Secondary intensive control should be undertaken in late autumn to primarily target females and juvenile hedgehogs while they are preparing for hibernation.
3. Use a minimum trap spacing of 100 metres, with a density of one DOC250 trap per hectare.
4. When establishing buffer protection areas for vulnerable native species, consider the largest home range estimates and distances travelled by hedgehogs.
5. Position traps near suitable hedgehog nesting sites, roads, and habitat edges to maximise the chance of encounters.

5.3 Future research directions

5.3.1 Methodological recommendations

- A thermal imaging scope was beneficial for detecting hedgehogs while searching at night. Although they can be costly, they improved the success of finding hedgehogs that may have been missed with only a spotlight. It also allows the researcher to observe the hedgehog's behaviour from a distance without disturbing the hedgehog.

5.3.2 Research

- Estimate how the home range size of male and female hedgehogs varies with the season in coastal duneland ecosystems. As hedgehog trap catch shows a clear seasonal trend, further research to estimate how the size of the home range changes with the season in northern New Zealand would help to optimise trapping efforts further.
- Further research into hedgehog hibernation in northern New Zealand is needed to fill knowledge gaps of invasive hedgehog ecology. An investigation into the duration of hedgehog hibernation, whether hibernation is intermittent, and the winter mortality rate would be valuable information for informing control measures.
- In the warmer climate of northern New Zealand, hedgehogs have a prolonged breeding season. Confirming whether hedgehogs in this region can produce more than one litter in a single breeding season would also be valuable information for informing control measures.
- To increase the effectiveness of trapping, I recommend trialling conspecific scents in traps when hedgehogs are actively searching for mating opportunities.

Chapter 6: Reference material

6.1 References

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6.2 Appendices

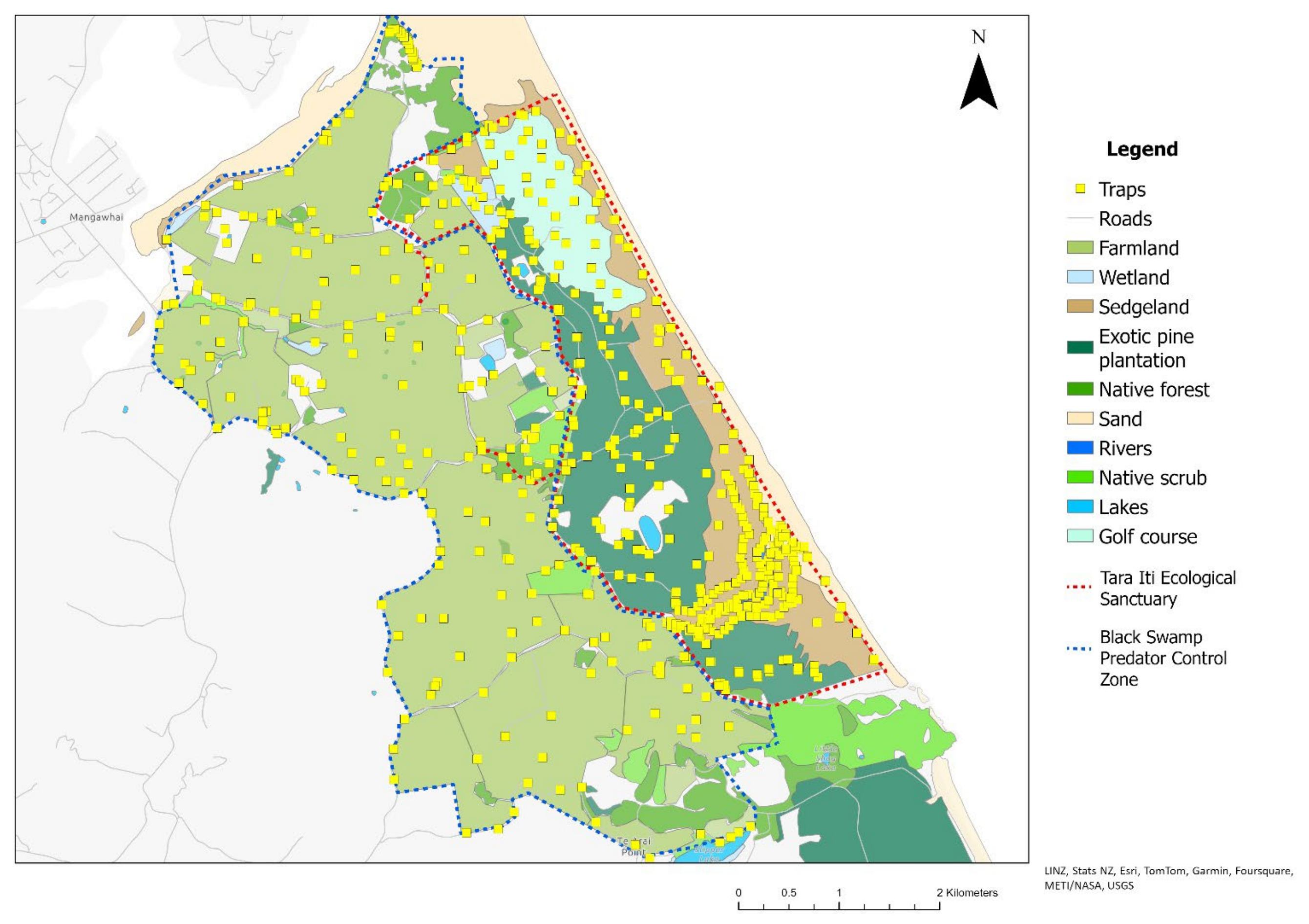
6.2.1 Study site trapping history

Tara Iti Golf Course has been recording the removal of animal pests at their site on *Trap.NZ* since mid-2016. From July 2016 to July 2023 over 2500 animal pest species were removed, with over 1300 hedgehogs, 400 rats, 200 possums, and 200 mustelids controlled. Tara Iti Ecological Sanctuary maintains a high-density network of 230 traps, 344 bait stations, and 300 monitoring stations. The number of different traps used is outlined in Figure 2.2. The majority of traps are DOC250 and DOC200 traps (Figures 6.2 and 6.3).

The Black Swamp Predator Control Zone was set up as a buffer zone to Tara Iti Ecological Sanctuary and traps were installed during 2020. In total, 230 traps and 20 monitoring stations are located on private properties and pastoral farmland. The traps are maintained by private landowners and by the conservation managers for Tara Iti Golf Course. The network is made up of predominantly DOC200 traps. The trapping program is a partnership between private landowners, the Shorebirds Trust, Auckland Council, and the Rodney Local Board, and is a component of an overarching project "the Conservation Coast", over 10,000 ha of coordinated community trapping efforts. Over 500 rats, 150 hedgehogs, and 80 mustelids have been removed (Flavell-Johnson, 2022).

Figure 6.1 A DOC200 trap (left) versus a DOC250 (right) trap. Note: the DOC200 is a "weka-proof" style with a longer distance between the first and second baffles.

Figure 6.2 Front-on view of the standard baffle aperture size for a DOC200 (left; 60 mm by 60 mm) versus a DOC250 (right; 80 mm by 80mm).



LINZ, Stats NZ, Esri, TomTom, Garmin, Foursquare, METI/NASA, USGS

Figure 6.3 Map of the trapping network (including all recorded trap locations) at the study site, Tara Iti Ecological Sanctuary and Black Swamp Predator Control Zone.

6.2.2 Search area

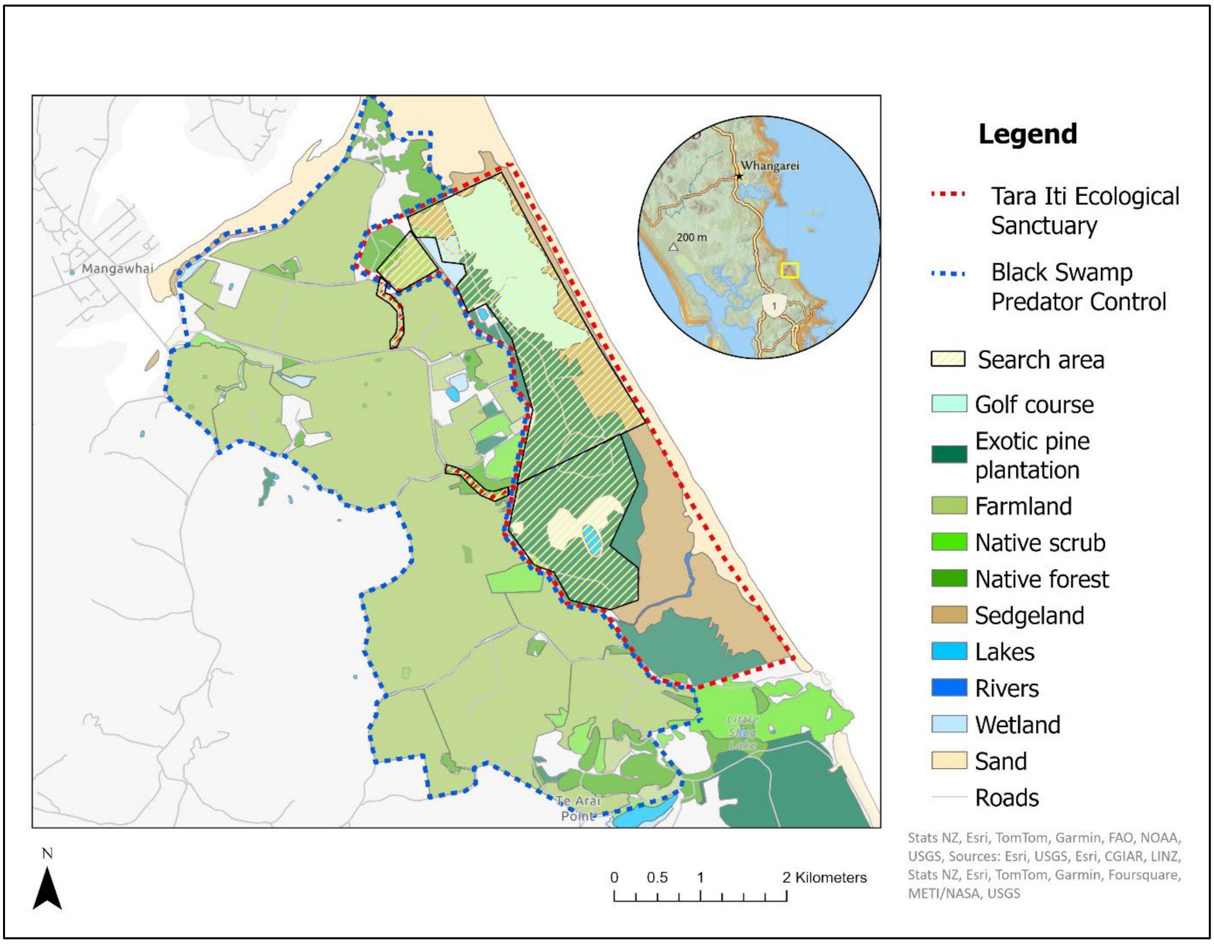


Figure 6.4 The approximate nightly search area during sampling. The area searched each night varied slightly based on weather and ground conditions.

6.2.3 Search effort

Table 6.1 Search effort information in detail.

Date	*Time*	*People*	*Search hours*	*Weather*	*Season*	*Hedgehogs*	*Notes*
24/09/2022	20:00-22:30	3	7.5	Windy, light rain	Spring	0	
31/10/2022	21:00-01:00	3	12	Fine, warm	Spring	1	
1/11/2022	21:00-01:00	3	12	Fine, warm	Spring	3	
2/11/2022	21:00-00:30	4	14	Fine, warm	Spring	2	
3/11/2022	21:00-00:00	4	12	Fine, warm	Spring	5	
8/12/2022	20:00-23:30	3	10.5	High wind, rain 11pm	Summer	0	1 juvenile outside of study area
9/12/2022	20:00-22:00	2	4		Summer	0	
10/02/2023	20:30-00:30	4	16	Windy, heavy rain 8pm, drizzles	Summer	0	Cyclone hit day after
17/02/2023	20:00-00:00	3	12	High wind, fine	Summer	0	
2/03/2023	20:00-00:30	3	13.5	low wind, fine, warm	Autumn	0	Surface flooding still present
5/05/2023	18:30-22:30	3	12	Showers, humid, 19degrees, windy	Autumn	0	thermal scope used
6/05/2023	17:30-23:00	3	16.5	Showers, humid, 18degrees, windy	Autumn	2	thermal scope used

6.2.4 Basic hedgehog data

Table 6.2 Detailed data on tagged hedgehogs in this study.

HEDGEHOG ID	TAG ID	TAG TYPE	SEX	DATE (CAPTURE)	TIME	DATE (RECAPTURE)	INITIAL MASS (G)	MASS (G) (RECAPTURE)
1	45328	Pinpoint VHF-75	Male	31/10/2022	21:31	4/11/2022	672	674
2	45688	Pinpoint VHF-75	Male	1/11/2022	21:23	4/11/2022	555	513
3	45689	Pinpoint VHF-75	Male	2/11/2022	0:13	4/11/2022	691	688
4	45684	Pinpoint VHF-75	Female	2/11/2022	22:22	5/11/2022	672	694
5	45687	Pinpoint VHF-75	Female	2/11/2022	23:10	5/11/2022	785	787
6	45686	Pinpoint VHF-75	Female	3/11/2022	21:15	5/11/2022	622	*
7	45326	Pinpoint VHF-75	Female	3/11/2022	21:15	5/11/2022	572	*
8	45331	Pinpoint VHF-75	Female	3/11/2022	21:15	5/11/2022	834	823
9	45685	Pinpoint VHF-75	Male	3/11/2022	23:10	5/11/2022	672	663
10	45331	Pinpoint VHF-75	Male	6/05/2023	22:10	12/05/2023	466	473
11	45326	Pinpoint VHF-75	Male	6/05/2023	22:15	12/05/2023	484	520

Table 6.3 Detailed data on tagged hedgehogs in this study continued.

HEDGEHOG ID	SAMPLING NIGHTS	LOCATION	MARKER	TOTAL POSSIBLE FIXES (CAPTURE TIME - END OF SCHEDULE)	FAILED FIXES	FSR (%)	HIGH LE	VALID FIXES
1	4	Rako Drive	Yellow	460	43	90.7	12	405
2	3	Rako Drive	Yellow	344	30	91.3	3	311
3	3	Petting farm	Yellow	315	4	98.7	4	307
4	3	Rako Drive	Yellow	332	2	99.4	2	328
5	3	Rako Drive	Yellow	326	24	92.6	2	300
6	1.5	Cam16	Yellow	224	2	99.1	0	222
7	1	Cam16	Yellow	103	2	99.1	1	100
8	2	Cam16	Yellow	224	8	96.4	7	209
9	1	Rako Drive	Yellow	81	4	95.1	2	75
10	6	Rako Drive	3R,3Y	305	63	79.3	1	241
11	6	Rako Drive	3B,3Y	306	91	70.3	3	212

6.2.5 Trail camera data

Table 6.4 Trail camera data on hedgehogs only.

Camera	Month	Date	Time	Species	Notes	Bait
Cam1	November	2/11/2022	05:00:00	Hedgehog		cat food (tin)
Cam5	November	3/11/2022	01:18:00	Hedgehog		cat food (tin)
Cam4	November	4/11/2022	01:06:00	Hedgehog		cat food (tin)
Cam9	November	4/11/2022	00:01:00	Hedgehog		cat food (tin)
Cam5	November	4/11/2022	04:16:00	Hedgehog	male	cat food (tin)
Cam7	November	4/11/2022	22:29:00	Hedgehog		cat food (tin)
Cam7	November	4/11/2022	23:23:00	Hedgehog	marked and tag	cat food (tin)
Cam9	November	4/11/2022	19:57:00	Hedgehog		cat food (tin)
Cam1	November	4/11/2022	22:09:00	Hedgehog		cat food (tin)
Cam1	November	4/11/2022	23:13:00	Hedgehog		cat food (tin)
Cam9	November	4/11/2022	23:14:00	Hedgehog		cat food (tin)
Cam4	November	5/11/2022	04:16:00	Hedgehog		cat food (tin)
Cam1	November	5/11/2022	00:35:00	Hedgehog		cat food (tin)
Cam1	November	5/11/2022	03:34:00	Hedgehog		cat food (tin)
Cam9	November	5/11/2022	03:49:00	Hedgehog	not marked	cat food (tin)
Cam9	November	5/11/2022	04:41:00	Hedgehog	marked	cat food (tin)
Cam9	November	5/11/2022	05:01:00	Hedgehog	not marked	cat food (tin)
Cam4	March	4/03/2023	20:39:00	Hedgehog		Bikkies
Cam3	March	6/03/2023	22:07:00	Hedgehog		Bikkies
Cam3	March	8/03/2023	22:59:00	Hedgehog		Bikkies
Cam4	March	8/03/2023	21:19:00	Hedgehog		Bikkies
Cam7	April	23/04/2023	02:04:00	Hedgehog		cat food (tin)
Cam10	April	23/04/2023	04:00:00	Hedgehog		Bikkies
Cam10	April	23/04/2023	18:59:00	Hedgehog		Bikkies
Cam9	April	24/04/2023	05:02:00	Hedgehog		cat food (tin)
Cam11	April	24/04/2023	21:40:00	Hedgehog		cat food (tin)
Cam7	April	25/04/2023	23:18:00	Hedgehog		cat food (tin)
Cam7	April	26/04/2023	18:54:00	Hedgehog		cat food (tin)
Cam8	April	26/04/2023	20:30:00	Hedgehog		cat food (tin)
Cam9	April	26/04/2023	18:23:00	Hedgehog		cat food (tin)
Cam3	April	27/04/2023	00:53:00	Hedgehog		Bikkies
Cam7	April	27/04/2023	20:57:00	Hedgehog		cat food (tin)
Cam9	April	27/04/2023	00:13:00	Hedgehog		cat food (tin)
Cam9	April	27/04/2023	18:25:00	Hedgehog		cat food (tin)
Cam7	April	28/04/2023	20:00:00	Hedgehog		cat food (tin)
Cam8	April	28/04/2023	22:54:00	Hedgehog		cat food (tin)
Cam9	April	28/04/2023	00:22:00	Hedgehog		cat food (tin)
Cam9	April	28/04/2023	01:18:00	Hedgehog		cat food (tin)
Cam5	April	29/04/2023	03:01:00	Hedgehog		cat food (tin)
Cam8	April	29/04/2023	03:06:00	Hedgehog		cat food (tin)
Cam8	April	29/04/2023	19:23:00	Hedgehog		cat food (tin)
Cam4	April	30/04/2023	00:18:00	Hedgehog		Bikkies

Cam11	April	30/04/2023	00:18:00	Hedgehog	cat food (tin)
Cam9	May	1/05/2023	01:21:00	Hedgehog	cat food (tin)
Cam9	May	2/05/2023	18:35:00	Hedgehog	cat food (tin)
Cam7	May	6/05/2023	04:08:00	Hedgehog	cat food (tin)
Cam7	May	6/05/2023	19:22:00	Hedgehog	cat food (tin)

6.2.6 GPS data

Table 6.5 Processed GPS point dataset from Hedgehog 11. One example dataset out of 11 in total.

Index	Status	Sats	NZST-date	NZST-time	Delta(s)	Latitude	Longitude	Altitude(m)	HDOP
19	Valid	7/7	6/05/2023	22:15:00	2.392	-36.1288	174.605	73.02	1.1
20	Valid	5/5	6/05/2023	22:30:00	2.386	-36.1285	174.6051	72.68	2.1
21	Valid	7/7	6/05/2023	22:45:00	1.805	-36.1287	174.6051	53.46	1.6
22	Valid	4/4	6/05/2023	23:00:00	2.207	-36.1294	174.6057	53.46	6.9
23	Valid	4/4	6/05/2023	23:15:00	2.401	-36.1294	174.6057	53.46	2.2
24	Valid	5/5	6/05/2023	23:30:00	2.187	-36.1293	174.6056	47.26	4.7
25	Valid	5/5	6/05/2023	23:45:00	2.185	-36.1293	174.6055	63.21	4.2
26	Valid	5/5	7/05/2023	00:00:00	1.99	-36.1293	174.6057	63.32	2.5
27	Valid	4/5	7/05/2023	00:15:00	2.008	-36.1293	174.6057	63.32	5.5
28	Valid	5/5	7/05/2023	00:30:00	1.996	-36.1296	174.6056	54.63	1.5
29	Valid	5/5	7/05/2023	00:45:00	2.003	-36.1299	174.6057	54.05	4.9
30	Valid	7/7	7/05/2023	01:00:00	1.992	-36.1301	174.6053	61.18	1.2
31	NotEnoughSats	0/1	7/05/2023	01:15:00	1.92				
32	NotEnoughSats	0/1	7/05/2023	01:30:00	1.84				
33	NotEnoughSats	0/0	7/05/2023	01:45:00	1.76				
34	NotEnoughSats	0/1	7/05/2023	02:00:00	1.68				
35	Valid	7/7	7/05/2023	02:15:00	1.597	-36.1302	174.6052	59.51	3.2
36	Valid	7/7	7/05/2023	02:30:00	1.234	-36.1301	174.6052	56.58	2.4
37	Valid	8/8	7/05/2023	02:45:00	1.183	-36.1297	174.6049	52.58	1.3
38	Valid	7/7	7/05/2023	03:00:00	1.126	-36.1297	174.6046	44.49	2
39	Valid	6/6	7/05/2023	03:15:00	1.124	-36.1296	174.6045	49.09	1.8
40	Valid	7/7	7/05/2023	03:30:00	1.598	-36.1295	174.6045	49.29	1.7
41	Valid	6/6	7/05/2023	03:45:00	1.037	-36.1296	174.6046	49.89	2.1
42	Valid	6/6	7/05/2023	04:00:00	0.995	-36.1293	174.6041	49.44	2.6
43	Valid	7/7	7/05/2023	04:15:00	0.946	-36.1294	174.6038	49.97	1.7
44	Valid	8/8	7/05/2023	04:30:00	0.915	-36.1293	174.604	51.8	1.1
45	Valid	8/8	7/05/2023	04:45:00	0.877	-36.1292	174.6042	54.71	1
46	Valid	8/8	7/05/2023	05:00:00	0.843	-36.1292	174.6044	55.99	1
47	Valid	7/7	7/05/2023	05:15:00	0.795	-36.1292	174.6046	60.69	1.2
48	Valid	6/6	7/05/2023	05:30:00	0.741	-36.1292	174.6047	57.14	2.1
49	Valid	7/7	7/05/2023	05:45:00	0.716	-36.1296	174.6052	55.63	1.6
50	Valid	5/6	7/05/2023	06:00:00	0.605	-36.1298	174.6053	58.93	1.9
51	Valid	7/7	7/05/2023	06:15:00	0.636	-36.1299	174.6053	58.49	1.4
52	Valid	5/5	7/05/2023	06:30:00	0.999	-36.1296	174.6047	58.5	2.7
53	Valid	4/4	7/05/2023	06:45:00	0.807	-36.1294	174.6047	58.5	5.1
54	NotEnoughSats	0/2	7/05/2023	07:00:00	0.4				

55	NotEnoughSats	0/1	7/05/2023	17:00:00	-1.2				
56	Valid	5/5	7/05/2023	18:00:00	-0.994	-36.1295	174.6046	57.83	2
57	Valid	6/6	7/05/2023	18:15:00	-1.187	-36.1294	174.6045	68.94	1.9
58	Valid	4/4	7/05/2023	18:30:00	-1.581	-36.1293	174.6046	68.94	5.8
59	Valid	4/4	7/05/2023	18:45:00	-0.898	-36.1289	174.6049	68.94	30.3
60	Valid	3/3	7/05/2023	19:00:00	-1.8	-36.1294	174.6043	68.94	2.9
61	Valid	7/7	7/05/2023	19:15:00	-1.446	-36.1295	174.6045	54.32	1
62	Valid	6/6	7/05/2023	19:30:00	-1.488	-36.1297	174.6049	53.3	1.9
63	Valid	8/8	7/05/2023	19:45:00	-1.52	-36.1299	174.6056	51.63	1
64	Valid	6/6	7/05/2023	20:00:00	-1.566	-36.1298	174.6058	44.66	1.3

65	Valid	7/7	7/05/2023	20:15:00	-1.595	-36.1297	174.606	48.03	1.6
66	Valid	6/6	7/05/2023	20:30:00	-1.191	-36.1297	174.6061	51.6	1.3
67	Valid	6/6	7/05/2023	20:45:00	-1.694	-36.1297	174.6061	53.54	1.8
68	Valid	8/8	7/05/2023	21:00:00	-1.727	-36.1298	174.6062	53.42	1.3
69	Valid	6/6	7/05/2023	21:15:00	-1.777	-36.1298	174.6062	57.03	3
70	Valid	7/7	7/05/2023	21:30:00	-1.816	-36.1298	174.6061	56.14	2.8
71	Valid	6/6	7/05/2023	21:45:00	-1.854	-36.1298	174.6062	53.88	2.9
72	Valid	7/7	7/05/2023	22:00:00	-1.885	-36.13	174.6061	47.18	1.2
73	Valid	8/8	7/05/2023	22:15:00	-1.922	-36.13	174.6056	48.15	1.1
74	Valid	4/4	7/05/2023	22:30:00	-1.601	-36.1301	174.6054	48.15	16
75	NotEnoughSats	0/2	7/05/2023	22:45:00	-2.2				
76	NotEnoughSats	0/1	7/05/2023	23:00:00	-2.12				
77	NotEnoughSats	0/0	7/05/2023	23:15:00	-2.04				
78	NotEnoughSats	0/0	7/05/2023	23:30:00	-1.96				
79	NotEnoughSats	0/2	7/05/2023	23:45:00	-1.88				
80	NotEnoughSats	0/2	8/05/2023	00:00:00	-1.8				
81	Valid	5/5	8/05/2023	00:15:00	-1.802	-36.1302	174.6052	47.94	2.1
82	Valid	6/6	8/05/2023	00:30:00	-2.293	-36.1302	174.6052	50.96	1.6
83	NotEnoughSats	0/2	8/05/2023	00:45:00	-1.8				
84	Valid	6/6	8/05/2023	01:00:00	-2.373	-36.1303	174.6051	51.3	1.9
85	Valid	7/7	8/05/2023	01:15:00	-2.413	-36.1302	174.6049	48.73	2.5
86	Valid	8/8	8/05/2023	01:30:00	-2.45	-36.1296	174.6046	47.24	2.3
87	Valid	7/7	8/05/2023	01:45:00	-2.48	-36.1294	174.6042	47.94	3.7
88	Valid	8/8	8/05/2023	02:00:00	-2.54	-36.1293	174.604	49.6	1.3
89	Valid	6/6	8/05/2023	02:15:00	-2.566	-36.1294	174.6037	48.15	2.8
90	Valid	7/7	8/05/2023	02:30:00	-2.616	-36.1293	174.6039	54.79	1.7
91	Valid	7/7	8/05/2023	02:45:00	-2.64	-36.1294	174.6039	54.18	1.7
92	Valid	6/6	8/05/2023	03:00:00	-2.688	-36.1293	174.604	53.87	1.7
93	Valid	6/6	8/05/2023	03:15:00	-2.723	-36.1294	174.604	53.3	1.7
94	Valid	6/6	8/05/2023	03:30:00	-2.765	-36.1293	174.6042	47.67	1.9
95	Valid	6/6	8/05/2023	03:45:00	-2.805	-36.1294	174.6043	47.67	2.2
96	Valid	6/6	8/05/2023	04:00:00	-2.842	-36.1293	174.6046	49.49	2.8
97	NotEnoughSats	0/2	8/05/2023	04:15:00	-3				
98	Valid	4/4	8/05/2023	04:30:00	-3.411	-36.1294	174.6045	49.49	5.5
99	Valid	3/3	8/05/2023	04:45:00	-3.4	-36.1294	174.6045	49.49	3.6
100	Valid	4/4	8/05/2023	05:00:00	-3.401	-36.1294	174.6045	49.49	2.6
101	Valid	6/6	8/05/2023	05:15:00	-3.051	-36.1296	174.6046	45.39	1.9
102	Valid	6/6	8/05/2023	05:30:00	-2.991	-36.1297	174.6046	46.27	2.2
103	Valid	6/7	8/05/2023	05:45:00	-3.117	-36.1297	174.6049	49.06	1.6
104	Valid	6/6	8/05/2023	06:00:00	-3.167	-36.1298	174.6053	48.53	1.5
105	Valid	6/6	8/05/2023	06:15:00	-3.216	-36.1301	174.6051	55.53	2.3
106	NotEnoughSats	0/2	8/05/2023	06:30:00	-3.4				
107	NotEnoughSats	0/2	8/05/2023	06:45:00	-2.6				
108	NotEnoughSats	0/1	8/05/2023	07:00:00	-3.6				
109	Valid	6/6	8/05/2023	17:00:00	-4.932	-36.1302	174.6053	54.38	1.9
110	Valid	4/4	8/05/2023	18:00:00	-5.397	-36.1302	174.6051	54.38	2.6
111	Valid	5/5	8/05/2023	18:15:00	-4.807	-36.1302	174.6052	53.75	1.9

112	Valid	5/5	8/05/2023	18:30:00	-4.81	-36.1302	174.6052	53.74	2.5
113	NotEnoughSats	0/0	8/05/2023	18:45:00	-5.2				
114	Valid	6/7	8/05/2023	19:00:00	-5.595	-36.1302	174.6052	53.47	1.2
115	Valid	8/8	8/05/2023	19:15:00	-5.302	-36.1302	174.6053	44.76	1
116	Valid	6/6	8/05/2023	19:30:00	-5.353	-36.1297	174.6056	44.66	2.5
117	Valid	8/8	8/05/2023	19:45:00	-5.372	-36.1297	174.606	53.73	1
118	Valid	6/6	8/05/2023	20:00:00	-5.414	-36.1299	174.6064	53.12	1.6
119	Valid	8/8	8/05/2023	20:15:00	-5.46	-36.13	174.6065	51.81	1.1
120	Valid	7/7	8/05/2023	20:30:00	-5.508	-36.1299	174.6065	54.52	1.3
121	Valid	8/8	8/05/2023	20:45:00	-5.532	-36.1299	174.6067	56.62	1.2
122	Valid	7/7	8/05/2023	21:00:00	-5.191	-36.1297	174.6062	47.47	1.2
123	Valid	6/6	8/05/2023	21:15:00	-5.614	-36.1297	174.6061	48.71	3
124	Valid	7/7	8/05/2023	21:30:00	-5.655	-36.1295	174.6062	56.15	1.6
125	Valid	6/6	8/05/2023	21:45:00	-5.194	-36.1294	174.6064	51.59	2.6
126	Valid	6/6	8/05/2023	22:00:00	-5.203	-36.1295	174.6064	49.03	1.8
127	Valid	6/6	8/05/2023	22:15:00	-5.762	-36.1296	174.6063	49.25	1.4
128	Valid	7/7	8/05/2023	22:30:00	-5.831	-36.1295	174.6062	53.78	1.1
129	Valid	6/6	8/05/2023	22:45:00	-5.851	-36.1294	174.6061	53.9	2.1
130	Valid	7/7	8/05/2023	23:00:00	-5.402	-36.1294	174.6061	53.4	1.5
131	Valid	6/6	8/05/2023	23:15:00	-5.947	-36.1294	174.6059	65.51	2.2
132	Valid	6/6	8/05/2023	23:30:00	-5.588	-36.1296	174.6057	59.03	2.8
133	NotEnoughSats	0/2	8/05/2023	23:45:00	-6.2				
134	Valid	4/4	9/05/2023	00:00:00	-6.149	-36.1297	174.606	59.03	7.5
135	NotEnoughSats	0/1	9/05/2023	00:15:00	-6.2				
136	Valid	6/6	9/05/2023	00:30:00	-6.224	-36.1298	174.6055	60.78	2
137	Valid	7/7	9/05/2023	00:45:00	-5.616	-36.1296	174.6049	58.68	1.2
138	Valid	6/6	9/05/2023	01:00:00	-6.216	-36.1295	174.6045	57.02	2.1
139	NotEnoughSats	0/1	9/05/2023	01:15:00	-6.2				
140	NotEnoughSats	0/2	9/05/2023	01:30:00	-6.2				
141	NotEnoughSats	0/0	9/05/2023	01:45:00	-6.2				
142	NotEnoughSats	0/0	9/05/2023	02:00:00	-6.2				
143	Valid	4/4	9/05/2023	02:15:00	-6.193	-36.1295	174.6045	57.02	2
144	Valid	5/5	9/05/2023	02:30:00	-6.604	-36.1294	174.6045	56.94	2.5
145	Valid	7/7	9/05/2023	02:45:00	-6.498	-36.1294	174.6042	54.92	1.7
146	Valid	7/7	9/05/2023	03:00:00	-6.556	-36.1293	174.6039	26.17	1.8
147	Valid	6/6	9/05/2023	03:15:00	-6.573	-36.1294	174.604	51.24	1.9
148	Valid	7/7	9/05/2023	03:30:00	-6.604	-36.1293	174.6041	51.37	2.9
149	Valid	6/6	9/05/2023	03:45:00	-6.649	-36.1294	174.6039	52.2	2.4
150	Valid	7/7	9/05/2023	04:00:00	-6.687	-36.1293	174.6039	49.61	2.8
151	Valid	7/7	9/05/2023	04:15:00	-6.728	-36.1292	174.6041	49.39	1.2
152	Valid	8/8	9/05/2023	04:30:00	-6.777	-36.1292	174.6043	60.59	1.1
153	Valid	6/6	9/05/2023	04:45:00	-6.796	-36.1293	174.6047	53.3	4.3
154	Valid	7/8	9/05/2023	05:00:00	-6.85	-36.1291	174.6048	52.39	1.1
155	Valid	7/7	9/05/2023	05:15:00	-6.894	-36.1295	174.605	52.74	1.8
156	Valid	6/6	9/05/2023	05:30:00	-6.932	-36.1295	174.6049	52.27	2.3
157	Valid	7/7	9/05/2023	05:45:00	-6.981	-36.1297	174.605	56.13	1.6
158	Valid	7/7	9/05/2023	06:00:00	-6.6	-36.1296	174.6045	56.07	1.7

159	NotEnoughSats	0/2	9/05/2023	06:15:00	-7.2				
160	Valid	4/4	9/05/2023	06:30:00	-7.403	-36.1295	174.6045	56.07	5.8
161	NotEnoughSats	0/0	9/05/2023	06:45:00	-7.42				
162	NotEnoughSats	0/1	9/05/2023	07:00:00	-7.45				
163	Valid	4/4	9/05/2023	17:00:00	-8.397	-36.1295	174.6046	56.07	17.7
164	Valid	4/4	9/05/2023	18:00:00	-8.62	-36.1296	174.6045	56.07	4.2
165	Valid	6/6	9/05/2023	18:15:00	-8.596	-36.1295	174.6045	49.69	1.7
166	NotEnoughSats	0/1	9/05/2023	18:30:00	-9.2				
167	Valid	6/6	9/05/2023	18:45:00	-9.032	-36.1292	174.6048	57.31	6
168	Valid	7/7	9/05/2023	19:00:00	-9.112	-36.1295	174.6045	60.58	2.4
169	Valid	7/7	9/05/2023	19:15:00	-9.146	-36.1296	174.6045	37.82	1.1
170	Valid	7/7	9/05/2023	19:30:00	-9.193	-36.1296	174.6045	52.33	1.1
171	Valid	8/8	9/05/2023	19:45:00	-9.223	-36.1297	174.6046	51.28	0.9
172	Valid	7/7	9/05/2023	20:00:00	-9.262	-36.1296	174.6048	51.23	1.5
173	Valid	6/6	9/05/2023	20:15:00	-9.348	-36.1296	174.6045	60.57	7.9
174	Valid	7/7	9/05/2023	20:30:00	-9.345	-36.1298	174.6052	55.43	1.3
175	Valid	3/3	9/05/2023	20:45:00	-9.8	-36.1302	174.6052	55.43	2.7
176	NotEnoughSats	0/0	9/05/2023	21:00:00	-9.84				
177	NotEnoughSats	0/0	9/05/2023	21:15:00	-9.88				
178	NotEnoughSats	0/1	9/05/2023	21:30:00	-9.92				
179	NotEnoughSats	0/0	9/05/2023	21:45:00	-9.96				
180	Valid	3/3	9/05/2023	22:00:00	-10	-36.1303	174.6052	55.43	13.5
181	NotEnoughSats	0/1	9/05/2023	22:15:00	-9.2				
182	Valid	4/4	9/05/2023	22:30:00	-9.998	-36.1302	174.6051	55.43	2
183	NotEnoughSats	0/2	9/05/2023	22:45:00	-10				
184	NotEnoughSats	0/1	9/05/2023	23:00:00	-10				
185	NotEnoughSats	0/0	9/05/2023	23:15:00	-9.93				
186	NotEnoughSats	0/2	9/05/2023	23:30:00	-9.87				
187	NotEnoughSats	0/1	9/05/2023	23:45:00	-9.8				
188	NotEnoughSats	0/1	10/05/2023	00:00:00	-9.73				
189	NotEnoughSats	0/1	10/05/2023	00:15:00	-9.67				
190	Valid	4/4	10/05/2023	00:30:00	-9.592	-36.1302	174.6053	55.43	7.2
191	Valid	6/6	10/05/2023	00:45:00	-10.023	-36.1302	174.6053	53.96	1.3
192	Valid	6/6	10/05/2023	01:00:00	-10.06	-36.1303	174.6053	58.09	2.5
193	Valid	6/6	10/05/2023	01:15:00	-10.104	-36.1302	174.605	54.09	1.3
194	NotEnoughSats	0/2	10/05/2023	01:30:00	-10.4				
195	Valid	5/5	10/05/2023	01:45:00	-9.809	-36.1301	174.6048	53.17	6.5
196	Valid	4/4	10/05/2023	02:00:00	-9.575	-36.1315	174.6059	53.17	38.7
197	Valid	6/6	10/05/2023	02:15:00	-9.798	-36.1302	174.605	42.88	3.3
198	Valid	6/6	10/05/2023	02:30:00	-10.301	-36.1302	174.605	54.75	1.8
199	Valid	5/5	10/05/2023	02:45:00	-9.809	-36.1302	174.605	71.12	2.3
200	Valid	4/4	10/05/2023	03:00:00	-9.812	-36.1301	174.6051	71.13	3.7
201	Valid	6/6	10/05/2023	03:15:00	-10.432	-36.1303	174.6051	69.83	1.8
202	Valid	7/7	10/05/2023	03:30:00	-9.999	-36.1303	174.6051	53.81	1.9
203	Valid	6/6	10/05/2023	03:45:00	-10.489	-36.1303	174.6048	52.81	2.5
204	Valid	7/7	10/05/2023	04:00:00	-10.535	-36.1305	174.605	52.37	1.1
205	Valid	7/7	10/05/2023	04:15:00	-10.572	-36.1303	174.6049	53.38	1.2

206	Valid	6/6	10/05/2023	04:30:00	-10.598	-36.1301	174.6051	53.56	3
207	Valid	6/6	10/05/2023	04:45:00	-10.651	-36.1296	174.6048	53.15	4.7
208	Valid	6/6	10/05/2023	05:00:00	-10.691	-36.1296	174.6047	49.85	3.3
209	Valid	6/6	10/05/2023	05:15:00	-10.721	-36.1296	174.6046	55.23	2.2
210	Valid	7/7	10/05/2023	05:30:00	-10.769	-36.1299	174.6053	53.79	1.6
211	NotEnoughSats	0/0	10/05/2023	05:45:00	-10.82				
212	NotEnoughSats	0/0	10/05/2023	06:00:00	-10.91				
213	NotEnoughSats	0/2	10/05/2023	06:15:00	-11				
214	NotEnoughSats	0/0	10/05/2023	06:30:00	-11.1				
215	NotEnoughSats	0/2	10/05/2023	06:45:00	-11.2				
216	NotEnoughSats	0/1	10/05/2023	07:00:00	-11.24				
217	Valid	6/6	10/05/2023	17:00:00	-12.611	-36.1302	174.6053	62.52	1.7
218	NotEnoughSats	0/1	10/05/2023	18:00:00	-12.82				
219	NotEnoughSats	0/1	10/05/2023	18:15:00	-12.85				
220	Valid	6/6	10/05/2023	18:30:00	-12.851	-36.1301	174.6055	52.38	3.4
221	Valid	7/7	10/05/2023	18:45:00	-12.889	-36.1299	174.6055	52.09	1.1
222	Valid	6/6	10/05/2023	19:00:00	-12.925	-36.1298	174.6052	52.83	1.3
223	Valid	6/6	10/05/2023	19:15:00	-12.96	-36.1297	174.6049	52.98	3.5
224	Valid	7/8	10/05/2023	19:30:00	-12.986	-36.1296	174.6048	52.83	1.8
225	Valid	8/8	10/05/2023	19:45:00	-13.024	-36.1301	174.605	52.39	1.1
226	Valid	6/6	10/05/2023	20:00:00	-13.065	-36.1298	174.6053	52.17	1.5
227	Valid	7/8	10/05/2023	20:15:00	-13.095	-36.1299	174.6054	57.71	1.4
228	Valid	6/6	10/05/2023	20:30:00	-13.141	-36.1303	174.6054	58.85	2.4
229	Valid	7/7	10/05/2023	20:45:00	-13.171	-36.1303	174.6053	57.73	1.4
230	Valid	6/6	10/05/2023	21:00:00	-13.214	-36.1303	174.6053	56.93	2
231	Valid	8/8	10/05/2023	21:15:00	-13.242	-36.1302	174.6052	57.1	1.3
232	NotEnoughSats	0/0	10/05/2023	21:30:00	-13.48				
233	NotEnoughSats	0/2	10/05/2023	21:45:00	-13.54				
234	NotEnoughSats	0/2	10/05/2023	22:00:00	-13.59				
235	NotEnoughSats	0/1	10/05/2023	22:15:00	-13.64				
236	NotEnoughSats	0/0	10/05/2023	22:30:00	-13.69				
237	NotEnoughSats	0/0	10/05/2023	22:45:00	-13.75				
238	NotEnoughSats	0/2	10/05/2023	23:00:00	-13.8				
239	NotEnoughSats	0/2	10/05/2023	23:15:00	-13.4				
240	NotEnoughSats	0/0	10/05/2023	23:30:00	-13.55				
241	NotEnoughSats	0/1	10/05/2023	23:45:00	-13.7				
242	NotEnoughSats	0/0	11/05/2023	00:00:00	-13.85				
243	Valid	4/4	11/05/2023	00:15:00	-13.965	-36.1302	174.6054	57.1	8.5
244	Valid	4/4	11/05/2023	00:30:00	-14.192	-36.1301	174.6053	57.1	6.1
245	Valid	4/4	11/05/2023	00:45:00	-13.217	-36.1302	174.6051	57.1	5.9
246	Valid	3/4	11/05/2023	01:00:00	-14	-36.1302	174.6052	57.1	5.3
247	Valid	5/5	11/05/2023	01:15:00	-13.403	-36.1301	174.6052	57.08	4.5
248	Valid	5/5	11/05/2023	01:30:00	-14.2	-36.1302	174.6052	57.27	4.3
249	Valid	4/4	11/05/2023	01:45:00	-13.419	-36.1301	174.6051	57.27	10.2
250	NotEnoughSats	0/0	11/05/2023	02:00:00	-13.43				
251	Valid	6/6	11/05/2023	02:15:00	-14.031	-36.1302	174.6053	52.66	2.8
252	Valid	7/7	11/05/2023	02:30:00	-14.078	-36.1303	174.6054	50.1	1.8

253	Valid	7/7	11/05/2023	02:45:00	-14.104	-36.1305	174.6054	50.25	1.6
254	Valid	7/7	11/05/2023	03:00:00	-14.141	-36.1308	174.6055	47.84	1.5
255	Valid	6/6	11/05/2023	03:15:00	-14.171	-36.1312	174.6055	47.36	1.8
256	Valid	7/7	11/05/2023	03:30:00	-13.595	-36.1311	174.6054	58.62	1.1
257	NotEnoughSats	0/0	11/05/2023	03:45:00	-13.73				
258	NotEnoughSats	0/0	11/05/2023	04:00:00	-13.87				
259	NotEnoughSats	0/0	11/05/2023	04:15:00	-14				
260	NotEnoughSats	0/0	11/05/2023	04:30:00	-14.13				
261	Valid	7/7	11/05/2023	04:45:00	-14.405	-36.1302	174.6052	54.39	1.2
262	Valid	6/6	11/05/2023	05:00:00	-14.439	-36.1303	174.6054	52.69	1.4
263	Valid	6/6	11/05/2023	05:15:00	-14.484	-36.1303	174.6053	53.42	2.1
264	Valid	6/6	11/05/2023	05:30:00	-14.511	-36.1303	174.6052	52.67	1.8
265	Valid	6/6	11/05/2023	05:45:00	-14.808	-36.1301	174.6052	45.83	1.7
266	NotEnoughSats	0/2	11/05/2023	06:00:00	-14.8				
267	NotEnoughSats	0/0	11/05/2023	06:15:00	-14.83				
268	NotEnoughSats	0/0	11/05/2023	06:30:00	-14.86				
269	NotEnoughSats	0/0	11/05/2023	06:45:00	-14.89				
270	NotEnoughSats	0/0	11/05/2023	07:00:00	-14.92				
271	NotEnoughSats	0/0	11/05/2023	17:00:00	-16.08				
272	Valid	5/5	11/05/2023	18:00:00	-16.197	-36.1302	174.6052	48.44	2.5
273	NotEnoughSats	0/0	11/05/2023	18:15:00	-15.94				
274	Valid	8/8	11/05/2023	18:30:00	-15.686	-36.1302	174.6053	55.39	0.9
275	Valid	7/7	11/05/2023	18:45:00	-15.398	-36.1303	174.6052	54.84	1
276	Valid	6/6	11/05/2023	19:00:00	-15.759	-36.1303	174.6054	51.26	1.9
277	Valid	6/6	11/05/2023	19:15:00	-15.798	-36.1303	174.6054	51.27	1.2
278	Valid	8/8	11/05/2023	19:30:00	-15.827	-36.1305	174.6054	53.23	1
279	Valid	6/6	11/05/2023	19:45:00	-15.872	-36.1305	174.6053	37.7	2.8
280	Valid	7/7	11/05/2023	20:00:00	-15.898	-36.1303	174.6053	50.38	2.2
281	Valid	7/7	11/05/2023	20:15:00	-16.823	-36.1303	174.6051	53.37	1.2
282	Valid	6/6	11/05/2023	20:30:00	-16.986	-36.1301	174.6051	63.37	1.9
283	NotEnoughSats	0/0	11/05/2023	20:45:00	-17.1				
284	NotEnoughSats	0/2	11/05/2023	21:00:00	-17.2				
285	Valid	4/4	11/05/2023	21:15:00	-16.397	-36.1302	174.6053	63.37	14.1
286	Valid	4/4	11/05/2023	21:30:00	-16.549	-36.13	174.6057	63.37	12.2
287	Valid	4/4	11/05/2023	21:45:00	-17.135	-36.1299	174.6057	63.37	12.7
288	NotEnoughSats	0/2	11/05/2023	22:00:00	-16.8				
289	NotEnoughSats	0/2	11/05/2023	22:15:00	-17.4				
290	NotEnoughSats	0/2	11/05/2023	22:30:00	-17.39				
291	NotEnoughSats	0/0	11/05/2023	22:45:00	-17.38				
292	Valid	7/7	11/05/2023	23:00:00	-17.248	-36.1302	174.6053	50.21	1.7
293	Valid	7/7	11/05/2023	23:15:00	-17.299	-36.1305	174.6054	56	2.9
294	Valid	7/7	11/05/2023	23:30:00	-17.333	-36.1303	174.6053	53.18	1.5
295	NotEnoughSats	0/2	11/05/2023	23:45:00	-17.6				
296	NotEnoughSats	0/2	12/05/2023	00:00:00	-17.6				
297	NotEnoughSats	0/1	12/05/2023	00:15:00	-17.6				
298	NotEnoughSats	0/0	12/05/2023	00:30:00	-17.47				
299	NotEnoughSats	0/0	12/05/2023	00:45:00	-17.33				

300	Valid	6/6	12/05/2023	01:00:00	-17.197	-36.1302	174.6053	48.72	1.4
301	Valid	6/6	12/05/2023	01:15:00	-17.604	-36.1304	174.6054	48.97	5.4
302	Valid	7/7	12/05/2023	01:30:00	-17.19	-36.1308	174.6055	46.89	1
303	Valid	8/8	12/05/2023	01:45:00	-17.669	-36.1312	174.6055	39.28	1
304	Valid	6/6	12/05/2023	02:00:00	-17.709	-36.1314	174.6053	39.92	4.6
305	Valid	7/7	12/05/2023	02:15:00	-17.751	-36.1311	174.6054	44.69	2
306	Valid	6/6	12/05/2023	02:30:00	-17.777	-36.1311	174.6053	47.43	2
307	Valid	6/6	12/05/2023	02:45:00	-17.803	-36.1309	174.6051	46.03	1.8
308	Valid	7/7	12/05/2023	03:00:00	-17.835	-36.1306	174.605	55.47	1.8
309	Valid	7/7	12/05/2023	03:15:00	-17.88	-36.1308	174.6051	55.58	1.2
310	Valid	5/5	12/05/2023	03:30:00	-17.393	-36.1302	174.6053	37.31	2.5
311	NotEnoughSats	0/0	12/05/2023	03:45:00	-17.43				
312	NotEnoughSats	0/0	12/05/2023	04:00:00	-17.47				
313	Valid	7/7	12/05/2023	04:15:00	-18.032	-36.1303	174.6053	45.4	2.7
314	Valid	8/8	12/05/2023	04:30:00	-18.072	-36.1302	174.605	50.87	1
315	Valid	6/6	12/05/2023	04:45:00	-18.101	-36.1307	174.6056	43.8	1.3
316	Valid	7/7	12/05/2023	05:00:00	-17.594	-36.1303	174.6054	52.78	1.2
317	Valid	8/8	12/05/2023	05:15:00	-18.159	-36.1304	174.6053	39.53	1.1
318	Valid	6/6	12/05/2023	05:30:00	-18.187	-36.1302	174.6053	40.84	2.1
319	NotEnoughSats	0/0	12/05/2023	05:45:00	-17.7				
320	NotEnoughSats	0/0	12/05/2023	06:00:00	-17.73				
321	NotEnoughSats	0/0	12/05/2023	06:15:00	-17.77				
322	NotEnoughSats	0/0	12/05/2023	06:30:00	-17.8				
323	NotEnoughSats	0/0	12/05/2023	06:45:00	-17.83				
324	NotEnoughSats	0/0	12/05/2023	07:00:00	-17.87				