To disturb or not disturb:
radio-telemetry based territory mapping and camera traps for monitoring cryptic species using Rakiura tokoeka
(*Apteryx australis australis)*

STEWART ISLAND
KIWI
RAKIURA TOKOEKA
RESEARCH TEAM

A thesis presented in partial fulfillment of the requirements for the
degree of Doctor of Philosophy in Conservation Biology at Massey
University, Albany, New Zealand

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2023

Abstract

Successful wildlife conservation is dependent on effective population monitoring. The objectives of monitoring can be multi-faceted, but population density is often coveted. However, estimating the density of species in which individuals cannot be identified is challenging without a complete census, which is rarely possible. In New Zealand, kiwi (*Apteryx* spp.) are morphologically and behaviourally cryptic species that are difficult to monitor, yet monitoring results are essential to their conservation. The gold standard of kiwi monitoring is territory mapping using radio-telemetry, yet this method had never been formally evaluated, and the alternative method is call counts, which are difficult to relate to population variables.

Using Rakiura tokoeka (*Apteryx australis australis*) as my case study species, I implemented territory mapping with radio-telemetry at two novel locations on Rakiura/Stewart Island, one a pest-free island. My aim was to establish ‘known’ populations (minimum densities), and evaluate the traditional territory mapping method (Robertson, 2018) by comparing different ways of establishing territory boundaries (field-workers-estimates, convex 100% and concave polygons) and incorporating increasing numbers of locations by extending the length of the surveys.

In these two study locations, and an additional two locations where historical territory mapping surveys of Rakiura tokoeka had provided minimum density estimates, I then trialled a novel method for monitoring kiwi populations, camera trap grids. I ran camera trap surveys for Rakiura tokoeka seasonally between 2018 and 2020 in the four locations, using the same study areas that were used for territory mapping. I used the data from the camera surveys in two ways, firstly for a relative abundance index (calculating camera trap rate), and secondly in a statistical abundance model that estimated point abundance and detection probability (Royle-Nichols, 2003). I also evaluated the use of radio-telemetry and camera traps for monitoring Rakiura tokoeka through the breeding season and providing information on the survival, growth, and dispersal of young Rakiura tokoeka.

I found that territory mapping using radio-telemetry is an effective monitoring method for establishing minimum densities of Rakiura tokoeka, but that current methods could be improved. Convex polygon territory boundaries were similar to field-workers-estimate boundaries but could be applied more objectively and increasing the number of location fixes decreased density estimates. Camera trapping was an effective monitoring method for

Rakiura tokoeka populations. Camera trap rates were an easy to apply index that is widely applicable to the many community and conservation groups working with kiwi that do not have access to radio-telemetry for monitoring. Camera trap rates indicated that the pest free island (Ulva Island) had lower detections of Rakiura tokoeka than the other three locations. This could have been due to lower densities of Rakiura tokoeka over some parts of the island, or lower detection probabilities. From the abundance model, estimates of density of Rakiura tokoeka at the four locations were not significantly different to those from territory mapping. This indicated that camera trap surveys could be used as a non-invasive alternative to territory mapping with radio-telemetry for Rakiura tokoeka, and potentially other kiwi species that has lower cost and requires less effort.

I found the use of radio-telemetry and camera traps effective for monitoring different aspects of breeding behaviour, nesting, and chick variables, with the best use being a combination of the two methods. From the data collected on age structure, breeding and survival, I found no reason for immediate concern or management intervention for the Rakiura tokoeka population.

This project shows the importance of questioning established methods, trialling new methods, combining methods, and considering whether the invasiveness of a method is warranted to meet the project objectives.

Acknowledgements

This project was driven by my passion to make a valuable contribution to my field, but it was not without struggle. Concussion makes many things challenging, so to those who supported me in my professional and personal life to finish this PhD despite the ongoing struggle with my brain capacity, I couldn't have done it without you. To Win most of all. And to those of you who experience post-concussion syndrome – don't give up! There are so many people & organisations beyond those listed here who helped make this possible – this goes out to you.

Supervisors

My primary supervisory team	ISABEL CASTRO
	AI GLEN
	STEPHEN MARSLAND
My secondary supervisory team	ROGAN COLBOURNE
	LUIS ORTIS-CATEDRAL

Funding

Primary funder & stalwart supporter	JOHN INNES & MAANAKI WHENUA/LANDCARE RESEARCH
Essential funder	MASSEY UNIVERSITY
Ancillary funders & appreciated support	BIRDS NEW ZEALAND
	JULIE ALLEY BURSARY
	HUTTON FUND
	NZFGW NORTH SHORE BRANCH
	JS WATSON TRUST
	AUSTRALIAN WILDLIFE SOCIETY

Rakiura community

Accommodation	MAMA & PAPA JOY & THE STEWART ISLAND BACKPACKERS
	THE CHITTENDENS
	KAIPIPI CREW
Logistics	RAKIURA & PETER & THE ULVA ISLAND FERRY
	IAN & PIP AND AURORA CHARTERS
	RAKIURA CHARTERS
	RAYMOND & STEWART ISLAND FLIGHTS
	SAME, CHARLOTTE & MY TRUSTY 4-WHEELS
	MIKE, THE MU, TY & THE KAIPIPI CREW FOR GETTING INTO KAIPIPI
Advice and support	THIS LIST IS SO LONG, WHAT AN INCREDIBLE COMMUNITY, THANK YOU!
Field assistance	MY ENTHUSIASTIC CREW OF LOCAL VOLUNTEERS, ESPECIALLY IAN HERBERT, THANK YOU!

Kiwi work

Training	ISABEL CASTRO ON PONUI ISLAND, ROGAN, HUGH, JAMES & TASH AT MASON BAY AND PORT ADVENTURE
Field assistance	SO MANY PEOPLE CAME FROM FAR & WIDE TO ASSIST IN THE FIELD, THANK YOU!

Friends & family

For your patience and understanding at not seeing me for many months/years at a time
For mum, for reading my whole thesis with your specialised eye
And for Win, I couldn't have finished this without your support, thank you.

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Chapter 1: Introduction

Preface: This thesis is primarily about population monitoring and the use of two different methods for estimating abundance and density: territory mapping using Very High Frequency (VHF) radio-telemetry, and camera trap surveys. The case study species was Stewart Island kiwi (*Apteryx australis australis*, previously *Apteryx australis lawyri*). This species is also known as 'Southern brown kiwi' and 'Rakiura tokoeka'; in this thesis I use 'Rakiura tokoeka'.

In this chapter, I provide a brief introduction to kiwi (*Apteryx spp.*) and kiwi monitoring, and introduce Rakiura tokoeka and the study location, Rakiura/Stewart Island. I then set out my research approach and objectives and provide a short overview of the content of each chapter.

1.1 Kiwi

Kiwi are endemic to New Zealand, and belong to a distinct family of paleognathous birds, the *Apterygidae* (Germano et al., 2018). Five species of kiwi have been formally described: North Island brown kiwi (NIBK, *Apteryx mantelli*), rowi (*A. rowi*), great spotted kiwi or roroa (GSK; *A. haastii*), little spotted kiwi/ kiwi pukupuku (LSK; *A. owenii*) and Southern brown kiwi, or tokoeka (SBK; *A. australis*), and 14 extant *Apteryx* taxa are currently recognised as separate management units (Germano et al., 2018; Weir, Haddrath, Robertson, Colbourne, & Baker, 2016). Kiwi nomenclature has been, and continues to be, in a state of flux. Until recently it was thought there were only three species, and it is likely there will be further divisions of the current five extant species in the future (Evans, 2021; Weir et al., 2016). When referring to all species generally I use the term kiwi and will otherwise distinguish using abbreviations of the species common names (NIBK, GSK, LSK, SBK, and Rakiura Tokoeka). The word kiwi is a te reo Māori word, and is the same in singular and plural. Between and within species, there are differences in terms of social, territorial, mating, and breeding behaviour (Burbidge, Colbourne, Robertson, & Baker, 2003; Colbourne, 2002). This is important because these differences may impact the effectiveness of monitoring methods and the reliability and relevance of results.

Figure 1. Three kiwi (Rakiura tokoeka) outside a burrow, Kaipipi, Stewart Island (image from camera trap footage installed as part of this project).

All kiwi are flightless, ground nesting, predominantly nocturnal and precocial birds that have poorly developed eyesight and an acute sense of smell (Castro et al., 2010; Potter, 1989; Taborsky & Taborsky, 1999). Kiwi most commonly reside as pairs but can have additional birds present some or all of the time depending on age and species. Groups of up to seven Rakiura tokoeka have been recorded in one territory (Colbourne, 2002; Jahn, Harper, & Gilchrist, 2013; Robertson, Coad, Colbourne, & Fraser, 2017; Ziesemann, 2011). Figure 1 shows three adults at a nest burrow. All five species share some propensity to site fidelity. However, it is not known whether they consistently defend boundaries, who they defend against, how the boundaries change temporally and spatially, or whether they represent the limits of a home range or a territory. This life history information may differ between species (Jahn et al., 2013; Robertson, Coad, Colbourne, & Fraser, 2018; Taborsky & Taborsky, 1999; Toy & Toy, 2020; Ziesemann, 2011).

The abundance of all kiwi species have dropped significantly in the last 100 years, and the geographically isolated populations that remain are now under a variety of management schemes (Germano et al., 2018; Innes, Eppink, & Robertson, 2015). Since the first Nationwide Kiwi Recovery Programme was launched in 1991 there has been considerable large-scale and widespread action from government and community towards the ongoing conservation of kiwi due to their distinctive taxonomy, contribution to biodiversity as an endemic NZ species, and importance to NZ culture (McLennan et al., 1996, Sales 2005). Accurately monitoring the remaining populations, identifying threats, and instigating effective management is essential to support government-led population growth goals (Germano et al., 2018). Kiwi monitoring is conducted nationwide by private landowners, community groups, private research institutes, universities, and the Government's Department of Conservation (DOC) under DOC permits.

Kiwi are challenging to monitor due to their cryptic appearance and behaviour. Their feathers are mottled brown/grey which acts as camouflage, and most species are inactive in underground burrows or surface roosts during the day. They are often sparse in the environment, which can impact the likelihood of detecting them during a survey (Ziesemann, 2011), resulting in under-detections or false absences (McComb, Zuckerberg, Vesely, & Jordan, 2010). Kiwi are usually shy, avoid people, and tend to run when disturbed. Furthermore, changes in behaviour associated with breeding such as incubation, which is long in kiwi (~75 days), can impact conspicuousness (Denes, Tella, & Beissinger, 2018). However, they have loud, sexually dimorphic calls that can be detected at long distances (Colbourne & Digby, 2016). The cryptic characteristics of kiwi have dictated monitoring methods for their populations.

1.2 Case study species: Rakiura tokoeka

The case study species was Stewart Island kiwi/Rakiura tokoeka (*Apteryx australis australis*), the only kiwi species on Stewart Is./Rakiura. Rakiura tokoeka were until recently described as a genetically distinct subspecies of SBK or tokoeka, the *Apteryx australis lawyri* (Weir et al., 2016). However, in-depth analysis of the original tokoeka specimen (identified as Rakiura tokoeka) has resulted in a change to the nomenclature to the original *Apteryx australis australis,* while the other tokoeka are now considered unresolved subspecies (Evans, 2021; Robertson et al., 2021; Scofield et al., 2021). Rakiura tokoeka are geographically isolated from any other kiwi, their nearest relatives are found along the Western side of the South Island of New Zealand in three geographically distinct populations: Haast, Northern Fiordland, and Southern Fiordland (Heather & Robertson, 2005) (Figure 2).

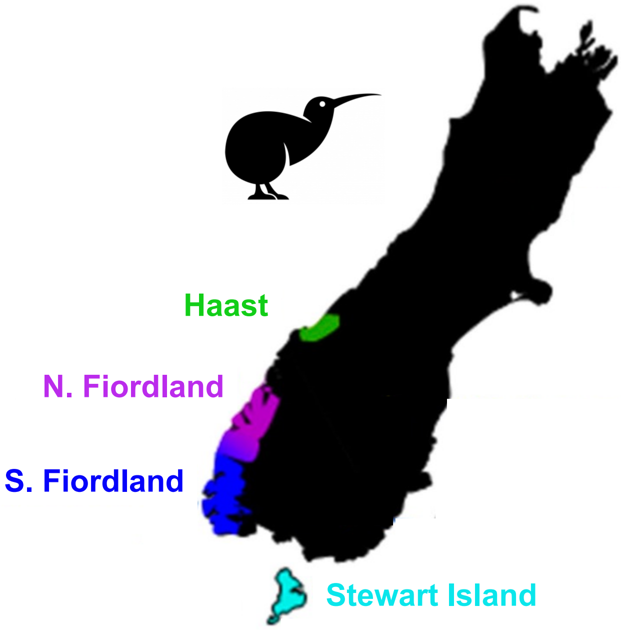

Figure 2. Geographic locations of tokoeka (Haast, North Fiordland & South Fiordland) along the West Coast of the South Island of New Zealand and Rakiura tokoekoa on Stewart Island (Figure adapted from Scofield et al. (2021)).

Anecdotal stories and some reports in the literature suggest that Rakiura tokoeka were not present in the Northern part of Stewart Island in the early 20th Century, but were common by the 1950s (Harper, 2009). By the early 21st Century they were reported as widespread (Harper, 2009), and have been observed in most available habitats on the island, including established and regenerating forest, coastal and alpine scrub, swampy wetlands, sand dunes and beaches, exposed alpine tops and around hunters' camps, Department of Conservation huts, and the sole township, Oban. In addition to mainland Rakiura, a population of Rakiura tokoeka lives on predator-free 259 hectare (ha) Ulva Island (46°57′S, 168°08′E), on the East Coast of Stewart Island in Paterson's Inlet (Figure 3). Prior to 1980 they were introduced to Ulva Island in small numbers by locals (P.Tait and U.Goodwillie pers. comm.). Official translocation records begin after 1980, when seven birds were translocated there, together with another ten in 2013 (Jahn, Cagua, Molles, Ross, & Germano, 2022).

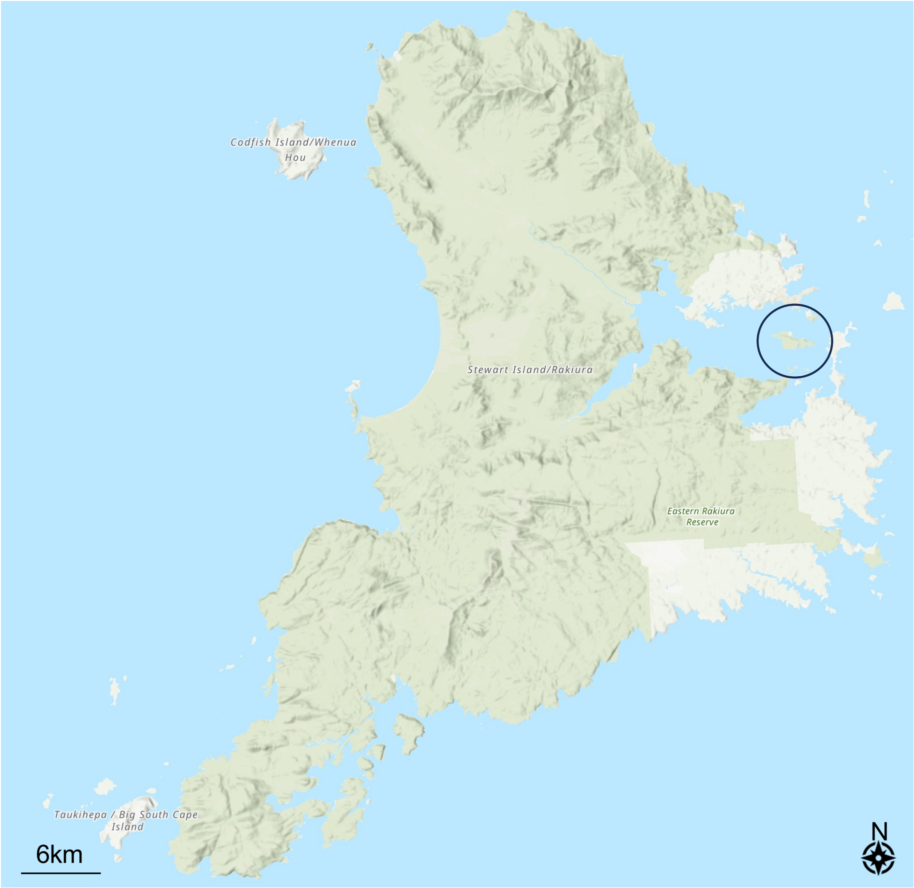

Figure 3. Map of Stewart Island/Rakiura, showing the location of Ulva Island circled in black.

Rakiura tokoeka are considered unique among kiwi for three reasons. Firstly, they are regularly active during the day, whereas other kiwi are usually nocturnal unless environmental conditions such as drought occur (Colbourne & Powlesland, 1988; Keye, Roschak, & Ross, 2011). Secondly, chicks are known to remain in natal territories for up to ten years (Robertson & Colbourne, 2022), whereas other kiwi disperse as juveniles. These extra family members may form a crèche system of raising young during the breeding season by sharing incubation duties, which has not been reported for other kiwi species (Colbourne, 1991, 2002; Germano et al., 2018). Finally, Rakiura tokoeka can live in large groups, which is unusual for kiwi, who more commonly occupy a territory as a pair or occasionally with one to two additional birds (Zeisemann 2011, Jahn et al., 2013).

The total population of *A. australis* (all tokoeka species) was estimated at c.29,500 in 2008, with an estimated 15,000 (Holzapfel et al., 2008) or 15,000 – 20,000 Rakiura tokoeka on Stewart Island (Robertson & Colbourne, 2022). At the implementation of this project, Rakiura tokoeka were classified as ‘Threatened - Nationally Endangered’ by the New Zealand Threat Classification System because they were considered to be a moderate population with ongoing decline (Innes et al., 2015). If the estimates of their rate of decline were correct, then the total number was expected to drop to 10,000 by 2030 under the current management regime (Germano et al., 2018; Innes et al., 2015). Rakiura tokoeka are now considered ‘At Risk - Naturally Uncommon’ (Robertson et al., 2021; Robertson & Colbourne, 2022), a downgrading of threat classification, although more information regarding their population is essential to be confident of their population status (Robertson & Colbourne, 2022). Given that government-led goals for kiwi conservation are for 2% population growth in all species (Germano et al., 2018), a possible decline in the Rakiura tokoeka population demands attention, or at minimum, additional information to confirm the decline and the possible reasons behind it.

The Rakiura tokoeka population receives little to no active conservation management (Germano et al., 2018). Rakiura tokoeka live in an unusual context for kiwi as the suite of mammalian pests on Rakiura is different from mainland NZ, which is probably the reason the population has persisted despite the lack of active management. Mustelids (*Mustelidae*) and dogs (*Canis lupus familiaris*) have the most significant impact on kiwi over the rest of the country, and both are absent from Stewart Island, except for residential dogs present around the sole township. At the time of writing, there is a small level of localised poison baiting targeting feral cats (*Felis catus*), limited cat trapping and periodic, localised possum (*Trichosurus vulpecula*) trapping, with most effort put into rat (*Rattus norvegicus, Rattus rattus*) trapping around the township by local community group Stewart Island Rakiura Community and Environment Trust (SIRCET) and on Ulva Island by DOC.

Effort at genetic management of the Ulva Island Rakiura tokoeka population was made in 2013 with the removal of 12 and introduction of 10 individuals from elsewhere on Rakiura (Germano et al., 2018). While the Rakiura tokoeka boasts the highest estimated population numbers among the tokoeka species, it is imperative to study and manage the four populations (Haast, North Fiordland & South Fiordland, Rakiura) separately. This approach is necessitated not only by geographical distinctions but also by the variation in potential threats facing each population, as highlighted in studies by Germano et al. (2018) and Holzapfel et al. (2008).

The 2018-2028 Kiwi Recovery Plan, which identifies priority action for the recovery of all kiwi species, suggests that a continuation of current conservation effort for Rakiura tokoeka will result in further decline (Germano et al., 2018). However, these projections, and the initiation of any management action, are hampered by inadequate information (Germano et al., 2018). Most of the published research on kiwi has been on North Island brown kiwi (*A.mantelli*). However, knowledge of the 'biology, population ecology and response to management' of the South Island species is a primary goal of the current Kiwi Recovery Plan (Germano et al., 2018). Innes et al. (2015) classifies Rakiura tokoeka as 'data poor', while Germano et al. (2018) states their current phase of recovery as 'Research'. As it stands, more research is required on the age structure, survivorship, and recruitment of Stewart Island's kiwi population (Harper, 2009). As Germano et al. (2018) points out, addressing knowledge gaps for kiwi means that conservation goals are reached more effectively.

1.3 Kiwi monitoring

The most widely used method for kiwi monitoring is call counts (Germano et al., 2018). Call surveys are frequently used because it is easier to hear kiwi than to find them, very little experience is required and they are simple to perform, which makes them broadly applicable by community and conservation groups. Kiwi call counts have been used for detecting the presence of kiwi and to estimate population variables such as abundance (De Rosa, 2021; Dent & Molles, 2016), changes in density over time (Colbourne & Digby, 2016), and more recently have been considered in occupancy and Spatial-Capture-Recapture models (Jahn, Ross, MacKenzie, & Molles, 2022; Juodakis, Castro, & Marsland, 2021).

However, there are significant variations in calling rates by individuals and populations for mostly unknown reasons (Colbourne & Digby, 2016). This means that changes in the number or distribution of calls could be falsely attributed to changes in the population. The detection of calls can also be affected by a number of different variables (Denes et al., 2018). Furthermore, chicks and juveniles do not call, therefore only adult kiwi can be surveyed with call counts. Although call counts are widely used and easily applied and replicated, little is known about how kiwi calls reflect true population variables (Germano et al., 2018), although see De Rosa (2021).

Very High Frequency (VHF) radio-telemetry is the gold-standard for spatio-temporal behavioural data (Caravaggi et al., 2017) and has been used for various kiwi monitoring and research purposes. These include; analysis of breeding and nesting behaviour (Ziesemann, 2011), chick survival (McLennan, Dew, Miles, Gillingham, & Waiwai, 2004; Robertson, Craig, Gardiner, & Graham, 2016), growth rates and dispersal of chicks (McLennan et al., 2004; A. Wilson, 2014), habitat utilisation of juvenile kiwi (Chan, 1999; Gibbs, 2000), and adult kiwi (Dixon, 2015), estimating survival and life expectancy (Robertson & Colbourne, 2004), survival pre- and post-predator control (Robertson & Colbourne, 2001; Robertson et al., 2016) dispersal, home range, pairing and breeding success post-translocation (Toy & Toy, 2020) and to determine the home range size, population density and behaviour of adults (Keye, Roschak, & Ross, 2011; Robertson, Coad, Colbourne, & Fraser, 2018). Radio-transmitters are also used to establish territory maps for kiwi (Figure 4).

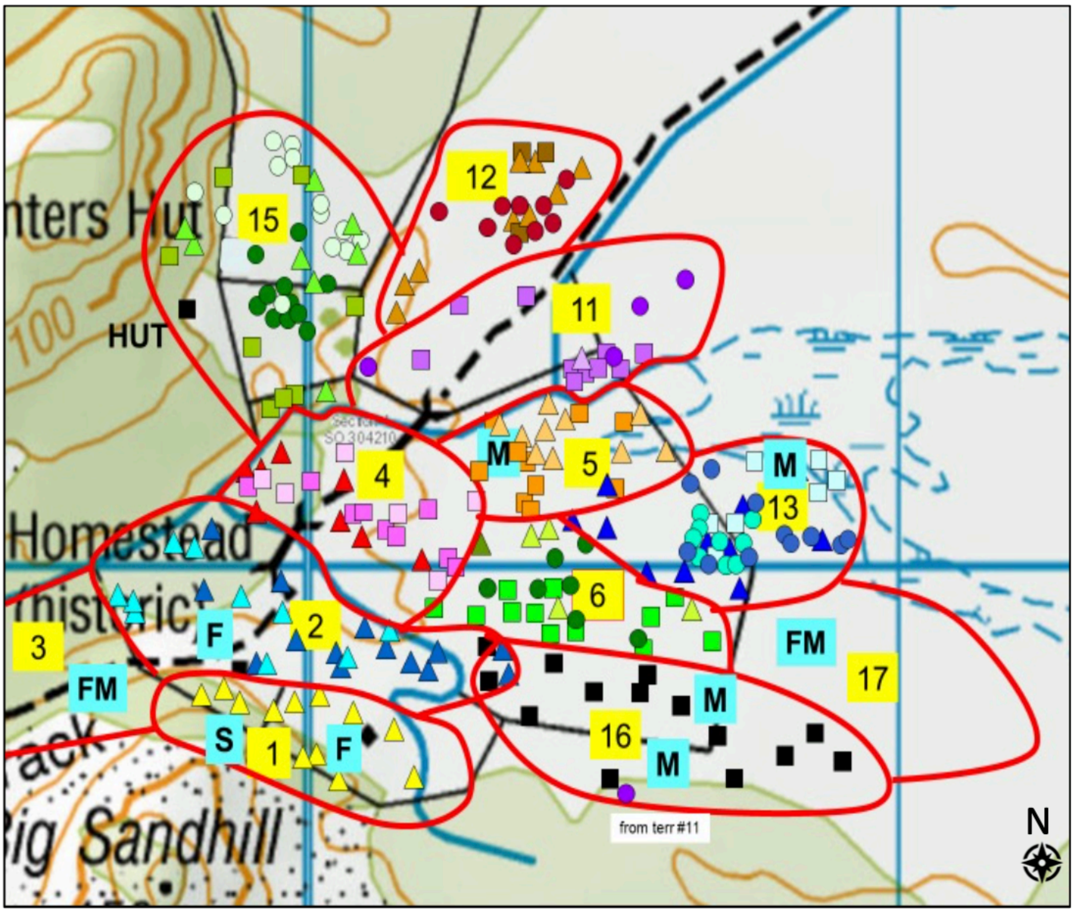

Figure 4. Territory mapping of Rakiura tokoeka republished from Robertson et al. (2018): Capture and radio-telemetry locations of Rakiura Tokoeka in the Mason Bay study area in February 2018. Each different coloured shape represents a different bird: females (squares), males (triangles) and subadults or juveniles (circles). Additional birds seen or heard are shown with approximate locations: adult female (F), adult male (M) and subadult (S).

Long-term (repeated) territory mapping is used to establish the conservation status and requirements for management intervention for some kiwi species (Robertson et al., 2018; Robertson & Colbourne, 2005). While territory mapping has long been used for passerines (*Passeriformes*) (usually based on direct observations rather than telemetry-based localisation) (Bibby, Burgess, Hillis, Hill, & Mustoe, 2000), and for other species of birds and mammals (Soisalo & Cavalcanti, 2006; Suwanrat, Ngoprasert, Sutherland, Suwanwaree, & Savini, 2015), its reliability as a method for kiwi population monitoring has not been evaluated.

When the methodology for monitoring a particular species is well-established, factors that should be considered in the implementation of surveys may be neglected. For instance, radio-transmitters may not always be the most ethical choice due to the requirement for catching and handling animals and the often-unknown impacts of these processes (Barron, Brawn, & Weatherhead, 2010). There is very little published information on the impact of transmitters on kiwi. One study suggests transmitters have been responsible for up to 20% of recorded fatalities, due to entanglement (Forbes, 2009). On Ponui Island, one NIBK was found deceased during a study by Cunningham (2010), tangled in vegetation by the leg with the transmitter attached. In their study, Cunningham et al. (2010) conducted a comparison of the tarsi in NIBK fitted with a transmitter against those without. Over a three-year period, they observed that 30% of the birds with a transmitter exhibited abrasions and calluses on the tarsus fitted with the device. Telemetry is an invasive method that can cause stress, disrupt breeding, requires experienced personnel, and significant investment in terms of cost and effort (Robertson & Colbourne, 2017; Vattiato, 2021).

Although data from tagged birds are immensely valuable, playing a critical role in conservation efforts (Sales, 2005), it is crucial to weigh the benefits against the drawbacks of invasive monitoring techniques (Witmer, 2005). This consideration becomes even more important in light of common assumptions, often without empirical support, that transmitters do not affect the behaviour or survival of tagged animals, or that any impacts are uniformly distributed across the radio-tagged population (Robertson & Colbourne, 2005). Given that current methods for monitoring kiwi populations have been criticised for being costly, inefficient, or unreliable (Innes et al., 2015), there is a clear need for methodological enhancements.

1.4 Location

Stewart Island/Rakiura is the third largest island of New Zealand (NZ) and is off the southern coast of the South Island (Figure 5). It is approximately 75 km long by 45km wide, and encompasses 1725 km^2 (Wilson, 1987), not including a number of off-shore islands. Approximately 85% of the island comprises Rakiura National Park, with one small township, Oban, located on the East Coast with around 400 permanent residents. Although the island has a significant history of both Māori and European settlers, it has never had the large-scale habitat loss and land clearance typical elsewhere in NZ (Harper, 2009).

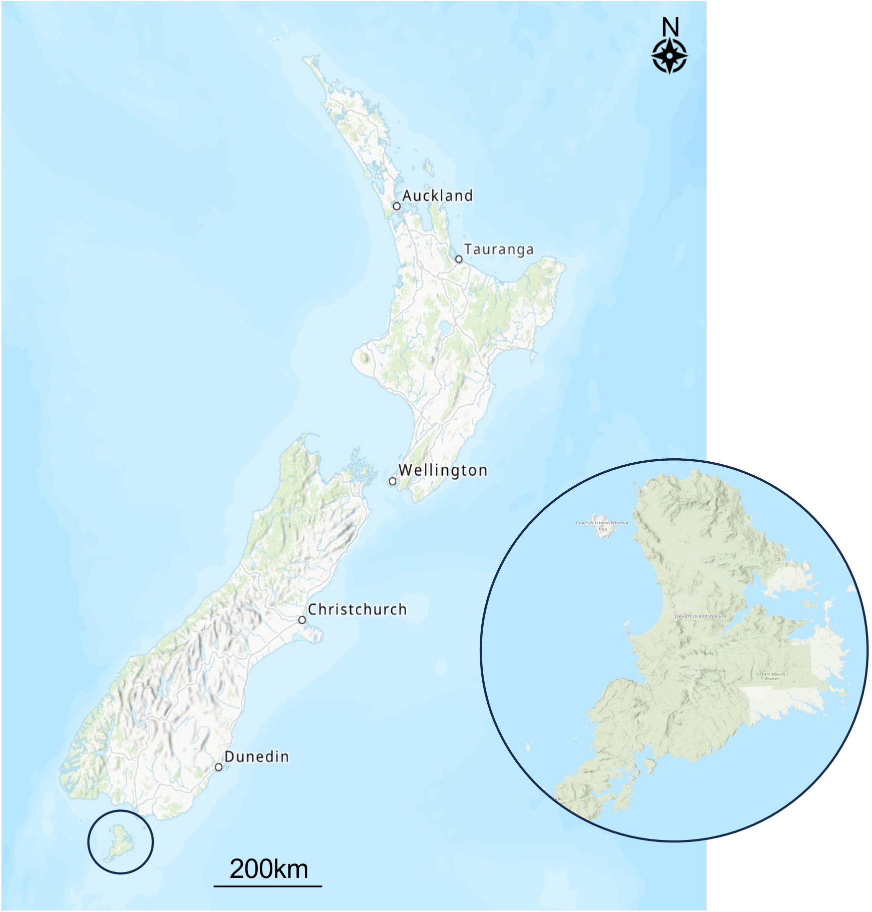

Figure 5. Map of New Zealand, showing Stewart Island/Rakiura circled at the bottom of the South Island and in the inset.

Rakiura remains predominantly forested, with many permanent wetlands, small lakes, streams and tidal rivers (Wilson, 1987). The forested areas are mainly podocarp, with low forest and scrub, with the remaining landscape components being wetland, bare rock, alpine heath and tussock grassland (Wilson, 1987). Native rimu (*Dacrydium cupressinum*), kamahi (*Weinmannia racemosa*), southern rata (*Metrosideros umbellata*), miro (*Podocarpus ferruginea*) and totara (*Podocarpus hallii*) make up the podocarp forest, with Southern beeches (*Nothofagus spp.*) notably absent. Manuka (*Leptospermum scoparium*), leatherwood (*Olearia colensoi*), *Dracophyllum longifolium*, *Myrsine divaricata, Coprosma spp*., pink pine (*Halocarpus biformis*), and yellowsilver pine (*Lepidothamnus intermedius*) in various combinations make up the low forest and scrub found in coastal, alpine and alluvial sites (Wilson, 1987). There are also sandy beaches and significant dune systems on the east, north and west coasts of the island, most notably Mason Bay, which stretches for 12 km. Winds from the west and southwest are both strong and frequent and deliver a cool temperate climate, with precipitation spread evenly throughout the year and a little snow possible in winter, usually restricted to the alpine areas (Wilson, 1987).

Despite retaining a large area of native forest and remaining largely undeveloped, Rakiura is inhabited by a suite of invasive pests that have left their mark on the landscape. Red deer (*Cervus elaphus*) and whitetail deer (*Odocoileus virginianus)* have become numerous, being introduced in 1901 and 1905 respectively (Harper, 2009). These species, along with the brushtail possum, released in the 1890s, have caused significant damage to the forest, which is now considered in poor condition (Harper, 2009). All three NZ rat species are present, ship rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*) and Pacific rat, or kiore (*Rattus exulans*). Ship rats are the most common of the three, as they dominate the podocarp forest (Harper, 2005a), and become even more abundant after a rimu mast year (Cockrem, 1995). Norway and Pacific rats became established prior to 1800 and before ship rats in 1890; however, they have largely been displaced to secondary vegetation types such as scrub (Harper, 2004).

Cats were also introduced to Rakiura in the 1800s and are still present in and around the settlement (Oban) and are feral throughout the National Park (Karl & Best, 1982). However, the array of invasive fauna present on Rakiura is different than that of mainland NZ, with some notable absentees being mice (*Mus musculus*), pigs (*Sus scrofa*), European rabbits (*Oryctolagus cuniculus*) and mustelids (Harper 2009, Wilson 1987, Taylor 1975). Despite the presence of feral cats and other invasive flora and fauna, Rakiura is home to many native species, and in some cases in higher numbers than would usually be seen on the mainland, for example, kererū (*Hemiphaga novaseelandiae*), kākā (*Nestor meridionalis*), and South Island robin

(*Petroica australis*) (Harper, 2009).

1.4.1 Study sites

Four sites on Rakiura were used for this study (Figure 6). The two sites established for this study, Kaipipi and Ulva Island, are on comparable latitudes to two historical sites used for DOC surveys, Mason Bay and Port Adventure* and largely represent novel locations for monitoring Rakiura tokoeka. (It is possible that some form of monitoring of the Ulva Island population has occurred, but no records were found). The habitat at Kaipipi is similar to that at Port Adventure, both have established, stable forest with a limited understorey due to browsing damage by deer and possums (*pers. obs.*) and the same suite of pests that are present across mainland Rakiura. Ulva Island is unique in the Rakiura landscape. It was made pest-free approximately 20 years ago, resulting in considerably more regenerating understorey than the mainland. Additionally, there is an abundance of the endemic Stewart Island weka (*Gallirallus australis scotti*) on Ulva Island, which are largely absent from the Rakiura mainland due to predation by cats (Harper, 2009).

*(NZTM, Ulva Is. 1229335E/4790896N, Kaipipi 1223234E/4795301N, Mason Bay 1204200E/4790040N, Port Adventure 1234396E/4777786N).

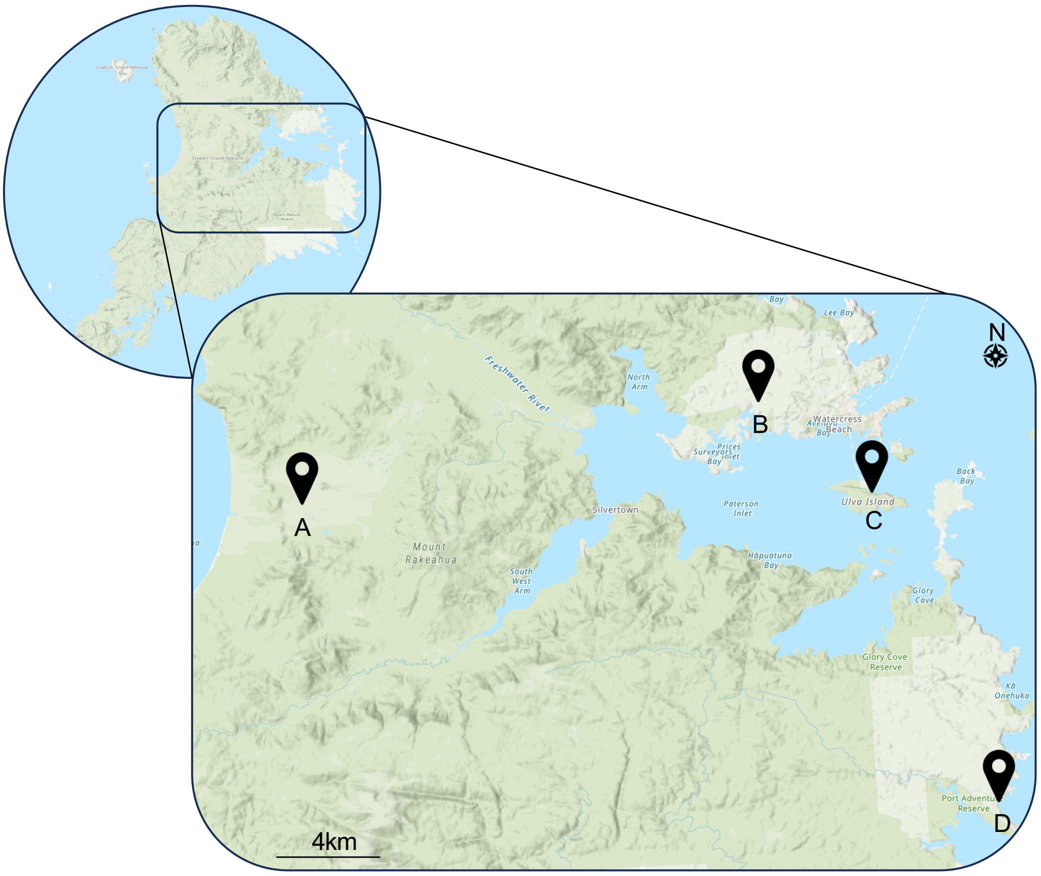

Figure 6. Map of Rakiura/Stewart Island in the top left-hand corner, with a cross-section showing the approximate center of Rakiura and the locations of the four study sites. A: Mason Bay, B: Kaipipi, C: Ulva Island, and D: Port Adventure.

Mason Bay is also unique on the island, being comprised of relatively open, regenerating farmland vegetation with coastal scrub, red tussock (*Chlionochloa rubra*) and old farm pasture inland, and pīngao (*Desmoschoenus spiralis*) and marram-grass (*Ammophila arenaria*) on the sand dunes towards the coast (Colbourne, 2002).

1.5 Research objectives

The overall aim of this project was to compare two population monitoring approaches for a cryptic species, one more invasive method that obtains direct data (radio-telemetry), and one less invasive method that collects data remotely (camera trapping). I used Rakiura tokoeka as the case study species, thereby obtaining valuable information on the Rakiura tokoeka population (age structure, survival of chicks, and population density). ‘Developing more cost-efficient and effective survey and monitoring tools for kiwi’ is a goal of the current Kiwi Recovery Plan that spans 2018 to 2028 (Germano et al., 2018).

To achieve this aim, I formulated the following objectives:

1. Critically analyse territory mapping with radio-telemetry, which is the current gold standard for kiwi monitoring (Chapter 3).
2. Trial the use of a camera trap grid to establish population estimates of Rakiura tokoeka (Chapters 4 and 5).
3. Compare the use of radio-telemetry and camera traps for monitoring young Rakiura tokoeka (Chapter 6).
4. Report on the age structure, chick survival and density of Rakiura tokoeka for population management (Chapters 3, 5, and 6).

1.5.1 Chapter overview

Chapter 2. Population monitoring

I introduce the subject of population monitoring, why it is key to wildlife conservation, and identify some of the challenges involved, particularly when working with cryptic species. The concept of invasive and non-invasive monitoring methods is introduced, along with reasons why this distinction is important. Population abundance and density are two of the most sought-after monitoring objectives, and the different ways in which population abundance is estimated are explained, from a complete census through to incomplete counts and indices. Spatial monitoring is discussed, because defining animals within an area (i.e., home range or territory) facilitates accurate estimates of density, especially with the use of technology for location data in the form of radio-telemetry or GPS tags. However, these methods are invasive, and their use is discussed in terms of the value of the monitoring outcomes.

Chapter 3. Density estimates for a cryptic species using radio-telemetry-based territory mapping

I explain the concept of a home range versus a territory and describe the monitoring method known as 'territory mapping'. I discuss how this is used for kiwi (*Apteryx*. spp.) populations. The different ways in which territory boundaries can be established are introduced, including field-workers-estimates, convex and concave polygons. The results from territory mapping using radio-telemetry for location data of Rakiura tokoeka (*Apteryx australis australis*) are reported, including the impact of the length of survey (increasing the number of location data points) and territory boundary method on territory size and density estimates. This chapter provides minimum baseline densities for the following chapters and provides suggestions to improve the use of this method for monitoring kiwi.

Chapter 4. Camera trap rates for a cryptic, ground dwelling bird, Rakiura tokoeka

In this chapter I introduce camera traps as a non-invasive method for monitoring kiwi at the population level. Using two locations where Rakiura tokoeka had previously been monitored (Mason Bay and Port Adventure), and the two locations established in Chapter 3 (Kaipipi and Ulva Island), camera trap grids were used to record camera trap rates (CTR) as indices of relative abundance between 2018 and 2020. Whether CTR and other indices were an effective monitoring method and accurately reflected the minimum populations known at the four locations through territory mapping (Chapter 3) is discussed.

Chapter 5. Estimating the abundance and density of a cryptic, unmarked species using camera traps

In this chapter I further explore the potential of cameras to monitor kiwi populations by using statistical models that estimate the abundance of unmarked species from detection histories. Three different models are considered, the Royle-Nichols model, Binomial mixture-model, and Beta-binomial mixture-model. Several common ways of establishing an effective sampling area for the cameras are presented and used to calculate density estimates for each of the four locations using the best fitted model. How close these estimates were to density estimates from territory mapping (Section 3.3.2) are discussed in the context of using camera surveys to monitor kiwi populations.

Chapter 6. Radio-telemetry and camera traps for monitoring young kiwi: Rakiura tokoeka survival

In chapter six I explore the use of radio-telemetry and camera traps for monitoring young Rakiura tokoeka (chicks and juveniles), presenting the strengths and weaknesses of each method and how a combination of the two methods can be useful to gain a more accurate impression of the age structure of a population. Novel results from radio-telemetry monitoring of breeding adults and new chicks are presented, describing incubation patterns, survival, growth, and dispersal.

Chapter 7: Synthesis

This is the final chapter and re-introduces the original objectives and discusses whether they were addressed and some of the pertinent limitations thereof. The main themes of the thesis are discussed; comparing monitoring methods, invasive and non-invasive monitoring, and how representative Rakiura tokoeka might be of other kiwi species. The most important points to consider when implementing either territory mapping via radio-telemetry or camera traps for kiwi monitoring are given, future studies are suggested, and the overall significance of the project is considered.

1.5.1.1 Permits

This project was carried out under New Zealand Department of Conservation permits: 67843-RES and 68160-FAU (Appendix E) and Massey University Animal Ethics Approval: 19/01.

Chapter 2: Population monitoring

Preface: In this chapter I discuss the rationale for population monitoring in the context of wildlife management. I also consider the advantages and limitations of different monitoring strategies, particularly for cryptic species.

2.1 Population monitoring

Population monitoring, as defined by McComb et al. (2010), is the assessment of the condition of a population through repeated observations or measurements of variables over time. It aims to identify whether a population of animals is declining, increasing, stable, or at carrying capacity (i.e., has reached the maximum number of animals that can be supported by available resources in that location). Population monitoring is fundamental in wildlife research and management (Mills, Godley, & Hodgson, 2016), and particularly crucial for threatened and endangered species (Engeman, 2005; Marsh & Trenham, 2008). By knowing the status of a population, wildlife managers can implement strategies for situations that require urgent management, for example, rapidly declining populations of valued species or rapidly increasing populations of undesirable species (Sodhi, Brook, & Bradshaw, 2009). Effective monitoring can promote the best outcomes for species conservation by providing strategic allotment of time, effort, and resource investments into management programmes (Gonzalez et al., 2016). As McComb et al. (2010) states: 'monitoring provides facts in order to aid decision making'.

Monitoring might include all populations of a species across its range (meta-population), or a single, disjunct local or sub-population (Noss, 1990). Assessing a meta-population is usually infeasible financially and logistically, particularly for species that cover large geographic areas (Sutherland, Newton, & Green, 2004). Therefore, smaller sample sites within the species range are frequently used (Pollock et al., 2002). Care should then be taken to ensure these sites are representative of the greater area, selected objectively (without bias), and of a suitable spatial scale for the species of interest and project objectives to allows repeatable measurements or observations (Blake et al., 2007).

In many cases in conservation management, decisions must be made within a short time frame. Short-term monitoring achieves the collection of information in a short time, using fewer financial resources and reducing confounding factors associated with time (e.g., population closure, natural seasonal fluctuations). However, valuable information may be missed or patterns undetected. Nonetheless, short-term monitoring may be sufficient depending on the project objectives (Bengsen et al., 2011). Longer-term monitoring is more likely to capture inter-annual variation and detect trends, particularly for long-lived species (Jouventin & Dobson, 2002).

Unfortunately, financial support for long-term monitoring is not always available; it can be resource intensive, and result in the redirection of effort from research, outreach, and active management (Elzinga, Salzer, & Willoughby, 1998).

There are a range of practical, field-based methods, and analytical strategies for population monitoring. All practical and analytical constructs reflecting a population rely on both explicit and implicit assumptions, and the validity of the monitoring output depends on the method's success at meeting these assumptions (Denes et al., 2018), because violation of assumptions may produce biased results (Buckland, Marsden, & Green, 2008). For example, it is common to monitor a sample of the target species and then extrapolate the results to draw inference about the wider population (Pollock et al., 2002). However, the assumption that a population will be distributed similarly across a landscape despite probable differences in habitat, terrain, resources, and predation risk is unlikely to be accurate, so these studies should also consider spatial heterogeneity. Another very common issue that needs to be addressed is detection probability; the natural variation in detection that occurs within and between species (Pollock et al., 2002). If unaccounted for, species can wrongly be assumed to be more or less abundant rather than more or less detectable (O'Brien, Baillie, Krueger, & Cuke, 2010), because detection can be related to many biotic and abiotic factors and the methods using for monitoring as well as abundance.

There are some general rules that can increase the reliability of population monitoring in addition to addressing assumptions. For instance, establishing clear objectives when developing a monitoring plan (Block et al., 2001; Marsh & Trenham 2008). Following this, selection of appropriate monitoring methods is imperative. Methods should be tailored by species-specific knowledge and directly capture the information required to fulfil the project's objectives. Importantly, studies that compare monitoring methods in terms of efficiency, accuracy and affordability are of significant value for informing conservation management (Joseph, Field, Wilcox, & Possingham, 2006) and for guiding future choice of methodology. By increasing the variety of potential survey methods, the likelihood of finding a technique that is particularly well suited to the objectives, species, time, and financial constraints of a study is increased (Mills et al., 2016). This is important, as discrete study populations may require methods that are considered unsuitable elsewhere (Witmer, 2005).

Comparing monitoring methods allows the evaluation of relative performance and can therefore guide method choice (Joseph et al., 2006), but seldom occurs (Gompper et al., 2006; Witmer, 2005). Ideally, potential methods would be calibrated against a known population (Keever et al., 2017; Wilson & Delahay, 2001). Unfortunately, comparing different methodological and analytical techniques against known populations is often not possible, as few of these are available (Engeman, 2005). More commonly, comparisons involve two or more methods being used to simultaneously monitor the same unknown population. In these cases, the method that most closely reflects the true population cannot be ascertained, but the methods can be compared in terms of cost, efficiency, precision of estimates, and applicability. If estimates from two methods are similar, this improves confidence in the results (Wilson & Delahay, 2001). More commonly, monitoring methods are endorsed through comparisons with more rigorous methods of population estimation (Witmer, 2005).

Further development of established methods, as well as development of novel, more efficient and affordable techniques is ongoing and contributes to effective monitoring in wildlife management and conservation programmes (Denes et al., 2018; McComb et al., 2010).

2.1.1 Monitoring cryptic species

Population monitoring relies on the successful detection of individuals or groups, and the characteristics of cryptic animals are a significant challenge for the probability of detection. Cryptic species may behave elusively (secretive, nocturnal), be morphologically cryptic (camouflaged, drab colouration, indistinguishable individuals), be rare (endangered, widely dispersed, low density), or parts of their life cycles may be impossible to observe; such as many marine animals (Chapple, Gleiss, Jewell, Wikelski, & Block, 2015; Thompson, Spoon, Goertz, Hobbs, & Romano, 2014; Witmer, 2005). The application of traditional sampling techniques to cryptic species results in various methodological and analytical challenges (Thompson, Royle, & Garner, 2012). For example, some carnivores are notoriously difficult to survey due to their secretive behaviour, wariness toward humans, and relative rarity in the landscape (Gompper et al., 2006).

The challenge of detecting cryptic species often hampers researchers' ability to gather adequate sample sizes during surveys. This can lead to inferences about individuals and populations that are criticised for their unreliability, lack of precision, and susceptibility to variability and bias (Thompson et al., 2014). Despite these limitations, the derived estimates often constitute the best available data, and the species in question typically urgently require conservation efforts (Thompson et al., 2012). Employing monitoring methods that enhance detection probability and, consequently, sample size is crucial. However, it is necessary to acknowledge that in many cases, relying on small sample sizes, variable estimates, or indices might represent the only or most feasible approach to acquiring essential information. Tailoring practical and analytical methods for population monitoring to the specific species in focus is especially vital for cryptic species, given the unique challenges they present.

2.1.2 Monitoring methods

There are a wide variety of specific monitoring tools available for surveying populations (Sutherland et al., 2004). What determines an appropriate method depends on: the range, mobility and behaviour of the species, environment, terrain, logistics, budget, experienced personnel required, consideration of the assumptions involved and to what level the method has been or can be validated (McComb et al., 2010; Witmer, 2005). In all cases, the intention should be to select the correct monitoring approach for meeting the objectives of the project (Block et al., 2001), and prioritising methods that will accurately represent the species and population of interest (McComb et al., 2010).

2.1.2.1 Invasive and non-invasive methods

Monitoring methods fall into two broad categories that I will refer to as invasive and non-invasive, based on the definition of human disturbance by Nisbet (2000). Invasive methods are those that directly interfere with an animal through catching and handling, likely changing the behaviour or physiology of an individual or individuals. Non-invasive methods are those that do not directly interfere with animals, i.e., there is no catching or direct handling, and in many cases, the species of interest is unaware of or unaffected by the monitoring. For example, annual counts of otter (*Lutra lutra*) spraints and burrows (Jenkins & Burrows, 1980). Non-invasive methods also include the use of passive data collection through remote recording devices, e.g., camera traps. In some cases, non-invasive methods can cause changes in behaviour based on how individuals respond to the scent or presence of humans or equipment in their habitat. Thus, species-specific knowledge is required to ensure any bias using these methods is reduced or eliminated.

Specific, direct, and conclusive data is provided by invasive methods, which Gompper et al. (2006) believes is ultimately more desirable. For example, catching an animal allows direct measurements and samples to be collected, and attaching a transmitter to that animal provides valuable knowledge on individual movement. However, invasive methods are also resource intensive, and often require specially trained personal. Additionally, as most monitoring studies are focused on threatened species, ethical questions have been raised about putting individuals at risk with invasive methods (Nisbet, 2000). Furthermore, the effect that direct interference by the researcher (through catching and handling) has on the natural state and movement of animals can bias results in unknown ways. However, the data obtained via invasive methods remains crucial in many circumstances.

Non-invasive methods are compared favourably to invasive methods by some as more economical and efficient (Cristescu et al., 2015), and unfavourably by others as imprecise, inaccurate, resource intensive and difficult to validate (Gonzalez et al., 2016). As opposed to the specific data obtained by catching and handling, non-invasive methods involve indirect sampling through records of field observations or using passive equipment like camera traps, with the data analysed and interpreted post-field work. For example, Brodie and Pangau-Adam (2015) made a density estimate for grizzly bears (*Ursus arctos*) in Glacier National Park by the collection and subsequent analysis of hair samples found both in the environment and in hair traps. Some non-invasive data is easier to obtain, particularly for cryptic species that are difficult to capture, widely dispersed, avoid people or are vulnerable to invasive methods, but they also require some assumptions to draw conclusions, which may not always be reasonable. Ultimately, the appropriate method for a project depends on the species of interest, resources available and the overall objective of the project.

2.2 Monitoring Abundance

There are several ways to estimate abundance. True abundance can be estimated using a census or incomplete count, or with a calculation of indices that are presumed (or proved) to relate to or reflect abundance (Wilson & Delahay, 2001) (Figure 7).

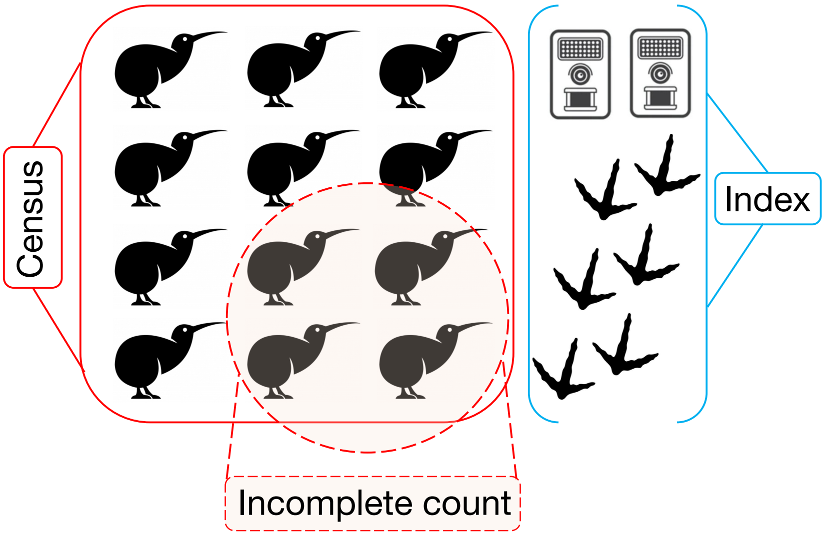

Figure 7. Estimating the abundance of wildlife populations can take the form of a complete count or census (red square with all individuals), an incomplete count (circle with a subsample of individuals) or an index (camera trap detections of kiwi, or kiwi tracks).

2.2.1 Estimating true abundance: censuses and incomplete counts

Identifying the true number of animals in a population is a highly prized objective in monitoring but is rarely achieved. A census or partial census aims to achieve this by counts of individuals, and a partial census may extrapolate this count to a wider area (assuming the distribution of animals is spatially consistent). A complete census is sometimes attempted in one or a few small areas but is usually limited by the difficulty of observing a population across its whole distribution (Pollock et al., 2002). Census counts are generally prohibitively expensive and therefore applied only to populations that exist in a restricted range or are at very low numbers, so costs can be validated against a high risk of extinction (McComb et al., 2010). In most cases, researchers accept that knowing the true number of wild animals in a population with a census is unachievable.

Incomplete counts are frequently used as an alternative. A count of individuals still occurs, but the method acknowledges that some will be missed and attempts to estimate total abundance by also accounting for the missed individuals. When incomplete counts are conducted well and account for the probability of detecting an individual if it is present (detection probability), they can produce useful estimates (Gibbs, Eagle, & Droege, 1998). However, they can be resource and labour demanding, practically difficult (Chandler & Royle, 2013; Pollock et al., 2002; Witmer, 2005), and it can be challenging to compile enough data for valid population size estimates (Kery, Gardner, Stoeckle, Weber, & Royle, 2010; McKelvey & Pearson, 2001). Furthermore, the assumptions associated with abundance-estimation methods are frequently violated and are often the reason indices are used as a substitute (Engeman, 2005).

2.2.2 Abundance indices

Population indices, which entail counts of animals or their sign at pre-determined stations across a study area, serve as a practical approach to wildlife monitoring for unmarked species (Engeman, 2005). Unlike censuses or incomplete counts, indices infer the presence of individuals without direct identification (Witmer, 2005), for example, evidence of burrows, nests, tracks, responses to audio playback, number of camera trap images or fecal counts. The efficiency and cost-effectiveness of indices make them preferable for large-scale studies, however, indices assume that the frequency of observations correlates with actual animal abundance (Wilson & Delahay, 2001; Pollock et al., 2002).

Indices may only indicate animal activity levels, with an unknown relationship to the precise number of individuals (Engeman, 2005; McComb et al., 2010). Furthermore, the accuracy of indices as a population monitoring tool is contingent upon the stability of detection rates over time, a condition rarely met in field studies (Pollock et al., 2002; Rosenstock et al., 2002). Factors such as observer efficiency, environmental conditions, and the behavioural patterns of the animals can influence detectability, introducing variability and potential bias into the data (O'Brien et al., 2010).

To counter these challenges, the implementation of standardised sampling protocols is critical, ensuring that variations in the data more likely reflect true changes in population rather than methodological inconsistencies (Rosenstock et al., 2002). Indices, therefore, are predominantly utilised for assessing relative abundance, allowing researchers to monitor population trends over time or compare different populations without specifying exact numbers (Sauer et al., 2013; Engeman, 2005; Wilson & Delahay, 2001). Such an approach is especially valuable in the study of cryptic species, where direct abundance estimation is challenging, demonstrating the need for a pragmatic yet sensitive measure that can detect population dynamics effectively (Allen, Engeman, & Krupa, 1996). The use of indices, particularly for elusive species, underscores the ongoing dialogue within conservation science about optimising monitoring methods within the constraints of available resources and the inherent complexities of studying wild populations (McComb et al., 2010; Royle & Nichols, 2003; Rosenstock et al., 2002).

2.2.3 Comparing and validating methods

The only way to know how an index relates to true population variables is to apply it to a population of known density, which rarely occurs (Gompper et al., 2006), because known densities of wild populations are rare. If specific knowledge on a target species is available, it may be possible to convert an index to a density estimate (Rovero & Marshall, 2009), but obtaining this data requires non-index methods, which removes the need for an index at all. Instead, comparisons of an index to estimates of true abundance from incomplete counts are used to validate indices. In these cases, the index measure that is closest to estimates of true abundance is considered the most successful (Suwanrat et al., 2015). While this is essentially comparing estimates from two or more monitoring methods, estimates of abundance are considered more robust than an index and therefore suitable to confirm their reliability (Rovero & Marshall, 2009; Warburton, Barker, & Coleman, 2004). To assess the ability of an index to track changes in a population, either a variety of densities are required to compare the index-density relationship (Palmer et al., 2018), or the population can be purposefully manipulated to test the response of the index (Bengsen et al., 2011).

2.3 Measuring density: animals in space

2.3.1 Spatial population monitoring: home range and territories

The size of areas used by animals and the distribution of intensity of use (i.e., preferred and less preferred habitat) is significant in most population studies (Harris et al., 1990). One way that animals may be distributed in space is within a home range or territory, areas in which an individual or group of animals spend most of their time (Figure 8). Generally, a territory is considered an area exclusively used and protected from intruders by the territory holder, within a wider area that includes all the necessary resources for an animal's life, the home range (see Section 3.1.1 for a detailed definition of a home range).

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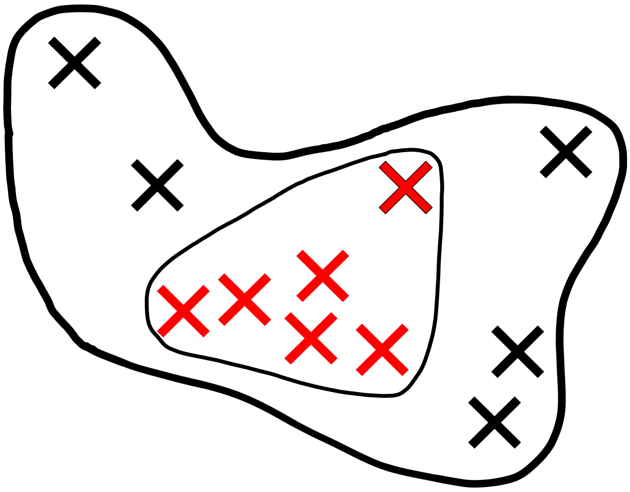


*Figure 8. The locations of an animal (X), which can be defined as a home range: an area encompassing all necessary resources (external boundary), or a territory (**X**): a smaller area within that range.*

Delineating animals by their home range or territory is a useful tool in population monitoring (Samuel, Pierce, & Garton, 1985), for various and diverse reasons (Harris et al., 1990; Rogers & White, 2007; Glenn et al., 2016; Girard et al., 2002), including the possibility that home range size can be an indicator of population health, as habitat supply and demand become equalised (McLennan & McCann, 1991). It is important to note that perhaps the most valuable output of home range/territory monitoring is the estimation of population density by estimating the abundance of animals within defined boundaries (Efford, 2019).

The size of a home range or territory is thought to be based on the availability of a limiting resource, which is often, but not always or exclusively food (Börger, Dalziel, & Fryxell, 2008; Powell, 2000). For example, in a review on the relationship of feral cats to resource availability, Bengsen et al. (2016) found that abundant resources resulted in a high density of female cats with smaller home ranges. However, home range and territory boundaries tend to vary in size and shape as a reflection of their complex relationship with biotic and abiotic factors (Glenn et al., 2016; Sunde, Zuberogoitia, & Martínez, 2011). Boundaries can shift in response to stochastic events such as flood, drought, season, breeding or non-breeding periods, age or stage of the animals, or a combination of the above (Bengsen et al., 2016; Börger et al., 2008). Additionally, resources are not uniformly distributed, nor will their distribution be constant in time (Samuel et al., 1985). The flexibility of home range and territory boundaries means the timing and duration of surveys must be carefully considered when using these frameworks to answer ecological questions.

Home range and territory boundaries can also differ depending on the methods used to estimate them, which have varied historically based on whether a home range or territory was being mapped (Section 3.1.1). This is important because density estimates can vary considerably depending on the boundaries used to define an area. Individuals will defend territories through distinctive and *observable* behaviours, including vocalisations, visual displays, scent marking, and direct confrontations (Powell, 2000). Such behaviours facilitate the delineation of territory boundaries, which are generally more straightforward to identify compared to home range boundaries (Powell, 2000). This approach has been widely applied in the large-scale monitoring of passerines (Bibby et al., 2000). Conversely, home ranges are usually mapped by tracking the locations of individuals, either through direct observation or with the aid of tools like camera traps. Progressively sophisticated methods are now available for collecting spatial data on animals that do not distinguish between a home range or territory based on visible behaviours, though traditional methods remain popular for some species (Bibby et al., 2000).

Location data in the form of home range and territories is so highly regarded it is regularly used as reference data from which to compare other monitoring methods. For example, Buckland (2006) used territory density maps of songbirds to compare various monitoring methods, and Newell et al. (2013) conducted a similar study in which baseline densities from territory maps were used to determine which monitoring methods could detect population change in seven species of songbird. This implies a level of accuracy that is difficult to attain in population monitoring, and the assumption that spatial monitoring methods are a reliable benchmark by which to test all other methods has itself not been tested (Streby, Loegering, & Andersen, 2012).

In some cases, territory maps have been shown to overestimate the abundance of species with high detection probability (Gottschalk & Huettmann, 2011), indicating that they may not be reliable in certain circumstances. However, the specificity available through monitoring locations means that they are regarded by some as the closest estimates to true density possible (Suwanrat et al., 2015). At a minimum, location data can provide researchers with estimates of both the number of animals in an area (through catch and release or multiple sampling occasions), and the size of their ranges (by tracking locations), which allows reasonable estimates of abundance and density.

2.3.2 Location data and technology

Technological developments have allowed increasingly accurate mapping of movement and location data for animals. Early methods for monitoring animals by direct observation evolved into the more sophisticated VHF radio-transmitters from the 1950s (Cochran & Lord Jr, 1963) and Global Positioning System (GPS) satellite tags from the 1980s (Fuller et al., 1984). To use these methods, animals must be caught and have the tracking device attached either permanently (until removed on recapture) or semi-permanently (designed to fall off after a period). The increased ease and accuracy of collecting individual location data facilitated by radio-transmitters and GPS tracking devices has significantly enhanced the relevancy and utility of spatial monitoring through the analysis of home range and territory data (Burgos & Zuberogoitia, 2020).

The incorporation of location data from radio-telemetry into population monitoring has made huge advances for population estimation (Robertson & Westbrooke, 2005; White & Garrott, 1990; Seber, 1986). Radio-transmitters can be multi-functional, providing information on location and movement as well as behaviour (Harris et al., 1990), for example, they can be programmed with specific capabilities, for example, providing a mortality signal (Robertson & Westbrooke, 2005). The requirement for direct physical tracking has the advantage that researchers are more likely to gain an intimate knowledge of the study environment and species. Once a transmitter is attached, individual animals can be detected over 1 km away (depending on the terrain) (Robertson & Westbrooke, 2005), and if resources allow, by a receiver/aerial mounted on an aircraft (White & Garrott, 1990). Although radio-telemetry is more expensive than monitoring the visible locations of singing birds to establish territories (Anich, Benson, & Bednarz, 2009), it is much lower cost than GPS, has been developed for numerous species, provides specific data on individuals, and allows minimal subjectivity in spatial data.

The use of tracking devices on animals allows several benefits compared to other monitoring methods. For example, a substantial amount of data on individuals can be captured while handling animals to attach transmitters. Morphological measurements, biological samples and confirmation of sex and age are hugely valuable and can be difficult, unreliable, time-consuming, or impossible to obtain without direct handling.

The shift from observation-based monitoring to direct marking of individuals has also meant that in some cases a more accurate representation of the population is likely to be captured in the data. For example, Bibby et al. (2000) found that mapping bird territories using direct observations of defensive behaviours tended to miss a large, non-breeding component of the population. Furthermore, being able to regularly determine the specific location of animals allows better estimates of population size because the issue of emigration and immigration (i.e., an animal’s presence on the study site and consequent availability for re-sighting) can be controlled (White, Franklin, & Shenk, 2002). As the cost of radio-transmitters and GPS tracking decreases and tags get smaller, with a longer battery life and more capabilities, both methods will only increase in applicability and utilisation for wildlife monitoring (Barron et al., 2010; López-López, 2016).

2.3.3 Radio-telemetry: an invasive method

As the use of radio-transmitters increases, it becomes even more important to understand how they affect the individuals to which they are attached (Barron et al., 2010). If the impact of the transmitters is not understood, it can introduce bias into the survey. Furthermore, catching animals to attach tags can have negative impacts on individuals (Caravaggi et al., 2017). A meta-analysis of 84 tracking studies on various bird species by Barron et al. (2010) showed that birds that were captured and restrained spent less time foraging, regardless of whether they had had a transmitter attached. If a transmitter was attached, the specific type used resulted in varying levels of disturbance, harm, or even mortality. Additionally, Barron et al. (2010) found that birds wearing tags had significantly higher energy expenditure, were less likely to nest than birds without, and had lower nesting productivity and offspring quality (Barron et al., 2010). Transmitters can also indirectly reduce the fitness of un-tagged individuals if they must compensate for decreased parental investment by a mate with a transmitter (Paredes, Jones, & Boness, 2005). Observer presence during the multiple tracking occasions usually associated with radio-transmitters could also impact animal behaviour and welfare in unknown ways.

The decision to employ telemetry should hinge on its relevance to solving specific research questions, acknowledging that, in many instances, it may represent the only feasible approach to garnering the necessary insights (White et al., 2002; Rogers & White, 2007). Given that the effect of catching and attaching transmitters can never be completely avoided (Kenward, 2000), the often-unknown biases these processes introduce and the fact that catching and marking animals is very time consuming (Bibby et al., 2000), it is worth carefully considering the benefit of using transmitters in a project, and whether another monitoring method could substitute it. Furthermore, an assessment of the likelihood that telemetry will lead to improved management outcomes for the population is recommended (Silvy, 2020).

2.4 Summary

Population monitoring should be a central component of any wildlife conservation, research, or active management project. Estimating population abundance and density over time is often the most desired outcomes of monitoring and can detect changes in the abundance of protected and pest species and inform management where, when, and how to intervene. The true abundance of populations is rarely known, and most often, incomplete counts and indices are relied on for abundance estimates or proxies for abundance instead of a census.

A wide variety of invasive and non-invasive methods are available for monitoring purposes, with a growing movement towards non-invasive methods (Gompper et al., 2006; Long, MacKay, Ray, & Zielinski, 2012). Comparing methods against one another or against known populations is a valuable way to evaluate monitoring options and validating indices in this way is essential for reliable estimates. Regardless of the project objectives and the practical and analytical methods chosen, there are specific challenges with all choices, and inherent difficulties in population monitoring generally. Cryptic species pose a particular challenge for population monitoring, adding to the suite of contending factors that require consideration in the instigation of monitoring programmes. Spatial monitoring of the home range or territories of a species is a valuable way to consider populations, particularly with the use of technology for tracking, although the benefit of the monitoring results should be considered against the invasiveness of the method. The most effective estimates of density for populations are achieved by applying a species-specific monitoring method, meticulous standardisation of surveys and, ideally, validation or comparison with independent estimates.

Chapter 3: Density estimates for a cryptic species using radio-telemetry-based territory mapping

Preface: The purpose of this chapter is to present population monitoring results generated from territory mapping using radio-telemetry. This method is frequently used for kiwi, and I used it for monitoring two populations of Rakiura tokoeka. The method of territory mapping is explored by determining the effects on territory size and population density estimates from changes in the way territory boundaries are established and by extending survey length.

3.1 Introduction

Estimating population density is a key goal for the management of kiwi in New Zealand. As a species requiring intervention for conservation and survival, kiwi have been formally monitored for their number and spatial distribution for decades. This has resulted in efforts to manage threats such as predation, and interventions such as captive breeding.

One way to assess the spatial distribution of animals is by identifying their home range or territory size and shape, and counting the number of individuals within it. Knowledge of home ranges or territories can be used to investigate habitat selection, resource distribution, compare populations and estimate the density of kiwi populations. Depending on the study species, project objectives, and resources available, there are several ways to establish the home range or territory of an individual or group. This chapter evaluates the original method for determining territory boundaries; ‘territory’ or ‘spot’ mapping (Williams, 1936), using one of the most accurate methods currently available for localisation of animals, Very High Frequency (VHF) radio-telemetry. This method has been used for kiwi since 1987 (McLennan, Rudge & Potter, 1987).

3.1.1 Home ranges and territories

Most animals do not range unpredictably, but base themselves within an area (Burt, 1943; Laver & Kelly, 2008; R. Powell & Mitchell, 2012). In the literature it is common to differentiate between a home range: the entire area used by an animal for reproduction and survival (Börger et al., 2008), and a territory: an area of priority use within a home range that is defended to maintain exclusivity (Powell, 2000). Individuals can have a home range but not be territorial, i.e., they do not defend or assert their home range against intruders, or defence may change under varying conditions such as resource availability (Newsome, Ballard, Dickman, Fleming, & van de Ven, 2013). The key difference between a home range and territory in a monitoring context is how the boundaries are delineated. The boundaries of home ranges are more flexible and tend to overlap with neighbours (Burt, 1943; Samuel et al., 1985), so the total home range area is determined by the locations where individual animals are found, excluding occasional excursions ‘outside’. Territories are typically those parts of a home range that are of higher value, such as nesting/breeding areas, refuges, or dependable food resources, and boundaries may be determined by territorial behaviours such as defensive displays, advertisement or reactions to intruders (Börger et al., 2008). Territories may also be referred to as ‘core areas’ based on frequency of use.

Historically, bird territories were mapped by recording the locations of visible defensive behaviours (Bibby et al., 2000), while a home range was primarily concerned with location, rather than behavioural data. Increasingly, animals are tracked using radio- and GPS-transmitters (Section 2.3.2), with the data collected representing an area or areas of activity that can be interpreted in various ways (Hinsch & Komdeur, 2017). Seasonal data showing how the landscape is used throughout the year may be used to determine home range, while core areas of high activity may indicate an area of priority use or territory. Perhaps as a result of this technological transition, it is not always clear in the literature whether a home range or territory is being estimated, or which term is most appropriate for the species in question. In this chapter I use the term territory ‘mapping’, which matches the literature on the method for kiwi, however, in this case, ‘activity area’ or ‘home range’ may be more accurate.

3.1.2 Territory mapping

Williams (1936) first described the method for estimating the territory size and number of breeding pairs of songbirds that later became known as ‘territory’ or ‘spot’ mapping (Thunhikorn, Grainger, McGowan, & Savini, 2016; Tomiałojć, 2004). Repeat visits are made to a site, and direct observations of individuals and indirect records of calls and nests are plotted onto maps. Approximate boundaries are drawn by hand around the clusters of mapped observations to represent the ‘territories’ of breeding birds (Bibby et al., 2000) (Figure 9).

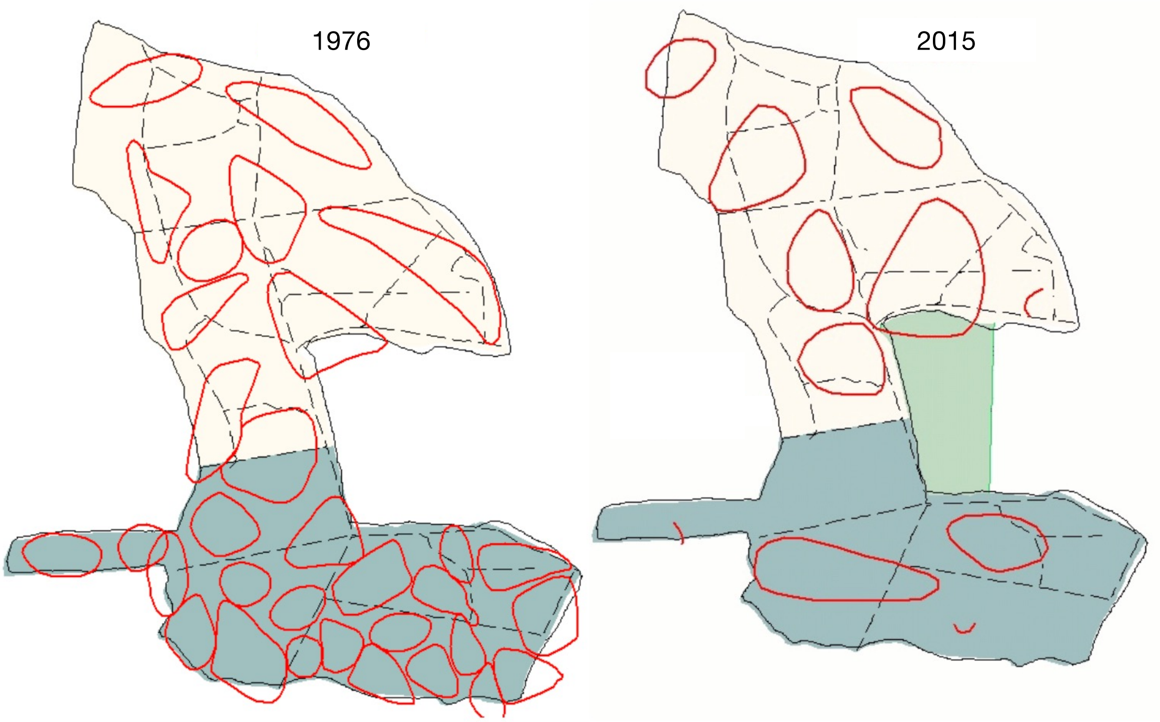


Figure 9. An example of territory mapping from the Breeding Bird Survey in Treswell Wood, England of Song Thrush (Turdus philomelos) showing fewer breeding territories in 2015 than there were in 1976. Red shapes denote breeding territories. (Figure from https://www.treswellwoodipmg.org/common-bird-census).

The terms territory or spot mapping can describe various approaches to monitoring territories. For example, Anich et al. (2009) and Burgos and Zuberogoitia (2020) considered the locations of bird vocalisations as the basis for territory maps. Lin, Hsu, and Ding (2011) only mapped the location of singing males, while Verner (1985) preferred mapping moving birds, and other studies have included field sign such as scats, tracks, burrows or nests, or aggressive interactions between conspecifics into territory maps (Gregory, Gibbons, & Donald, 2004; Robertson et al., 2018; Tomiałojć, 2004). Although historical methods typically used unmarked birds, Peele, Marra, Sillett, and Sherry (2015) referred to territory mapping as a method that maps 'marked' individuals only. For example, Streby et al. (2012) mapped the locations of song perches chosen by banded birds. Location data from radio-transmitters has been used to map the locations of both tagged and untagged individuals, i.e., as many animals as possible (Fuller, York, Powell, Decker, & DeGraaf, 2001; Greene & Pryde, 2012), and by using a single tagged individual to represent a group of territory holders (Suwanrat et al., 2015).

The primary purpose of territory mapping is understanding territory densities (McComb et al., 2010; Thunhikorn et al., 2016), which have been used to determine the abundance and density of individuals, pairs and groups of birds (Gottschalk & Huettmann, 2011; Gregory et al., 2004; Suwanrat et al., 2015; Tomiałojć, 2004), changes to populations and population trends (Fuller et al., 2001; Newell et al., 2013), community composition, and the relative abundance of different bird species (Lin et al., 2011; Svenson & Williamson, 1969; Tomiałojć, 2004). Territory mapping has been frequently been used for bird census at both small and large scales using mapped locations of direct observations of territorial behaviours (e.g., (Bibby et al., 2000; Svensson, 1979)). While territory mapping is considered by some to be predominantly a survey technique for song-birds (Bibby et al., 2000), it has also been used for ground-dwelling birds (Suwanrat et al., 2015), and mammals (Fuller et al., 2001).

Territory mapping is a non-statistical method. As Gottschalk and Huettmann (2011) point out, the absence of confidence intervals or any other statistically based assessment raises questions over the use of territory mapping for management decisions. Interpreting results can be subjective and the difficulty in quantifying precision and bias makes it challenging to compare results across studies (Buckland, 2006; Gregory et al., 2004). Despite this, territory mapping is considered an international standard for conducting large-scale, long-term bird censuses (Bibby et al., 2000; Svenson & Williamson, 1969), has been used for baseline estimates to test other monitoring methods (Buckland, 2006; Newell et al., 2013), and is sometimes regarded as a ‘true’ census or as close to true density as is possible to achieve through monitoring (Greene & Pryde, 2012; Suwanrat et al., 2015). Although it is not considered as statistically rigorous as other monitoring methods, territory mapping has also been favourably compared to capture-mark-resight surveys using cameras (Fuller et al., 2001).

Territory mapping relies on determination of territory boundaries, which traditionally relied upon field observations. Boundaries would be hand-drawn onto maps, and so accounted for knowledge and experience of the field site by the observer as well as direct observations of individuals (Bibby et al., 2000). This method of drawing boundaries is sometimes referred to as the ‘field-workers-estimate’ or ‘observers method’ (Keye et al., 2011; Macdonald et al., 1980). Observations of field sign may be included, such as scat, burrows, or footprints (based on the assumption of exclusive use), as well as projected locations of animals from calls or telemetry signals, positions of territorial behaviours and other observations. Territory boundaries are often adapted to align with natural topographical borders (e.g., rivers), eliminate overlap or space between neighbouring territories and account for local geographical features. Macdonald et al. (1980) advocate for this method as the closest approximation of the reality of animal societies due to the incorporation of knowledge based on non-specific location data.

Boundaries that are fixed by location points and are not manually adjusted for environmental features, neighbouring territories, or field sign provide a less subjective way of establishing boundaries. The Minimum Convex Polygon (MCP) is one of the oldest methods and remains commonly used for comparisons with previous studies (Harris et al., 1990; Kenward, 2000; Mohr, 1947; Powell, 2000), although it has largely been superseded by more complex methods that focus on frequency of use within boundaries (Worton, 1989). MCP (100%) boundaries are created by connecting the furthest outlying location points of individuals, pairs, or groups in a territory in the smallest polygon that encloses the points using straight lines (Macdonald et al., 1980).

MCPs are particularly sensitive to outliers (Macdonald et al., 1980) and the size and shape of a territory using MCPs can vary widely based on only a few location points. To reduce the impact of outliers, 95% MCP polygons are often applied. However, MCPs are still largely considered simplistic and unrealistic. Regardless, MCP boundaries have been used to explore the size, overlap and density of territories of the ground dwelling Siamese Firebacks (*Lophura diardi*) (Suwanrat, 2013), to monitor the survival, dispersal, and breeding of GSK (*Apteryx haastii*) (Toy & Toy, 2020) and they are utilised for a range of species including songbirds, tawny owls (*Strix aluco*) and jaguar (*Panthera onca*) (Burgos & Zuberogoitia, 2020; Soisalo & Cavalcanti, 2006; Streby et al., 2012). Minimum Convex Polygons remain popular due to ease of calculation and importantly, their capacity for comparison between studies (Harris et al., 1990; Rogers & White, 2007).

In order to avoid the over-estimation of territory size that can occur with convex polygons, concave polygons can be used. Concave polygons also encompass all the location points using straight lines but minimise the distances so that they are essentially a conservative version of a convex polygon (Kenward, 2000). As a result, concave polygons have been regarded as correcting or reducing the disadvantages of convex polygons (Harris et al., 1990), by avoiding the inclusion of large areas that are potentially unused by the animal (Keye et al., 2011). More contemporary methods such as kernel estimators use multiple factors to exclude areas that are unlikely to be used be used by animals and can be fitted to certain types of data (Yang et al., 2020; Worton, 1989). However, these focus less on territory boundaries and more on internal use of territories, and may require large sample sizes (Seaman et al., 1999; Girard et al., 2002).

Concave and convex polygons join external location points and so do not describe the intensity of use within the range (Kenward 2001). This makes them useful options for territory mapping that uses the size and shape of territories. Both polygon options can be used to join observation points that are based on true locations, projected estimates of locations, territorial behaviours or observations of field sign, but they are most commonly applied to location data from radio-telemetry or GPS satellite and so, in most cases, more accurately describe a home range as opposed to a territory.

3.1.3 Territory mapping for kiwi

Kiwi (*Apteryx spp*.) are generally considered territorial, although various levels of territory overlap have been reported among the different species (Dixon, 2015; Potter, 1989; Taborsky & Taborsky, 1999; Ziesemann, 2011). In general, the original concept from Williams (1936) for territory mapping holds true for kiwi, as clusters of locations indicate the area an individual is usually found in, and their propensity to share burrows or roost sites with other individuals assists greatly in establishing co-territory holders.

Territory mapping has been used in some form to monitor kiwi for decades. Powlesland (1988) described an estimate of population density determined from ‘call frequencies and territory mapping’ by the Wildlife Service of a local population of Stewart Island kiwi between 1977 and 1981 (original report unavailable). The first published territory map available in the literature is from Colbourne and Kleinpaste (1983), who captured and marked NIBK (*Apteryx mantelli*) with metal bands and used capture and recapture locations, re-sightings, and estimated positions of calling birds to map the distribution of territories. Methods were developed further with the introduction of radio-telemetry: McLennan et al. (1987) used locations of radio-tagged NIBK and field sign (faeces, footprints, and probe holes), to map territories in the Hawkes Bay. In the years since, variations of direct and indirect location data and methods of drawing territory boundaries have been used for mapping kiwi territories, predominantly by the Department of Conservation (DOC).

Territory mapping using radio-telemetry is used by DOC throughout New Zealand to map the territory boundaries of individuals, pairs, and groups of kiwi, and is currently considered the most reliable method for determining population density (Robertson et al., 2018; Robertson & Colbourne, 2005). Repeat surveys at specific locations provide long-term territory mapping data that is used to make population estimates for different kiwi species. These estimates are relied upon to establish the conservation status for each species and indicate where management might be required (Innes et al., 2015; Robertson et al., 2021; Robertson et al., 2018; Robertson & Colbourne, 2005).

The Department of Conservation has outlined a protocol for using territory mapping to monitor kiwi populations (Robertson et al., 2018). DOC territory mapping surveys are rapid; approximately two weeks in duration, and surveys always occur in summer during the non-breeding season to avoid unnecessary disturbance to nesting birds. Territory maps are constructed primarily from locations of individuals with radio-transmitters, although sightings of un-tagged birds and estimated locations of calls may be included (Robertson et al., 2018). Territory boundaries are established using field-workers-estimates; encompassing location points while adjusting for neighbouring territories (removing overlap or assimilating small gaps) and accommodating geographical features using site-specific knowledge.

Despite the territory mapping methods used by DOC being readily available since 2005 (Robertson & Colbourne, 2005), there has not been an uptake of standardised methods across locations or species outside of DOC. For example, combinations of triangulated (indirect) and homed (direct) locations of radio-tagged birds have been favoured for mapping territories of GSK, with boundaries made by convex polygons preferred in some cases (Jahn et al., 2013; Toy & Toy, 2020), and concave in others (Keye et al., 2011). Survey duration has also differed, with some studies lasting a few months (Jahn et al., 2013), while others extend over a year (Keye et al., 2011), or multiple years (Toy & Toy, 2020). This means that the breeding season may or may not be included, which could affect the results if populations undergo changes in territory shape or size throughout the year (Ziesemann, 2011).

Territory mapping is effective, but also time and resource intensive (Gottschalk & Huettmann, 2011; Greene & Pryde, 2012), and invasive, and therefore its utilisation should be carefully considered. Sutherland (2006) suggested territory mapping was only feasible in small areas because of the effort required, and that less intensive monitoring methods should be considered when working in larger landscape-scale areas, even if they provided less precision. Territory mapping requires experienced personnel, and the birds can be hard to catch, which can limit the applicability of the method. If telemetry is being used the cost of devices and equipment can be prohibitive. Additionally, when territory mapping involves marked birds, the method relies on a high proportion of the population being marked, and that all unmarked individuals are identified (Fuller et al., 2001; Greene & Pryde, 2012), which requires intensive survey effort. These issues particularly affect kiwi conservation, which involves many community groups and volunteers. The benefits of territory mapping and the outcomes of its employment for kiwi monitoring are therefore worth exploring.

3.1.4 This project

To have confidence in the results of current territory mapping methods for kiwi (Robertson et al., 2018), an exploration and assessment of the method is needed. While DOC's protocols may prove adequate both for rapid surveys and longer-term population estimates for kiwi, the use of territory mapping for ground-dwelling birds is questioned by Thunhikorn et al. (2016) in a review of four methods (although they do not consider the use of radio-telemetry data), and Denes et al. (2018) encourage researchers to challenge the status quo of widely accepted methods. There is a large number of groups and individuals working in kiwi conservation in New Zealand, which makes it increasingly important to consider the effectiveness of monitoring methods and to work towards consistent monitoring for comparability of results. Furthermore, it is essential to determine if the benefits of telemetry-based territory mapping justify its high costs, need for experienced personnel, resources, labour, and invasiveness compared to other forms of population monitoring that could be used as alternatives (Engeman, 2005).

Rakiura tokoeka (*Apteryx australis australis*) are a species of kiwi that are resident on Stewart Island/Rakiura (see Section 1.2 for more details). Until recently, results from territory mapping surveys by DOC on Rakiura raised concerns over an island-wide declining population due to a gradual decrease in numbers at Mason Bay since five-yearly surveys began in 1993 (Colbourne & Robertson, 2013). This prompted the establishment of a second territory mapping location at Port Adventure, where the first survey in 2011 caused further concern with a single chick recorded (Robertson & Colbourne, 2011). Changes to the different components of a population, i.e., adults, young, females, can indicate issues with predation or recruitment that require management intervention (McComb et al., 2010). However, the most recent DOC territory mapping in 2017 at Port Adventure and 2018 at Mason Bay contributed to a downgrading of threat classification from 'Threatened - Nationally Endangered' to 'At Risk - Naturally Uncommon' (Robertson et al., 2021) as the population is now considered potentially stable due to an increased proportion of young birds at Port Adventure and no further decline at Mason Bay (Robertson et al., 2017, 2018) (Table 1).

Table 1. The number of territories and the estimated minimum number of Rakiura tokoeka in the 125 ha study area at Mason Bay, Stewart Island, from 1993 to 2018. The minimum number of birds assumes marked birds that were missed during a survey did not leave the study area and return. The age composition of birds is given each survey period: chicks are estimated to be 0-50 days old, juveniles 50 days to 6 months old, and subadults are 6 months to 5 years old (Robertson et al., 2018).

Year	# Territories	Min # Birds	Adults	Subadults	Juveniles	Chicks
1993/94	17	41	38	2	0	1
1997/98	16	45	43	2	0	0
2002/03	14	38	33	5	0	0
2007/08	13	36	33	2	1	0
2012/13	11	35	31	3	1	0
2017/18	12	38	30	7	1	0

Rakiura tokoeka monitoring in the last two decades has been limited to DOC's territory mapping surveys at the previously mentioned locations (except for yearly call counts run by community group Stewart Island Rakiura Community and Environment Trust). The initiation of any management action for Rakiura tokoeka is hampered by inadequate information and the uncertainty reflected in the conflicting reports of population decline versus stability from DOC. Despite the recent conclusion that habitat change caused localised population decline of Rakiura tokoeka at Mason Bay by Robertson and Colbourne (2022), this was based on a slight (7.5%) reduction in average body mass for males and females between 1988 and 2018, which had no comparison to birds outside of Mason Bay or independent measures of food availability. Further research is required on the age structure, survivorship, and recruitment of the island's population (Harper, 2009), and additional information from Rakiura would assist with confident statements around long-term population viability (Germano et al., 2018; Innes et al., 2015; Robertson et al., 2021).

3.2 Methods

3.2.1 Radio-telemetry & tracking

In February 2019 I set out to replicate as closely as possible the territory mapping methods used by Robertson et al. (2017, 2018) at Kaipipi and on Ulva Island (see Section 1.4.1 for a description of study sites).

Individuals were caught in a pre-determined area, as described in Appendix A.1, and radio-transmitters (North Island Brown Kiwi Chick Timers from Lotek and Kiwitrack Ltd., Havelock North, NZ) were attached. Methods included night catching using pre-recorded kiwi calls to elicit territorial behavior from kiwi, daytime use of kiwi detection dogs, and burrow/roost checks.

Birds were measured and weighed, and their age and sex were estimated as part of the transmitter attachment process. Post-catch feather testing was used to confirm sex. To establish a consistent and objective method for categorising the age of birds I determined <800 g as a chick, 800 – 1800 g as juvenile, and >1800 g as either sub-adult or adult depending on the weight, sex, growth between measurements and condition of leg scales and toe nails (worn/calloused versus supple and shiny). This is in contrast to previous Rakiura tokoeka surveys (Robertson et al., 2017, 2018) and what is outlined in the Kiwi Best Practice Manual (Robertson & Colbourne, 2017), where age is determined more subjectively based on the experience of the handler.

The aim for monitoring the birds with a transmitter was to collect a minimum of 5 different locations per bird and 10 different locations per territory (H. Robertson, pers. comm.). The birds with a transmitter were tracked to their location and their positions were recorded using a GPS unit. During tracking to location, the burrow or roost site was checked for additional birds, which could then be recorded and fitted with a transmitter. Territory maps were based on adult and sub-adult locations only. Chicks and juveniles found during the initial catching trips (<1.8 kg) were weighed and measured, but did not receive a transmitter. The locations of chicks caught later in the study (Section 6.2.4) were also not included.

Locations of tagged Rakiura tokoeka were recorded and individuals were assigned to a territory based on clusters of locations and records of which individuals were found with other known birds either at initial catch or on later tracking occasions. Some initial catch sites occurred at night (44% at Kaipipi, 65% on Ulva Island) and so represent nocturnal locations, otherwise locations were primarily from daytime fixes, which for Rakiura tokoeka could mean roost or burrow sites as well as active foraging locations.

The locations of individual Rakiura tokoeka were recorded for 17 months, until transmitters were removed or dropped off. The goal was to track each bird at least twice weekly. However, this was not always possible due to logistic and personnel constraints or because individual signals could not be detected on occasion.

3.2.2 Location fixes

To compare how the number of location fixes affected estimates of study area size, territory size and density, I used three categories: (10 – 20), (20 – 40) and (> 40) of fixes per territory. While I retained the recommended minimum of 10 location fixes per territory recommended by Robertson et al. (2018), I exceeded this in territories where the first 10 fixes were unevenly shared between individuals. In these cases, I increased the sample size to be ⩾ 20, resulting in a minimum number of fixes of 10 – 20 per territory. This is as comparable as possible to results from other mapping studies for Rakiura tokoeka (Robertson et al., 2017, 2018) given that the number of fixes collected for territories tends to be variable and can span 5 – 30 (H. Robertson, pers. comm.). The two categories of 20 – 40 and > 40 fixes were based on the incremental area analysis for the number of location fixes (see Section 3.3.5), with 20 – 40 representing approximately 80 – 90% of territory size, and > 40 fixes reaching 100% or close to of territory size for Kaipipi and Ulva Island.

Within each category of location fixes, an equal number of locations was contributed from each bird (except in one circumstance where a single individual on Ulva had a total of six location fixes and the other inhabitants had 18 – 21). Consecutive location fixes were used for each territory, so that the 10 – 20 category included the first 10 – 20 recorded fixes for that territory.

For all analyses that do not discriminate between location fix category, the maximum amount of location data available per territory was used. Two cases of extreme outliers and one case of a moderate outlier from three individuals at Kaipipi were excluded as singular occasions of ranging outside the territory. These were considered outliers as the locations were 1.8 – 12.5 standard deviations from the range of individuals at Kaipipi.

3.2.3 Territory boundaries

Three methods of establishing territory boundaries were applied to the data: field-workers-estimate, convex and concave polygons. For field-workers-estimates, territory boundaries were mapped in Google Earth Pro V 7.3 using the external locations of transmitted birds within a group/territory. Overlap between adjacent territories was removed if present (rarely applicable) (Robertson, 2018), manual adjustments were made to extend Ulva Island boundaries to the coastline if the distance was less than the average territory size, and reasonable gaps between territories were incorporated (distances <75 m). This distance was used because the smallest distance between subsequent location fixes for an individual was >80 m.

Convex (100%) and concave polygon territory boundaries were mapped using Ranges V.9 (www.anatrack.com), the main difference to field-workers-estimates being that only external location data was used to join boundary lines, no manual adjustments were made for neighbouring territories or geographical features. Convex polygons were set to 100% to avoid making the assumption that 95% adequately represented territory extent given this is the first application of convex polygons to Rakiura tokoeka territory boundaries. Convex polygons were used as an alternative to field-workers-estimate boundaries to enable comparisons, and to avoid the emphasis on nest sites (through localised activity), and high sample sizes required by more complex methods.

The maximum number of locations per territory was included in the analyses with a tracking resolution of 10 m to account for GPS error. For concave polygons, 100% of the location data was used (set by default) and the ‘edge restriction’ was set to 0.5 (proportion of the maximum range width).

Incremental area analyses were conducted in Ranges V.9 for each polygon type to indicate how accurately the number of location fixes represented the average territory size. One territory at Kaipipi was removed from these analyses due to having 50% more locations than the other territories because of the higher number of birds within that territory, which biased the average.

3.2.4 Breeding and non-breeding territories

Convex (100%) polygons were used to compare breeding and non-breeding territory size and overlap in Ranges V.9. Location data was categorised into breeding (July - January) and non-breeding (February - June). Two extreme outliers were removed, both from female birds at Kaipipi (due to being 1.8 - 12.5 standard deviations from maximum range of all individuals at Kaipipi), but other movements outside estimated territory boundaries were included to represent the range of transmitted individuals most accurately during both periods. All territories from Kaipipi and Ulva Island were included, because even in territories where no breeding attempts were recorded, it was not possible to rule out that breeding attempts had occurred.

The size of convex polygon (100%) breeding and non-breeding territories was compared using a Wilcoxon matched pair test in R version 4.2.2 (R Development Core Team, 2021). Results were considered significant when $p < 0.05$.

3.2.5 Density and territory size

Densities were estimated using the most common method, the number of mapped territories or pairs divided by the study area, which provides reasonably accurate estimates of population size (Gregory et al., 2004; Kasper, Schneider, & Oliveira, 2016; Thunhikorn et al., 2016). Estimates were grouped by age (adult, subadult and young [juveniles and chicks]) and transmitter category (with transmitter or unidentified [UID]: recorded but not with transmitter). While territory maps were created using only birds with a transmitter (Section 3.2.1), density estimates also included UID birds. The first category was for all radio-tagged individuals >1800 g, (adult and subadult), the second included all radio-tagged *and* UID birds >1800 g and the last group contained all radio-tagged and UID birds of all weights (including juveniles and chicks).

The total area used for density estimates from field-workers-estimates was taken by drawing an external line around all the territories (Robertson et al., 2018). If the space between adjacent territories was greater than 75 m (see Section 3.2.3), these remained separate, and the study area was calculated from unconnected components. The estimate for the total study area was re-calculated as the number of location fixes was increased, providing three separate estimates for each of the categories of fixes (see Section 3.2.2). To obtain a total study area from convex and concave polygons I used 95% polygons that encompassed all the location fixes from every territory (Suwanrat, 2013). As a result of having non-adjacent territories at both Kaipipi and on Ulva Island, a 95% polygon was deemed more suitable than a 100% polygon for total area, to reduce the effect of the inclusion of empty spaces between territories into the total study area size.

The overall study area at each location included the area of the territories plus an additional ‘empty’ area (Figures 10 and 11) between territories that was thoroughly surveyed for kiwi in the initial stages of the project (and later used to establish a camera trapping survey: see Chapters 4 and 5), but radio-tagged tokoeka were not found in those areas. The empty areas could have been incorporated into adjoining territories, following the methods of Robertson et al. (2018). However, I preferred to leave the integrity of mapped territories intact to enable future comparisons of territory size and to leave the ‘empty areas’ separate.

Average territory size was calculated by dividing the total study area size by the number of territories (Robertson et al., 2017, 2018) as well as a more standard measure that divides the total sum of territory sizes by the number of territories (and therefore does not need to account for empty spaces between non adjacent territories).

Results are presented as means ± standard error unless otherwise stated.

3.3 Results

Fifty-five Rakiura tokoeka were caught and processed (measured, weighed, aged & sexed) (Appendix A.2). Forty-eight adults and sub-adults had transmitters attached, the remaining birds were chicks or juveniles and were released after processing.

An additional eight adult/subadult birds that were not caught were identified at Kaipipi and on Ulva Island in known territories and so classed as unidentified (UID). Four additional juveniles at Kaipipi and two on Ulva Island were also recorded in the months following the initial catching periods (one juvenile at Kaipipi was caught in 2020 and so was probably a UID chick in 2019) (Table 2).

Table 2. The total number of adult (A), subadult (SA), juvenile (J) and chick (C) Rakiura tokoeka observed at each location, with the number of adult/subadult birds that had transmitters (TX) attached, or were unidentified (UID) (F = female, M = male). Adults and subadults >1800 g, Juveniles 800 – 1800 g and Chicks <800 g.

	Total No. birds	A/SA TX	A/SA (UID)	J	C
Kaipipi	43	26 (16F, 10M)	8	6	3
Ulva Island	33	22 (10F, 12M)	8	2	1

The mean group size of adult and subadult birds (> 1800g, fitted with transmitter or UID) was 3.8 ± 1 at Kaipipi, and 3.0 ± 1 on Ulva Island. With the addition of chicks and juveniles from 2019 (pre-breeding season) mean group size was 4.8 ± 2 at Kaipipi and 3.3 ± 1 on Ulva Island (Table 3). The maximum number of adult/subadult (>1800 g) birds detected in a territory was six at Kaipipi and four on Ulva Island.

Table 3. The mean number of adult/subadult males (M) and females (F) with a transmitter, UID adult/subadults, juveniles and chicks and mean group size per territory/home range

	Adult M	Adult F	Adult UID	Juvenile	Chick	Group size
Kaipipi	1.1 ± 1	1.8 ± 1	0.9 ± 1	0.7 ± 1	0.3 ± 1	4.8 ± 2
Ulva Is.	1.1 ± 0	1.1 ± 1	0.8 ± 0	0.2 ± 0	0.1 ± 0	3.3 ± 1

Adult and subadult kiwi with transmitters were tracked for an average of 373 ± 96 days at Kaipipi and 397 ± 63 days on Ulva Island. In two cases at Kaipipi, dropped transmitters were found at significant distances from the known territories of individual females (3.2 km and 1.3 km from the closest location fix, see Figure 10 below).

Between February 2019 and May 2020, I obtained a total of 840 location fixes for transmitted birds, 477 from Kaipipi and 363 from Ulva Island. There was a slightly higher percentage of female compared to male location fixes from Kaipipi (62% F, 38% M), likely as a result of having more females with transmitters than males, and a more even spread across the sexes on Ulva Island (48% F, 52% M). The number of location fixes obtained during the breeding season (July - January) was lower than the number obtained during the non-breeding seaason (Feb - June) for both locations (Kaipipi 39% versus 61%, Ulva Island, 37% versus 63%). The mean number of location fixes per individual Rakiura tokoeka was 19 ± 7 at Kaipipi and 17 ± 5 on Ulva Island. The mean number of location fixes per territory was 51 ± 22 (range 29 – 103) at Kaipipi and 36 ± 17 (range 13 – 60) on Ulva Island.

3.3.1 Territories

I recorded nine territories in a 180 ha area at Kaipipi (Figure 10) and ten territories in 128 ha on Ulva Island (Figure 11). Not all territories had > 40 fixes due to low numbers of birds with a transmitter, dropped transmitters or limited tracking occasions; at Kaipipi, 3/9 had less than forty fixes in total (29, 35, 39) and on Ulva Island, 6/10 had less than forty fixes (13, 15, 19, 34, 35, 37). However, identifying approximately 80 – 90% of territory size required 27 – 28 fixes for both locations (see Section 3.3.5).

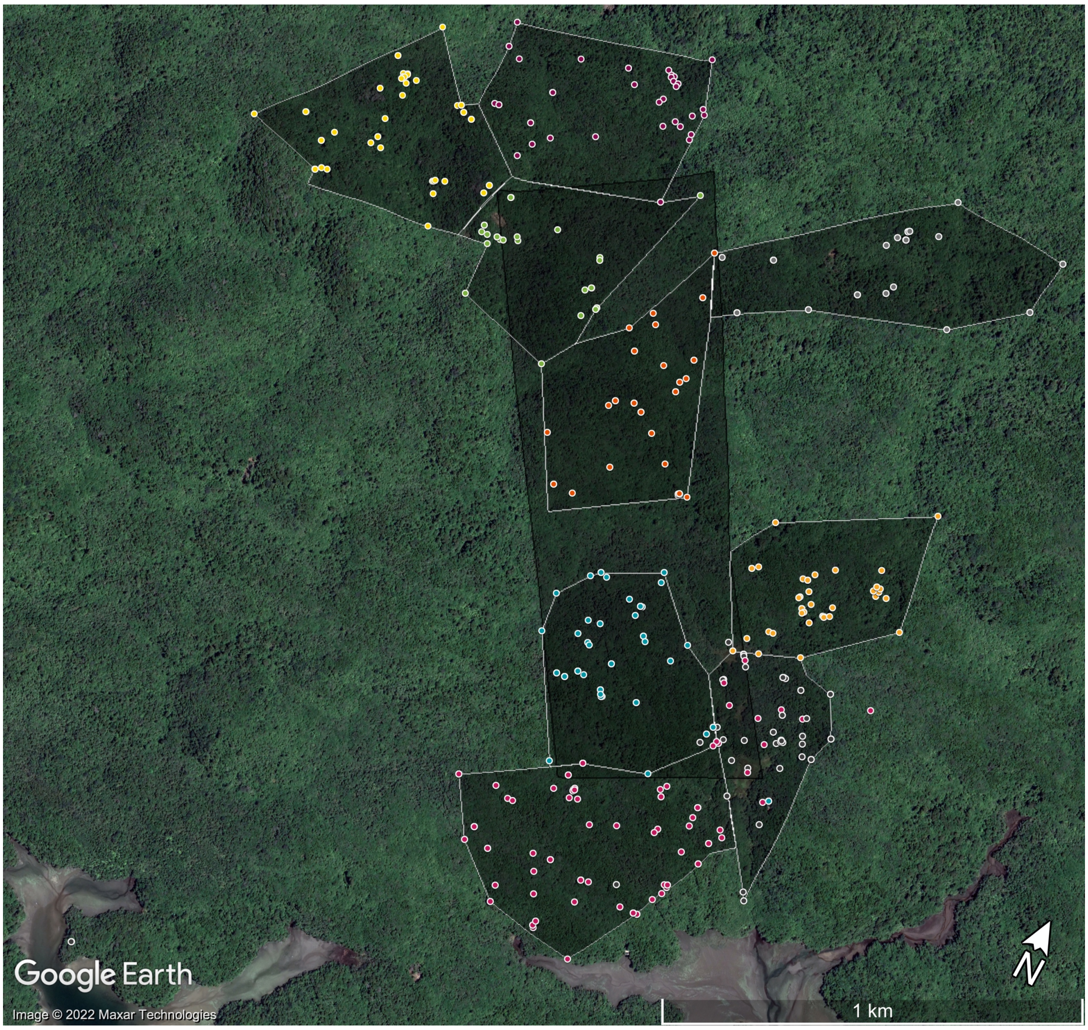


Figure 10. Kaipipi study site, Stewart Island, showing nine Rakiura tokoeka territories (outlined in white), with field-workers-estimate boundaries. The 'empty area' which was included in the total study area of 180 ha is the black background rectangle. Coloured dots denote location fixes from all the members in a territory, different colours indicate separate territories. Note that there is one individual who moved from the left to right bottom territories and so red dots are present in both. There is one location outlier (1.2km from the nearest territory boundary, bottom left corner).

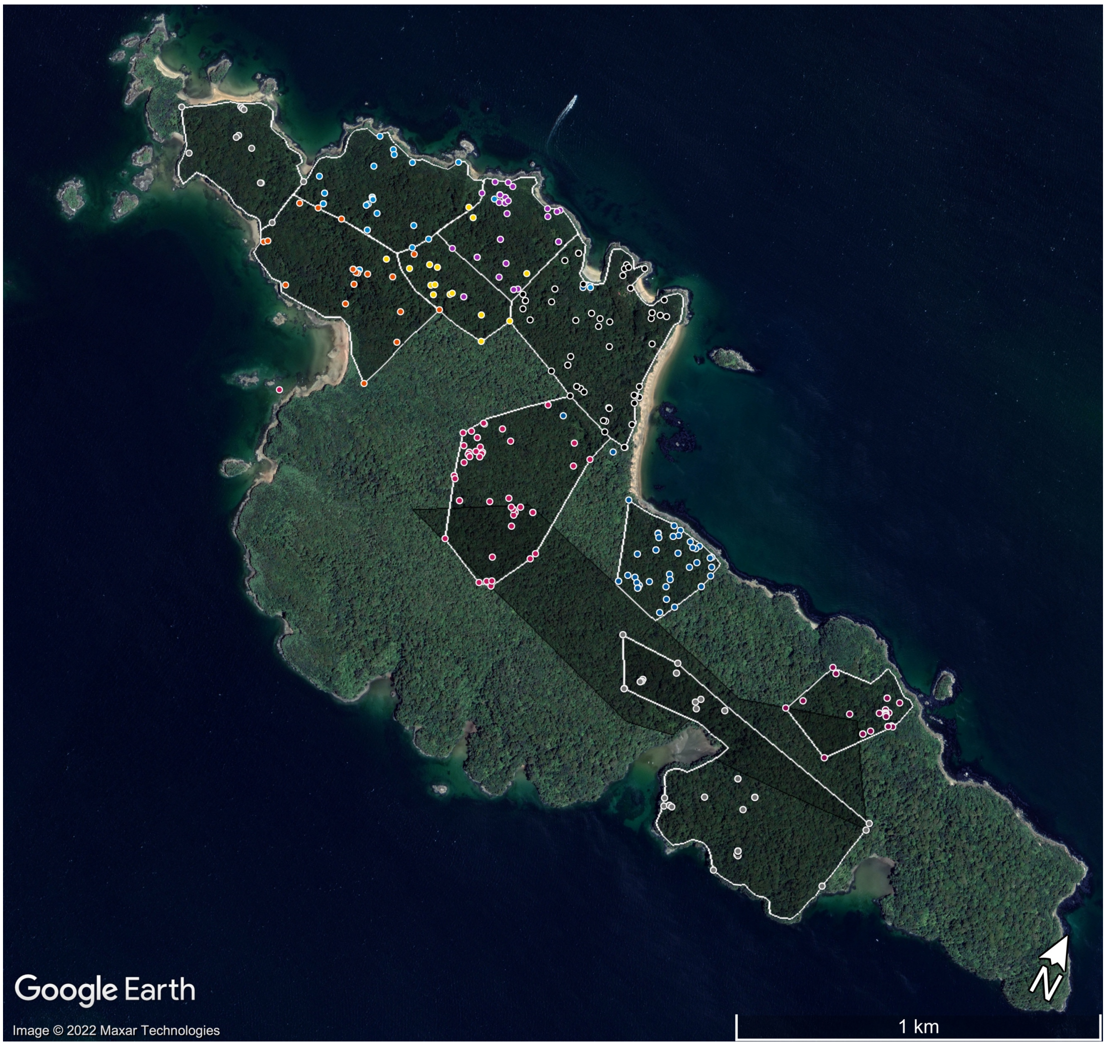


Figure 11. Ulva Island study site, Stewart Island, showing ten Rakiura tokoeka territories (outlined in white) with field-workers-estimate boundaries. The 'empty area' which was included in the total study area of 128 ha is the black background shape in the centre of the island. Coloured dots denote location fixes from all the members in a territory, different colours indicate separate territories.

Study area sizes from convex and concave polygon territories were much larger than from field-workers-estimate territories (Table 4).

Table 4. Total study area size (ha) at Kaipipi and on Ulva Island using > 40 location fixes and three methods for territory boundaries: field-workers-estimate, minimum convex (100%) and concave polygons.

	Study area (ha)	
Method	**Kaipipi**	**Ulva Island**
Territory mapping	180	128
Convex 100%	287	208
Concave	242	195

Dividing the study area by the number of territories gave an average territory size of 20 ha at Kaipipi and 12.8 ha on Ulva Island. Dividing the sum of territory sizes by their number instead suggested an average territory size at Kaipipi was 16.5 ± 3 ha and 10.4 ± 5 ha on Ulva Island. The furthest distance between two location points (span) of an individual *within* its territory was 853 m at Kaipipi (mean 646 ± 145 m) and 662 m (mean 468 ± 113 m) on Ulva Island.

Average territory size using 100% minimum convex polygons (MCP) for territory boundaries were similar to results from field-workers-estimate (FWE) (Kaipipi MCP: 18.9ha, FWE: 20 ha and Ulva Island, MCP: 11.6 ha, FWE: 12.8 ha). Concave polygon territories were the smallest of the three methods for both locations (Kaipipi 16.2 ha, Ulva Island, 10 ha) (Figure 12).

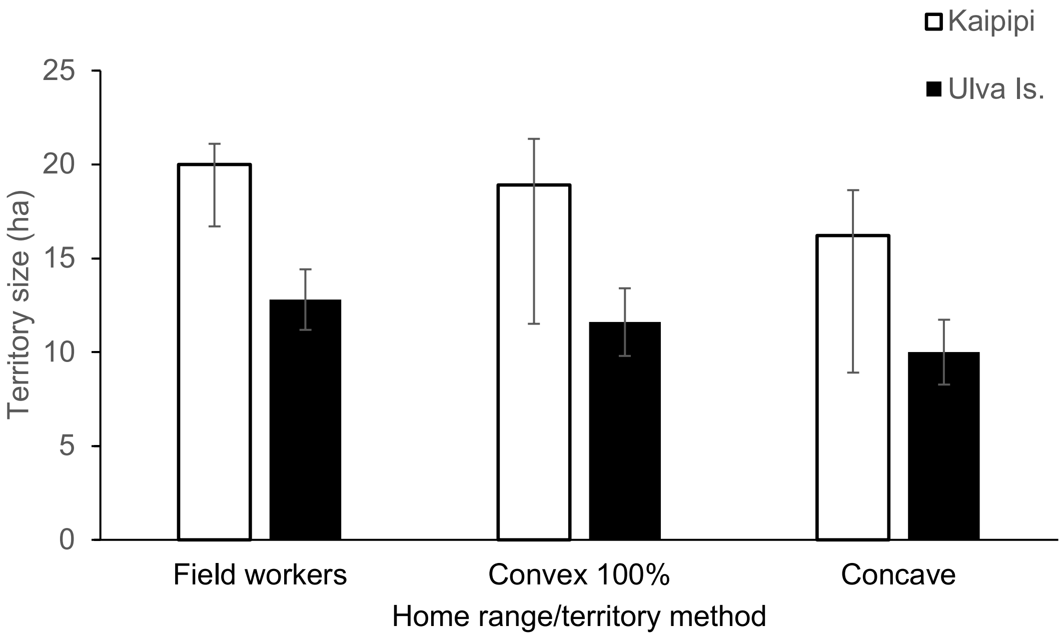


Figure 12. The average territory size per group of Rakiura tokoeka at Kaipipi and on Ulva Island using the maximum number of location fixes (> 40) and three methods for territory boundaries; field-workers-estimate, convex (100%) and concave polygons ± standard error.

Convex polygon territories are similar in appearance to the field-workers-estimate territories, however, both polygon methods show the degree of overlap between location points in neighbouring territories that is removed for field-workers-estimates (Figure 13, Figure 14).

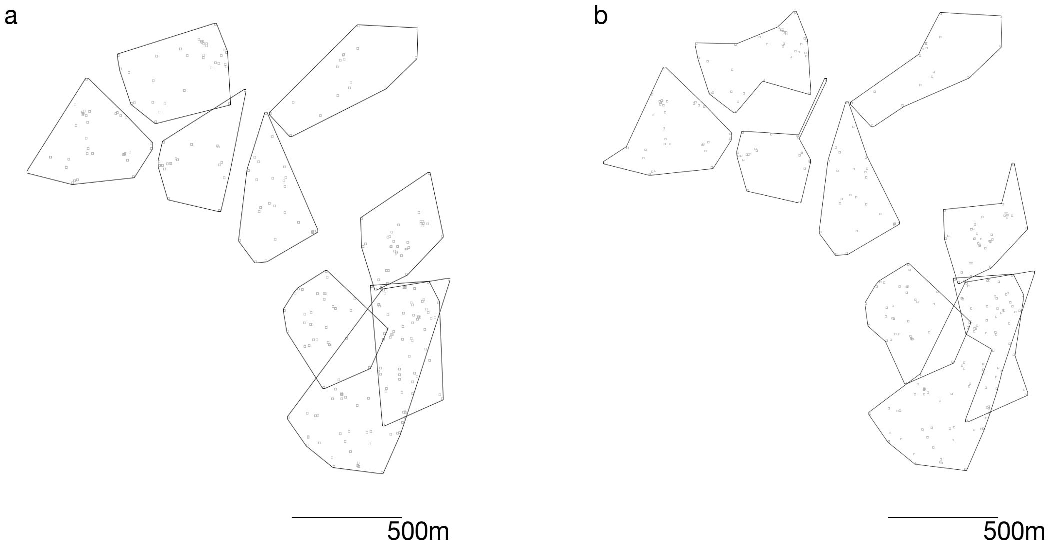


Figure 13. Convex 100% (a) and concave (b) polygons for average territory sizes of nine groups of Rakiura tokoeka at Kaipipi.

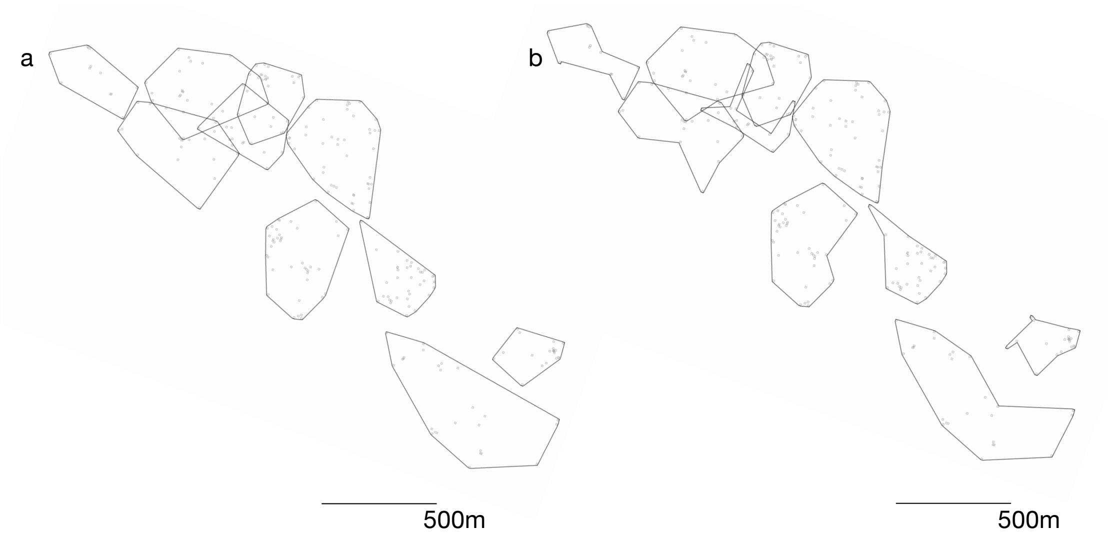


Figure 14. Convex 100% (a) and concave (b) polygons for average territory sizes of ten groups of Rakiura tokoeka on Ulva Island.

3.3.2 Density estimates

The density (number of birds per hectare) of Rakiura tokoeka at Kaipipi and on Ulva Island based on field-workers-estimates of territory size was similar, with Ulva Island slightly higher (Table 5).

Table 5. Density estimates (birds per ha) for Rakiura tokoeka at Kaipipi and on Ulva Island using three categories; adults and subadults with a transmitter (TX), adults and subadults unidentified (UID) or with a transmitter, and the previous group with the addition of UID juveniles and chicks.

	Kaipipi	Ulva Island
Density adult/subadult (TX)	0.14	0.17
Density adult/subadult (TX/UID)	0.19	0.23
Density adult/subadult (TX/UID) and young (UID)	0.24	0.26

Considering the slight difference in estimates, there was a maximum of one adult/subadult per 7 ha at Kaipipi and one per 6 ha on Ulva Island.

As a result of the larger study areas, density estimates from convex and concave polygon territories were lower than from field-workers-estimate territories (Figure 15).

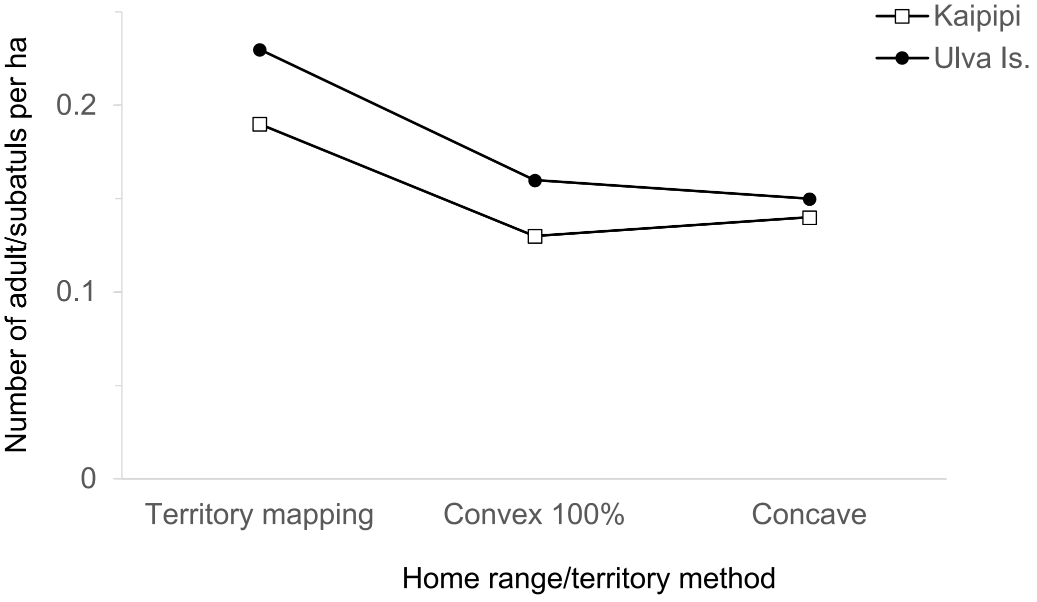


Figure 15. The density (number of birds per ha) of adult/subadult Rakiura tokoeka using > 40 location fixes and three methods for estimating territory boundaries; field-workers-estimate, minimum convex (100%) and concave polygons.

3.3.3 Survey duration

Increasing the number of location fixes per territory caused an increase in the size of mapped territories and overall study area for both Kaipipi and Ulva Island. As the number of location fixes per territory increased, density estimates decreased (Figure 16).

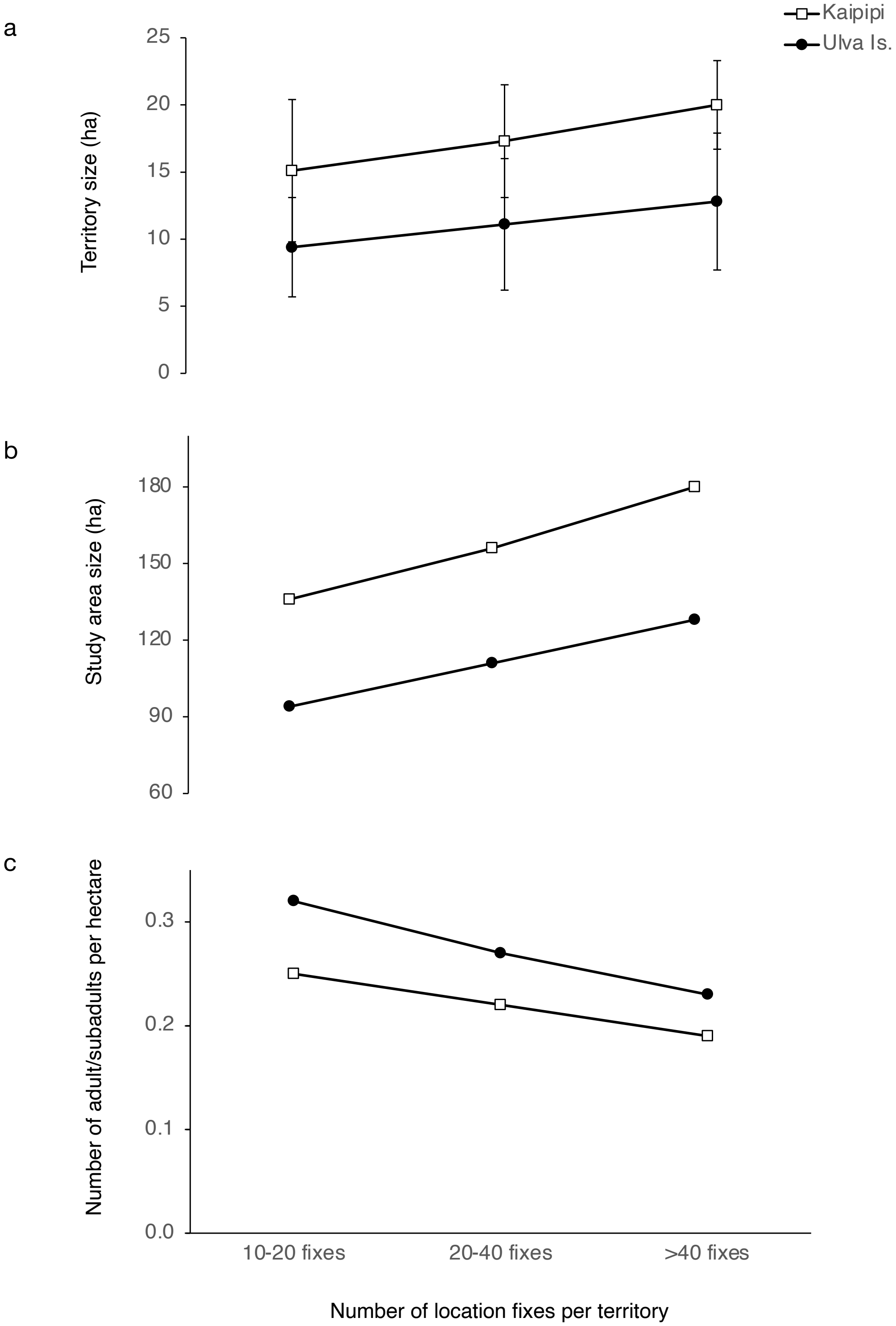


Figure 16. (a) Average territory size per group of Rakiura tokoeka ± standard deviation, (b) study area size, and (c) density (number of tokoeka per ha) of adult and subadult Rakiura tokoeka using increasing numbers of location fixes per territory at Kaipipi and on Ulva Island using field-workers-estimates.

The density of adults/subadults at Kaipipi and on Ulva Island estimated using minimum (10 – 20) location fixes was higher than with the maximum (> 40) location fixes (Table 6). Converting densities to the number of birds per km^2 shows how these differences could be interpreted within a site (Table 6).

Table 6. The density (number of adult/subadult Rakiura tokoeka per ha) and the number of adult/subadult Rakiura tokoeka per km^2 at Kaipipi and on Ulva Island using increasing numbers of location fixes per territory.

	Density (per ha)		Adults/subadults per km^2	
	Kaipipi	**Ulva Island**	**Kaipipi**	**Ulva Island**
10 - 20 fixes	0.25	0.32	20	25
20 - 40 fixes	0.22	0.27	17	20
> 40 fixes	0.19	0.23	14	17

3.3.4 Breeding versus non-breeding

Territories during the breeding season (June - January) were smaller than during the non-breeding season at Kaipipi (mean 9.5 and 15.3 ha respectively, n = 9, P = 0.5, Wilcoxon matched pair test) and on Ulva Island (mean 4 and 11.9 ha, n = 10, P = 0.5). More location fixes were captured during the non-breeding season than the breeding season at both locations (Table 7).

Table 7. The number of location fixes collected during the breeding (July - January) and non-breeding (February - June) seasons for Rakiura tokoeka at Kaipipi and on Ulva Island.

	Breeding	Non-breeding	Total
Kaipipi	185	292	477
Ulva Island	135	228	363

In most instances (16 out of 19) breeding and non-breeding territories greatly overlapped (Kaipipi: mean 78% overlap, range 47 – 100%), (Ulva Island: mean 92%, range 80 – 100%). In one instance at Kaipipi and two on Ulva Island, breeding territories were totally encompassed within non-breeding. However, in three instances at Kaipipi, breeding and non-breeding territories only overlapped between 45 – 60%.

The shape of territories between breeding and non-breeding seasons was slightly different (Figure 17, Figure 18). The proportion of breeding range that was within the non-breeding territory was higher on average at Kaipipi (mean 42%, range 7 - 62%) than on Ulva Island (mean 26%, range 4 - 58%).

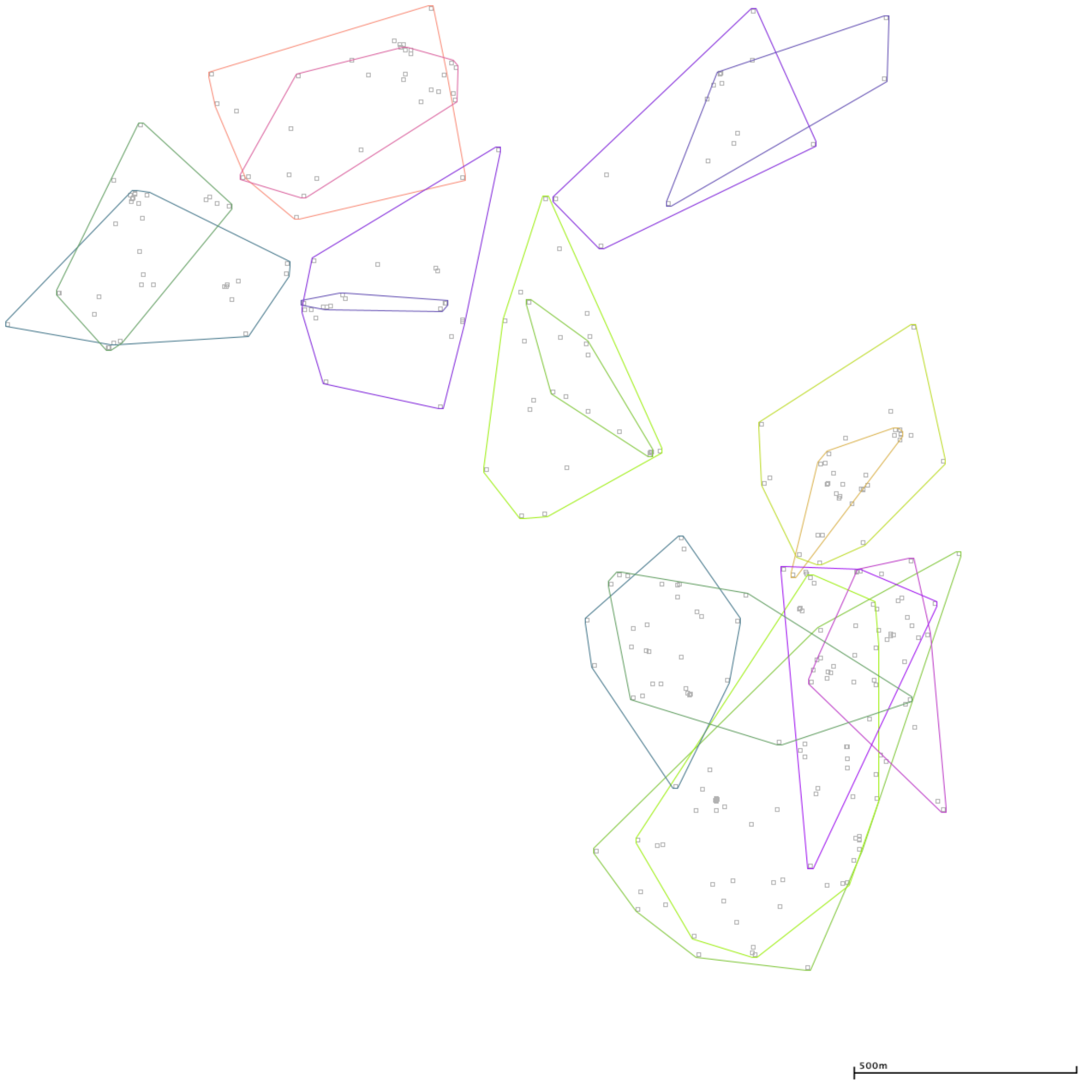


Figure 17. Minimum Convex Polygons (100%) of overlapping breeding and non-breeding territories of Rakiura tokoeka at Kaipipi. Each pair of polygons representing a territory are shown in a different colour, and always overlap each other.

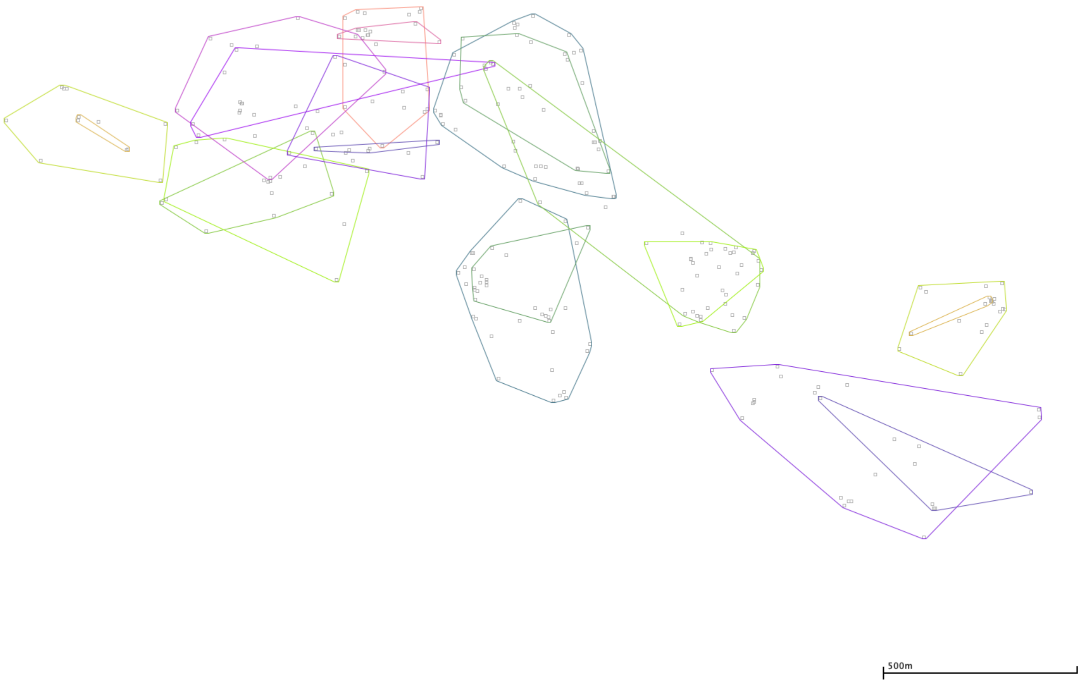


Figure 18. Minimum Convex Polygons (100%) of overlapping breeding and non-breeding territories of Rakiura tokoeka on Ulva Island. Each pair of polygons representing a territory are shown in a different colour, and always overlap each other.

3.3.5 Incremental area analysis

Incremental area analysis (IAA) results were similar for Kaipipi and Ulva Island. For concave and convex analyses, 28 location fixes at Kaipipi were required to reach 80 – 85% of the mean territory size respectively, where it stabilised until reaching 100% at 51 – 54 fixes. For Ulva Island, 27 – 29 location fixes were required to reach 90% of mean territory size, where it stabilised until reaching 100% at 56 – 57 fixes (see Appendix A.3 for IAA figures).

3.4 Discussion

3.4.1 Territory boundary and area methods

In this study, territories defined by convex boundaries and field-workers-estimates were a similar size. Typically, convex polygons provide larger estimates of territory size than other methods, including for NIBK, due to their tendency to include large areas that may not be utilised (Kenward, 2000; McLennan et al., 1987). However, a few study design features probably account for the similarity. Straight lines were incorporated into both types of territory boundaries (more commonly a convex polygon method), the average territory size may have been influenced by the empty spaces between territories included in estimates of study area, and field-workers-estimate boundaries were formed conservatively. Although the estimates were similar, convex polygons were less subjective to apply.

Field-workers-estimates boundaries may be the most biologically relevant method (Macdonald et al., 1980) and more accurately represent the area actually utilised by animals (McLennan et al., 1987). However, manually drawing boundaries based on field knowledge and interpretation is a subjective practice. In this study, only direct locations of birds with radio-transmitters were used to establish territory size and shape. However, in other studies that territory map kiwi estimated (indirect) locations from calls and sightings of un-untagged or unidentified birds may also be included (Robertson et al., 2018). Perhaps this would be unlikely to have a significant impact on territory boundaries, but for territory mapping to be an effective method for population monitoring, methods need to be consistent over time and between sites (Bibby et al., 2000; Gregory et al., 2004), and estimating the location of unidentified birds is difficult to maintain consistently. Years of data in which observers changed or methods deviated have been discarded from some studies (Bibby et al., 2000) because sampling effort can have a significant impact on results (Girard et al., 2002) and because the methods were not consistent or replicable.

None of the methods are statistically rigorous, but, overall, polygon methods are less subjective and easier to compare between studies (Harris et al., 1990). Importantly, MCPs are reliable for comparisons both within and between studies because the boundaries are usually based solely on location fixes. For this reason, it is often recommended to include their estimation in any home range estimates (Harris et al., 1990; Laver & Kelly, 2008). In this study MCPs were well suited to the data as there were very few outliers and extreme cases were removed. McLennan et al. (1987) used both field-workers-estimates and MCPs for NIBK, relying on the latter when they had low numbers of location fixes, indicating they believed MCPs were more reliable with smaller sample sizes (though overall they preferred field-workers-estimates). In some cases, MCPs have proved accurate and robust for small sample sizes compared to other methods (Harris et al., 1990; Suwanrat et al., 2015) and in other cases large sample sizes have been required to reach reliable estimates (Gasson, 2005; R. Powell, 2000).

Concave polygons are less often utilised than convex ones, but they were favoured for a survey of GSK by Keye et al. (2011), who considered them to provide the most convincing results while mapping territories using radio-telemetry location data. For both GSK (Keye, 2008) and Rakiura tokoeka at Kaipipi and on Ulva Island, concave polygons gave the smallest estimates for territories. Although concave polygons might seem an effective way to minimise the ‘inclusion of large, unused areas’ of MCPs (Keye, 2008), the assumption that areas *are* unused and the application of the more conservative concave polygon risks underestimating territory size. This results in overestimates of density, and therefore caution must be used when making conclusions from concave polygon territories. Furthermore, there is no objective method for establishing the edge restriction for concave polygons (Kenward, 2000), which makes comparisons within and between studies difficult. In conservation, it is safer to underestimate density than overestimate it with the use of constricted territory boundaries such as the concave polygon.

While the average territory size was similar for all three methods, estimates of the total study area size were vastly different, resulting in much smaller density estimates for both polygons than with field-workers-estimates. Replicating the method used by Suwanrat et al. (2015) and Quaglietta, Hájková, Mira, and Boitani (2015) for determining total study area by calculating a single polygon that encompasses all territories proved ineffective for disparate, non-adjoining territories such as occurred at both Kaipipi and on Ulva Island. A more accurate method would be to create separate polygons that capture adjoining territories and then sum the areas together for the total study area. Correctly establishing the total area being sampled is essential for obtaining accurate estimates of density (Ivan, 2011). As a result, the following discussion on territory mapping results are from field-workers-estimates unless explicitly stated otherwise.

It is possible that territory sizes at Kaipipi and on Ulva Island were biased slightly higher by including 'empty areas' in the calculations for total study area size (because average territory size = total study area/ number of territories (Robertson et al., 2018). However, attempts were made to balance this effect by more conservative application of field-workers-estimate boundaries; limiting manual extension to meet neighbouring territories or incorporate geographical features, as opposed to assuming territory boundaries fall between location records (Bibby et al., 2000; Robertson et al., 2017, 2018). Fuller et al. (2001) assumed empty spaces between mapped territories were occupied if they were large enough to fit the mean annual territory size of fishers. Applied to future territory mapping studies of kiwi, empty spaces between territories could be incorporated into neighbouring territories only if the area is less than the average territory size at that location.

3.4.2 Territory size and population density

Kaipipi had a larger average group size per territory and more young birds were found compared with Ulva Island. However, the average territory size at Kaipipi was larger than on Ulva Island, resulting in a lower density of Rakiura tokoeka on the mainland. This difference was less extreme than expected, given that Ulva Island is a pest-free sanctuary with abundant regenerating forest and therefore assumed to have improved food availability and reduced predation pressures (McLennan et al., 1987). This was expected to translate into higher numbers of tokoeka, greater recruitment and a larger proportion of chicks and juveniles. However, densities on islands may not be as high as expected when some environmental factor or factors are unfavourable or the restricted area means marginal habitat must be used, which may have limited resources or increased predation risk (Gliwicz, 1980).

Potentially weka (*Gallirallus australis scotti*), which are present on Ulva Island but largely absent from mainland Rakiura, are having a significant impact on young kiwi through the predation of eggs and chicks (Section 6.3). However, Rakiura tokoeka at Kaipipi live alongside feral cats (*Felis catus*), which are known to predate on kiwi chicks and have been responsible for adult mortalities of NIBK (A. Wilson, 2014). Additionally, possums (*Trichosurus vulpecula*) compete for burrows, can eat eggs (Robertson et al., 2018), and cause nest disturbance, and rats (*Rattus rattus*) forage in the leaf litter for the same food sources as chicks and juveniles (Shapiro, 2005). However, NIBK can persist even with high predation of chicks (Wilson, 2014), and a small sample size of Rakiura tokoeka chicks could not adequately compare predation pressure on mainland Rakiura versus Ulva Island (Chapter 6).

The (vegetation-eating) impact of deer (*Odocoileus virginianus, Cervus elaphus*), possums (*Trichosurus vulpecula*), and rats (*Rattus norvegicus, Rattus rattus, Rattus exulns*) at Kaipipi could explain the larger territory size if tokoeka required a greater area to meet their requirements in a resource-poor habitat. Alternatively, larger group sizes at Kaipipi could result in increased territory sizes, related to social dynamics. The relationship between group size, territory size and resource availability has not been thoroughly investigated for kiwi (Johnson, Macdonald, Newman, & Morecroft, 2001; Newsome et al., 2013). Toy & Toy (2020) found no difference in territory size between individuals versus pairs for GSK, but single kiwi are likely to be prospecting for mates and do not provide a fair comparison to different sized groups.

Alternatively, Ulva Island could be close to or at carrying capacity due to the restricted space available, resulting in smaller territories than Kaipipi. However, smaller group sizes on average indicate this may be unlikely, at least for part of the island. Another possible and unexpected theory is that resources are limited or competition for resources is fiercer on Ulva Island as opposed to at Kaipipi. The species-rich dynamic on Ulva Island may act to limit the niche of Rakiura tokoeka by increasing competition for resources with other protected bird species, e.g., food, space, burrows, or roosts (MacArthur, Diamond, & Karr, 1972). Interestingly, the cause of a Rakiura tokoeka chick mortality on Ulva Island in 2019 was partly starvation (Section 6.3.3). Clearly, more specific research on resource availability and the relationship with territory size and densities is required.

It is possible that the detection probability for Rakiura tokoeka on Ulva Island was different than on mainland Rakiura. The increased vegetation and lack of a kiwi detection dog team on Ulva Island could have inhibited detection. This could have particularly impacted the detection of young birds, as they are much less conspicuous than adult kiwi (Colbourne, 1992). It is also possible that kiwi on Ulva Island are more averse to humans, perhaps as a result of interactions during translocation. However, this seems unlikely given the anecdotal observations of kiwi along popular walking tracks and location of nests close to areas of high use.

3.4.3 Survey duration

The minimum location fixes I used were as comparable as possible to previous territory mapping estimates for Rakiura tokoeka and other kiwi species by DOC (Robertson et al., 2017, 2018). Minimum location maps indicated a slightly different story than when I used the maximum amount of data, which could lead to inaccurate conclusions. Increasing the number of location fixes in territory maps increased territory sizes and subsequently decreased density estimates. How vital the scale of difference is between the minimum and maximum location maps is open to interpretation and dependent on the objectives of a project.

Given that the primary goal of long-term, five-yearly territory mapping surveys by DOC seems to be to monitor change in the population, using the minimum maps may serve this purpose adequately without being overly concerned with accuracy. However, if the purpose were to obtain the most accurate estimates possible for territory sizes and density, increasing the number of location fixes to 20 – 40 at a minimum and ideally > 40 location fixes per territory is useful. The effect that this has on density is important when conservation management is the primary goal. If estimates are used to extrapolate to larger areas, errors in estimates will only increase in this instance. For example, in this study extrapolated estimates for individuals per 100 km^2 for Ulva Island fluctuates from 1,700 using the maximum amount of location fixes available to 2,500 using the minimum amount.

The incremental area analysis from convex and concave territory boundaries corroborated a higher number of location fixes for more accurate territory maps. Quaglietta et al. (2015) considered boundaries stable when they reached either a fixed value or at least 70% of the final estimate for Eurasian otters (*Lutra lutra*). At both Kaipipi and on Ulva Island, approximately 28 locations were necessary to reach a at least 80% of the final value, while over 50 were necessary for 100%. Rakiura tokoeka commonly live in groups and therefore comparisons to other kiwi species in this regard should perhaps be considered from an individual perspective. Interestingly, the number of location fixes required to reach 80 – 90% of the final values using convex polygons for individual Rakiura tokoeka territories, as opposed to groups, was 15 (Appendix A.3: Figure 43, Figure 44). Colbourne (2002) recommended 15 locations while mapping NIBK territories and in kiwi mapping studies for GSK that used minimum convex polygons, a minimum of 15 – 16 location fixes per territory was considered adequate for reasonably accurate estimates of range (Jahn et al., 2013; Keye, 2008; Toy & Toy, 2020). These recommendations for minimum location fixes are consistent with individual Rakiura tokoeka, although length of study should be considered; Jahn et al. (2013) predominantly used locations from a 4-month period (May - August), while Keye (2008) and Toy and Toy (2020) tracked individuals for at least a year, including the breeding season.

Because territory maps in this study included both the breeding season and the non-breeding season and represent a group living species, this may explain why a high number of fixes were needed. As the sample size increases, temporal or seasonal effects may confound efforts to estimate when territory size stabilises (Barg, Jones, & Robertson, 2005). As Powell (2000) points out, short time frames for location data may not build a realistic map of an animal's range, but long time periods can also be challenging as the likelihood of change to the range increase. McLennan et al. (1987) would not consider field-workers-estimates for territory boundaries of NIBK when there were less than 50 locations and Seaman et al. (1999) recommended a minimum of 30 locations and ideally over 50 as a rule when mapping animal ranges (using kernel density estimators), which is conservative compared to other recommendations (Girard et al., 2002).

3.4.4 Breeding versus non-breeding

One benefit of monitoring over a longer survey duration was that territories could be measured during both breeding and non-breeding seasons. Territories during the breeding season were largely contained within the area of the non-breeding territory and appeared to be slightly smaller. An established year-round territory that becomes smaller in the breeding season is characteristic of cooperative breeding birds (Ekman & Ericson, 2006), so this is reasonable to expect for Rakiura tokoeka.

It is unclear whether the difference in this study is due to a real effect or due to tracking bias. One challenge of radio-telemetry is that survey effort can vary and there is a risk of missing detections of individuals in unexpected locations. During the breeding season, there was a focus on nest monitoring with minimal disturbance to the birds. This means that activity readings would be taken from the transmitter signal output (which can be done at distance), as opposed to tracking specific locations. Birds were generally found in fewer locations, and more commonly tracked to their single nest burrow site. In contrast, more search effort was required during the non-breeding season to track Rakiura tokoeka in multiple burrows and roosts, which likely increased the extent of the locations in which they were found.

However, the reduction in size of breeding and non-breeding territories was observed even in territories where breeding attempts were not observed. Although, it is possible that there were nests or nesting attempts that were never detected, as a result of having untagged birds within known territories. Alternatively, if there was no breeding event, perhaps non-breeding birds still reduce their range seasonally in response to environmental triggers such as weather conditions, food availability or distribution, or increased avoidance of conspecifics due to the potential for antagonistic encounters during breeding. Importantly, fewer location fixes were obtained during the breeding season and this could have impacted the size of territory detected.

Future research where all individuals in a territory have a radio-transmitter and are tracked consistently through both seasons would help to clarify the effect of breeding season on territory size. In this study, it is possible that individuals were ‘missed’, which could bias the results as it is not known which sex or age best represents the breeding territory for Rakiura tokoeka. Furthermore, a future study should more precisely define ‘breeding’ and ‘non-breeding’ seasons based on the behaviour of the group as the exact timing of laying, incubating, and hatching will vary between groups. Ideally, both diurnal and nocturnal locations would be used, as this study used only diurnal locations for breeding seasons, which has an unknown effect on the location fix data.

Historically, territory mapping was used for breeding birds, because during the breeding season not only did songbirds tend to hold defended territories, but they displayed observable territorial behaviours (Bibby et al., 2000). Some species may only be mildly territorial, or only maintain a territory during the breeding season, and therefore, territory mapping would only be applicable at that time (Suwanrat et al., 2015; Bocca, Carisio, & Rolando, 2007; Tomiałojć, 2004). Rakiura tokoeka in this study showed enough site fidelity for territory mapping to be an effective method.

3.4.5 Previous estimates and population status

Using the minimum territory maps, I could make general comparisons with the most recent territory mapping surveys of Rakiura tokoeka by DOC (Robertson et al., 2017, 2018). Territory sizes at Kaipipi were close to the most recent estimates at Port Adventure, which is a very similar environment (Kaipipi 15 ha, Port Adventure 14.4

ha) (Robertson et al., 2017). Ulva Island had the smallest average territory size (~9.4 ha) when compared with previous territory mapping estimates at Port Adventure and Mason Bay. However, estimates for Mason Bay are similar, with an average of 10.4 ha (and 7.4 ha in 1993) (Robertson et al., 2018). Unlike Ulva Island, Mason Bay is a site of regenerating coastal farmland, which may support a higher density of kiwi in smaller territories due to an abundance of food, preference for a specific food unique to that area, a difference in predation pressure or some other unknown reason. Interestingly, recent research suggested there could be a decline in average body mass in the Mason Bay population as a result of habitat change and reduced food availability (Robertson & Colbourne, 2022). Identifying the relationship between territory size, available resources and predation pressure is beyond the scope of this study, but could be addressed with invertebrate sampling and multi-species surveys.

Although territory sizes from this study are compared with previous estimates by DOC for Rakiura tokoeka, there are important differences in survey effort and design that have already been mentioned. It is also unclear how accurately previous territory mapping estimates can be interpreted given the size of the study area is not re-calculated at each survey, despite changes to the number and shape of territories within. Given the natural flux of kiwi territories over time (Toy & Toy, 2020), it is highly likely the total study area would differ as a direct result.

Density estimates from Kaipipi and Ulva Island were reasonably similar to the most recent surveys of Rakiura tokokea by DOC at Port Adventure and Mason Bay (Robertson et al., 2017, 2018). The density of adults and subadults (radio-tagged and unidentified) at Kaipipi and Ulva Island (0.2 birds per ha, or 5 ha per bird) was the same as Port Adventure in 2017, while Mason Bay had a slightly higher density (0.3 birds per ha, or 3.3 ha per bird) in 2018. When young birds were included for estimates of total density of Rakiura tokoeka, Kaipipi still had 0.2 birds per ha while the other three locations had 0.3 per ha. Colbourne (2002) refers to a density of 0.4 adult pairs of Rakiura tokoeka per ha (territories of 5 ha per pair) at Mason Bay, calculated from earlier work using bands and transmitters and not including additional birds present in territories (R. Colbourne pers. comm.), a higher density than recorded recently.

In general, densities of Rakiura tokoeka at all locations surveyed in recent years by this study and DOC are higher than other reports (Colbourne and Powlesland, 1988; Innes et al., 2015), although it is important to note that comparisons of density are inherently unreliable given the inconsistencies between survey methods and duration. Colbourne and Powlesland (1988) estimated one pair per 20 – 40 ha (at Scollay's Flat in Southern Rakiura), based solely on call rates and sightings. Innes et al. (2015) estimated a higher mean density of 0.09 Rakiura tokoeka per ha (1 bird per 11 ha) using an estimated total population size of 13,000 individuals. The total population size was based on an original population estimate of 15,000 (Holzapfel et al., 2008), with a 2% rate of decline suggested from territory mapping at Mason Bay (Robertson & Colbourne, 2011), divided by an area of 151,100 ha, (H. Robertson pers. comm). without a description of which parts of the 174,600 ha of Rakiura that includes (Innes et al., 2015).

Crucially for unmarked species like kiwi, and particularly group living species where the number of group members is variable, territory mapping provides estimates of *minimum* densities, because it is impossible to know the true number of unidentified individuals present (Peele et al., 2015). True densities could be underestimated due to conservative inclusion of a minimum number of unmarked individuals at each location. The morphological cryptic-ness of kiwi makes individual identification difficult, though sexing of adults is usually accurate due to the difference in size and bill length between males and females. Nevertheless, one unmarked kiwi observed in a territory is difficult to distinguish from subsequent sightings of unmarked birds. However, minimum densities are still useful for conservation purposes (Kasper et al., 2016).

Although local densities can be used to extrapolate total population density (Skirrow, 2018), these estimates should be made with significant caution. Extrapolating local density estimates assumes that there is a consistent density of individuals across the island. This is likely to be inaccurate given that Rakiura consists of many different areas such as swamp, sand dune, coastal scrub, granite domes, alpine areas, and a township. Before a reasonable extrapolation of the Rakiura tokoeka population could be made, these areas would need to be considered, or perhaps excluded from estimates, which could result in overestimating or underestimating population density. If the minimum density estimate of 0.2 Rakiura tokoeka per ha was extrapolated across an area of 151,100 ha (e.g., Skirrow (2018) with two parakeet species on islands), the total number on Rakiura would be ~30,220, which is much higher than the total estimate of 13,000 in 2015, 15,000 in 2008 (Holzapfel et al., 2008), and 15,000 – 20,000 in 2022 (Robertson & Colbourne, 2022).

As a result of the most recent territory mapping surveys by DOC in 2017 and 2018

(Robertson et al., 2017, 2018), and this study over 2019 – 2020, it would appear the Rakiura tokoeka populations are at least stable. Rakiura tokoeka, like other kiwi, are a long-lived species, and therefore a consistently lower level of recruitment than was found at either Kaipipi or on Ulva Island would be necessary to consider the population at risk. Given the low mortality of adults and chicks (Sections 3.3 and 6.3), the preponderance of multi-bird territories and high ratio of young birds (chick, juvenile and subadults) to adults (except at Port Adventure in 2011 (Robertson et al. 2017)), it appears there are good levels of recruitment into the breeding population of Rakiura tokoeka at both locations, at least periodically.

3.4.6 Territory mapping considerations

The radio-telemetry data met most of the assumptions associated with territory mapping; the observer is skilled at finding the birds, records are plotted accurately, there is reasonable chance of detecting a territory owner, the population is closed, and birds live in pairs in fixed, discrete, and non-overlapping ranges (Thunhikorn et al., 2016). Clearly, group living species like Rakiura tokoeka violate the assumption for pairs, which makes knowledge of the species and efforts to identify the correct number of birds in each territory essential. The DOC two week territory mapping surveys avoid the issue of time when considering a closed population, however, it is important to establish a balance between survey duration and acquiring enough location fixes to meet the project objectives (Mander, 2016). As Powell and Mitchell (2012) point out, mapping ‘real’ animal ranges is likely to be irregular, complex, messy, and difficult.

Importantly, territory maps at Kaipipi and on Ulva Island were built predominantly using daytime locations, therefore assuming that space use is similar diurnally and nocturnally (Kochanny et al., 2009). Most kiwi species roost in burrows or shelters during the day and are active during the night. Rakiura tokoeka are regularly active during the day as well as at night, though are primarily nocturnal. Individuals that were tracked during the day were often found active or in surface roosts e.g., under a fern. Toy and Toy (2020) found that GSK regularly moved outside their daytime territory at night, although they had a small sample size and were working on a translocated population. However, McLennan and McCann (1991) and Gasson (2005) also found GSK at night in places they did not roost during the day. It is also possible that roost and burrow sites may not be representative of territories. Taborsky and Taborsky

(1995) included both day and night locations in territories of NIBK, finding that different habitat types within territories were preferred for day roosting versus night foraging. Territory maps for Kaipipi and Ulva Island, should be considered a minimum territory given the lack of nocturnal location fixes, though it is unknown how significant the difference may be for Rakiura tokoeka compared with other more strictly nocturnal kiwi species such as NIBK and LSK (*Apteryx owenii)*.

Another potential bias in territory mapping is the impact of the invasiveness of the method (particularly catching and handling, but also regular tracking) on individuals. It is important to consider the sensitivity of a species to the monitoring method being used, for example, some birds may leave a territory after being caught and handled, or desert a nest or burrow, which may skew their distribution in an unrealistic way (Keye, 2008). Even attempting to catch kiwi can cause changes in behaviour that bias a survey, for example, wary birds may not approach people again (Robertson & Colbourne, 2005). Increased avoidance of people could seriously impact repeat surveys if individuals are assumed to have died or have left the area, and is problematic when considering the consistency of the method. If the responses of a group of animals to the processes involved in territory mapping are known, it could be possible to account for these in some way, for example, by extending the survey to increase the likelihood of capturing natural behaviour. However, it is also worthwhile to consider alternate methods that reduce or eliminate this bias (Chapters 4 and 5).

A combination of night catching with call playback and day searching with kiwi detection dogs appears to be a reasonable way of establishing a random sample of birds of all ages and both sexes and tracking transmitted birds to burrows to detect new birds that may not be responsive to playback (such as juveniles) is highly successful. There is some concern that the use of telemetry causes too much separation from a field-based understanding of animal ecology (Hebblewhite & Haydon, 2010), because animals are monitored remotely, and that sudden large-scale movements as well as fine scale movements between sampling occasions may not be captured (Kochanny et al., 2009). However, territory mapping incorporating telemetry was an effective and informative method for Rakiura tokoeka.

3.5 Conclusion

In this study, radio-telemetry proved vital in successfully using territory mapping for the morphologically and behaviourally cryptic Rakiura tokoeka. While there are challenges related to the selection of territory boundaries and study areas, these did not drastically affect the overall estimates. Establishing clearer protocols for monitoring that are more reproducible would be advantageous, particularly where the goal is to monitor change in populations. There have been some inconsistencies in previous territory mapping surveys for kiwi (e.g., duration of survey and subsequent number of birds detected (Robertson et al., 2017, 2019b)) and this should be considered when interpreting results (including this study). The repeatability of territory mapping could be improved by establishing a common method for dealing with both territory boundaries and empty spaces between territories. While field-workers-estimates make the most of site-specific knowledge, convex polygons were the most replicable and objective of the methods trialled.

Territory mapping is currently the most reliable tool to establish knowledge of individuals and their locations in an area (Bibby et al., 2000), and is the method of choice when sufficient resources are available (Gregory et al., 2004). However, the high cost and resource demands limit the applicability of territory mapping for many kiwi conservation groups, which increases the requirement for monitoring methods that are easier to apply and provide similar results (Chapters 4 and 5). Whether territory mapping represents a reasonable baseline for comparing other monitoring methods remains open to debate (Buckland, 2006; Streby et al., 2012).

In this study, I believe it is acceptable to use territory mapping estimates as the closest possible estimates of ‘true’ density for Rakiura tokoeka (Chapter 4), with the caveat that these represent ‘minimum estimates’, given the unknown number of unmarked birds. To accurately represent the territories of group-living species, it is essential to catch as many group members per territory as possible. For this species, where group size is variable and ‘missed’ birds may bias the data, this is a challenging task. It is worth noting that it is possible to combine monitoring methods to reduce the unknowns, for example, camera traps within territories can help to identify (by size, bill length, and presence or absence of a transmitter) how many unmarked individuals are resident (Section 6.3.4.2).

Engeman (2005) considers the most useful monitoring methods to be those that account for the spatial characteristics of a species. An animal’s use of space over time forms the foundation of many wildlife monitoring programmes and can be used to fulfil multiple objectives. Monitoring the density of a population is often considered critical for their management and conservation (Glenn et al., 2016) and determining the home range/territory of a species can fulfil this and other objectives simultaneously.

Chapter 4: Camera trap rates for a cryptic, ground dwelling bird, Rakiura tokoeka

Preface: The purpose of this chapter is to introduce camera trapping as a novel monitoring method for kiwi, and to explore the validity of camera trap rates as an index measure for four local populations of Rakiura tokoeka.

4.1 Introduction

4.1.1 Kiwi & camera traps

Camera trapping surveys are potentially a useful monitoring method for kiwi and the implications of being able to use cameras for kiwi populations are significant. Camera trapping could offer an alternative to current methods, which are either expensive, invasive, require experienced personnel (e.g., radio-telemetry) or have a poorly understood relationship to population dynamics (e.g., call surveys) (see Section 1.3: kiwi monitoring). Due to the non-invasive nature of cameras, they can be used for surveying kiwi throughout the year. Furthermore, camera traps can be low effort to install and analyse, and that can be added to the arsenal of monitoring tools for the many community groups and organisations that do not have ready funds or other resources to instigate telemetry-based projects. At the very least, camera monitoring could offer novel insights into the behaviour of wild kiwi (Znidersic, 2017).

4.1.2 Camera traps

Camera traps offer a promising alternative to telemetry-based studies because they involve minimal disturbance, avoid the stress associated with capture and handling, require less effort, and can detect animals that are difficult to find or are rare in the environment (Mills et al., 2016; Noss et al., 2003; Thunhikorn et al., 2016). Noss et al. (2003) found that camera surveys provided more precise estimates of density than telemetry for their study on lowland tapir (*Tapirus terrestris*) in Bolivia. While cameras have most notably been used to monitor rare mammals such as tigers (*Panthera tigris*) (Carbone et al., 2001; Karanth, 1995), they are also a promising tool for terrestrial, visually and behaviourally cryptic birds that are otherwise difficult to monitor (Alves, López-Iborra, & Silveira, 2015; O'Brien & Kinnaird, 2008; Thunhikorn et al., 2016).

Historically, bird detections on camera traps were considered by-catch during mammalian surveys and not further analysed (O'Brien & Kinnaird, 2008). However, some studies have shown how useful this by-catch data can be; Murphy et al. (2017) investigated the distribution and occupancy of a range of Madagascan forest birds that were non-target species from carnivore surveys. A growing number of studies have used camera trapping successfully for surveys targeting large, ground-dwelling birds. For example, Pérez-Irineo and Santos-Moreno (2017) investigated the occupancy, relative abundance and activity of the Great Curassow (*Crax rubra*) in Southeast Mexico; Mere Roncal et al. (2019) assessed the daily activity patterns, composition and dynamics of medium-large terrestrial birds across seasons and habitats in south-eastern Peru; Dinata, Nugroho, Haidir, and Linkie (2008) calculated an abundance index comparing the diversity of bird species in different habitats in West-central Sumatra, and Znidersic (2017) recorded the cryptic behaviours of a little-known wetland species, the Lewins rail (*Lewinia pectoralis*), on Tasman Island, Australia. Camera traps are currently used for kiwi primarily to monitor nest burrows for predators and the emergence of chicks, and to get pictures for publicity purposes, but there are no reports on their use for population monitoring at the time of this study.

4.1.3 Relative abundance indices

Incorporating marked animals into camera trap studies produces more robust estimates of abundance (Chandler & Royle, 2013; Royle, Chandler, Sollmann, & Gardner, 2014). However, unmarked animals are frequently the target of monitoring, and in these cases relative abundance indices are commonly used (O’Brien & Kinniard, 2008; Bengsen et al., 2011; Burton et al., 2015). Rather than estimating the true abundance or density of a population, these indices make relative comparisons within a population over time or between populations (Engeman, 2005; Gilbert, Clare, Stenglein, & Zuckerberg, 2021; McComb et al., 2010). The most common relative abundance index in camera trap surveys is the detection rate i.e., the number of independent detections of a given species over a specific sampling period, usually 100 camera days (Gilbert et al., 2021; Rovero & Marshall, 2009). This can also be referred to as the photographic rate, mean trapping rate, trap success, relative abundance (RA/RAI), or camera trap rate (CTR) (Burton et al., 2015; Murphy et al., 2017; Pérez-Irineo & Santos-Moreno, 2017; Samejima, Ong, Lagan, & Kitayama, 2012; Sollmann, 2018).

The premise of an index like camera trap rate (CTR) is that a fixed search effort will detect a fixed proportion of the population and that detection rates are proportional to the true density of the population (Caughley, 1977). The most important component of this relationship is that if population abundance/density changes, the index will be sensitive enough to vary proportionately (Bengsen et al., 2011; Engeman, 2005). Proponents of CTR suggest that as population density increases, the number of encounters with cameras should also increase, thereby resulting in higher CTR (Rovero & Marshall, 2009). Therefore, all site and survey variables being equal, areas with more individuals would have higher trapping rates (O'Brien & Kinnaird, 2008). Without standardisation or explanation of the variables associated with the study site/s or survey methods and space use by the species, changes in an index cannot be attributed confidently to changes in a population versus changes in detection (O'Brien & Kinnaird, 2008). Ideally, the probability of detection would remain constant and so detection rates would provide a valid index of abundance (O’Brien, 2011). Despite these concerns, indices can provide reasonable representations of relative abundance (Palmer 2018), although it is more accurate to describe CTR as an index of activity (Sollmann, 2018; Witmer, 2005).

The most reliable relative abundance indices are correlated to independent estimates of abundance or density. For example, Bengsen et al. (2011) trialled CTR alongside the Capture-Mark-Recapture (C-M-R) of feral cats (*Felis catus*) before and after a trapping operation on Kangaroo Island, Australia. The significance of this study is that the CTR index tracked the same population reduction as the independent density estimate from C-M-R. Although comparisons between CTR and independent density estimates are a comparison between two estimates as opposed to the true population density (Palmer, Swanson, Kosmala, Arnold, & Packer, 2018), they are still valuable. Comparing CTR with methods that are considered to provide more robust population estimates such as C-M-R increases confidence in CTR when the results are comparable, and CTR is much cheaper and simpler to implement. Furthermore, if estimates from both methods are similar then there is more confidence that the results are close to representing true population variables (Rovero & Marshall, 2009).

Although relative abundance indices are generally considered less robust than methods that directly estimate abundance, in some circumstances they may be more valuable and applicable (Gilbert et al., 2021). For example, when the objective of monitoring is to detect change in abundance, such as before and after control or management intervention, the value of a precise and reliable index is potentially greater than estimates of absolute abundance (Bengsen et al., 2011). Furthermore, if a relative abundance comparison is simple, quick, and sensitive to changes in the population (Allen et al., 1996), it is appealing for conservation biologists as well as community groups and other organisations that conduct wildlife population monitoring: many of the models for estimating the abundance of unmarked species from camera trapping are complex and based on assumptions that are difficult to meet (Denes, Silveira, & Beissinger, 2015). However, imperfect data is a permanent reality for conservation projects. Indices can, at the very least, identify areas that require further investigation and action despite not being entirely accurate (Carbone et al., 2002) and can still be used to inform conservation management (Gilbert et al., 2021).

CTR is the most commonly used relative abundance index for camera trap studies. However, other indices are also useful. Complementary indices can help describe the activity captured in the population, all based on the intuitive assumption that higher densities should result in more activity. For example, time until capture of the target species is expected to decrease if density is higher, which is considered a possible measure of abundance (Carbone et al., 2001; Kays & Slauson, 2008). Other commonly reported indices include the total number of independent detections and the proportion of camera stations with successful detections (Burton et al., 2015). Both of these measures are expected to increase with population density.

4.1.4 Case study

I used Rakiura tokoeka (*Apteryx australis australis*) (Section 1.2), as the case study species to explore the use of camera monitoring for kiwi. I chose this species due to the opportunity to compare CTR with independent estimates of density that had been made at four locations on Stewart Island/Rakiura using radio-telemetry-based territory mapping (Robertson et al., 2017, 2018). Previous research on Rakiura tokoeka indicated a slow but gradual decline at one of the four locations (although more recently this population appears stable (Robertson et al., 2018; Robertson & Colbourne, 2022), and more information on this subspecies would be valuable for conservation and management purposes. My goals were to: (1) trial the use of a grid of camera traps for monitoring the activity of Rakiura tokoeka at four locations, (2) consider the relationship of activity to independent estimates of density, and (3) provide guidelines for future camera surveys for Rakiura tokoeka.

4.2 Methods

4.2.1 Location and study species

I conducted camera trap surveys at four locations on Rakiura: Mason Bay, Port Adventure, Kaipipi and Ulva Island (Figure 19) (see Section 1.4.1 for a description of study sites). These sites were chosen as they are the only locations where estimates of Rakiura tokoeka density are available through radio-telemetry based territory mapping. Density estimates were made in 2018 at Mason Bay (Robertson et al., 2018) 2017 at Port Adventure (Robertson et al., 2017), and 2019 at Kaipipi and on Ulva Island (see Sections 3.3.2 and 3.4.5).

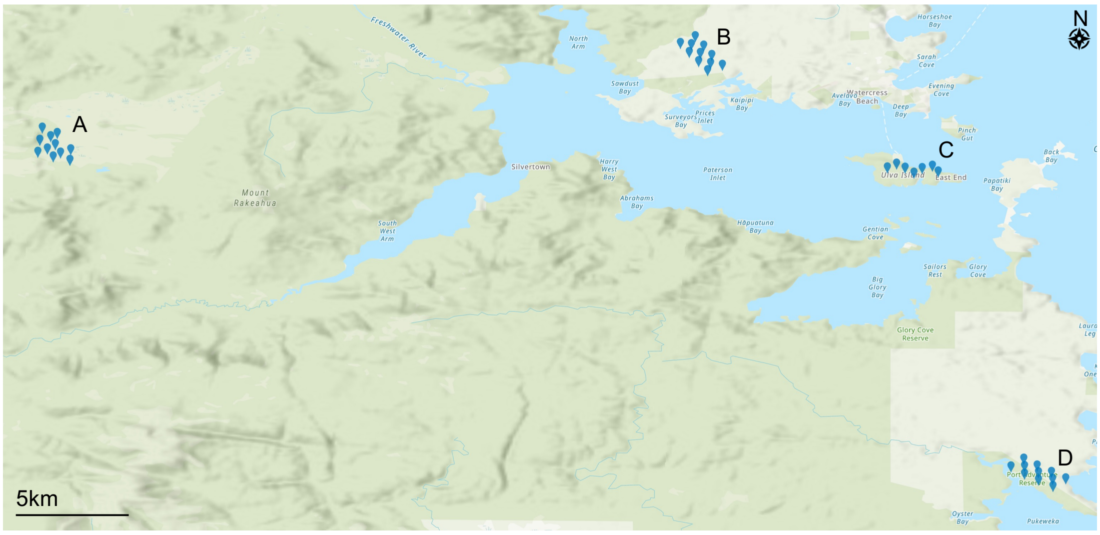


Figure 19. Map showing a cross section of Stewart Island/Rakiura with the location of four camera trap grids. A: Mason Bay, B: Kaipipi, C: Ulva Island, and D: Port Adventure.

4.2.2 Establishment

The size and shape of the territory mapping sites dictated the layout of camera grids at each location. I used regular grids with approximately equal distances between cameras (Rovero, Zimmermann, Berzi, & Meek, 2013; Whittington, Hebblewhite, Chandler, & Lentini, 2018). Camera stations were 350 or 500 m (±25m) apart depending on their location within the grid (external or internal) (Figure 20).

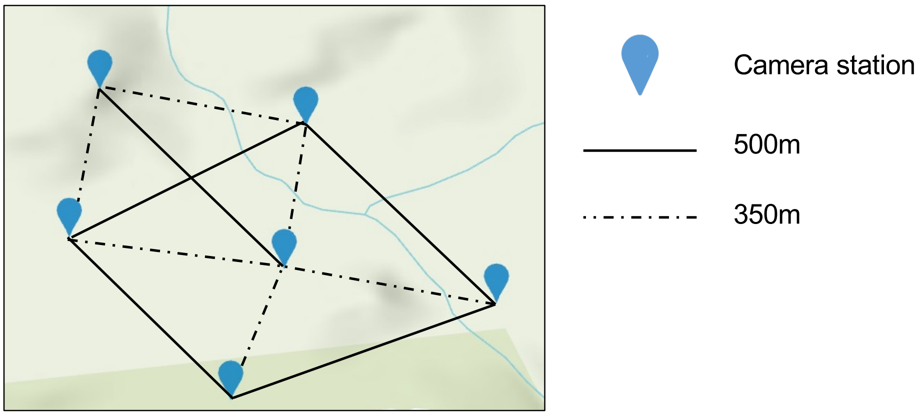


Figure 20. Part of the camera trap grid at Kaipipi showing the distance between camera stations (350 or 500 m) depending on their location in the grid.

Mason Bay, Kaipipi and Port Adventure had square formations with a central, internal camera, while Ulva Island had a zigzag line due to the size and shape of the island (Figure 21). The inter-station distance was set in an attempt to both avoid gaps larger than the smallest average home range of Rakiura tokoeka (7.4 ha, diameter: 307 m, Mason Bay) where no encounters with a camera would be possible (Bengsen et al., 2011; Robertson et al., 2017; Sollmann, 2018; Suwanrat et al., 2015), and reduce the possibility of individuals being captured in multiple cameras because they were unable to be individually identified (Suwanrat et al., 2015). I could therefore reasonably assume that most individuals in the study area had a >0% chance of being photographed (Anile, Ragni, Randi, Mattucci, & Rovero, 2014),

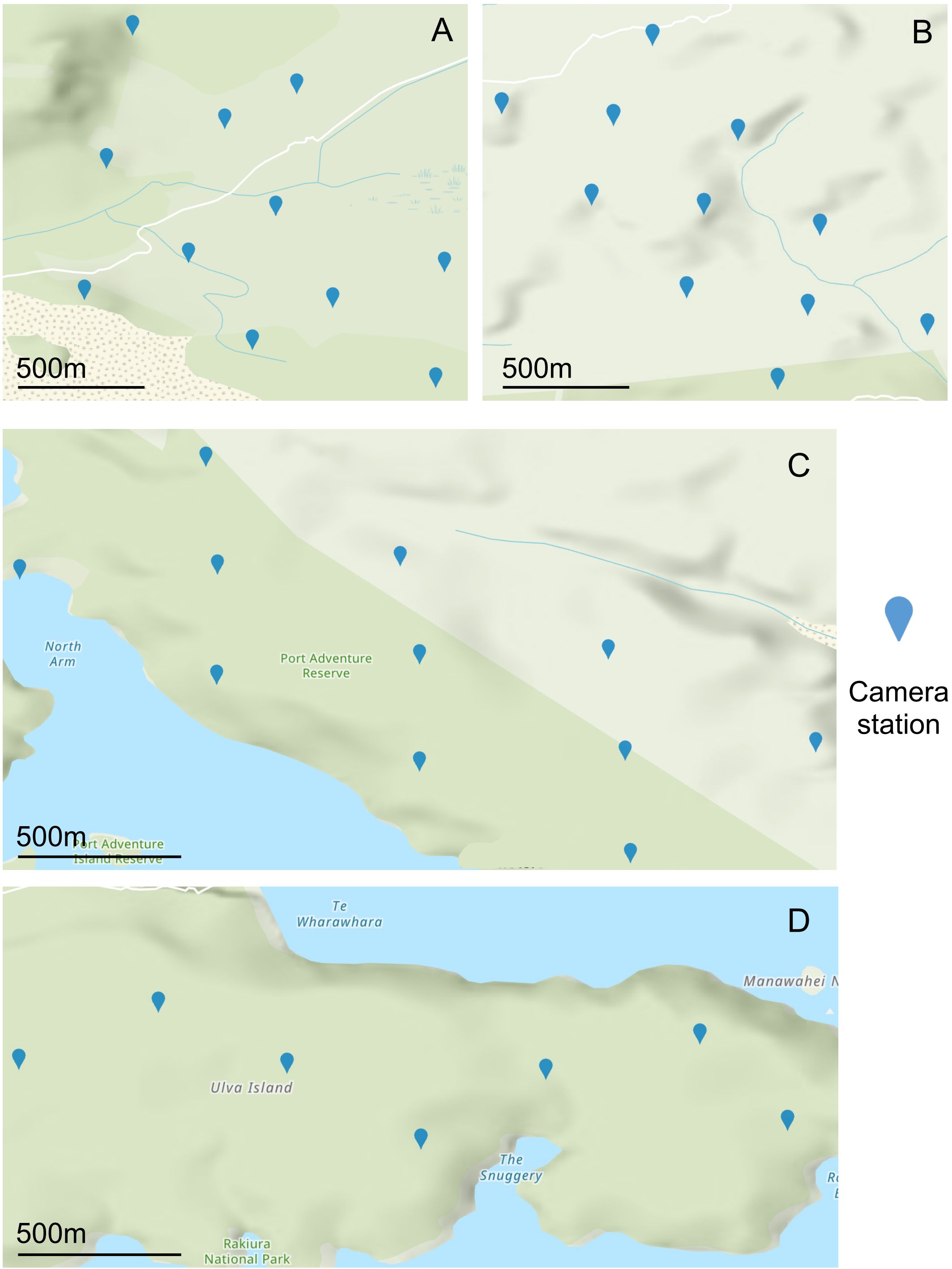


Figure 21. Camera trap grids for monitoring Rakiura tokoeka on Stewart Island at Mason Bay (A), Kaipipi (B), Port Adventure (C) and Ulva Island (D).

Mason Bay, Kaipipi and Port Adventure had 11 camera stations while Ulva Island had seven stations (due to the size and shape of the island). Rowcliffe, Field, Turvey, and Carbone (2008) found 3 – 6 'setting points' provided camera trap rates that had a good correlation to density estimates using simulations for four ungulate species, and Rovero and Marshall (2009) had the same result using 5 – 8 setting points for Harvey's duiker (*Cephalophus harveyi*).

Cameras were attached to trees, branches, or posts at a height of approximately 30 cm within 25 m of predetermined locations based on set distances from other camera stations (350 or 500 m). Cameras faced straight ahead and parallel to the ground, directed towards the most likely area nearby to detect Rakiura tokoeka, i.e., clear areas. Placement of cameras was semi-random, with a preference for possible animal trails, open areas or cut tracks if available, to maximise detection probability and reduce exposure to vegetation that would trigger the camera excessively through movement. I used a combination of camera models: Bushnell (Trophy Cam HD Aggressor Low-Glow and Trophy Cam Essential HD 10MP Low-Glow), Little Acorn (5210A) and Exodus (Lift 2). Cameras were enabled for 24 hours/day, and once triggered, cameras were programmed to capture a 20 second video (termed 'captures'), with a minimum delay between records of 1 second. These settings were chosen to help determine if Rakiura tokoeka were moving alone, in pairs or in groups, which has not been established for this species. Furthermore, video increases the chance of species detection and identification and allows observations of behaviour (Caravaggi et al., 2017; Mills et al., 2016). Lures and baits were not used as there are no commonly accepted methods of attracting wild kiwi, and this could have biased results in an unknown way (Bengsen et al., 2011).

4.2.3 Surveys

Five surveys were completed between February 2018 and March 2020 at Mason Bay and on Ulva Island, and four at Kaipipi and Port Adventure, for a total of 18 sampling periods (Table 7). The same camera stations were used consistently for each survey as recommended by Engeman (2005) for any type of monitoring station. Surveys were conducted biannually in opposing seasons, winter (breeding) and summer (non-breeding). There were three surveys in summer: summer 2018, summer 2019, and summer 2020, and two surveys in winter: winter 2018 and winter 2019. When referring to a sampling period I refer to the location specific survey, for example, Kaipipi summer 2019. Summer monitoring was established to coincide with the long-term monitoring of Rakiura tokoeka at Mason Bay and Port Adventure, which always occurs in February. Winter is breeding season for kiwi and monitoring is usually limited to avoid disturbing breeding birds and nests, making cameras a potentially effective tool to monitor Rakiura tokoeka and other kiwi during this time. Furthermore, monitoring in opposing seasons can help account for seasonal variation (Kays et al., 2020; Noss et al., 2003).

Table 7. The maximum number of survey days for 18 seasonal camera trapping surveys at four locations on Rakiura. Zero indicates no survey occurred.

	Summer 2018	Winter 2018	Summer 2019	Winter 2019	Summer 2020
Mason Bay	11	8	57	25	24
Port Adventure	27	13	76	0	29
Ulva Island	22	14	74	24	22
Kaipipi	0	8	77	21	21
Average	*20*	*11*	*71*	*23*	*24*

Surveys ranged from 8 – 77 days in length based on logistics, camera availability, and the desire to determine the impact of a longer survey. According to Samejima et al. (2012), any effect of weather or breeding cycles that may impact detection between locations can be reduced by longer surveying periods. Surveys were not quite simultaneous between locations; the timing was based on logistics and surveys began within six days of one another. Once equipment was deployed in the field it was left to remotely monitor for a minimum of eight days and ran until collected or until the batteries failed. Surveys were always initiated to avoid the full moon, which is potentially a time that kiwi are less active (McLennan & McCann, 1991). Of course, longer surveys also covered the full moon period.

4.2.4 Data analysis

Camera trap footage was manually screened and any species visible in each video was identified and counted, or videos were classified as false triggers if no species were visible. Where there were camera malfunctions, such as recording the wrong date and time, the days of data that were unreliable were removed from analysis. I considered captures of Rakiura tokoeka at the same camera station as independent events if they were (i) taken more than 0.5 hours apart (O'Brien et al., 2003), (ii) showed two or more individuals in the same video, (iii) they were clearly different individuals through size or distinguishable marking (Brook, Johnson, & Ritchie, 2012; Foster, Harmsen, & Doncaster, 2010). I used only independent captures for further analyses.

I calculated the activity of Rakiura tokoeka, defined as camera trap rate (CTR), as the number of independent captures divided by the number of camera days (i.e., the number of 24-hr periods during which the cameras were operating) multiplied by 100 (Rovero & Marshall, 2009). This provides the number of Rakiura tokoeka captures per 100 camera days. I used camera trap rate to compare activity between the four locations, between and within locations for the different surveys, between seasons (summer/breeding and winter/non-breeding), during the day (summer: 5:00 - 21:00, and winter: 8:00 - 18:00) and night, with different temperatures, precipitation, and moon phases.

To explore variation in CTR between camera stations I used (a) visual 'hotspot' figures, (b) independent sample t-tests, and (c) one-way ANOVA.

(a) I used ArcGIS (https://www.esri.com/en-us/home) to map the average CTR of individual camera stations (from all surveys combined) as hotspot images, with larger circles representing higher CTRs. For Kaipipi and Ulva Island I plotted the locations of known nests (Section 6.3.1) on the maps to help identify potential relationships between distance to nest and CTR, hypothesizing that camera stations closer to nests would have higher CTRs. I also used different coloured hotspots to represent distance to known territories (Section 3.3.1), hypothesizing that stations within territories would have higher CTRs.

(b) I used independent sample t-tests to compare the CTR of camera stations with or without the following variables: open space, on a track, near a nest (within 50 m), dense foliage, on a territory boundary, on a beach, close to water, on a slope, on a ridge or within a known territory.

(c) I used a one-way ANOVA to compare the CTR of camera stations with distance to known nests using: 0 – 100 m, 101 – 200 m or >200 m.

Temperature data was obtained from either location-specific i-buttons (DS1921G-F5# Thermochron,4K), or the weather station in Oban (https://www.wunderground.com/weather/nz/stewart-island), the sole township on Rakiura. Precipitation accumulation data was also obtained from the weather station in Oban. The difference in recorded temperature from i-buttons and the weather station was usually less than 1°C, but occasionally up to 4°C. I had no independent precipitation measure to compare to values from the weather station. I used all available temperature information from the weather station: high, average, and low temperatures per day, and when i-buttons were used the same values were extracted. I grouped daily temperatures and accumulated precipitation as shown in Table 8.

Table 8. Categories for daily low, average and high temperatures (degrees Celsius) and accumulated precipitation (mm), with four categories for temperature and five for precipitation.

Temperature (C)	Precipitation (mm)
< 11	0
11 - 16	0 - 10
16 - 20	10 - 20
> 20	20 - 30
-	> 32

To compare CTR over different moon phases I classified survey days by the primary phases of the moon using https://www.timeanddate.com/moon/phases/new-zealand/auckland, as either first, full, new, third or intermediate. I established the intermediate category because when the period between moon phases is longer than seven days, there is an extra day where the illumination level is intermediate between the two phases.

I compared the mean CTR from smaller samples of camera stations (mixed camera models) within location to the overall CTR from that location using Wilcoxon signed rank tests to see if the same results could be produced with fewer stations. I used the following subsamples:

(i) Odd and even numbered stations (i.e., Stations 1,3,5,7,9,11 and 2,4,6,8,10)

(ii) Lower and upper consecutive stations (e.g., stations 1,2,3,4,5 and 6,7,8,9,10,11)

(iii) Smaller versions of the same camera grid pattern used at Mason Bay, Port Adventure and Kaipipi using five cameras as opposed to eleven (Ulva Island had a different grid configuration and was not included in this subsample).

> This pattern was a square of camera stations 500 m apart, with a central station in the centre (350 m from all external stations).

The length of survey was analysed by comparing CTR in increasing 7-day increments with 95% confidence intervals. Stabilisation of the mean CTR over time and the width of confidence intervals was considered in assessing appropriate survey length.

Cameras vary according to sensitivity and trigger speed amongst other parameters, all of which affect the success of animal detections. Because I used different camera models during the surveys, I ran comparisons between models at five random stations. Each comparison had two different models of camera on the same settings set side-by-side to run simultaneously. These comparisons occurred at Kaipipi (Stations 1,8,9) and Port Adventure (Stations 3,8). I compared Bushnell and Exodus (x3), Acorn and Bushnell (x1) and Acorn and Exodus (x1). The data from these paired cameras was compared for the mean number of captures, the temporal distribution of captures, the proportions of different species and the number of false triggers.

Additionally, I report on other basic indices from the camera trap data that are assumed to relate to abundance and detection probability including; proportion of sites with detections, latency to first detection (using a generalised linear model with a poisson distribution, one-way ANOVA and post-hoc Tukey's HSD pairwise comparisons to compare the four locations), and detection rate (the number of independent detections per survey day).

The data did not follow a normal distribution, so Wilcoxon-Mann-Whitney and Wilcoxon signed rank tests were used to compare the difference between estimates. I used Welch t-tests for mean CTRs and Chi-squared goodness of fit to compare proportions for the camera subsamples (comparison (iii)). I bootstrapped correlation estimates and corresponding confidence intervals using 1000 – 10,000 resamples. Where Wilcoxon-Mann-Whitney tests were used I report the U statistic, and solely to distinguish with the Wilcoxon signed rank tests (for paired samples) I report the W statistic.

Significance is reported for values $p \leq 0.05$.

4.3 Results

4.3.1 Surveys

There were a total of 4213 camera days (number of cameras x number of days recording) from the five seasonal survey periods (Table 9).

Table 9. The number of camera days per location and survey period at four study sites on Stewart Island, New Zealand.

	Summer 2018	Winter 2018	Summer 2019	Winter 2019	Summer 2020	Total
Mason Bay	86	65	459	182	214	1006
Kaipipi	0	54	840	214	196	1304
Port Adv.	218	77	688	277	0	1260
Ulva Island	89	60	217	134	143	643
Total	304	196	1987	673	410	**4213**

4.3.2 Camera trap rates

Overall, Ulva Island had a significantly lower CTR than Mason Bay (Estimate = -10.77, U: 74, p = 0.01), Kaipipi (Estimate = -7.20, U: 76, p = 0.01) and Port Adventure (Estimate = -6.49, U: 73, p = 0.02) (Table 10). There were no significant differences between the other locations.

Table 10. The total overall camera trap rate (CTR) of Rakiura tokoeka at four locations on Stewart Island from five seasonal survey periods. CTR = number of independent kiwi captures/number of camera days x 100.

	Camera days	Independent kiwi detections	CTR
Mason Bay	1006	174	17.3
Kaipipi	1304	179	13.7
Port Adventure	1260	164	13.0
Ulva Island	643	42	6.5

Between individual surveys, the mean CTR for Ulva Island was consistently lower than Mason Bay, Port Adventure and Kaipipi (Table 11), but the difference was not always statistically significant to the 0.05 level (see Appendix B.1 for all the significant survey comparisons). Importantly, the mean CTR within locations did not differ significantly between surveys.

Table 11. Mean CTR for each seasonal survey at four locations on Stewart Island (N/A = no survey). CTR = number of independent kiwi captures/number of camera days x 100.

	Summer 2018	Winter 2018	Summer 2019	Winter 2019	Summer 2020
Mason Bay	15.6	12.5	16.9	17.5	19.6
Kaipipi	N/A	14.8	14.3	15.8	9.3
Port Adventure	12.7	21.2	10.1	N/A	12.7
Ulva Island	6.7	5.3	4.8	3.4	7.4

The range and variation in CTR for individual camera stations at all the locations was high, particularly at Mason Bay (Table 12, Figure 22).

Table 12. The maximum, minimum and mean camera trap rate (CTR) from all camera stations at four study sites on Stewart Island from five seasonal survey periods. CTR = number of independent kiwi captures/number of camera days x 100.

	Max. CTR	Min. CTR	Mean CTR	SE
Mason Bay	44.0	1.9	15.7	3.5
Kaipipi	26.6	5.5	12.9	2.2
Port Adventure	25.5	3.7	12.6	2.0
Ulva Island	12.8	0.0	5.9	1.7

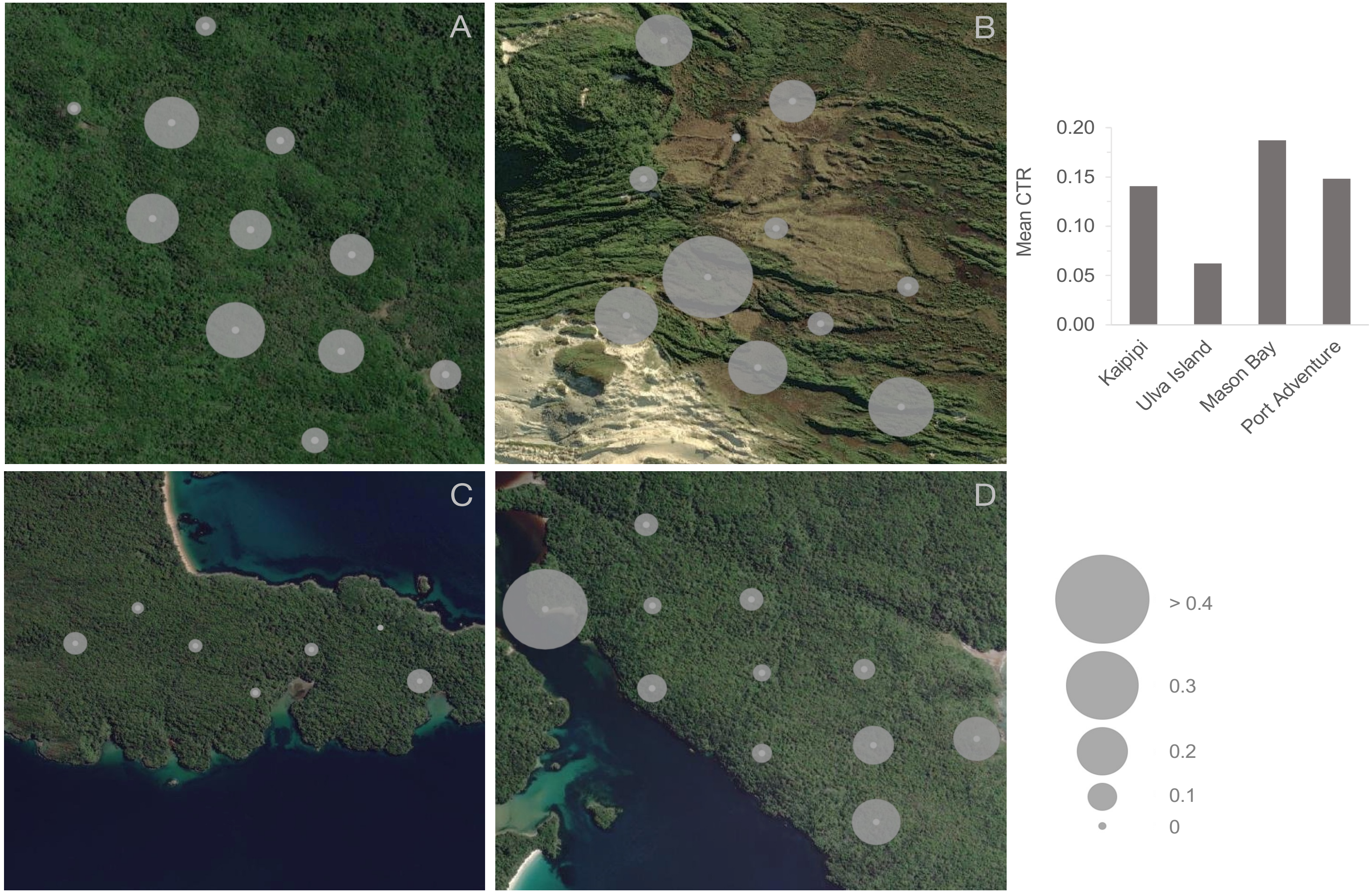


Figure 22. Hotspot figure showing the variation in average CTR between stations and locations (from all surveys combined), with larger circles representing a higher CTR (A = Kaipipi, B = Mason Bay, C = Ulva Island, D = Port Adventure). CTR = number of independent kiwi captures/number of camera days x 100.

The high variation in CTR within and between stations made it difficult to relate any of the camera station variables to CTR. However, there was a significant difference in CTR for stations on a track or a slope. Camera stations that were on tracks had a higher CTR (n = 53, mean: 0.21) than those not on tracks (n= 86, mean: 0.11) (t- 2.642, df 72.5, p = 0.01). Camera stations on a slope had lower CTR (n = 45, mean: 0.07) than those not on a slope (n = 94, mean: 0.17) (t- -4.240, df 137, p <0.001). There was no significant difference in CTR with distance to nest, or for stations within territories at Kaipipi or on Ulva Island (Figure 23).

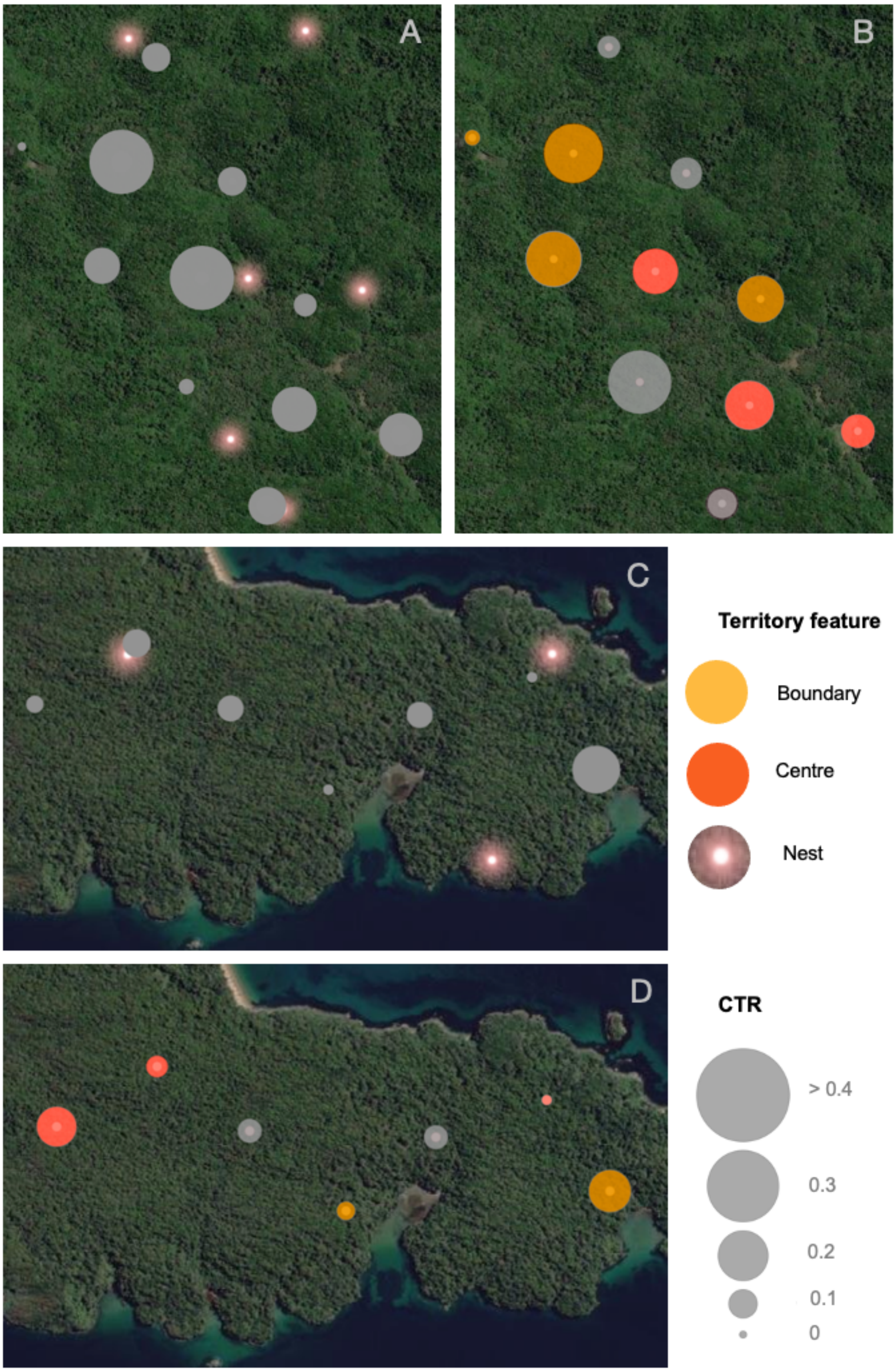


Figure 23. Hotspot figures showing average CTR per camera station (from all surveys combined), in relation to known nest locations (A = at Kaipipi, C = on Ulva Island) and known territories (B = Kaipipi, D = Ulva Island), with larger circles representing a higher CTR. CTR = number of independent kiwi captures/number of camera days x 100.

Rakiura tokoeka were detected in all four locations and 39/40 of the camera trap stations. The single station that did not have any captures was on Ulva Island. The median number of independent captures per station at each location was lowest for Ulva Island and very close between the other three locations, with a highly variable range, from 0 – 48 (Table 13).

Table 13. The median number and range of Rakiura tokoeka detections (captures) per camera station and location from all surveys combined.

Location	Median no. captures	Range
Mason Bay	14.3	(1 – 48)
Kaipipi	12.9	(6 – 34)
Port Adventure	10.6	(4 – 38)
Ulva Island	4.6	(0 – 13)

The median value for the number of days that a camera was operational until its first capture of Rakiura tokoeka followed a similar pattern, with Ulva Island having the longest period until first capture at 10.2 days (range 5 – 16.5), and the other locations around 3 to 4 days (range 1.5 – 8) (Figure 24). However, the overall difference between locations was not significant ($F_{(3,104)} = 2.598$, p = 0.06).

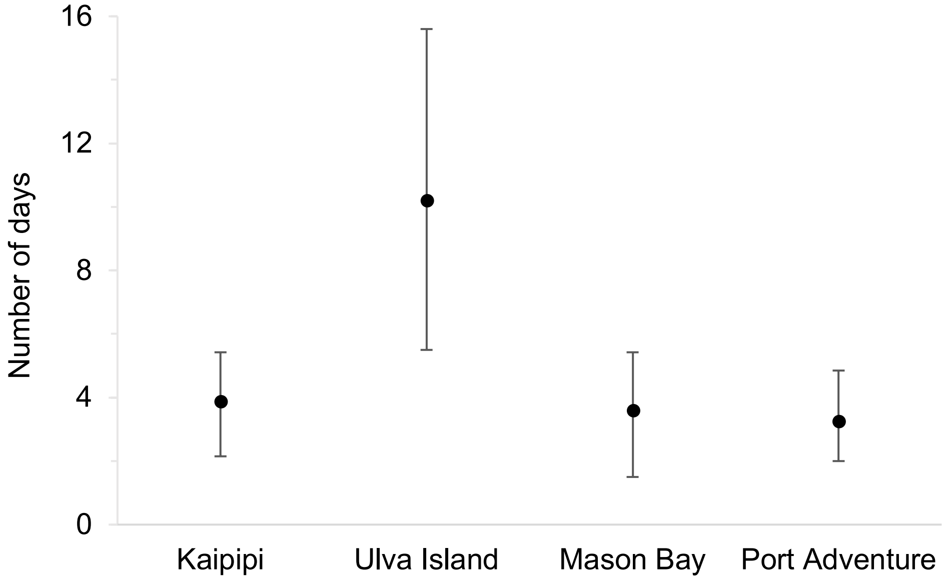


Figure 24. The median number of days until the first Rakiura tokoeka capture from camera trapping at four locations on Stewart Island ± 90% confidence interval, based on the 5th and 95th percentiles.

The detection rate of kiwi (number of independent kiwi detections per survey day) was significantly different between locations ($F_{(3,10)} = 18.77$, $p = < 0.001$), but not between surveys. Tukey's HSD showed that the detection rate was lower on Ulva Island than the other three locations (Figure 25). The difference in detection rate between Ulva Island and Kaipipi was 0.90 ($p = 0.001$), Ulva Island and Mason Bay 0.95 ($p <0.001$) and Ulva Island and Port Adventure 0.94 ($p = 0.001$).

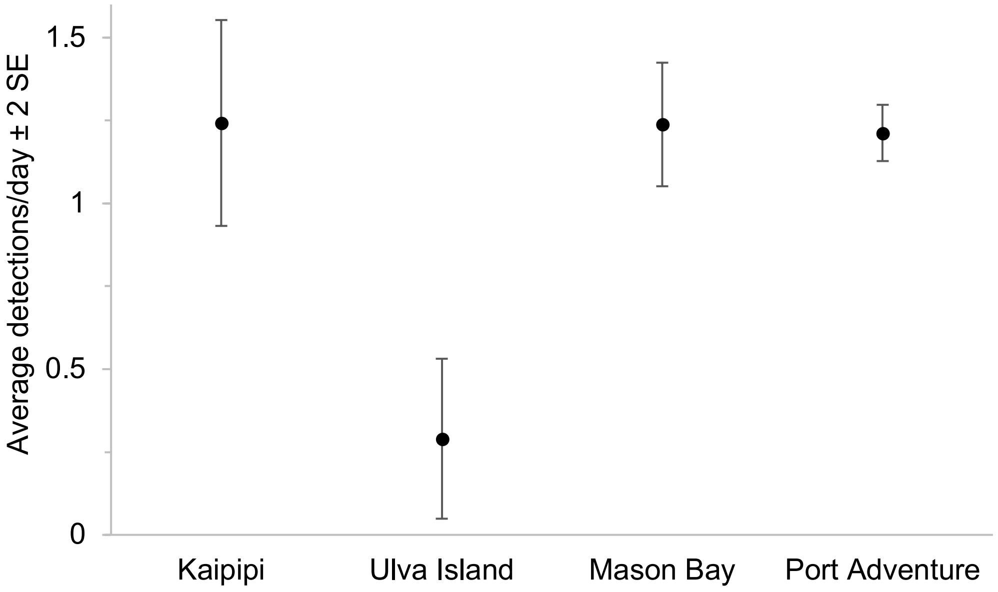


Figure 25. The average number of Rakiura tokoeka detections per survey day from camera trapping at four locations on Rakiura ± two standard errors.

There was no significant difference between CTR in the winter/breeding and summer/non-breeding seasons (CTR breeding: 13.83, non-breeding: 12.20, W = 652.5, $p = 0.38$). CTR also did not differ between moon phases, or across any of the temperature or precipitation comparisons. The CTR of Rakiura tokoeka was significantly higher during the hours of darkness compared to daylight hours (CTR day: 6.58, night: 26.41, W = 5,451, $p < 0.001$).

4.3.3 Subsamples and survey length

Mean CTR's from the subsamples of camera stations, (i) odd and even numbered and (ii) upper and lower consecutively numbered, were not significantly different from the overall CTR for each location. For the mini-grids (iii), only one configuration at Mason Bay during the summer 2018 survey had a significantly different CTR from the total (total CTR = 15.63, mini-grid CTR = 2.08, W = 1872.5, p = 0.04). In all other comparisons, the mini-grid CTR was not significantly different. This means that in general, a similar CTR could be obtained using fewer cameras. However, the confidence intervals tended to be large due to the low number of stations in each sample.

The most effective and efficient length of survey was approximately 21 – 28 days (Figure 25). Mean CTR and confidence intervals became stable around this time in all locations. At 49 – 56 days, CTR began to fluctuate slightly at all locations.

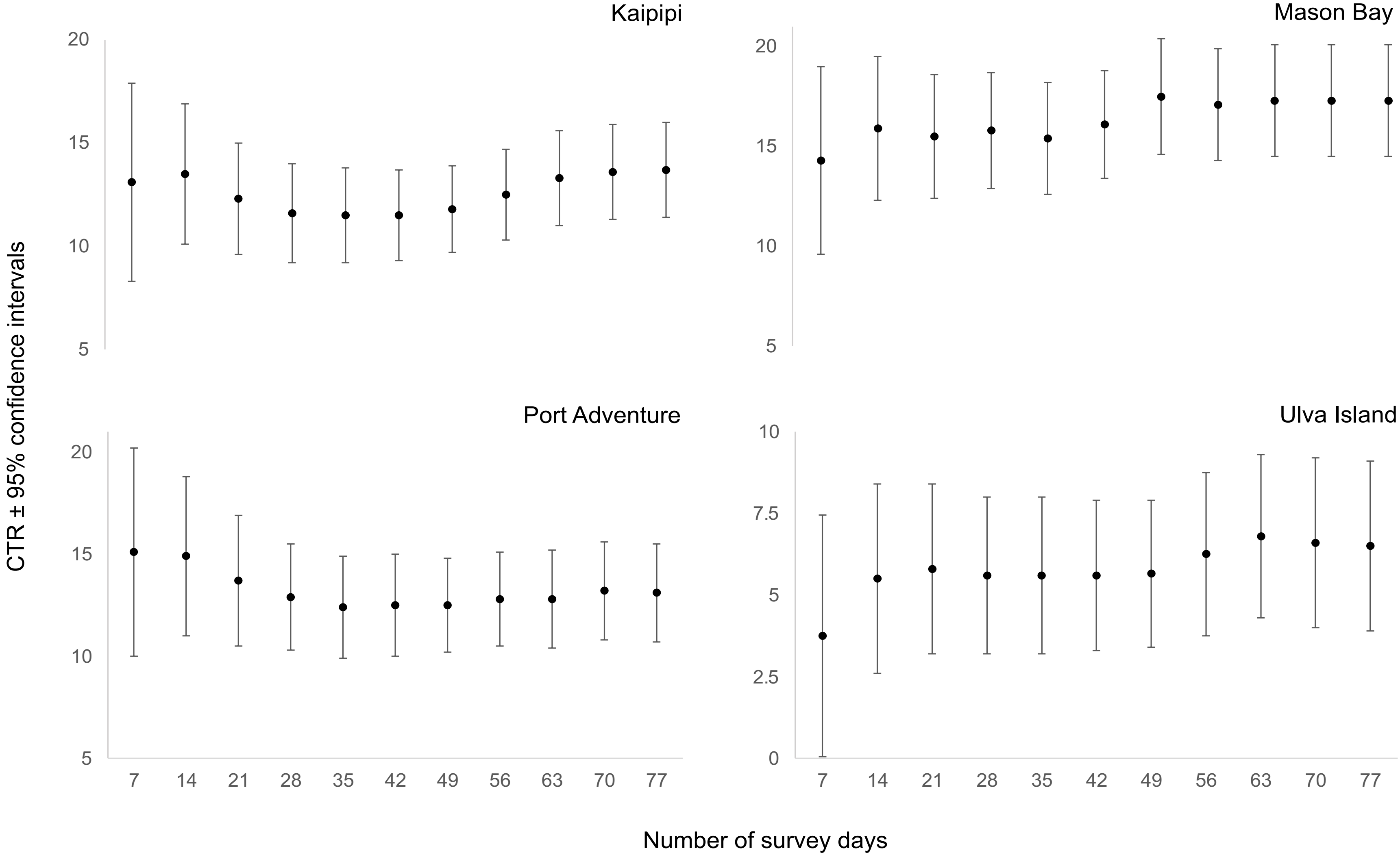


Figure 25. The CTR ± 95% confidence intervals of independent captures of Rakiura tokoeka in increments of seven survey days for four locations on Stewart Island. CTR = number of independent kiwi captures/number of camera days x 100.

4.3.4 Cameras

Wilcoxon signed rank tests showed no significant differences in the mean number or distribution of captures between camera models except in the case of the Acorn and Exodus comparison with two independent kiwi captures by the Exodus camera and no captures by the Acorn (Mean number $t= -3.2707$, $df = 9$, $p < 0.01$, distribution $V = 1.5$, p-value < 0.01). As a result, the Exodus camera data was used for all further analyses from that survey. There were no other Acorn cameras used at Port Adventure during later surveys. Acorn cameras were never deployed at Kaipipi, however, Mason Bay had four stations with Exodus cameras and three stations with Acorns in the summer survey of 2018. Chi-squared goodness of fit tests found no evidence of a difference in the proportions of species captured or the number of false triggers between any camera model comparisons.

There was a 12% rate of camera failure (19/157), and a further 6 cameras part-malfunctioned during surveys (turned off or rotated to face in a different direction by possums (*Trichosurus vulpecula*), recorded with incorrect date/time, or failed for unknown reason part-way through a survey).

4.4 Discussion

4.4.1 Rakiura tokoeka activity (CTR)

According to the camera trap rate (CTR) and related activity indices, the activity of Rakiura tokoeka was lower on Ulva Island than at Mason Bay, Port Adventure and Kaipipi. If camera and site variables are controlled and the use of space is consistent, changes in detection rates should be driven by density (Broadley, Burton, Avgar, & Boutin, 2019; O'Brien et al., 2010). From independent density estimates using radio-telemetry-based territory mapping, Ulva Island had a comparable density to the other three locations (Section 3.3.2). However, the study area used for territory mapping and that of the camera grid survey did not align completely, with the camera grid overlapping approximately 50% of the territory mapping area (due to the camera trapping being initiated prior to the radio-telemetry, and low numbers of birds in the area resulting in extending the search effort for birds beyond the camera trapping zone). This means that only part of the area covered by the camera grid included known Rakiura tokoeka territories, and these were two of the largest territories, which contain a lower density of birds than some of the other mapped areas not covered by the cameras. The density of Rakiura tokoeka may not be consistent across Ulva Island, and the cameras may be capturing a lower density more representative of the area where the cameras were located as opposed to where the territory mapping occurred. If this was the case, cameras could have captured a more accurate representation of the density on Ulva Island than telemetry.

However, camera trap rate can also vary independently of density (Noss et al., 2003), and instead be related to other factors affecting detection rates (Sollmann, 2018). Although the activity of Rakiura tokoeka on Ulva Island was consistently lower than the other locations according to the indices, it cannot be assumed that this reflects a lower density. Importantly, the absence of detections on Ulva Island does not necessarily mean that Rakiura tokoeka are not present in these areas (Newton, Nguyen, Roberton, & Bell, 2008; Tobler, Carrillo-Percastegui, Leite Pitman, Mares, & Powell, 2008).

Ulva Island has several unique characteristics that could impact detection probability. For example, regenerating native saplings are common due to the lack of browsing pest species present on mainland Rakiura, and therefore the understorey tends to be denser. Dense vegetation can reduce the detection zone of cameras (Burton et al., 2015; Glen, Cockburn, Nichols, Ekanayake, & Warburton, 2013) and slow the movement rate of animals (Broadley et al., 2019) which could have limited the opportunities for individual Rakiura tokoeka to be exposed to camera stations. The lack of large, browsing pest species also reduces the number of obvious animal trails and clearings that were used for camera placement when available at the other locations to maximise detection potential. Two camera stations on Ulva Island were established on cut tracks, but the other five stations were in denser vegetation and hence may not have had the same probability of detection as at the other locations where more open areas were available.

The behaviour of Rakiura tokoeka could also have reduced detection rates on Ulva Island, for example, through the avoidance of weka (*Gullirallus australis scotti*) which are largely absent from mainland Rakiura and not present at the other three locations. Weka were captured frequently on camera footage from Ulva Island, making repeat visits and spending long periods of time investigating the cameras. It is unknown how Rakiura tokoeka and weka are distributed spatially or temporally, but the predation of Rakiura tokoeka eggs and chicks has been recorded at burrows (Section 6.3.2) and it is possible that the presence of weka at camera stations was a deterrent for Rakiura tokoeka. Additionally, avoidance of people and areas with human scent could have been a reason for reduced detections, as all Rakiura tokoeka on Ulva Island have been either directly translocated or are descendants of translocated birds and this experience could have impacted their future willingness to interact/approach human scent. However, if this did occur, it was not apparent for all individuals as one male that was translocated in 2013 nested within 2 m of a popular walking track in 2019 (*pers. obs.*). Furthermore, Rakiura tokoeka at Mason Bay have been subject to intensive telemetry-based surveys five yearly since 1993, and at Port Adventure since 2011, so this bias would not necessarily be restricted to Ulva Island alone.

Finally, it is important to consider that the size and shape of the camera grid on Ulva Island was different to the other locations and fewer cameras were used (7 as opposed to 11). Camera trap rates per camera are highly variable and using a lower number of cameras may not have captured enough of the variability on Ulva Island to represent the mean camera trap rate with enough precision. However, subsamples using fewer camera stations at Mason Bay, Port Adventure and Kaipipi did not have a significantly different capture rate in most cases to the total, indicating fewer cameras would capture the same mean. Similarly, Kays et al. (2020) did not find a relationship between the number of cameras and precision in detection rate. Nonetheless, the set-up of the survey differed on Ulva Island and the number of stations and shape of the grid could have influenced all the calculated indices in unknown ways. Additionally, territory size on Ulva Island tended to be smaller, and there were less individuals per territory (Section 3.3).

There was no significant difference in CTR or other activity indices between Mason Bay, Kaipipi and Port Adventure. Independent density estimates from territory mapping were also comparable for these locations (Section 3.3.2). Port Adventure and Kaipipi are similar in terms of habitat with mostly open forest, while Mason Bay has sandy soil and unique areas of regenerating farmland with tussock and native grasses. In this case, the different habitats did not seem to impact detection rates of Rakiura tokoeka, perhaps due to the presence of animal trails through the tussock at Mason Bay where camera stations could be placed. Achieving constant detection probability across locations is difficult, even with consistent monitoring protocols (Zwerts et al., 2021), although I was able to use animal trails at all three locations for some camera placements. Including variables that could impact detection such as temperature, precipitation and moon phase can help account for differences in camera trap rates across surveys, but not between locations, as these features were reasonably consistent due to the proximity of sites and single source of most of the weather data.

Kaipipi, Mason Bay and Port Adventure had consistent estimates of both density (Section 3.3.2) and CTR, which could lead to the conclusion that these measures are correlated. However, that relationship needs to be more thoroughly investigated with a wider range of density estimates and camera trap rates than was found during this study (O'Brien, Kinnaird, & Wibisono, 2003; Palmer et al., 2018; Rovero & Marshall, 2009). Furthermore, it is not yet known how density affects kiwi movement or home range size or vice versa and these factors can impact detection rates in different populations. Broadley et al. (2019) found that in 10 out of 11 studies that reported movement rates with density, lower movement rates were present in higher density populations. This could falsely decrease camera trap rates in higher density populations compared to lower density populations with higher movement rates (and therefore more camera encounter opportunities). Methods that adjust for the typical movement rate of a species in camera detections have been presented (Chandler & Royle, 2013; Rowcliffe et al., 2008), but estimates of movement must be accurate for reliable results (Rovero & Marshall, 2009), and these do not yet exist for kiwi.

4.4.2 CTR variables

Camera trap rates per station were highly variable at each location. This is reasonable when cameras are placed randomly in the environment without prior knowledge of proximity to food, water, nests, or other areas that may dictate activity levels (Samejima et al., 2012). Consequently, establishing adequate camera stations and multiple surveys to capture site variability is important. Placing un-baited cameras in semi-random positions at set intervals is the most effective way to capture the natural variability in animal activity and provide reasonably unbiased estimates (Kays et al., 2020). In this study, there were sufficient cameras and camera days to capture the variability between stations (except perhaps for Ulva Island). In a meta-analysis of 41 studies using cameras for monitoring terrestrial mammals, spatial heterogeneity between camera stations was common and the authors suggested local habitat variables could be used to explain the differences in detection and make comparisons between locations more valid (Kays et al., 2020). Although placement on a trail or slope had an effect on the CTR of Rakiura tokoeka, proximity to a nest or territory did not, and it is likely that the relationship of CTR to these variables (as well as true density, movement rates, behaviour et cetera) is much more complicated than could be captured during this study.

Seasonal differences in detection rate are common in camera trap studies (Kays et al., 2020). This does not necessarily mean that density changes seasonally (although this can occur), but that detectability can vary depending on various factors that change throughout the year (Noss et al., 2003). Across the 18 sampling periods that covered summer, autumn (due to the length of the summer 2019 survey) and winter, CTR was consistent within each location, i.e., there was no seasonal variation. This is despite range contraction during the breeding season (winter) suggested by territory mapping surveys at Kaipipi and on Ulva Island (Section 3.3.4). The effectiveness of monitoring methods can differ seasonally (Smith & Weston, 2017), for example, the results from spotlighting surveys for red fox (*Vulpes vulpes*) varied between autumn and winter, but camera trap outcomes did not (Vine et al., 2009). If seasonal range reduction did occur for Rakiura tokoeka, movement rates would be likely to simultaneously decrease, resulting in less exposure of individuals to cameras and a lower CTR (Broadley et al., 2019), but this was not this case.

However, there are some irregularities when considering seasonal changes in Rakiura tokoeka activity. Firstly, the territory mapping results indicating a reduced range are somewhat unreliable given the primary purpose was not to detect seasonal change and therefore the effort towards locating individuals was not consistent across seasons (becoming limited and selective towards nesting sites during the breeding season). Furthermore, Rakiura tokoeka incubation patterns are unusual among kiwi; it was rare that individuals reduced their activity to the levels of other kiwi species (Section 6.3.1), probably because of shared incubation. Additionally, some of the individuals in group territories may not be involved in incubation, and hence do not change activity during the breeding season. Until there is more conclusive evidence of how Rakiura tokoeka territories change throughout the year, it is difficult to conclude whether (i) the cameras did not detect a seasonal difference in activity that did occur,

(ii) the cameras were a reliable monitoring method throughout the year and the territory mapping results did not represent a true range reduction, or (iii) there was some difference in Rakiura tokoeka activity patterns during the breeding season but this did not affect CTR.

The lack of seasonal difference in CTR for Rakiura tokoeka has two important implications. Firstly, seasonal differences in weather, environment, and breeding behaviours did not affect CTR so camera trapping has the potential to be a useful monitoring tool for kiwi populations during the breeding season when other more invasive methods like tracking and catching for radio-telemetry are minimised (Robertson & Colbourne, 2017). Secondly and speculatively, stable activity levels over time could indicate population stability, or at least, stability in CTR index estimates.

Temperature, precipitation, and moon phase were considered to determine how these variables impacted the likelihood of detection of Rakiura tokoeka. By controlling and explaining variables that can impact detection, variation in CTR is more likely to be driven by animal specific effects (Broadley et al., 2019; Meek et al., 2014). However, none of these factors influenced the CTR of Rakiura tokoeka, although sample sizes were small, and it is possible larger comparisons would yield different results. Temperature and precipitation on Rakiura do not vary extremely throughout the year and are therefore perhaps unlikely to influence activity (Pérez-Irineo & Santos-Moreno, 2017). Cloud cover can negate illumination levels and not including this factor when considering the impact of moon phase on the activity of Rakiura tokoeka could be the reason no effect was found. Although, given that this species is routinely active during the day, it would be surprising if they purposefully avoided bright moonlight. Notwithstanding this, Rakiura tokoeka were more active at night than during the day.

4.4.3 Subsamples & survey length

Camera station subsamples (5 versus 11 cameras) resulted in a comparable CTR in most cases, but estimates were less precise with wide confidence intervals. Although using fewer cameras may not require as much time, effort or investment, and may possibly achieve the same CTR, precision is essential for an index to detect underlying population change (Caughley & Sinclair, 1994). According to Engeman (2005), increasing observations improves precision, and the best way to increase observations is by increasing the number of locations, as opposed to extending the duration of a survey (Kays et al., 2020). Therefore, having a higher number of cameras is worth the effort to increase the precision of estimates.

The appropriate duration of survey to capture CTR for Rakiura tokoeka was a minimum of 3 – 4 weeks, and there was no benefit of going beyond six weeks. Kays et al. (2020) also suggested a minimum of 3 weeks for camera surveys after analysing the survey design and outcomes of 41 camera trap studies. There were some slight changes to CTR after 7 weeks at Mason Bay, Kaipipi, and on Ulva Island but not at Port Adventure, although these differences were not significant. This may not be the case for populations at different densities, as the detection rate of a species can impact how long a survey needs to run before a precise estimate is reached, and higher detection rates require shorter surveys (Kays et al., 2020). This means that when surveying for animals at lower densities and detection rates, surveys may need to be of longer duration.

4.4.4 Camera models

Ideally, camera model would be kept consistent within a population monitoring project. Where this has not been possible, some studies have found differences in detection rate between models (Robley et al., 2010; Vine et al., 2009) whereas others have found no effect on detection (Farris et al., 2015). In other examples, data from cameras is pooled without considering what differences might exist between models, which jeopardises the reliability of results (Meek, Ballard, & Fleming, 2015). In this project, there were no detectable differences between Bushnell and Exodus or Bushnell and Acorn models. However, it was of some concern that the mean number and distribution of captures differed between an Exodus and Acorn model in a single comparison at Port Adventure in the summer 2018 survey. The Acorn camera missed two captures of Rakiura tokoeka that were captured by the Exodus. However, I do not believe the CTR from Port Adventure was affected as only one Acorn camera was deployed and I could use the data from the paired Exodus instead.

The only other survey in which Acorn cameras were used was at Mason Bay in summer 2018, where four stations had Acorn models. The CTR from this survey was not significantly different from subsequent surveys at Mason Bay, so if there were missing captures from Acorn cameras this was not detectable. I believe that the Acorn camera used in the comparison with the Exodus model at Port Adventure was likely faulty, given that in the other comparisons there was no difference between the Bushnell with the Acorn or Exodus models. Context-specific field trials have been suggested to avoid camera models with incomplete detection rates (Fancourt, Sweaney, & Fletcher, 2018). Cameras will never have completely accurate detection, and performance can differ both between and within models. Future studies for

Rakiura tokoeka would benefit from using a consistent camera model (of higher quality) and seeing if and how detection changes.

4.4.5 Limitations

When working with a species where individuals cannot be identified, such as kiwi, it is usually impossible to determine if multiple captures at a single station are different individuals or the same animal repeatedly. Higher detection rates could be a result of repeated use of some camera stations by individuals (Kays et al., 2020; Tobler et al., 2008). Alternatively, higher detection rates could be due to a single individual being captured on multiple cameras. I used two strategies to help mitigate these possibilities: I first tried to avoid detections of the same individual in two adjacent camera traps, which is important when working with unmarked species (Thunhikorn et al., 2016). To achieve this, I aimed for camera stations to be at least one home range diameter apart from one another (Sollmann, 2018) with approximately one camera per territory (Karanth & Nichols, 2011). The second strategy was to use a time delineation (30 minutes) on capture records, under which all captures were assumed to be the same individual (O'Brien et al., 2003). However, there are other methods to deal with repeat captures that are worth exploring in future camera surveys for kiwi that may deal more appropriately with multiple captures of the same individuals that quite likely occurred regardless of the 30 minute delineation in this study (see Brook et al., 2012).

Camera trap indices assume equal detection probability across space and time. However, there are many factors that result in imperfect detection. Variables such as weather, terrain, and camera placement in relation to habitat features can impact detection rates, as well as sampling method and error. Cameras may not capture individuals that are in their detection zone (camera failure/malfunction), animals may enter the detection zone but not stimulate the passive infrared (PIR) sensors or enter the field of view of the camera (Meek et al., 2015), or individuals may be present but not enter the detection zone (Burton et al., 2015). It is also possible that not all individuals have the same probability of detection due to unknown and unmeasured factors such as size, illness, neophilia or neophobia. Further studies on these factors, including the heat signature of kiwi (important for helping to trigger the PIR sensors), would be beneficial to understand the detection of kiwi on camera traps.

Despite the issue of imperfect detection, camera trap rates assume that activity is related to abundance (Burton et al., 2015). In some cases where camera trap rates have been correlated to independent density estimates (O'Brien et al., 2003; Palmer et al., 2018; Rovero & Marshall, 2009), this has been a reasonable conclusion. However, the relationship between abundance and CTR needs to be tested in species- and site-specific contexts (O'Brien & Kinnaird, 2008). Without a proven correlation to abundance, CTR indices should only be interpreted as activity and alternative explanations for CTR results other than the density of animals present should be explored*.

*I *was not able to correlate CTR with density estimates from territory mapping using formal analyses due to the lack of variation in density and CTR estimates, except for Ulva Island where the study areas were not consistent. But this would be an invaluable way to enhance the use of relative abundance indices for kiwi monitoring.*

4.4.6 Camera traps for kiwi monitoring

The use of camera trapping for monitoring kiwi deserves further exploration. As knowledge of kiwi species and population dynamics grows, the use and application of camera trapping for their monitoring will become more effective and reliable. A basic understanding of how kiwi respond to and interact with cameras is clearly important and could differ between individuals, populations, and species (Meek et al., 2014). Rakiura tokoeka did not appear overly affected by the presence of camera traps on trails or nest burrows. A better understanding of how movement rate, territory size, and activity change with density and in response to other variables will enable more reliable indices and utilisation of camera data in more complex ways. For example, the detection distance and movement rate of Harvey's duiker (*Cephalophus harveyi*) was used to convert camera trap rates to density estimates by Rovero and Marshall (2009) using an equation from Rowcliffe and Carbone (2008).

However, the simplicity of CTR makes it an easy to implement method (Broadley et al., 2019) that can be widely used by the numerous community groups and organisations that monitor kiwi. During the implementation of CTR, validation against independent density estimates would greatly increase the robustness of estimates. If camera trapping indices are compared to density estimates from radio-telemetry, it is important to consider that telemetry-based studies are based mostly on daytime locations, which do not necessarily represent the nocturnal range (Jahn et al., 2013; Toy & Toy, 2020) that cameras record. Ideally, camera monitoring trials would incorporate a range of different kiwi densities that could be used to test the accuracy of results.

A distance of 350 – 500 m between stations seemed to work well for Rakiura tokoeka at Mason Bay, Kaipipi and Port Adventure. However, further research is required to determine how they perform in areas with different densities and when there are fewer birds per territory. The difference in CTR for Ulva Island could have been partially due to the differences in territory size found during territory mapping (Section 3.3.1), resulting in a less appropriate camera spacing. It would be tempting in an area of low kiwi density to deploy more cameras per unit area. However, this would likely result in more than one camera per territory, repeated captures of the same individuals, and inflated estimates of activity or abundance (Silveira, Jácomo, & Diniz-Filho, 2003). Realistically, cameras may need to be more widely spaced in low density populations. The spacing of cameras tends to follow different recommendations depending on analyses of the data, target species, and source (Meek et al., 2014). It is important to establish the appropriate spacing and number of cameras for specific species and locations and then to keep this consistent.

Many kiwi populations are partially marked with bands or transmitters and these populations offer exceptional opportunities to explore the use of camera surveys. For example, the probability of capturing kiwi with transmitters on specific cameras could be determined based on their proximity to those cameras when tracked (Popescu, Valpine, & Sweitzer, 2014). Furthermore, incorporating marked individuals into more complex population models makes a substantial difference in the accuracy of density estimates (Chandler & Royle, 2013). In this study, although many Rakiura tokoeka at Kaipipi and on Ulva Island had transmitters or metal bands for 3/5 camera surveys (Section 3.2.1), in the majority of camera footage they were either not present or present but not visible (Appendix B.2). Sollmann et al. (2013) also struggled to obtain a reasonable sample size of marked individuals in a study on tagged racoons (*Procyon lotor*). If enough captures of tagged kiwi could be attained (perhaps by using a paired, multi-angle camera set up) then spatial-mark-resight models could be used, which are the most promising method for estimating the density of partially marked populations (Chandler & Royle, 2013; Gilbert et al., 2021). There are various statistical models available for estimating the abundance of unmarked populations that warrant consideration for kiwi populations. They have a tendency towards untested and difficult to meet assumptions (Broadley et al., 2019) but may become more attainable with greater knowledge of kiwi.

4.5 Conclusion

Although this was the first study using cameras to investigate population variables for a kiwi species, some initial recommendations can be made for Rakiura tokoeka. Based on the home ranges I found in Chapter 3, camera grids with a 500 x 500 m distance between camera stations, with a central camera in each square (350 m distance) worked well (Figure 20), though exploration of different spatial set-ups may be useful. Ideally, a single camera model would be used, or if there is more than one model, a formal comparison should be undertaken. Surveys should run for a minimum of three weeks, but no more than six, and more than one survey per location is important to capture the variation in activity between and within camera stations. Although there were more detections captured during night-time hours, until it is known whether different individuals are active at night versus the day, I recommend 24 hr monitoring for this species. Further research as to how camera station variables (i.e., slope) and environmental factors (as specific as possible to location) relate to activity levels and explain detection variability would be valuable. It is essential to standardise camera trap methodology within a project and ideally and if applicable, within a species, both to detect population change accurately and to make reliable comparisons (Dillon & Kelly, 2008).

Importantly, the use of relative abundance indices for kiwi would be greatly enhanced by correlating CTR with independent density estimates using formal analyses, which could be done with populations that are at known varying densities (O'Brien et al., 2003; Palmer et al., 2018; Rovero & Marshall, 2009). As camera trap monitoring becomes progressively vital in conservation decision making (Gilbert et al., 2021), trialling and developing these methods for kiwi becomes increasingly valuable.

Monitoring populations of unmarked species is challenging and without being able to identify and count individuals, relying on relative abundance indices like CTR is oftentimes necessary. Conservation biologists still need to provide population parameters even when less than perfect data is all that is available (Carbone et al., 2002). However, relative abundance indices can offer insights into the activity of a species spatially and temporally and identify where further investigation or management action is required (Carbone et al., 2002) and CTR is a particularly useful tool when resources for more intensive methods are not available. No single method is ideal for every project, species, or objective (Gilbert et al., 2021) but trialling different methods is a worthwhile exercise and post-survey data can also be used to assess the credibility of different options (Bengsen et al., 2011). Cameras are increasingly being used to monitor birds (Murphy et al., 2017; O'Brien & Kinnaird, 2008; Samejima et al., 2012; Suwanrat et al., 2015;

Thunhikorn et al., 2016), and are an exceptional tool for studying the behaviour and activity patterns of cryptic species (Kross & Nelson, 2011).

In the next chapter I continue to show the plausibility of camera surveys for kiwi populations by demonstrating the use of two models, the Royle-Nichols (RN model) (Royle & Nichols, 2003) and N-mixture model (Royle, 2004), which can estimate population abundance from repeated detection/non-detection and sparse count data respectively.

Chapter 5: Estimating the abundance and density of a cryptic, unmarked species using camera traps

Preface: The purpose of this chapter is to test if a model for estimating the abundance of unmarked species from detection/non-detection data can successfully estimate the abundance and density of Rakiura tokoeka at four locations where minimum group sizes and densities were available from territory mapping via radio-telemetry.

5.1 Introduction

Population scale monitoring with camera traps has not been used for kiwi (*Apteryx* spp.) before, and the previous chapter suggests it can be useful (Section 4.5). The abundance and density of kiwi are difficult to estimate because kiwi exhibit behaviours, use habitats, and have morphology that hinder many estimation methods (Section 1.1). Camera traps allow the passive collection of data without the intrusive effects of human observers or handling. Cameras have shown significant potential for other cryptic, nocturnal, and rare species (O'Brien et al., 2010; Thunhikorn et al., 2016) and are recommended for unmarked species that are difficult to detect (O'Brien & Kinnaird, 2008). Furthermore, point counts from cameras are a logical transition from the point counts by observers commonly used for avian species, including kiwi (Pollock et al., 2002; Royle & Nichols, 2003).

If abundance and density estimates can be generated from camera surveys that approximate estimates from the gold standard of kiwi monitoring, radio-telemetry, then it may be possible in some circumstances to replace telemetry surveys with less invasive, lower cost, and more widely applicable camera surveys. This would mean a greater ability to monitor and therefore manage kiwi populations, which in most cases (i.e., on mainland New Zealand), require direct management intervention to avoid decline (Robertson & Colbourne, 2017). Camera trap rates (CTR) can be used as a relative abundance index for kiwi (Chapter 4), but only provide surrogate estimates of abundance and are frequently criticised for ignoring detection probability (Pollock et al., 2002; Rosenstock et al., 2002). An alternate method of analysing camera data that is more robust and provides absolute estimates of abundance would be a valuable monitoring tool (Rovero, Tobler, & Sanderson, 2010).

This detection history from camera traps, as either a presence/absence record or a count, can be used by statistical models that estimate the number of animals in an area by the independent detections of multiple cameras. Examples of such models include the Royle-Nichols (Royle & Nichols, 2003) and Binomial mixture models (Royle, 2004), which have been used to estimate the abundance and density for other territorial and ground-dwelling birds (Dillon & Kelly, 2008; O'Brien & Kinnaird, 2008; Suwanrat et al., 2015). An extension to the Binomial mixture model is the Beta-binomial mixture model, which has additional potential for group-living species like kiwi, where individual detections may not be independent (Martin et al., 2011;

Suwanrat et al., 2015). These estimation tools are of great potential use for community and conservation groups that may not have the resources for radio-telemetry monitoring of kiwi populations. Furthermore, kiwi do not need to be caught or handled for camera surveys, and sparse count data (from low density populations) is adequate for the models (Royle, 2004).

5.1.1 Estimating the abundance of unmarked species

Camera data is biased to an unknown degree by the inherent variability in the detection of animals (Pollock et al., 2002). Detection rate can be related to abundance (Royle, 2004) and to other variables that affect the probability of individuals being detected, including weather, season, and behaviour (Denes et al., 2015). Further complicating camera detections is that (a) non-detections do not mean the animal is not present, (b) for unmarked species, multiple detections at a single camera could be one individual or many (Gilbert et al., 2021), and the placement of cameras in relation to the target species is usually unknown. Methods of analysing camera data that account for false-negative (individuals that are present but not detected) and false-positive (double counting of individuals) errors in the detection probability, and include covariates for identifying factors that impact detection, are more reliable than indices like CTR (Nakashima, Fukasawa, & Samejima, 2018; Rosenstock et al., 2002).

For species that cannot be individually identified there are several methods for analysing camera data to estimate abundance. Occupancy models are often used as a proxy for abundance for unmarked species and are considered a reliable method (MacKenzie et al., 2002; MacKenzie & Nichols, 2004; MacKenzie et al., 2006). However, traditional occupancy models do not provide *direct* estimates of abundance and are instead useful for relative/proportional occupancies over spatial or temporal scales (Rovero et al., 2013; Royle & Nichols, 2003). However, this approach was extended by Royle and Nichols (2003) and Royle (2004) with two different models that yield estimates of absolute abundance as opposed to relative abundances or proportions. Both models are widely used for unmarked species because they require only simple detection data from repeated counts to implement, reducing the effort and cost of monitoring (Gilbert et al., 2021; Link, Schofield, Barker, & Sauer, 2018; Rogan et al., 2019).

The RN model (Royle & Nichols, 2003) and the Binomial-N-mixture model (Royle, 2004), (hereafter Binomial mixture model) use the heterogeneity in detection/non-detection data to make estimates of both abundance and detection probability within an occupancy analysis framework (Appendix C.1). The main concept behind these models is that detection is related to abundance (higher abundance will result in greater detection probability) and therefore detection can inform us about abundance. Covariates can be included to more precisely explain variation in abundance and detection during surveys (Royle, 2004; Royle & Nichols, 2003).

These models are ideal for camera data because they rely on replicated visits to sites to undertake what are essentially point counts (the number of individuals detectable at a point), which is how camera trapping surveys operate (Sollmann, 2018). The RN and Binomial mixture model provide point estimates of mean abundance (Royle, 2004; Royle & Nichols, 2003) which is an estimate of abundance per camera station for camera surveys. The point estimates produced by the models can be multiplied by the number of points/cameras for an overall estimate of abundance for the study site (Royle, 2004; Royle & Nichols, 2003). The assumptions of the models are the same; (1) population closure during the sampling period, (2) equal detection probability for all individuals, (3) individuals are not counted at more than one point/camera, and (4) detections of individuals are independent.

Both models have been applied to camera survey data for a range of species and have been compared directly. RN and Binomial mixture models were compared with a traditional occupancy model for detecting population growth trends in a Great argus pheasant (*Argusianus argus*) population (O'Brien & Kinnaird, 2008) with the RN preferred over the Binomial mixture model. Suwanrat et al. (2015) also compared both models for estimating the group density of Siamese fireback (*Lophura diardi*), where the RN outperformed the Binomial mixture. The RN model was used to successfully estimate the population abundance and densities of fishers (*Pekania pennanti*) by Furnas, Landers, Callas, and Matthews (2017) and Linden, Fuller, Royle, and Hare (2017). The latter study compared estimates with spatial capture-recapture (SCR) analysis of marked individuals. For white-tailed deer (*Odocoileus virginianus*), both the RN and Binomial mixture model have been recommended by different projects (Duquette, Belant, Svoboda, Beyer, & Albright, 2014; Keever et al., 2017).

Issues with both models have been reported: some studies suggest the RN model is unreliable when abundance is high (Kéry, Royle, & Schmid, 2005), and Binomial mixture models may produce unreliable estimates when detection probability is low or only a small number of survey sites are used (Denes et al., 2015). For both models, the assumption of independent detections (the detection of any individual is independent of that of any other individual), is easily violated by species that live in groups, as the detection of one group member could mean the detection of other group members is more likely (Linden et al., 2017; Martin et al., 2011), although see Rogan et al. (2019). The Binomial mixture model may be very sensitive to violation of this assumption (Martin et al., 2011).

This potential problem led to the development of an extension to the Binomial mixture model that does not assume detections are independent and accommodates correlated detections; the Beta-binomial mixture model (Martin et al., 2011). If the standard Binomial mixture model is used when there are correlated detections, estimates can be biased (towards low detection probability and high abundance) and unreliable (Martin et al., 2011). The Beta-binomial model was used by Suwanrat et al. (2015) along with the RN and Binomial (Poisson) mixture model for the Siamese fireback, because these gregarious, mostly terrestrial, territorial birds live in groups, and therefore the detection of an individual was likely to be related to the detection of other individuals from that group. Although the authors preferred the Beta-binomial model as the estimates were closest to those from radio-telemetry, model fit could not be accurately compared because there was no consistent ranking criterion.

The reliability of estimates of the abundance and detection probability of an unmarked species is questionable when the results are not compared to those from an independent monitoring method. Comparing model estimates with those from other monitoring methods is not like a comparison with a true census of the population, which is rarely available (but see Keever et al. (2017)). However, when the model estimates are compared with estimates from methods that are considered robust and reliable, such as S-C-R (Linden et al., 2017; Rogan et al., 2019), radio-telemetry (Duquette et al., 2014; Keever et al., 2017; Suwanrat et al., 2015) or GPS-tracking (Bassing et al., 2022), it lends support to the model results. And in many cases, the different methods add complementary information to the study that would not have been gained by using one of the methods alone (Bassing et al., 2022; Linden et al., 2017). If no independent estimates are available, the suitability of the estimates is usually judged by the researcher using their knowledge of the study site and species (Kafley et al., 2019; Perera, Karawita, & Jayasinghe, 2022; Zou et al., 2019).

Radio-telemetry or GPS tags are particularly useful methods to use alongside abundance models because the location data can serve multiple purposes. Marked animals in the study area provide minimum estimates of abundance to which estimates from statistical models can be compared (Duquette et al., 2014; Suwanrat et al., 2015). For example, Duquette et al. (2014) compared abundance estimates from the RN model with radio-telemetry estimates and reported that the RN model tracked the same trend in population growth as the telemetry data. Furthermore, knowledge of animal movement from tracking allows more strategic camera spacings to avoid violating the assumption that animals are not detected at more than one site/camera (Suwanrat et al., 2015). Importantly, animals with tracking devices also allow territory/home range estimates that can be used to calculate the effective sampling area (ESA) of cameras so that total abundance estimates from the models can be used for density estimates (Dillon & Kelly, 2008; Soisalo & Cavalcanti, 2006).

Density estimates are only possible with a known ESA, yet the true area sampled by the cameras is unknown (Gilbert et al., 2021), and establishing this has long been recognised as one of the most challenging aspects of camera trapping data (Wilson & Anderson, 1985). There are multiple ways of estimating the ESA, and a lack of consensus around the best method (Sollmann, 2018). Typically, a buffer is established either around an external polygon formed by the camera stations (Bengsen et al., 2011; Dice, 1938) or as a circular buffer around each individual camera station (Rebecca J. Foster & Harmsen, 2012). The size of the buffer is commonly decided using estimates of territory/home range size from either tracking data (with radio-telemetry or GPS tags) or from the movement of individuals between cameras (for individually identifiable species), referred to as MMDM (mean maximum distance moved) (Thunhikorn et al., 2016; Wilson & Anderson, 1985). In comparisons of ESA based on tracking data versus MMDM they have resulted in vastly different estimates, with MMDM overestimating density (Dillon & Kelly, 2008; Soisalo & Cavalcanti, 2006). If density estimates are intended, then establishing territory/home range size with specific tracking data is recommended (Dillon & Kelly, 2008; Soisalo & Cavalcanti, 2006).

5.1.2 This project

I assessed the performance of the RN, Binomial mixture, and Beta-binomial models for point abundance and total density estimates of Rakiura tokoeka (*Apteryx australis australis*) using detection data from camera traps. Because the effective sampling area is so critical to density estimates from camera traps, I compared three methods to calculate this parameter, based on localised territory/home range estimates (Section 3.3.3). Density estimates from the different statistical approaches and effective sampling areas were compared to independent estimates from territory mapping (Section 3.3.2).

5.2 Methods

The camera survey data used in this analysis was the same data described in Section 4.2 from the camera trap grids at four locations on Rakiura (Kaipipi, Ulva Island, Mason Bay, and Port Adventure). I used data from five bi-annual (winter/breeding, summer/non-breeding) camera surveys that spanned summer 2018 to summer 2020. See Section 1.4.1 for a detailed description of the study locations, Section 1.2 for study species, and Section 4.2 for the establishment of the camera grids and survey details.

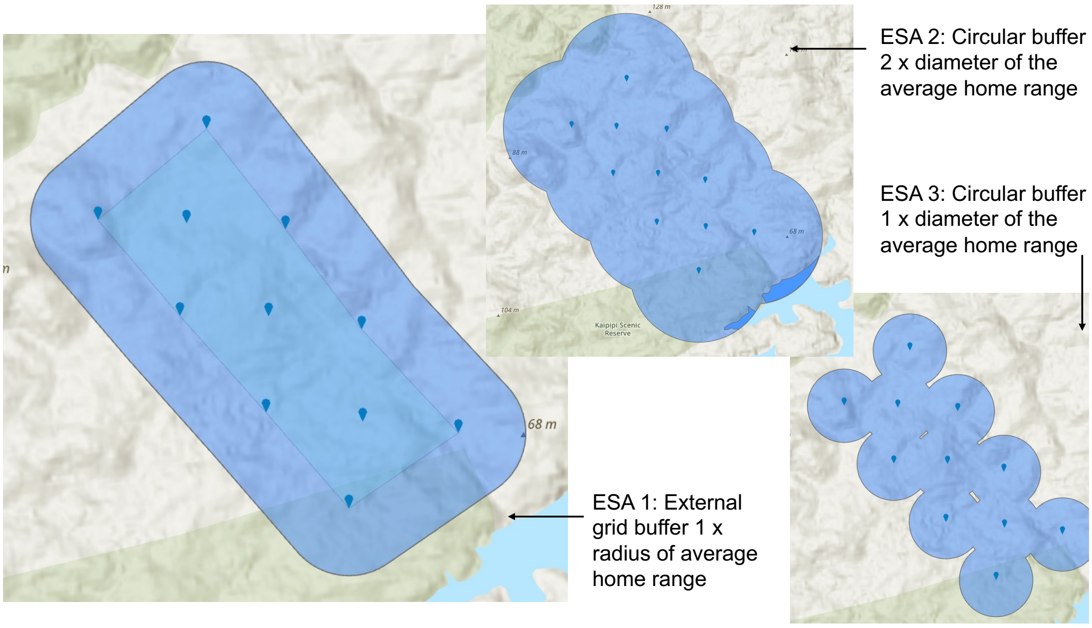
5.2.1 Models

To estimate the abundance and detection probability of Rakiura tokoeka from camera trapping I fitted three types of models that are used to estimate the abundance of unmarked species. The RN model (Royle & Nichols, 2003) uses repeated detection/non-detection data, and the Binomial mixture model and Beta-binomial mixture models use replicated count data (Royle, 2004) (Appendix C.1). For both mixture models, I compared Poisson, Negative-binomial and Zero-Inflated-Poisson (ZIP) distributions. Both Poisson and Negative-binomial distributions are reasonable for the consideration of animals in space (Royle, 2004) and the ZIP distribution can be useful if there are excessive zeros in the data (Royle & Nichols, 2003). I used a 24-hour timeframe for repeat sampling, which provided replicate occasions of repeated count data (Suwanrat et al., 2015). This meant a detection/non-detection of Rakiura tokoeka per camera station during that time for the RN model, or a count of the number of independent detections of Rakiura tokoeka per camera for the Binomial mixture model.

A Bayesian approach was used for all models and model fit was compared using the Deviance Information Criterion (DIC) (Spiegelhalter, Best, Carlin, & Van Der Linde, 2002). The posterior parameter estimates were based on a Markov chain Monte Carlo (MCMC) analysis with three separate chains of 50,000 iterations (the first 5000 were discarded as burn in), run using JAGS from R (version 4.2.2) using rjags (Kruschke, 2014; Plummer, Stukalov, & Denwood, 2016; R Development Core Team, 2021). Model convergence was assessed using the Rhat value, where values close to 1 indicate convergence (Gelman & Hill, 2006). The DIC minimum value was used to identify the model that would make the best short-term predictions (similar to Akaike's Information Criterion). A difference in DIC of more than 10 rules out the model with the higher DIC, differences between 5 and 10 are substantial, while differences of less than 5 are not definitive (Spiegelhalter et al., 2002). Goodness-of-fit was evaluated using Bayesian P-values where models appear to fit the data well when the value is close to 0.5 (Gelman, Carlin, Stern, & Rubin, 1995). Bayesian p-values are calculated based on the posterior predictive distribution, which incorporates both the likelihood of the data given the model (likelihood) and the prior distribution of the model parameters. When Bayesian p-values are close to 0.5, it suggests that the model fits the data well in the sense that the observed data are neither too surprising nor too predictable under the model. It represents a balance between underfitting and overfitting, indicating a reasonable level of model complexity given the data (Gelman, Carlin, Stern, & Rubin, 1995).

I ran a version of each model including covariates, and a naïve version with no covariates. Naïve models do not account for location and so produce the same point estimate for all cameras at each study site, but in some cases meaningful covariates are not available and then the naïve estimates are useful (Kafley et al., 2019; Kéry et al., 2005). For abundance estimates, the covariate was location (Kaipipi, Mason Bay, Port Adventure, Ulva Island), which I considered a surrogate for many inherent covariates, for example, the difference in invasive pests, vegetation, and presence of different native species between the three mainland sites and Ulva Island. For detection probability the covariates were location, season (winter/breeding and summer/non-breeding), survey, temperature, and precipitation. The models provided an estimate of the average abundance of Rakiura tokoeka per camera station and the supposed detection probability per individual.

To convert estimates of abundance to density I multiplied the point estimates per camera by the number of camera stations (Kaipipi, Mason Bay and Port Adventure n = 11, Ulva Island n = 7) (Royle, 2004; Royle & Nichols, 2003) and then divided it by the effective sampling area (ESA) of the camera grid. I compared three methods of establishing the ESA: (1) an external polygon of the camera grid with a buffer width the radius of an average home range (Bengsen et al., 2011; Dice, 1938) (2) circular buffers around each camera station with a radius equal to the diameter of an average home range (Suwanrat et al., 2015) and (3) circular buffers around each camera station with a radius equal to that of an average home range (Foster & Harmsen, 2012) (Figure 26). The total ESA given by the three different methods were compared using one-way ANOVA and Tukey's HSD pairwise comparisons. Average territory/home range sizes were location and species specific from a concurrent territory mapping study at Kaipipi and on Ulva Island (Section 3.3.1), and from the most recent territory mapping surveys by the Department of Conservation at Mason Bay and Port Adventure (Robertson et al., 2017, 2018). Field-workers-estimates of territory/home range size were used as they were available for all four locations.



ESA 2: Circular buffer 2 x diameter of the average home range

ESA 3: Circular buffer 1 x diameter of the average home range

ESA 1: External grid buffer 1 x radius of average home range

Figure 26. An example of three methods for establishing the camera trap grid effective sampling area (ESA) at Kaipipi, using a grid polygon and external buffer (ESA1) or circular buffers (ESA2, ESA3), all based on average territory/home range data for Rakiura tokoeka.

Density estimates calculated from the camera survey data were then compared to those available for the four study locations from territory mapping using radio-telemetry (Section 3.3.2) (Robertson et al., 2017, 2018) using the overlap of 95% confidence intervals, where a lack of overlap signifies a significant difference at least at the 5% level (Goldstein & Healy, 1995). Density estimates are presented as number of Rakiura tokoeka (of all ages) per hectare.

I did not assume that camera trap grids and territory mapping surveyed the same sized areas, and so estimated the sampling area separately for both methods using the most appropriate method for each (discussed in Section 7.2.1).

5.2.2 Assumptions

The spacing of the cameras was designed to accommodate assumptions; equal detection probability for all individuals, and individuals are not counted at more than one point/camera. Thus, the inter-station distance was set to avoid gaps larger than the smallest average home range (Bengsen et al., 2011; Sollmann, 2018; Suwanrat et al., 2015) so it could be assumed that all individuals in the study area had a >0 chance of being photographed (Anile et al., 2014) except perhaps young birds (Section 6.3.4.3). Prior knowledge of the average territory/home range size of Rakiura tokoeka at Mason Bay and Port Adventure (Colbourne & Robertson, 2013; Robertson et al., 2017, 2018; Robertson & Colbourne, 2011) allowed me to try to place one camera in each territory, but with little knowledge of where territory boundaries were this was unlikely to be perfect. In some of the camera surveys individuals with transmitters and metal bands were present and could be individually identified. None of these individuals were captured on more than one camera, but it was impossible to guarantee that this was the case for most indistinguishable individuals.

5.3 Results

5.3.1 Camera surveys

There was a total of 4213 camera days and an average of 105 survey days per camera. The number of independent kiwi detections overall was low, n = 559, occurring on 474 camera days.

5.3.2 Model fit

The Royle Nichols model was the best fit for the data according to the DIC and Bayesian P-values (Table 14).

Table 14. Model fit for estimating the abundance and detection of Rakiura tokoeka, with values in order of lowest DIC (Deviance Information Criterion) where lower values indicate a better model fit. pD = measure of the complexity of the model where higher is more complex, delta DIC = difference with the most parsimonious model, Rhat = values close to 1 indicate model convergence, Bayesian p value = values close to 0.5 indicate good model fit. P = Poisson, NB = Negative-binomial, ZIP = Zero inflated Poisson.

Model	**pD**	**DIC**	**∆ DIC**	**Rhat**	**P value**
Royle Nichols	41.20	240.45	0	1.00	0.45
Naïve Royle Nichols	42.31	241.31	0.86	1.00	0.42
Naïve Binomial mixture/NB	42.71	2930.22	2,689.78	1.00	0.94
Naïve Binomial mixture/ZIP	43.06	2930.30	2,689.86	1.00	0.94
Naïve Binomial mixture/P	43.00	2930.33	2,689.88	1.00	0.94
Binomial mixture/ZIP	59.32	2957.07	2,716.62	1.11	0.93
Binomial mixture/P	54.55	2959.79	2,719.35	1.02	0.93
Naïve Beta-Binomial/P	100.10	2978.89	2,738.44	1.00	0.93
Naïve Beta-Binomial/NB	132.39	3005.69	2,765.25	1.06	0.91
Binomial mixture/NB	178.38	3050.48	2,810.04	1.02	0.91
Naïve Beta-Binomial/ZIP	196.87	3069.97	2,829.52	1.01	0.93
Beta-Binomial/NB	325.37	3194.57	2,954.12	1.08	0.92
Beta-Binomial/P	634.40	3501.82	3,261.37	1.13	0.93

The naïve models outperformed the associated covariate models according to DIC (Table 15), indicating the covariates did not assist with model fit. For the RN model, the difference between the naïve and covariate versions according to DIC values was indistinguishable (< 5), and the Baysian p-values were very similar.

Table 15. Difference in DIC between the naïve and covariate models (covariate minus naïve). NB = Negative binomial, ZIP = Zero inflated Poisson.

Model	Difference to covariate model
Naïve Royle Nichols	-0.86
Naïve Binomial mixture/NB	120.26
Naïve Binomial mixture/Poisson	29.47
Naïve Binomial mixture/ZIP	26.77
Naïve Beta-Binomial/Poisson	522.93
Naïve Beta-Binomial/NB	188.87

The difference in DIC between the RN model and the next best model (naïve Binomial mixture model/Negative-binomial) was large enough (2689.78) to suggest a substantial difference between the two. According to the Rhat values, nearly all models converged reasonably (Rhat 1.0 – 1.13). Running the Binomial mixture/ZIP and Beta-binomial/Poisson models for longer would have produced better fits, but they are sufficient (Rhat ≤1.13), and computational costs precluded longer runs. The only model that did not converge was the Beta-binomial mixture model/ZIP, despite over 50,000 iterations.

5.3.3 Abundance estimates

Estimates are reported for the best fit model, the Royle Nichols. The difference in model fit between the naïve and covariate model was indistinguishable, and so both are reported. The Royle Nichols naïve model predicted that at any camera station there was 95% confidence of between 2.55 and 5.82 Rakiura tokoeka, with an average abundance of 4.10 individuals (SE = 0.86).

The model with covariates predicted an average of 6.8 (Kaipipi), 4.9 (Mason Bay), 7.8 (Port Adventure) and 5.2 (Ulva Island) Rakiura tokoeka per camera station/location, generally with low precision (Figure 27).

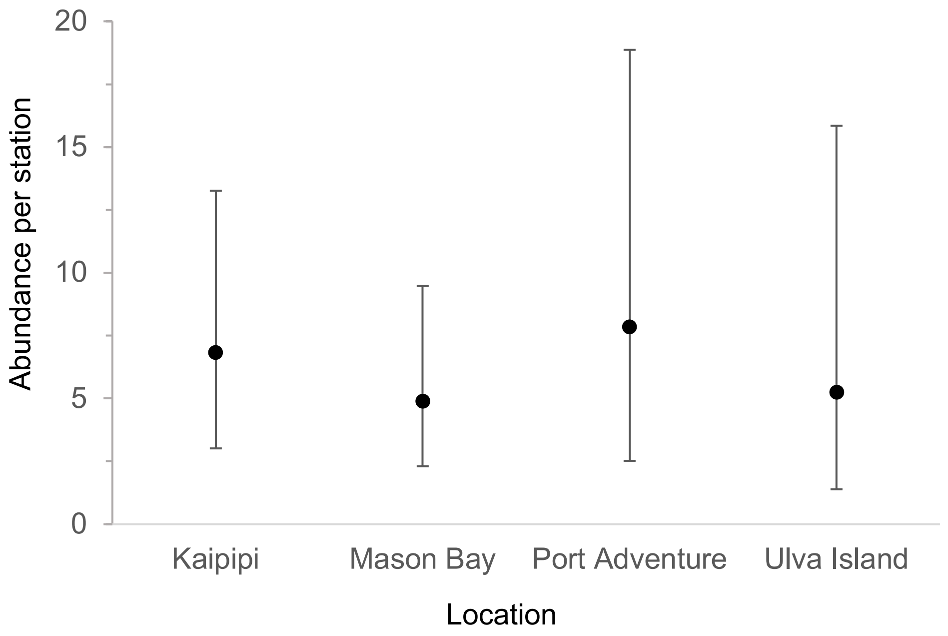


Figure 27. Abundance estimates of Rakiura tokoeka per camera station using the RN covariate model from four locations on Stewart Island, with 95% confidence intervals.

For the naïve RN model, the total abundance of Rakiura tokoeka for the sampled area at the three locations with 11 camera stations (Kaipipi, Mason Bay and Port Adventure) was n = 45.09 (SE 9.5) and for Ulva Island n = 28.69 (SE 6.1), because it only had 7 stations.

The total abundance estimates for each of the four locations from the covariate RN model (point abundance × number of camera stations [Kaipipi, Mason Bay and Port Adventure n = 11, Ulva Island n =7) were variable (Figure 28), and although Ulva Island had lower abundance and Port Adventure higher, using Kaipipi as the reference location, the RN model found no significant difference in abundance estimates between them. The parameters reported by the model were: Kaipipi and Mason Bay (B = -0.676, p = 0.3637, Exp(B) = 0.51), Port Adventure (B = -0.036, p = 0.9695, Exp(B) = 0.96) or Ulva Island (B = 0.225, p = 0.9551, Exp(B) = 0.9110).

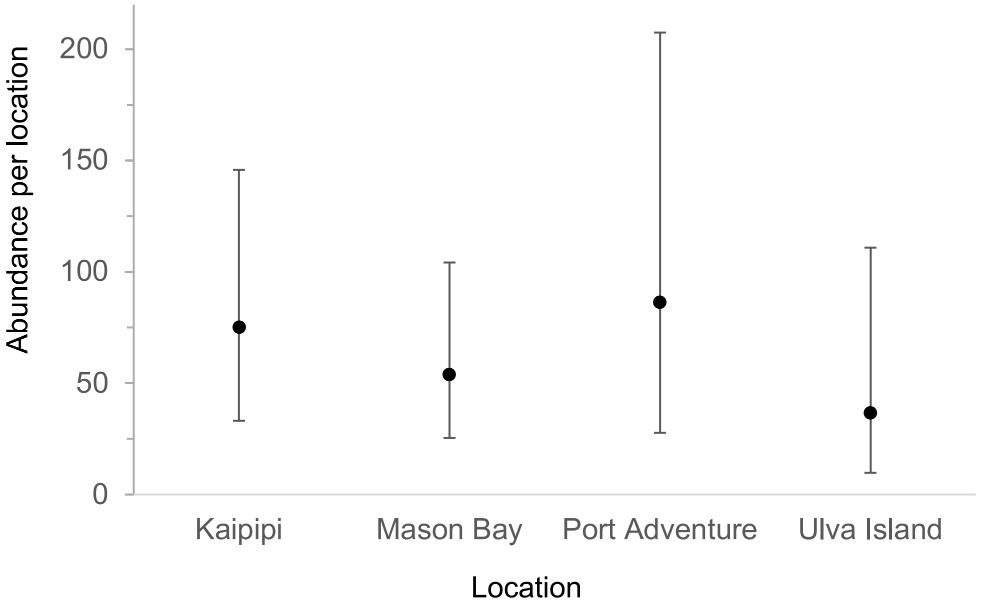


Figure 28. Total abundance estimates for Rakiura tokoeka using the RN covariate model from four locations on Stewart Island, with 95% confidence intervals.

5.3.4 Detection probabilities

The detection probability of individual Rakiura tokoeka was low for both the naïve and covariate RN model. The naïve model estimated a detection probability of 0.03 per individual per day (SE = 0.01, 95% CI = 0.02 – 0.04).

According to the RN covariate model, the detection probability of individual Rakiura tokoeka was highly variable but did not differ significantly between locations: Kaipipi and Mason Bay (B = 0.928, p = 0.2082, antilogit = 0.7166), Port Adventure (B = -0.0048, p = 0.9959, antilogit = 0.4988) or Ulva Island (B = -0.7596, p = 0.6445, antilogit = 0.3187) (Figure 29).

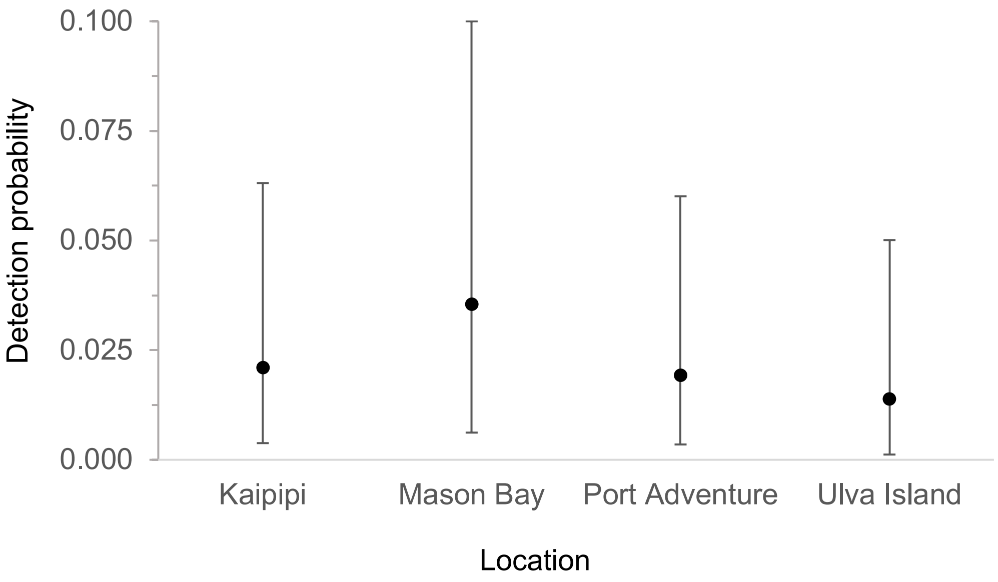


Figure 29. Detection probability of Rakiura tokoeka from the covariate Royle Nichols model for four locations on Stewart Island.

Detection probability did not differ significantly across winter/breeding or summer/non-breeding seasons (B = -0.123, p = 0.4536, antilogit = 0.4693), or survey, and temperature and precipitation showed no significant impact on detection.

5.3.5 Comparison of models

For the naïve abundance estimates, the Royle Nichols model gave the highest estimate of any of the models, the other estimates were all similar to each other, but different to the Royle Nichols model (Table 16).

Table 16. Abundance estimates for Rakiura tokoeka per camera station from the naïve RN, Binomial mixture, and Beta-binomial mixture models, with standard error (SE) and 95% confidence intervals.

Naïve model	Abundance	SE	95% lower	95% upper
Royle Nichols	4.10	0.86	2.55	5.82
Binomial mixture/Poisson	2.83	0.74	1.63	4.51
Binomial mixture/NB	2.96	0.78	1.67	4.67
Binomial mixture/ZIP	2.81	0.73	1.63	4.48
Beta-Binomial/Poisson	2.77	0.59	1.72	4.02
Beta-Binomial/NB	2.15	0.46	1.39	3.17
Beta-Binomial/ZIP	2.57	0.66	1.42	3.87

Although the naïve models were in all cases a better fit for the data (except in the case of the RN model where there was no distinguishable difference), they only provide a single abundance estimate. Therefore, abundance estimates from the covariate Binomial mixture and Beta-binomial models are provided for comparison with results from the RN model. Generally, abundance estimates were lower from the other models than for the RN, except in some cases for Ulva Island and Port Adventure where there was also very low confidence, e.g., Binomial mixture/Poisson and ZIP (Table 17). In some cases, for the Binomial mixture model, the standard error was higher than the abundance estimates, suggesting uncertainty (Kafley et al., 2019) (see underlined values in below table).

Table 17. Abundance estimates for Rakiura tokoeka per camera station from four locations on Stewart Island using the RN, Binomial mixture, and Beta-binomial mixture covariate models, with standard error (SE) and 95% confidence intervals. Underlined values indicate standard error that was higher than the abundance estimates.

Royle Nichols	**Abundance**	**SE**	**95% lower**	**95% upper**
Kaipipi	6.83	2.71	3.01	13.26
Mason Bay	4.9	1.85	2.31	9.47
Port Adventure	7.85	4.34	2.52	18.86
Ulva Island	5.24	4.03	1.39	15.84
Binomial Mixture/ Poisson				
Kaipipi	2.32	0.96	1.19	4.91
Mason Bay	4.66	4.13	1.43	17.95
Port Adventure	97.36	76.77	14.22	314.7
Ulva Island	8.91	15.36	1.05	60.74
Binomial Mixture/ Negative-binomial				
Kaipipi	2.51	1.07	1.13	5.25
Mason Bay	2.84	1.11	1.38	5.81
Port Adventure	2.39	1.16	0.9	5.06
Ulva Island	4.93	5.41	0.97	22
Binomial Mixture/ Zero-Inflated Poisson				
Kaipipi	3.21	1.72	1.22	7.62
Mason Bay	3.18	1.45	1.35	6.82
Port Adventure	73.72	88.57	1.3	322.42
Ulva Island	3.49	2.11	1.01	8.9
Beta-binomial/ Poisson				
Kaipipi	1.93	0.6	1.01	3.33
Mason Bay	2.51	0.96	1.14	4.81
Port Adventure	2.75	1.85	0.88	7.36
Ulva Island	3.62	3.06	0.89	12.26
Beta-binomial/ Negative-Binomial				
Kaipipi	2.4	0.87	1.16	4.52
Mason Bay	2.8	1.15	1.24	5.82
Port Adventure	3.66	2.64	1.1	12.12
Ulva Island	4.65	3.27	1.14	12.6

In the two models with inflated estimates of abundance for Port Adventure (Binomial mixture/Poisson and ZIP), detection probability was lower than for the other locations, and significantly lower than at Kaipipi and Mason Bay for the Binomial mixture/Poisson model (Figure 30). Furthermore, model convergence for the Binomial ZIP model could have been better (Rhat 1.1).

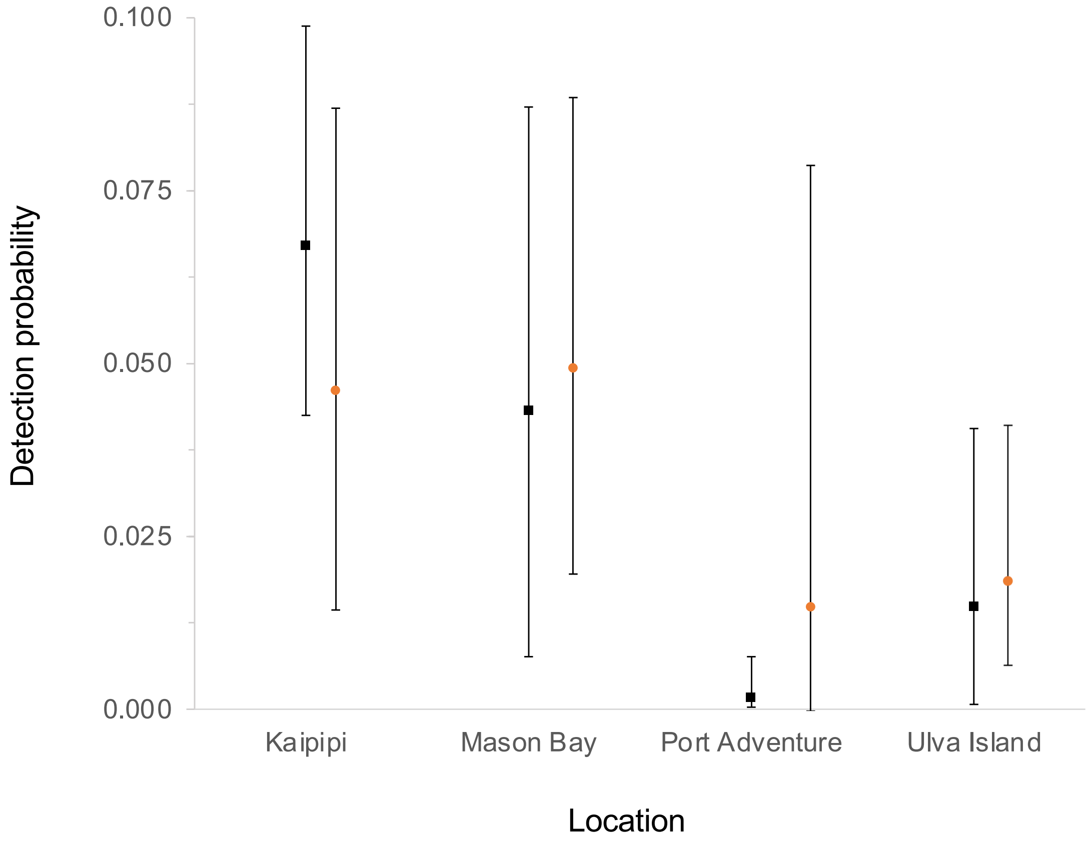


Figure 30. Detection probability for Rakiura tokoeka at four locations on Stewart Island estimated from a Binomial mixture model with Poisson (black square) and Zero-Inflated-Poisson distributions (orange circle) ± 95% confidence intervals.

There was no significant difference in detection probability between seasons or surveys from any of the models. Ulva Island had a much lower detection probability than the other locations in some models (Binomial mixture/Negative-binomial, Beta-binomial/Negative-binomial and Poisson); however, the variability was high and the difference not significant (Figure 31).

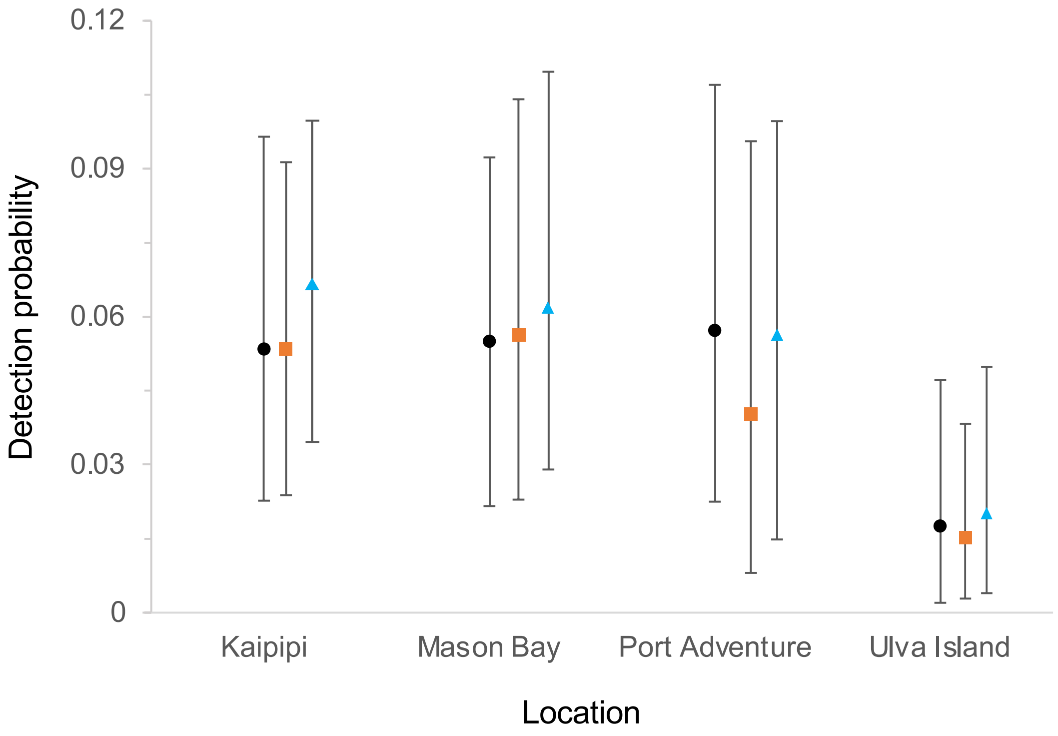


Figure 31. Detection probability for Rakiura tokoeka at four locations on Stewart Island estimated from a Binomial mixture model with a Negative-binomial distribution (black circle), and a Beta-binomial mixture model with a Poisson (blue triangle) and Negative-binomial (orange square) distribution ± 95% confidence intervals.

5.3.6 Density estimates

Densities using both the naïve and covariate RN model abundance estimates are reported using the calculated effective sampling area of the cameras. The three methods of establishing the effective sampling area of the camera grids produced different sized areas for density estimates (Table 18).

Table 18. Effective sampling area (ESA) size for camera survey grids (ha) at four locations using three different ESA methods* and location specific estimates of the average home range radius for Rakiura tokoeka per location from territory mapping (Chapter 3).

Location	Average home range radius (m)	Method 1 (ha)	Method 2 (ha)	Method 3 (ha)
Kaipipi	252.5	192	338	172
Ulva Island	202	109	162	77
Mason Bay	182	157	249	109
Port Adventure	214	153	227	128

**Method 1: External polygon of the camera grid with a buffer width the radius of an average home range of kiwi from that location*

Method 2: Circular buffers around each camera station with a diameter twice the diameter of the average home range

Method 3: Circular buffers around each camera station with a diameter twice the radius of an average home range

There was a significant difference between the three effective sampling areas ($F_{2,19}$ = 9.15, p <0.01). Method two resulted in a much greater sampling area than the other two methods (method 2-method1, p = 0.016, method 3-method2, p = 0.002). Density estimates based on the three methods for ESA were calculated for the covariate RN model to show how the different methods can impact results. Density estimates from the camera grids were higher than telemetry estimates when ESA methods 1 and 3 were used, and closest to telemetry densities using method 2 (Table 19). None of the camera grid densities were significantly different from telemetry densities as 95% confidence intervals included both estimates, but variance was high, particularly for Port Adventure and Ulva Island.

Table 19. Density estimates for Rakiura tokoeka (number of birds per ha) from camera trap grids and covariate Royle-Nichols model abundance estimates using three methods for effective sampling area, compared to density estimates from territory mapping using radio-telemetry at four locations on Stewart Island.

	Telemetry	Method 1		Method 2		Method 3	
	Density	Density	95% CI	Density	95% CI	Density	95% CI
Kaipipi	0.28	0.39	0.17 - 0.76	0.22	0.11 - 0.43	0.44	0.19 - 0.85
Mason Bay	0.23	0.34	0.16 - 0.66	0.22	0.10 - 0.42	0.50	0.23 - 0.96
Port Adv.	0.24	0.57	0.18 - 1.36	0.38	0.12 - 0.91	0.68	0.22 - 1.62
Ulva Island	0.30	0.34	0.09 - 1.01	0.23	0.06 - 0.69	0.48	0.13 - 1.44

Densities from the naïve RN model using Method 1 for effective sampling area (the preferred method) were very close to telemetry densities (Table 20).

Table 20. Density estimates for Rakiura tokoeka (number of birds per ha) from camera trap grids and naïve Royle-Nichols model abundance estimates and Method 1 for ESA, compared to density estimates from territory mapping using radio-telemetry at four locations on Stewart Island.

	Density		
	Telemetry	Naïve	95% CI
Kaipipi	0.28	0.23	0.15 – 0.33
Mason Bay	0.23	0.29	0.18 – 0.41
Port Adventure	0.24	0.29	0.18 – 0.41
Ulva Island	0.3	0.26	0.16 – 0.37

5.4 Discussion

5.4.1 The Royle-Nichols model

Results from camera trapping four local populations of Rakiura tokoeka show that the Royle Nichols model (Royle & Nichols, 2003) is a promising method for estimating the abundance and density of this kiwi species from camera survey data. The RN model was the best fitting model according to both DIC and Bayesian p-values, and provided abundance estimates comparable to those from the more established method of territory mapping.

The naïve model predicted an average of four (between 2.5 and 6) Rakiura tokoeka per camera station. This is a realistic estimate assuming there was approximately one camera per territory, and the average minimum group size in a territory was 4.8 ± 2 at Kaipipi, 3.3 ± 1 on Ulva Island (Section 3.3), and 4 ± 1.9 at Port Adventure in 2017 (Robertson et al., 2017) (group size for Mason Bay is not available). The covariate model also provided abundance estimates per location that were reasonable, but towards the higher end of the minimum group sizes listed above (5.2 – 7.8 birds per camera station), and variance was high, especially for Port Adventure and Ulva Island, for unknown reasons. Detections were low on Ulva Island, and the sample size was smaller (7 cameras as opposed to 11), but Port Adventure appears anomalous. Although the naïve model only provides a single estimate for all locations, it is not improbable that there was little or no significant difference in abundance between the locations. However, the variability and lack of precision present in estimates from the covariate RN model could have masked any difference that may have existed between locations.

The covariates included in the models were not useful for explaining the estimates and the simplest naïve model was ranked higher for model fit or was indistinguishable from the covariate version in all the model comparisons. Not all covariates chosen will necessarily be meaningful for a particular species. For example, Kafley et al. (2019) used Binomial mixture models for four different species, and while covariates offered more precise estimates for three, the naïve model was the most parsimonious for wild boar (*Sus scrofa*), providing valuable insight on the lack of importance of elevation or proximity to water for boar abundance. For Rakiura tokoeka, it was not surprising that temperature and precipitation had no significant impact on detection given that (i) neither occurs in any extreme on temperate Rakiura, (ii) they had no impact on CTR using the same data (Section 4.3.2) and (iii) there was a small sample size in any given temperature or precipitation category.

However, environmental factors should always be considered as possible covariates for detection, especially those that could influence movement (Broadley et al., 2019; Jakob, Ponce-Boutin, & Besnard, 2014; Jean-Pierre, Loranger-Merciris, & Cézilly, 2022). High temperatures and low precipitation can reduce the availability of invertebrates in the leaf litter and upper soil layers and affect the foraging success and survival of NIBK (*Apteryx mantelli*), particularly of young (Wilson, 2014). If kiwi became more active during dry periods as a result, seeking food or water, they could encounter more camera stations or be captured by the same station more frequently, impacting detection rates. Furthermore, weather conditions could influence the thermal signature of kiwi and subsequent detection rate by the camera's passive infrared sensors (Swann et al., 2010).

The lack of large fluctuations in weather throughout the year on Rakiura could also partly explain why season was not an important factor for detection probability. However, 'season' also represented breeding and non-breeding periods. Although Rakiura tokoeka territories were observed to be reasonably stable throughout the year, some range contraction may occur during the winter/breeding season (Section 3.3.4). This did not significantly impact camera trap detections, suggesting that cameras could be a useful tool for year-round monitoring of Rakiura tokoeka. This is valuable because the use of radio-telemetry needs to be carefully managed during the breeding season (Robertson & Colbourne, 2017), and call rates can vary in detectability with breeding season (Jahn et al., 2022), both of which constitute the most popular methods for monitoring kiwi (Section 1.3).

Importantly, detection probability within locations was reasonably stable throughout the study period, suggesting that the assumption of population closure was not violated (Brodie & Pangau-Adam, 2015). This could potentially indicate that these local populations were stable during the study period (not considering young kiwi, which were rarely detected, Section 6.3.4.3), which is likely given their long lifespan and low annual adult mortality. Alternatively, estimates lacked the precision to reveal any true differences that existed.

It was somewhat unexpected that Ulva Island did not have a significantly lower abundance or detection probability estimate. Although densities at Kaipipi, Mason Bay, Port Adventure and Ulva Island were similar during territory mapping surveys (Section 3.4.6), detections of Rakiura tokoeka by camera traps on Ulva Island were low (Section 4.3.2). While the RN model had the lowest lower bound for 95% confidence, the difference in estimate is not large. Indices that are assumed to relate to abundance like Camera Trap Rate (no. of independent captures/no. of camera days) and detection rate (no. of independent kiwi detections per survey day) were significantly lower for Ulva Island using the same camera survey data (Section 4.3.2). Although other indices such as latent time to first detection and median number of independent captures per camera were lower for Ulva Island, these differences were not significant, probably due to high variability. The habitat and other species present on Ulva Island make it a different type of environment than mainland Rakiura, but according to the RN model these differences did not significantly impact the abundance or detection probability of Rakiura tokoeka.

Detections of Rakiura tokoeka by the camera grids were generally low. The detection probability for an individual Rakiura tokoeka from the naïve RN model was 0.03 (95% CI 0.02 – 0.04). The probability of detection for animals in camera surveys is always less than one, reflecting the fact that it is highly unlikely that all individuals in a survey will be detected because individuals may (a) not encounter cameras during a survey, (b) be present but not captured by cameras that malfunction, or (c) be temporarily absent (Denes et al., 2015; Duquette et al., 2014). While detections were low for Rakiura tokoeka, this likely reflects the reality of having approximately one station per territory, the random space use of individuals (Duquette et al., 2014), and imperfect detection (Jakob et al., 2014).

It is not possible to conclude whether variation was masking any true difference in abundance or detection between locations, or if the RN model accurately depicted consistent estimates across locations. Individuals that cannot be distinguished individually (like kiwi) cannot be counted with certainty (Kafley et al., 2019), which leaves us with best estimates as opposed to true censuses. The RN model provided estimates that were largely consistent with our expectations, and I suggest that, although some improvements could potentially increase precision, the variability in the data is natural variability in detection that I would expect to be reflected in model estimates. Some researchers state the RN model only makes realistic estimates when abundance and detection are low and territorially well defined (Furnas et al., 2017; Kéry et al., 2005; Royle & Dorazio, 2008). Although what constitutes low abundance is unclear, I consider the latter two factors relevant for Rakiura tokoeka at these study locations.

5.4.2 Precision

It is common for low detection probabilities during camera surveys to result in imprecise model estimates (Duquette et al., 2014; Kafley et al., 2019; Kéry et al., 2005; O'Brien & Kinnaird, 2008; Randler & Kalb, 2018; Rogan et al., 2019), even in cases when covariates successfully explain some model fit (Duquette et al., 2014; Linden et al., 2017). Low detections increased the variability in estimates in this study and may have prevented the models from detecting change between or within locations. However, Duquette et al. (2014) successfully detected changes in population growth for a group of radio-marked white-tailed deer using the RN model, despite variability in estimates. Furthermore, even when the RN was not the best performing model, it detected the same trend in declining abundance over time as the most parsimonious model for the highly territorial Great argus pheasant despite low precision (O'Brien & Kinnaird, 2008).

Variability is common in camera survey data, because of the distribution and movement of animals, environmental variables, survey set-up, species abundance, and detection probability (Broadley et al., 2019; Denes et al., 2015; Duquette et al., 2014; Kéry et al., 2005; Rogan et al., 2019). In a camera survey experiment with strict controls on survey design (i.e., camera placement, orientation, ground cover, and spacing), and a large sample size, Kolowski, Oley, & McShea (2021) still found high levels of variation in capture rates for a range of species in Virginia, USA, that could not be explained by site characteristics. They hypothesised that the variability was due to spatial heterogeneity in abundance, i.e., individuals were not evenly distributed in space. Within an animal’s home range, some areas are used more than others, and this creates heterogeneity in probability. Somewhat intuitively, this detection or non-detection is what informs the RN model, which uses the heterogeneity in detection to estimate abundance (Royle & Nichols, 2003) and explains the variability in the estimates, which naturally reflect the reality of non-random space use.

Precise estimates could theoretically be achieved with increased detection for a given level of effort (O'Brien & Kinnaird, 2008). Bait is sometimes used to increase detection probability, but is not always successful (Duquette et al., 2014), could bias results in an unknown way, and has not yet been established as a method for kiwi. Furthermore, because the RN model uses detections to estimate abundance, it is important to avoid increasing detection probability in a way that could falsely lead to overinflated abundance estimates.

Alternatively, precision could be improved with more sampling occasions (Lyons et al., 2012), an increased number of sites (O'Brien & Kinnaird, 2008; Rovero et al., 2010), or density of cameras (Duquette et al., 2014). However, large sample sizes do not always result in precise estimates (Kolowski et al., 2021) and the assumptions of population closure and independence of stations and detections could be violated (O'Brien & Kinnaird, 2008). A more strategic way of improving detections for kiwi would be to deploy more than one camera per station, i.e., side-by-side, to avoid missed detections (Nichols, Ross, Glen, & Paterson, 2019) and to try and identify alternative covariates that help explain the detection and abundance of Rakiura tokoeka, which can improve the precision of estimates (Linden et al., 2017; Lyons et al., 2012).

5.4.3 Addressing assumptions

Reliable estimates rely on model assumptions being met (Nichols et al., 2019). The first model assumption was population closure (Royle, 2004). Rakiura tokoeka had established territories that were maintained throughout the study period, and therefore the four local populations were assumed to be closed. It is possible that ‘drifters’ also moved through the camera grid areas and were detected, but the number of these was likely to be small based on tracking data on individuals from territory mapping (Section 3.3). More pertinent to the population closure assumption was the seasonal hatching of chicks and subsequent presence of juveniles/sub-adults. Our sampling period covered two breeding seasons and the addition of 5 chicks to Ulva Island and 6 chicks to Kaipipi, at least temporarily, was recorded (Section 6.3). However, young Rakiura tokoeka were rarely caught on camera, so their addition to the population may not have significantly violated this assumption.

Future surveys may prefer to use captures of adult and sub-adult kiwi only, or to reduce the timing of their survey period to avoid the breeding season. The first option would also address the probable issue of equal detection probability for young kiwi, which are not often detected (Section 6.3.4.3). Although inter-station spacing was set to allow equal detection probability for all individuals, young kiwi likely have different movement patterns and ranging distances than adults (Section 6.3.4.1.2) which makes it challenging to space cameras to target all ages simultaneously. A greater density of cameras could increase the detection of young but would risk violating the assumption of independent stations for adults.

Detecting individuals at multiple stations is to be avoided for the abundance estimation of unmarked species (Rogan et al., 2019; Royle, 2004; Royle & Nichols, 2003) and it was difficult to establish if this occurred in this study. However, based on the few cases of distinguishable individuals and movements during territory mapping (Chapter 3), I believe violation of this assumption was largely avoided. Regardless, the RN model can make reasonable estimates even if this assumption is violated. For example, Linden et al. (2017) made similar estimates of abundance with the RN model to SCR estimates for fishers, where the cameras were purposefully spaced at a density for detections of individuals on multiple cameras.

The RN and Binomial mixture models assume that the detection of one individual is independent of the detection of any other (Royle, 2004). This may not be a reasonable assumption given that Rakiura tokoeka can live in groups (Section 3.3). However, it is unknown whether group members move around their territory/home range together, in proximity, or completely independently. If their movement is correlated, then the detection of one individual at a camera station would mean the detection of a second group member is more likely. The Beta-binomial mixture model (Martin et al., 2011) does not assume independence of detections, and this is the reason it was used.

It was likely that the same individual was detected at a single camera multiple times, given that the camera stations were in stable territories. However, the RN model may be robust to this (Linden et al., 2017) and it has been recommended by Denes et al. (2015) for situations where it is impossible to preclude double counting of individuals. The Binomial mixture model may be less robust to violations in counts but can be effective for data with a high proportion of zeros and variation in sampling effort between locations (Brodie & Pangau-Adam, 2015; Royle, 2004).

5.4.4 Alternate model estimates

Most abundance estimates from the Binomial and Beta-binomial mixture models were reasonable, though more conservative than from the RN model. In all three distributions (Poisson, Negative-binomial, and ZIP) for the Binomial mixture model, low detection probabilities appeared to contribute to inflated abundance estimates, large standard errors, and inflated confidence intervals. Estimates with low precision that are biased high when detection probability is low have been reported from Binomial mixture models in other studies (Denes et al., 2015; Keever et al., 2017). It is possible that the sensitivity of these models to violation of assumptions could be more significant than for the RN model. For example, Link et al. (2018) determined a 2% rate of accidental double counts of the same individuals had profound consequences on Binomial mixture model estimates using data simulations, whereas the RN model can tolerate double counts (Denes et al., 2015).

The Beta-binomial model accounts for non-independent detections (Martin et al., 2011), that could have reduced the effectiveness of the other models if Rakiura tokoeka detections were correlated. This model provided the most precise estimates; however, this could have been a result of the model overfitting the data, and in most cases the estimates of abundance were lower than expected. For example, the point abundance estimates for Kaipipi were 1.9 – 2.4, suggesting an average camera station captured approximately two individuals, a value that is lower than mean group size and likely underestimated reality. The Beta-binomial mixture with a Poisson distribution was favoured by Suwanrat et al. (2015) for Siamese fireback, a mostly terrestrial, gregarious bird. However, this species moves in groups, which definitively violates the assumption of independence for the RN or Binomial mixture models. I found no evidence that this was the case for Rakiura tokoeka. This highlights the importance of species-specific knowledge in the selection of models.

There is no consistent model or distribution that performs best in every study with each species (Denes et al., 2015; Kafley et al., 2019) and it is worthwhile exploring the different options when establishing the use of models to estimate the abundance and detection of specific unmarked species.

5.4.5 Densities

Estimates of the density of Rakiura tokoeka using the RN model were within the range of density estimates from territory mapping with radio-telemetry (Section 3.3.2). Densities from the RN covariate model reflected the pattern found in the point abundance estimates; they were generally higher from the cameras than from telemetry (except when using ESA method 2), as was expected. However, variation was also high, for example, using ESA method one (external grid polygon with buffer the radius of an average home range) resulted in 95% confidence intervals ranging from 0.1 to 1.4 birds per ha, the interpretation of which would greatly influence conservation management decisions for a species. The naïve RN model density estimates using ESA method one were very close to the estimates from telemetry. Possibly, the reasonable estimates reflect appropriate camera spacing. If camera spacing is too close or too far apart, estimates can be biased high if some individuals are double counted, or low if some individuals are not detected (Keever et al., 2017).

Density estimates were strongly influenced by the size of the buffer applied, and by the method used (external grid polygon or circular buffer). Although ESA method two (circular buffer with radius equal to the diameter of an average home range) provided the most precise and closest estimates to telemetry for the covariate RN model, the estimates were mostly smaller than known minimum densities from territory mapping (Section 3.4.3) and importantly, the ESA itself was unrealistically large given the known movements of Rakiura tokoeka in the four locations (Chapter 3). Suwanrat et al. (2015) used method two to calculate Siamese fireback densities from camera surveys, comparing estimates to those from radio-telemetry, and they also resulted in vastly larger sampling areas and smaller densities, but they used no methods for comparison. ESA methods one and three (three = circular buffer with radius equal to that of an average home range) provided comparable density estimates, but those from method one had lower variation and were closer to those from telemetry. Method one was therefore the overall preferred method. This method was also found to be the most reliable and used as a benchmark by which to compare other ESA methods by Soisalo and Cavalcanti (2006) for jaguar (*Panthera onca*) densities.

The size of the buffer area is best informed by home range data from the local population (Dillon & Kelly, 2008; Soisalo & Cavalcanti, 2006). Direct territory/home range data for Rakiura tokoeka from radio-telemetry territory mapping (Section 3.4.2)

(Robertson et al., 2017, 2018; Robertson, Colbourne, Graham, Miller, & Pierce, 2011) was essential for determining the spacing of cameras, the buffer width of the effective sampling areas, and interpreting whether the sampling areas were realistic. While it is possible to estimate these variables without specific tracking data, for example, by using the mean maximum distance moved (MMDM) between detections from camera trap footage or movement rates to estimate home range size (Karanth & Nichols, 1998, 2002; Wilson & Anderson, 1985), this is much less reliable (Dillon & Kelly, 2008; O'Connell, Nichols, & Karanth, 2011; Soisalo & Cavalcanti, 2006). The effective survey area and buffer width are the largest sources of variation in density estimates from camera surveys (Dillon & Kelly, 2008). Although density estimates are often sought and are useful for comparisons temporally, spatially, and between species, model point abundance estimates should always be included as a useful reference that avoids the variability inherent in density estimates from cameras.

5.5 Conclusion

Overall, results modelling the abundance and detection probability of Rakiura tokoeka from camera survey data are promising. Although the covariates I chose were not useful for explaining the estimates, future camera surveys may be able to identify covariates that are more informative. Abundance estimates from the RN covariate model were at the higher end of what I would have expected per camera station, while the naïve estimates were closer to the average group size per territory (Section 3.3). However, caution should always be used when making inference about the abundance of unmarked populations (Gilbert et al., 2021) and although I was able to compare estimates to those from territory mapping using radio-telemetry, the true population density remains unknown. Therefore, the estimates in this study may only be as good as indices of abundance (Dillon & Kelly, 2008) and although they take detection probability into account, they require additional computational effort and interpretation compared to simple indices such as CTR. The RN model did not consider lower detection probability on Ulva Island to be significant, unlike the CTR and associated indices (Section r 4.3.2). However, which method more accurately represents the true population variables is unknown.

Gilbert et al. (2021) suggest using simulations to compare the performance of different methods and models, followed by rigorous empirical testing in real systems. For Rakiura tokoeka and other kiwi, this would be particularly valuable as camera surveys for population monitoring of kiwi are in their infancy. Different models can be selected by considering the model output against project objectives, whether the model assumptions can be met, and the sensitivity of the model to violation of those assumptions (Nakashima, 2020). Although the Royle-Nichols model was the most successful in this instance, it may not be the best performing model with different camera spacing, population densities, movement of individuals or detection probabilities (Denes et al., 2015; Kéry & Royle, 2015). Importantly, Rakiura tokoeka are predominantly group living, whereas other kiwi species live mostly in pairs or sometimes trios, which could affect model outcomes. Furthermore, the number of detections of Rakiura tokoeka in this study were low.

Future trials of models to estimate the abundance and detection of kiwi from camera surveys have several other factors to consider. These include:

- The low detection of young kiwi by cameras (Section 6.3.4.3), which is problematic for camera spacing and model assumptions.
- Trials to understand the thermal signature of kiwi to better capture the heat differential and how it relates to camera placement for successful captures in varied environmental conditions.
- Whether the movement rate of kiwi (used as a measure of MMDM: mean maximum distance moved) could be used as an alternative to radio-telemetry data to estimate average territory/home range size to inform the ESA buffer estimate. This would need to be trialled alongside the home range method gathered specifically from tracking devices (Dillon & Kelly, 2008; Soisalo & Cavalcanti, 2006) to establish a robust MMDM.
- Providing a comparison of estimates from different effective sampling areas is wise when sampling area dictates density estimates. However, if the future study objective is density, point abundance should also be reported to enable comparisons without the issue of comparable ESA.
- It would be worthwhile establishing whether individuals are being detected on multiple cameras where possible, using combinations of transmitter leg (left or right), colour, and sex (size and bill length) to differentiate between birds. It was difficult to detect individuals in multiple cameras with Rakiura tokoeka, but this should be simpler with other kiwi species when there are fewer individuals per territory. This may also become increasingly possible with the advance of AI systems.
- Increasing the precision and decreasing the variability of estimates is a worthwhile pursuit, which could perhaps be achieved through meaningful covariates, different camera set-ups (i.e., two cameras per station) or variation in survey length, while respecting the assumptions of the model chosen.
- This field would benefit from future trials using populations at different densities and identifying covariates that can impact the abundance and detection probability of different populations.

The predominant methods of current kiwi monitoring are expensive and invasive, requiring certified practitioners (radio-telemetry) or have unknown connections to true population variables (call counts and acoustic call monitoring). Cameras are a non-invasive, easy to implement monitoring method that provides data on remote and difficult to monitor populations. The use of cameras for estimating the abundance and density of unmarked species is promising (Furnas et al., 2017; O'Brien & Kinnaird, 2008; Suwanrat et al., 2015). This chapter shows that density estimates for Rakiura tokoeka can be obtained using camera survey data and the RN model that are not significantly different from those from radio-telemetry. Camera surveys are increasingly being used on unmarked avian species for population scale monitoring and are worth developing further for Rakiura tokoeka and other kiwi species.

Chapter 6: Radio-telemetry and camera traps for monitoring young kiwi: Rakiura tokoeka survival

Preface: The purpose of this chapter is to investigate the survival of Rakiura tokoeka (*Apteryx australis australis*) chicks at two locations on Rakiura, one a pest-free island, while considering the most effective ways to monitor young kiwi to meet a variety of different objectives.

6.1 Introduction

Information on young individuals is essential to understanding the Rakiura tokoeka (*Apteryx australis australis*) population because it provides insights into population dynamics, reproductive success, and recruitment rates. Both telemetry and cameras can be used to monitor young Rakiura tokoeka, though each may be best suited to different research objectives. For young kiwi (*Apteryx* spp.*)*, the monitoring objectives are usually (a) finding nest burrows, (b) determining nest fate, (c) monitoring chick survival, and hence (d) establishing the recruitment and the proportion of young birds in a population. This chapter considers the use of radio-telemetry and camera traps towards these common objectives.

6.1.1 Monitoring young animals

For long-lived species like kiwi, adults are usually considered the vital component when considering population growth and fitness (Carpenter et al., 2021; Robertson et al., 2011; Street, Riecke, Williams, Behnke, & Sedinger, 2022). Kiwi populations can sustain themselves even when a high proportion of young are not surviving (Wilson, 2014). However, for a population to remain stable, the level of recruitment must at least balance the rate of adult mortality. When a species is of conservation concern, it is imperative to identify the reproductive rate, the level of recruitment, and degree of mortality for each life stage (McComb et al., 2010). These factors allow estimates of the speed of decline and identify if a species requires management intervention and a change in status (i.e., vulnerable, threatened). Without intervention, extinction can occur if mortality exceeds recruitment (Sodhi et al., 2009). If an understanding of these factors is lacking, then there is a blind spot in effective management of that species.

Monitoring the growth and dispersal of young animals also provides valuable information about a population. Dispersal is important for understanding population spread, spatial dynamics, habitat requirements and preferences, resource distribution, population density, competition, gene flow and mating systems (Göth & Vogel, 2003; Greenwood, 1980; Sutherland, Harestad, Price, & Lertzman, 2000). As most kiwi chicks grow older they tend to move out of their natal territories. This is a natural process that brings them closer to joining the breeding population, provided they survive this stage (Wilson, 2014). The dynamics behind growth rates include energy requirements, resource selection and availability, competition, population fitness and survival.

Many population studies focus on the adult population, probably largely due to the difficulties involved with monitoring young animals. They are smaller, tend to have a limited range and prefer denser vegetation in order to stay hidden from predators, and are more secretive and evasive than adults (Chan, 1999; Göth & Vogel, 2003; Williams, 2016). Precocial species are even more challenging to monitor as they hatch or are born in a relatively mature state where they are mobile and largely independent (Göth & Jones, 2001). Furthermore, young animals tend to be more fragile than their adult counterparts and invasive monitoring methods can jeopardise their survival, reducing the options available (Ewing, Clark, & Vohls, 1994; Gregg & Crawford, 2009; Mattsson, Meyers, & Cooper, 2006). For young kiwi, the options are more limited than for adults, because adults have loud, sexually dimorphic calls that can be monitored using call counts but young kiwi do not call.

6.1.2 Telemetry for young animals

In many cases, individuals fitted with radio-transmitters are relied on to monitor the early life stages of animals. In some cases, adults with radio-transmitters are tracked regularly and the survival of their young is monitored through direct observations as long as they remain with the parent/s (Street et al., 2022; Williams, Schroeder, & Jackson, 2020). In other cases, chicks are caught and have transmitters attached so they can be monitored directly (Göth & Vogel, 2003). However, these can be difficult to attach (Göth & Jones, 2001), only last a short period, (Göth & Vogel, 2003; Lees, Sherman, Maguire, Dann, & Weston, 2017) and impact fitness and survival (Mattsson et al., 2006).

The specific impacts of transmitters on different species have rarely been addressed (Lees et al., 2017). While some studies show significant effects on individuals (Mattsson et al., 2006), others suggest there are no discernible impacts (Göth & Jones, 2001; Lees et al., 2017). The benefits; the ability to measure growth during handling (Göth & Jones, 2001; Wilson, 2014), tracking dispersal movements (Göth & Vogel, 2003), and determining survival (Lees et al., 2017; Robertson & Colbourne, 2011) are often considered enough to outweigh the risks. Furthermore, because animals with transmitters can be located, a cause of death can often be established through post-mortem (Robertson & Westbrooke, 2005). This enables managers to confirm chick and juvenile mortality as well as identifying threats.

6.1.3 Camera traps for young animals

Camera traps provide a non-invasive alternative for monitoring young animals. According to Caravaggi et al. (2017), some of the advantages that cameras have over radio-tracking are: lower cost, less survey effort, surveying multiple species simultaneously, and observations of natural behaviours. Cameras are particularly well suited to capture animals that are elusive, secretive, and rare (O'Brien & Kinnaird, 2008). If cameras can be placed near bird nests, they can monitor hatch success and survival (Teunissen, Schekkerman, Willems, & Majoor, 2008); if placed in areas likely to be used by family groups (Znidersic, 2017) they can record the number of chicks still with the parent (Street et al., 2022). However, the use of camera traps means much less specific information on individuals than can be obtained from transmitters (Ellis & Marsland, 2022; Oliveira-Santos, Tortato, & Graipel, 2008), and it is difficult to tell most individuals apart. Further, slight changes in camera locations and set-up can significantly impact results (Thomas, Baker, Beattie, & Baker, 2020). Although concerns have been raised about the ability of cameras to capture very small animals (Kelly et al., 2008; Swann, Hass, Dalton, & Wolf, 2004; Tobler et al., 2008), they are frequently employed successfully for such surveys (Table 21).

Table 21. Examples of studies that have used camera trapping for the successful monitoring of small animals. Highlighted rows indicate the most captured species in that study.

Author & year	Species	Adult weight (g)
Larrucea & Brussard (2008)	Pygmy rabbit (*Brachylagus idahoensis*)	<500
Oliveira-Santos et al. (2008)*	Lesser Wilfred's mouse (*Juliomys pictites*)	29
	Tate's woolly mouse opossum (*Micoureus paraguayanus*)	110
	White-eared opossum (*Didelphis albiventris*)	900
	Little yellow-shouldered bat *(Sturnira lilum)*	20
De Bondi et al. (2010)**	Agile antechinus (*Antechinus agilis*)	20
	Yellow-footed antechinus (*Antechinus flavipes*)	45
	Dusky antechinus (*Antechinus swainsonii*)	59
	Southern brown bandicoot (*Isoodon obesulus*)	400 - 1500
	Long-nosed potoroo (*Potorous tridactylus*)	660 - 1600
	Heath mouse (*Pseudomys shortridgei*)	68
	Swamp rat (*Rattus lutreolus*)	110
	House mouse (*Mus musculus*)	19
	Black rat (R*attus rattus*)	230
Meek et al. (2012)***	Swamp rat (*Rattus lutreolus*)	110
	Hastings River mouse (Pseudomys oralis)	95
	Bush rat (*Rattus fuscipes*)	76
	Antechinus spp.	<170
Mills et al. (2016)	Hazel dormouse (*Muscardinus avellanarius*)	27
	Wood mouse (*Apodemus sylvaticus*)	23
Thomas et al. (2020)	Brown antechinus(*Antechinus stuartii*)	28
	Black-tailed antechinus (*Antechinus arktos*)	44 - 120
	Fawn-footed mosaic-tailed rat (*Melomys cervinipes*)	71
	Bush rat (*Rattus fuscipes*)	76

*Only the top four most commonly captured species included
**Only the 9 smallest animals included
**Combines data from two previous studies (Meek et al., 2010) and (Zewe, 2010)

6.1.4 Monitoring young kiwi

Threats to kiwi populations and to adults versus young differ depending on species and location. Predation is the main concern for young kiwi (chicks and juveniles), and it can also be an issue for egg viability (Forbes, 2009; McLennan et al., 1996; Robertson & Colbourne, 2011). Resource availability is also an important factor, access to and competition for food can impact growth, fitness, survival, and ultimately abundance (Robertson & Colbourne, 2004; Robertson & Colbourne, 2011; Shapiro, 2005; Wilson, 2014), particularly when the weight of an individual is related to their likelihood of predation by some predators (McLennan et al., 1996; Robertson & Colbourne, 2011). Because of this, the rate of growth is important for the survival of young.

Kiwi are precocial, and young kiwi are independent from when they start leaving the nest burrow at approximately 5 days old, although they may come back to roost with adults and subadults from their nest. As they get older they leave the burrow for longer periods and most species (not Rakiura tokoeka (Robertson et al., 2018)) will permanently leave their natal territory within a period of 1.5 to 24 months (Robertson & Colbourne, 2017). This precocial independence leaves chicks and juveniles vulnerable, particularly to predators such as mustelids (McLennan et al., 2004) and feral cats (Wilson, 2014) that are less likely to attack adult kiwi.

Radio-telemetry has been fundamental for understanding, monitoring, and mitigating the threats to kiwi and kiwi recruitment. Adults that have been fitted with transmitters can be tracked to nest burrows where breeding can be monitored and any chicks can be caught, have transmitters attached and tracked to determine growth, dispersal, and survival. It was through such a study that Robertson and Colbourne (2011) found only 6% of kiwi chicks in a NIBK (*Apteryx mantelli*) population without predator control survived to adulthood, and that stoats (*Mustela erminea*) were the most significant threat to kiwi under one kilogram. The authors also determined which predator control scenario resulted in the best population outcomes. Wilson (2014) used transmitters on chicks for a novel study on the growth, dispersal, and survival of NIBK chicks in a high-density population on Ponui Island and identified drought as a significant problem affecting food availability/access and cats (*Felis catus*) as more of an issue for chick survival in the absence of mustelids. For a cryptic species with precocial young, radio-telemetry is currently the best monitoring method to gain specific information on individuals (Göth & Jones, 2001; Robertson & Westbrooke, 2005).

Radio-transmitters are an invasive method that requires animals to be handled (Caravaggi et al., 2017), can cause regular disruption to normal behaviours through tracking (Lees et al., 2017), and have resulted in the mortality of young kiwi through entanglement (Forbes, 2009). There are no dedicated studies on the impact of transmitters on kiwi growth, movement, fitness or survival, or the effects of being regularly handled and tracked, despite research showing that these factors are species and transmitter style/weight specific (Barron et al., 2010; Göth & Jones, 2001; Lees et al., 2017). In addition, telemetry is not always possible to use because of the high associated costs, the need for experienced personnel, and amount of effort required (Ellis & Marsland, 2022; Robertson & Fraser, 2009).

Camera traps have also been used to understand the threats to kiwi eggs, chicks, and juveniles by using them to monitor the area directly in front of nest burrows. They are particularly useful in this context for helping to identify egg fate (Caravaggi et al., 2017) because of the activity records of both kiwi and predators at the nest. Once a chick has emerged from the burrow, cameras can monitor their survival without the need for a transmitter, while they continue to return to the burrow. However, both successful dispersal and death result in the chick/juvenile no longer appearing on the camera.

In most cases, cameras have been successfully established on kiwi burrows by tracking the locations of radio-transmitted birds, or by finding kiwi with detection dogs to attach transmitters (Robertson & Fraser, 2009). However, Ellis and Marsland (2022) recently used a combination of cameras and call monitoring to help identify the location of NIBK burrows. Camera trapping is a remote monitoring alternative that cause minimal disturbance, are more accessible for many kiwi conservation groups than telemetry and are increasingly being employed in studies on small animals and young, ground dwelling avian species (Göth & Vogel, 2003; Gregg & Crawford, 2009; Kelly et al., 2008; Oliveira-Santos et al., 2008; Suwanrat et al., 2015).

6.1.5 This project

Rakiura tokoeka have been subject to 5-yearly territory mapping surveys using radio-telemetry at two locations on Rakiura (Robertson et al., 2017, 2018). During these approximately two-week surveys, kiwi of all age groups were targeted, including chicks and juveniles. Based on the most recent of these surveys, the Rakiura tokoeka population was described as stable (Robertson et al., 2018; Robertson & Colbourne, 2022). However, this followed a period of long, slow decline at one of the two locations (Mason Bay) (Colbourne & Robertson, 2013) with an unknown cause assumed to be related to habitat change or chick mortality through predation by feral cats (Robertson et al., 2018; Robertson & Colbourne, 2022). Although feral cats are generally considered to have a relatively small impact on kiwi populations, they predate on kiwi chicks, juveniles, and occasionally adults and they may take on a larger predatory role in the absence of mustelids (McLennan et al., 1996; Robertson, Colbourne, Graham, Miller, & Pierce, 2010; Strang, 2018; Wilson, 2014), of which Rakiura has none. Historical reports that examined feral cat scats for evidence of Rakiura tokoeka proved unfruitful (Harper, 2005b; Karl & Best, 1982), however, these studies relied on the visual examination of scats. Cat scats collected on Rakiura between 2016 and 2020 have contained Rakiura tokoeka (Appendix D.4), identified through genetic analysis, though whether these individuals were predated or scavenged could not be determined.

The survival of Rakiura tokoeka chicks has not been investigated to address this proposed decline, and the possible missed detection of chicks or juveniles during historical territory mapping surveys (i.e., recorded as absent when actually present) has not been considered. Even with the use of kiwi detection dogs many individuals can be missed (Robertson & Fraser, 2009), and young kiwi are notoriously difficult to detect. Furthermore, it cannot be assumed that a sample of the population captured during monitoring is representative of the wider population (Powell & Gale, 2015). For populations believed to be in decline, understanding the threats to recruitment is essential (Wilson, 2014). The possible cause of decline of young Rakiura tokoeka, even if no longer occurring, warrants further exploration.

In this chapter, I considered the use of radio-telemetry and camera traps for monitoring young Rakiura tokoeka to address research objectives pertaining to their survival and recruitment. These were (a) identifying potential nests, (b) nest fate, (c) chick survival, and (d) recruitment, including growth and dispersal.

This chapter follows a different layout than the previous chapters. The results are discussed alongside the data in the results section, to clarify the contribution of each monitoring method towards the objectives. This is followed by a summary of Rakiura tokoeka chick survival and the use of camera traps and radio-telemetry for young kiwi.

6.2 Methods

To monitor young Rakiura tokoeka and address the objectives I used (a) an established population of adults/subadults with radio-transmitters (Section 3.2.1), (b) camera traps placed outside nest burrows, referred to as burrow cameras, (c) radio-transmitters on chicks, and (d) a grid of camera traps overlaying the home ranges of adults/subadults (Section 4.2.2). Refer to Section 1.4.1 for a detailed description of the study sites on Stewart Island/Rakiura mentioned in this chapter: Kaipipi, Ulva Island, Mason Bay and Port Adventure, and the study species, Rakiura tokoeka. Kaipipi and Ulva Island were the locations for (a), (b) and (c), while (d) took place at all four locations.

6.2.1 Establishing a sample of chicks

To establish a sample of chicks, it was necessary to track the adults/subadults from Chapter 3 through the 2019 - 2020 breeding season. There were 29 birds at Kaipipi and 22 on Ulva Island with radio-transmitters (see Section 3.2.1 for methods of radio-tracking).

Potential nests were identified using a combination of radio-telemetry using 'Chick Timer' transmitters and burrow cameras. Chick Timer™ (Lotek Ltd and Kiwitrack Ltd, Havelock North, NZ) is a software program often utilised in NIBK transmitters to track the activity, incubation, and hatching success of individuals. Sensors in the transmitter package detect motion and translate this into the number of hours of activity and time of nest emergence, reporting this information in the radio signal so it can be captured via telemetry. They also detect potential incubation behaviour through consistent reductions in activity.

Prior to this study the activity of incubating Rakiura tokoeka was largely unknown except for some information provided by Colbourne (1991, 2002) who monitored breeding Rakiura tokoeka with intermittent trips to Mason Bay to manually check nests and birds. Colbourne (1991) suggested that for Rakiura tokoeka, the time of emergence (when they exit the burrow) may change when incubating, but consistent predictive patterns to identify breeding birds were unknown. Breeding behaviour amongst different kiwi species is not consistent, but Chick Timer was used for LSK

(*Apteryx owenii*) (Taylor, Nelson, & Ramstad, 2014), and it reports on time of emergence, and so I deemed it suitable for Rakiura tokoeka. There is a software program available for Haast tokoeka (*Apteryx australis 'Haast'*) but it does not report on time of emergence.

6.2.2 Classifying age

For this study, Rakiura tokoeka were classified by weight into general age groups (Table 22), except for the distinction between subadult and adult, which was made from a combination of variables including weight, the condition of leg scales (worn/calloused for older birds versus supple and shiny for young), bill length, and growth over the study period. I found this system less subjective than trying to classify them by age in days/months (Robertson et al., 2017) since the age for individuals that were born before the study period was unknown, I found they did not fledge the nest at specific ages, and there is no published information on Rakiura tokoeka growth rates to know how they compared in size at certain ages to more well studied kiwi species (e.g., NIBK).

Table 22. Rakiura tokoeka age categories used in this study, using weight (g) and additional variables used for grouping adults and subadults.

	Weight	Other
Chick	< 800 g	–
Juvenile	800 – 1800 g	–
Subadult	>1800 g	Shiny leg scales, shorter bill and/or lower weight than adult of the same gender, growth between measurements
Adult	> 2200 g for M, > 3000 g for F	Worn/calloused leg scales, at or above average adult weight and measurements by gender, no growth between measurements

However, birds could not be classified in this way from camera footage. Therefore, individuals were classified as ‘young kiwi,’ being chicks or juveniles based on their body size, bill length (both smaller than adult and subadult birds) and movement (Table 23).

Table 23. Categories used to assign Rakiura tokoeka to age categories from camera trap footage.

	Kiwi characteristics
Young kiwi	(a) Very short bill, 'fluffy' appearance, sometimes wobbly on feet (b) Shorter bill and smaller body size than adults, sometimes hesitant or uncoordinated
Adult/subadult	Larger relative body and leg size to footage of young kiwi or known landmarks, longer bill, and confident movement

6.2.3 Burrow cameras

Over the June 2019 – January 2020 breeding season, 17 burrows were monitored as potential nests, 10 at Kaipipi and 7 on Ulva Island. When more than one individual in a territory was found in the same burrow on at least five consecutive occasions (or fewer if there was also an incubation signal from the transmitter), camera traps were established outside the burrow to monitor the entrance. At each suspected nest burrow, one or two (depending on the number of burrow exits) Exodus Lift 2 cameras were set up approximately 1.5 – 2 m from the burrow entrance facing towards it at a slight angle, at a height of around 15 – 30 cm depending on the angle of the burrow entrance (if the entrance sloped downward, cameras were placed higher on trees to have a level viewpoint). Cameras were programmed to operate 24 hr/day with minimum time delay (1 second) between triggers and a 20-second video setting so they could capture as much footage as possible. SD cards were changed weekly, and footage manually reviewed for the number of individual Rakiura tokoeka, whether they appeared to be incubating (i.e., were present daily), the presence of other species, and the emergence of chicks or evidence of possible nest fate.

For each burrow camera, footage of Rakiura tokoeka was reviewed and the suspected age, sex (based on size, bill length, or sexually dimorphic call) and presence of a transmitter (left or right leg and colour) or no transmitter (unidentified: UID) was recorded. To determine the occupants of a burrow, individuals were grouped into three categories: (1) residents with a transmitter, (2) residents with no transmitter (UID), or (3) transients, which were non-residents with no transmitter. Residents were individuals that were detected at the nest burrow on a daily or weekly basis, while sporadic or one-off footage indicated transients. The UID birds could in some cases be distinguished from other UID birds at the same burrow by size, colour, call, or simultaneous footage. If they could not be distinguished in these ways, only one UID bird was assigned to that burrow to avoid overestimation.

Burrow cameras were established as soon as a potential nest was suspected and stayed in place until it was clear that the burrow was not a nest burrow or was no longer a nest burrow because of sporadic or irregular use.

6.2.4 Chick telemetry

Chicks were expected to remain within the burrow post-hatch for around five days before emerging outside for the first time, as is the case for other kiwi species (Robertson et al., 2017). Once chicks had emerged from the nest burrow attempts were made to catch them to attach a chick radio-transmitter. These attempts were made from 8 – 21 days post-hatch depending on personnel and logistics and occurred during the chick's entry to or exit from the nest burrow, or opportunistically when they were foraging near the nest. One to three people would sit quietly near the burrow entrance and attempt to catch the chick when it went past. Once in the hand, chicks were processed like an adult/subadult Rakiura tokoeka (Appendix A.1), with measurements of body weight, bill length and tarsus depth, width, and length taken. Each chick received a chick transmitter, which are smaller in size and weight (~5.5 g Lotek Ltd.) than the adult version, have an external ariel, and no Chick Timer technology. Chick transmitters were changed frequently as the birds grew, following instructions from the Best Practice Manual (Robertson & Colbourne, 2017).

Chicks with radio-transmitters were tracked at least once weekly to their locations, which were recorded with handheld Garmin GPS devices (accuracy to ~3.65 m). On these occasions an attempt was made to sight each chick to confirm survival. Records were kept on whether chicks were found active or roosting, and, if roosting, whether they were in a ground burrow or surface roost, and if there were any other birds present (Appendix A.2). Chicks were caught approximately every four weeks to check and change the transmitter attachment, adjusting for growth. When chicks reached 700 – 900 g the chick transmitter was replaced with a juvenile version that weighed 11 g (Kiwitrack Ltd.) and could produce a 'mortality signal' triggered by lack of motion over a 24-hr period. This meant that visual confirmation of survival was no longer required. Once a juvenile was over 800 g, the interval between checks was at times extended to 6 – 8 weeks as the growth rate was not as rapid.

Chicks were tracked for a period of 21 to 218 days depending on the date of initial capture and mortality. Birds were approximately 3.5 (chick from second clutch) to 8.5 months of age when the transmitters were removed. All chick and juvenile transmitters remaining (i.e., not removed or dropped earlier) were removed at the conclusion of the study period (May 2020). Deceased chicks were photographed in-situ, transmitters removed, and remains sent as soon as possible to Wildbase Pathology (Massey University, Palmerston North) to determine the cause of death.

6.2.4.1 Growth

At each 4-weekly catch, growth measurements were collected for chicks. The sample size of chicks with transmitters was small (n = 10) and therefore analysis was kept simple to clearly display the data captured by the sample.

The average growth rate (AGR) was calculated by:

$\mathrm{AGR} = (\mathrm{w}_2 - \mathrm{w}_1)/\ (t_2 - t_1)$,

where *w* is weight (in grams) and t is time (in days) (McLennan et al., 2004).

I compared the average growth rate between locations (Kaipipi and Ulva Island) and genders, as well as the trend in growth rate and weights over time between locations using means and 95% confidence intervals (Goldstein & Healy, 1995).

6.2.4.2 Dispersal

The locations of chicks during tracking events were mapped using Google Earth Pro. Territories in which chicks were detected on burrow cameras and caught were considered their natal or home territory. Chick locations were compared to those of the adults and subadults with transmitters in their natal territories using field-workers-estimates of territory boundaries (see Section 3.2.3 for the establishment of territory boundaries). Locations > 50 m from the boundary were considered outside their natal territory. This distance was used because chicks over this distance were always found alone, but less than 50 m would sometimes be found with an adult from their territory. It is important to note that the territory boundaries were *estimates* based on intermittent radio-telemetry tracking and while I assumed that locations within 50 m of the estimated boundary were more likely to be within the natal territory, there was no way to know if locations were outside a territory unless they were in a known neighbouring territory.

6.2.5 Camera trap grid

Between 2018 and 2020, seasonal surveys using a grid of camera traps were carried out at Kaipipi, Ulva Island, Mason Bay and Port Adventure (see Section 4.2 for detailed methodology), for a total of 18 surveys of varying lengths (Table 24).

Table 24. The maximum number of survey days for 21 seasonal camera trapping surveys at four locations on Rakiura. Zero indicates no survey occurred.

	Summer 2018	Winter 2018	Summer 2019	Winter 2019	Summer 2020
Kaipipi	0	8	77	21	21
Ulva Island	22	14	74	24	22
Mason Bay	11	8	57	25	24
Port Adventure	27	13	76	0	29
Average	20	11	71	23	24

The intention of these surveys was to estimate the relative abundance (Chapter 4) and total abundance and density of Rakiura tokoeka (Chapter 5), including chicks and juveniles. In this chapter, the detections of young kiwi are covered in more detail to determine how useful the camera grid was for monitoring chicks and juveniles specifically. The camera grid surveys targeted all ages, but masking tape was used over the flash to reduce glare, which has been implemented in some studies to help with the detection and identification of small animals moving close to the camera (De Bondi, White, Stevens, & Cooke, 2010; Mills et al., 2016).

Video footage from the cameras was manually reviewed and detections of kiwi were recorded for each survey with the date, time, camera station (1 – 11), age (young kiwi, adult or subadult) and if a transmitter could be detected (if so, transmitter colour and which leg were also recorded). Detections of kiwi within a 30-minute period were considered to be of the same individual unless there were distinguishable differences or there was more than one kiwi in the frame (O'Brien et al., 2003).

The *minimum* number of young birds present at each location that were assumed to be available for detection by the camera grid was known for some surveys and locations from telemetry studies (Section 3.3) (Robertson et al., 2018) and could be compared to the number of captures by the camera grid per survey. Young kiwi were not assumed to be present at consecutive surveys unless their identity was known and confirmed from burrow camera capture or telemetry.

6.3 Results & discussion

6.3.1 Identifying nest burrows

A combination of radio-transmitter tracking, Chick Timer data, and burrow cameras were necessary to identify Rakiura tokoeka nests.

6.3.1.1 Radio-telemetry and nest burrows

The 51 adult and subadult birds were tracked 1 – 5 times per week throughout the breeding season (approximately June 2019 to January 2020) to establish if and where they were incubating. In this study, Rakiura tokoeka laid an egg in a nest burrow after mating and the egg was then incubated for approximately 75 days. The incubation process was non-synchronous among individuals, and there was sometimes a second clutch. Burrows were not manually checked for the presence of an egg as it was unknown how sensitive Rakiura tokoeka were to nest disturbance, and most nests were consistently occupied.

Telemetry was essential for locating nests by tracking adults and subadults with transmitters. Potential nests were first identified when individuals were tracked repeatedly to the same burrow as opposed to various roosts. This indicated the birds could be starting to establish a nest, or had begun to incubate, as they would otherwise use multiple burrows in their territory.

Although the information on activity from the Chick Timer transmitters helped identify individuals that were incubating, it is not designed for Rakiura tokoeka. In NIBK kiwi populations, the male(s) are the sole incubator (but see Colbourne (2002)), and transmitters on males are highly effective at identifying the start and end of incubation by the distinct reduction in the activity of males when sitting on eggs. When used for LSK, the software was not 100% accurate and acted more as an approximate guide (Taylor et al., 2014). For Rakiura tokoeka, which tend to live in groups, incubation had a different behavioural signature. However, various combinations of males and females in each territory were being monitored via transmitter/Chick Timer data, and there were UID birds without transmitters in most territories, making it difficult to identify predictive patterns.

At the ten confirmed nests there were 26 (13M, 13F) resident individuals with transmitters, 9 UID adults or subadults, and 12 UID young kiwi (not including the chicks that hatched in the nests). For the individuals with transmitters, the Chick Timer went into incubation mode (INC) for 7 male and 9 female adult/subadults, while 10 individuals had no incubation signal (Table 25). This could have occurred because the birds were not incubating, or because with so many 'helpers' individuals did not reduce activity levels to the point where the incubation signal would be triggered.

Table 25. Confirmed nest burrows of Rakiura tokoeka at two locations on Rakiura (Nest), with the number of adults/subadults with transmitters (TX), the total number present in brackets (total), and the number of birds with transmitters that had at least one instance of incubation mode (No. INC). The following columns show the number of females (F) and males (M) that went into INC mode at least once, or never went into INC mode (Non-INC), and the number of females and males for which the first date of INC mode could predict hatch date. In one case, a female incubated twice and on both occasions, hatch could be estimated (shown with x2), and in two cases for males, the Chick Timer software accurately predicted hatch dates (shown with black boxes).

			INC		Non-INC		Hatch	
Nest	**TX (total)**	**No. INC**	**F**	**M**	**F**	**M**	**F**	**M**
Kaipipi (1)	4 (4)	4	2	2	0	0	1	1
Kaipipi (2)	2 (3)	2	2	0	0	0	0	0
Kaipipi (3)	3 (3)	2	1	1	0	1	1	0
Kaipipi (4)	2 (3)	0	0	0	2	0	0	0
Kaipipi (5)	4 (6)	2	1	1	1	1	0	**1**
Kaipipi (6)	2 (3)	0	0	0	0	1	0	0
Ulva Is. (1)	2 (3)	2	1	1	0	0	1(x2)	**1**
Ulva Is. (2)	3 (4)	2	2	0	0	1	1	0
Ulva Is. (3)	3 (3)	1	0	1	1	1	1	0
Ulva Is. (4)	1 (3)	1	0	1	0	0	0	0
Total:	26 (35)	16	9	7	4	5	6	3

For the 16 birds whose transmitters entered incubation mode, 4 females and 3 males went into INC mode twice, and the remaining went into INC mode once during the nesting period. The number of days that individuals were in INC mode varied from 1 – 97 days. The average length of time for females was 17.31 days (SD 10.77), and males 34.67 days (SD 33.06). In only two cases were individuals in INC mode for the expected duration of incubation (~75 days). Both were males, and in both cases, the Chick Timer estimated hatch dates for the chicks that were within 3 and 5 days of the actual hatch date (as estimated from calculating the first date chicks were detected by burrow cameras minus 5 days).

When a hatch date was not predicted via Chick Timer, 7/14 hatches could be estimated by adding 75 days to the first date that a bird went into INC mode and were accurate to within 6 days (assuming chicks emerged 5 days post-hatch). However, there was no way to identify which individuals could be used for accurate predictions, for example, in Nest 1, 2M and 2F went into INC mode, but the hatch predictions of only 1M and 1F were accurate, and in Nest 2 and 10, none of the INC mode start dates could be used to predict the hatch date accurately (Table 25).

It was difficult to establish if the activity and time of emergence (TOE) of the nesting Rakiura tokoeka were considerably different to non-breeding patterns, as the data available for the non-breeding period only spanned a short period (~ 2 - 9 records) prior to and post nesting. Regardless, there were some indications of probable nesting behaviour. For TOE, 6/26 nesting individuals with transmitters (M and F) kept a consistent (within 2 hours) TOE throughout the whole period they were monitored, while for 16 birds, they had at least 2 occasions where the TOE was 4 hours different from their normal TOE. Most commonly for these birds, the TOE became erratic during the period of incubation, with no consistent hour of emergence.

The 'normal' amount of activity for Rakiura tokoeka was over 10 hours a day, according to the small amount of data pre and post breeding season. The activity of 22/26 birds dropped below 10 hours (Table 26) during incubation, but generally, activity was higher than is expected from other kiwi species, and only 4 birds ever dropped below 4 hours activity per day.

Table 26. The number of Rakiura tokoeka with transmitters that showed minimum activity (hours per day) in particular time ranges during the 2019-2020 breeding season via Chick Timer records.

Activity	No. of birds
10 hrs	22
8 hrs	16
6 hrs	11
4 hrs	4

Without having all individuals at a nest with radio-transmitters, any of these changes in activity, INC mode or TOE could easily be missed depending on which birds are being monitored and is likely the reason that more nests were not identified.

6.3.1.2 Burrow cameras and nest burrows

Burrow cameras helped to confirm nests after potential nesting burrows were found via radio-telemetry. The cameras could monitor the activity of birds remotely, and the nesting behaviour captured on footage (e.g., picking up and tossing leaves), and the consistent presence of at least one bird at a burrow helped identify groups that were nesting in all cases, and the likely start of incubation, and hence predict chick hatching times.

6.3.2 Nest fate

6.3.2.1 Radio-telemetry and nest fate

If adults and subadults with transmitters stopped being located at a particular burrow, it indicated that the burrow was not a nest, or no longer a nest, but this could not be confirmed with radio-telemetry alone, as there were also UID individuals in most territories that could have still been present. An increase in activity or change out of incubation mode for individuals via Chick Timer data also warranted scrutiny, but was too inconsistent to rely on, because these changes also occurred for birds that were part of successful nests.

6.3.2.2 Burrow cameras and nest fate

Burrow cameras were useful for determining nest fate. They were relied on to detect the emergence of chicks from a nest: it was not known conclusively that a burrow was a successful nest until it was confirmed by burrow camera footage.

Ten burrows (of the 17 monitored) were confirmed as successful nest burrows by footage showing the emergence of chicks: six chicks at Kaipipi and five on Ulva Island; two of the chicks on Ulva Island were from the only successful double clutch recorded (Figure 32).

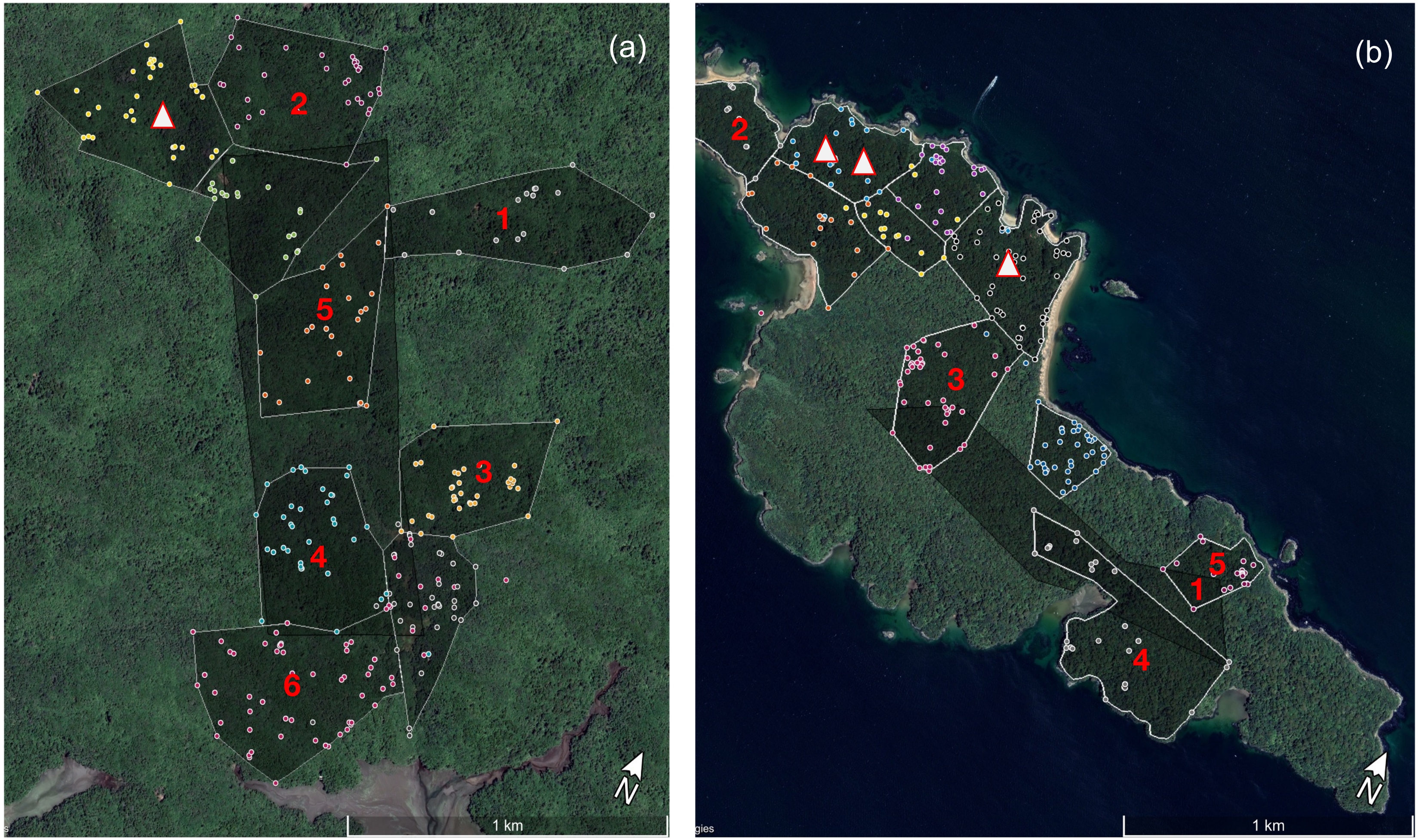


Figure 32. Maps of Kaipipi (a) and Ulva Island (b) territories during 2019 - 2020, with territories shaded and outlined in white. The red numbers indicate locations where chicks were captured by burrow cameras emerging from the nest, in increasing temporal order. White triangles mark what were thought to be nests, but chicks were never observed.

Whether the remaining 7 burrows were nests is unknown, but chicks were not captured on burrow cameras at these locations. The first chick on Ulva Island emerged on the 11/09/2019 and at Kaipipi on the 22/09/19. The last chick from the first clutch emerged on the 24/10/19 and 07/11/2019 respectively, and the second clutch chick on Ulva Island emerged on the 06/01/2020. It was likely that other territories produced chicks or attempted to do so during the monitoring period. The lack of success finding more nests was probably due to not having all individuals in a territory fitted with a transmitter, which made identifying incubating birds and nest locations in some territories challenging.

If no chick emerged despite obvious signs of incubation on burrow camera footage, then observations of the activity of individuals and other species present at nest burrows could be used to make reasonable inferences. In at least one instance at Kaipipi and three on Ulva Island, burrow cameras suggested that incubation was occurring due to the regular presence of multiple individuals at one 'nest' for extended periods. This was corroborated by incubation signals from some of the attending adults/subadults from telemetry. Despite monitoring these probable nests for the imminent arrival of a chick, this never occurred, and the adults gradually dispersed. In these cases, burrow cameras provided probable evidence of nest fate, as recorded in Table 27. Although possums (*Trichosurus vulpecula*), cats, rats (*Rattus norvegicus, Rattus rattus*), and weka (*Gallirallus australis scotti*) were present at other nest burrows, they were not observed entering the burrow pre-hatch/emergence of a chick as in the following cases. In the case of 'Nest 2 – Ulva Island', egg fragments were found inside the burrow.

Table 27. The activity record of Rakiura tokoeka and potential problem species (Kaipipi: possums, rats, cats, Ulva Island: weka) noted from three burrow cameras placed on expected nests at Kaipipi (n = 1 nest) and Ulva Island (n = 2 nests) in the 2019 breeding season, with suspected nest outcomes in italics.

Month	Activity kiwi	Activity other
Nest 1 - Kaipipi		
September	Regular activity, apparent nesting/incubation	possums inside burrow, rats
October	Regular activity, apparent nesting/incubation	possums inside burrow, rats, cat
November	Increasing absence, some days absent completely	Increasing/frequent possums inside burrow, cat, kitten
December	No kiwi. Camera removed	
Suspected outcome: Nest failure, probable possible possum disturbance or predation		
Nest 2 - Ulva Island		
September	Regular activity, apparent nesting/incubation	weka
October	Regular activity, apparent nesting/incubation	weka inside burrow
November	Regular activity, apparent nesting/incubation	weka inside burrow
December	Frequent disturbance by weka, increasing absence	Increasing/frequent weka inside burrow/ egg fragments
Suspected outcome: Weka predation of newly hatched chick around the 21st December		
Nest 3 - Ulva Island		
September	Regular activity, apparent nesting/incubation	weka
October	Regular activity, apparent nesting/incubation	weka
November	Increasing absence until absent completely	weka inside burrow
Suspected outcome: Nest failure, possible weka predation of egg or chick		

The burrow cameras captured the activity of other species that could be responsible for the nest failure of Rakiura tokoeka. At Kaipipi, burrow cameras captured significant nest disturbance from possums at every monitored burrow. This can cause trampling of eggs by the possums themselves or kiwi that actively give chase. Burrow cameras could not be used to determine whether the intent of possums was predation of the egg or to occupy the burrow (Jolly, 1989; McLennan et al., 1996), but they did capture two occasions where possums appeared to cause so much disturbance that kiwi abandoned probable nest burrows. However, it is possible that kiwi could have abandoned burrows for other reasons. Possums were recorded using the same burrow as kiwi at Mason Bay by Morrin (1989) and in this study, burrow sharing/swapping was seen later in the season once burrows were not being used every night by kiwi. There was no evidence in this study of egg or chick predation by possums; however, nest contents in most cases could not be checked because burrows were too deep or there were too many birds present.

Cats were recorded on 7 of 10 burrow cameras at Kaipipi, at times appearing to have followed adults to their burrows and then sniffing around and inside the entrance, sometimes with kittens. No interactions between cats and kiwi were captured, and no predations of individuals of any age with radio-transmitters were recorded (see section on survival below).

On Ulva Island, weka were captured on burrow cameras making repeat visits (often multiple times in a 24-hr period) to all the monitored burrows (7/7). They frequently attempted to enter and were actively deterred by the resident kiwi, but were sometimes successful. Cameras captured increased weka visitation around the time chicks were expected to hatch at some burrows and this helped to determine weka as a highly probable predator of an egg/newly hatched chick on at least one occasion. Jolly (1989) recorded the same behaviour by weka directed to the nests of LSK on Kapiti Island. In this case on Ulva Island, only a pair of birds was present at the nest, whereas all other monitored nests had at least three adults/subadults. As a result, there appeared to be times when the nest was unattended, leaving the egg more vulnerable to weka predation.

6.3.3 Chick survival

Transmitters were essential for monitoring chick survival, by tracking chicks to their locations where visual confirmation of survival was possible, and then once chicks grew sufficiently to carry a juvenile transmitter, they could be checked remotely using the mortality mode.

The sample size of chicks with transmitters in this study was too small to draw conclusions about the survival of the wider population of young Rakiura tokoeka in general, but some general observations could be made.

6.3.3.1 Radio-telemetry and chick survival

In total, there were eleven chicks available for monitoring survival. Nine had transmitters (Kaipipi n = 4, Ulva Island n = 5), and two additional chicks were detected on burrow cameras at Kaipipi (Table 28).

Table 28. Location, sex, and total number of Rakiura tokoeka chicks recorded on burrow cameras and with transmitters attached (TX).

	No. chicks	No. TX	Female	Male
Kaipipi	6	4	2	2
Ulva Island	5	5	2	3

Two mortalities were detected by tracking chicks with transmitters, which allowed the scene to be evaluated and the remains to be analysed to determine cause of death. One mortality was at Kaipipi and one on Ulva Island. The deceased chick (sex unknown) on Ulva Island was caught and a transmitted attached on 30/10/2019 foraging near the nest burrow, where it appeared in a reasonable condition and weight (295 g) for its estimated age of 10 days. Five weeks later, on the 09/12/19 the chick was found ~10 m from the nest burrow in the open, freshly dead with two weka nearby. Locating the chicks meant they could be sent for necropsy; the provisional diagnosis was predation by weka, with severe dorsal lumbar and thoracic trauma with subcutaneous and pleural hemorrhage and evisceration of the abdomen via the cloaca (Appendix D.2). Notably, the chick had zero body fat reserves, indicating starvation, and the lungs were severely congested, signifying that it had likely been in a poor and weakened state. It weighed 290 g minus the viscera, demonstrating it had gained at least some weight since it had last been handled.

The mortality at Kaipipi occurred much later in the season. The deceased chick (a female) was found on 19/05/2020 at an estimated 6 months old, approximately 579 m from the natal territory boundary, in an area where it had not been tracked before (nor any of its known territory cohabitants). The chick was last handled on the 29/02/20 for a transmitter change, when it weighed 625 g, having gained 105 g from measurements four weeks prior. It was last tracked on the 18/03/2020, after which field work was suspended due to the COVID-19 related lockdown. When fieldwork resumed, the chick was found deceased. It was immediately sent for necropsy at Wildbase Pathology (Massey University, Palmerston North), where pathologists found its condition too deteriorated to determine the cause of death but reported that it had adequate fat reserves and there were no obvious indications of trauma (see Appendix D.3).

6.3.3.2 Burrow cameras and chick survival

Burrow cameras could monitor chick survival remotely so long as chicks returned to the nest, though the fate of chicks once they were no longer captured on camera was unknown without radio-telemetry. Two of the six chicks from Kaipipi detected by burrow cameras were not caught for transmitter attachment. Of those, one abandoned the nest with the adults following the first attempted catch and was not seen again, the camera was removed after five weeks of recording frequent possum activity. The other chick evaded capture but was recorded on burrow camera returning to the nest burrow intermittently for the following four months. The camera was removed after a further three months with no detections.

6.3.4 Recruitment & population structure

Recruitment of chicks into the breeding population is important for the continuation of the species, and the proportion of young to adult kiwi can indicate how much recruitment has recently occurred. The growth and dispersal of chicks are key parts of their process towards successful recruitment.

6.3.4.1 Inferences from radio-telemetry

Radio-transmitters allowed the ongoing monitoring of chicks as they grew into juveniles, left the nest burrow, and started moving around within and occasionally outside their natal territories. Specifically, growth and dispersal could be monitored directly.

6.3.4.1.1 Growth

Although the sample size of chicks in this study was small, and growth can be expected to vary from year to year, some conclusions could be made. Individuals grew at different rates both within and between locations, although the differences were not statistically significant. The average growth rate in grams (g) per day was highly variable, particularly on Ulva Island. There was no significant difference between the growth rates at Kaipipi and Ulva Island or between male and female chicks (Figure 33), although weights on Ulva Island in general tended to be above those at Kaipipi at similar ages, particularly in the first 100 days (Figure 34).

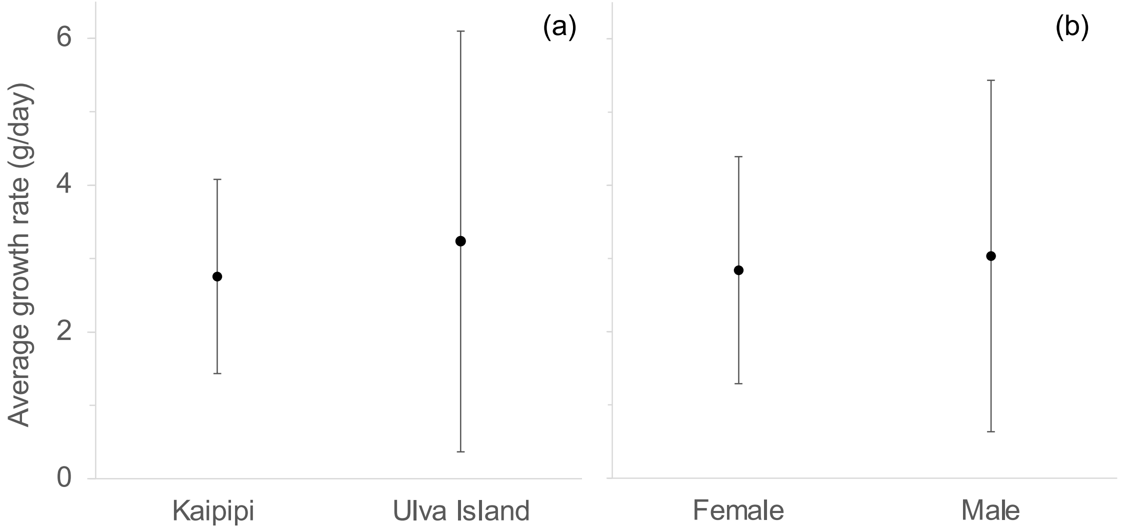


Figure 33. The average growth rate (grams/day) ± standard deviation for Rakiura tokoeka chicks by location (a) (Kaipipi n = 4, Ulva Island n = 5) and by gender (b) (females n = 4, males n = 5).

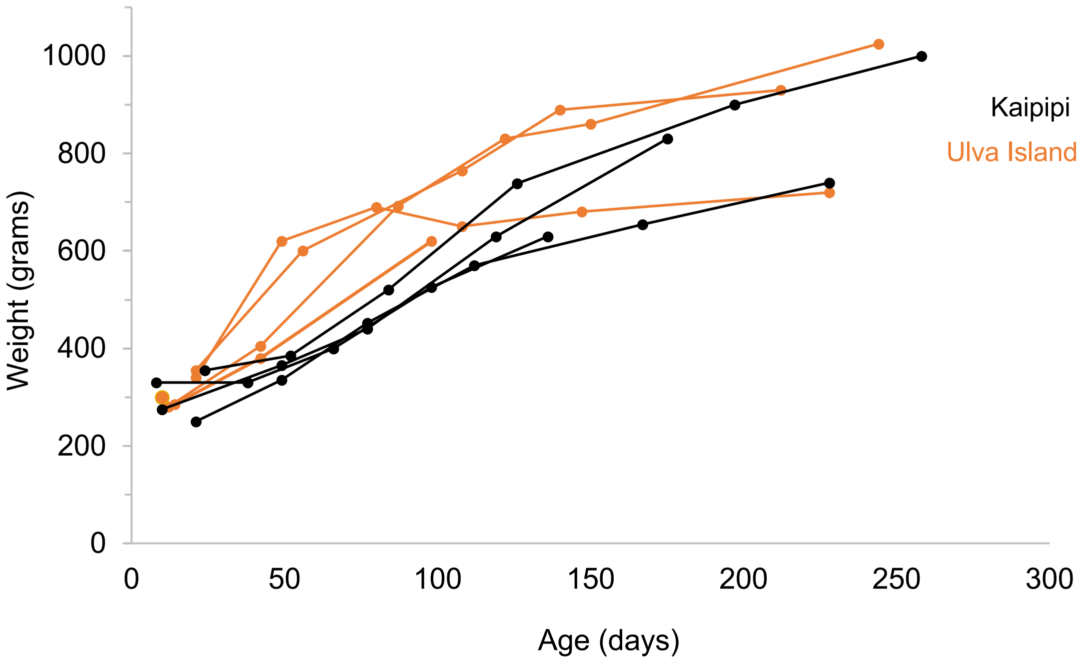


Figure 34. The weight (g) of chicks at Kaipipi (n = 4 chicks) and on Ulva Island (n = 5 chicks) with suspected age (days).

The average growth rate decreased with age from 5.85 to 0.52 g day^{-1} (10 – 228 days) for the Ulva Island chicks (and increased again to 1.76 g day^{-1} for the one measurement taken over this age, at 244 days), while Kaipipi chicks increased from 1.78 to 3.96g day^{-1} (8 – 126 days), then decreased to 1.64g day^{-1} until the final measurement at 258 days of age (Figure 35), although these differences were not statistically significant.

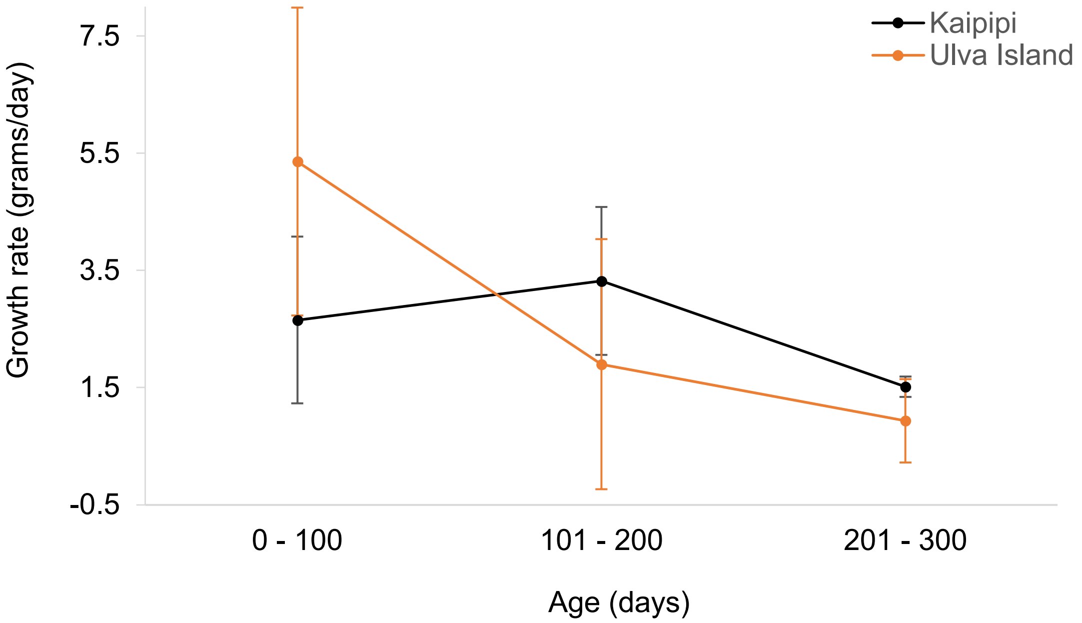


Figure 35. The average growth rate (grams/day) of Rakiura tokoeka chicks in different age categories for Kaipipi (n = 4 chicks) and Ulva Island (n = 5 chicks) ± standard deviation.

Overall, the rate of growth was highest in the first 100 days for Ulva Island, the first 150 days for Kaipipi, and gradually decreased at both locations with age (Figure 35 above, Figure 36 below).

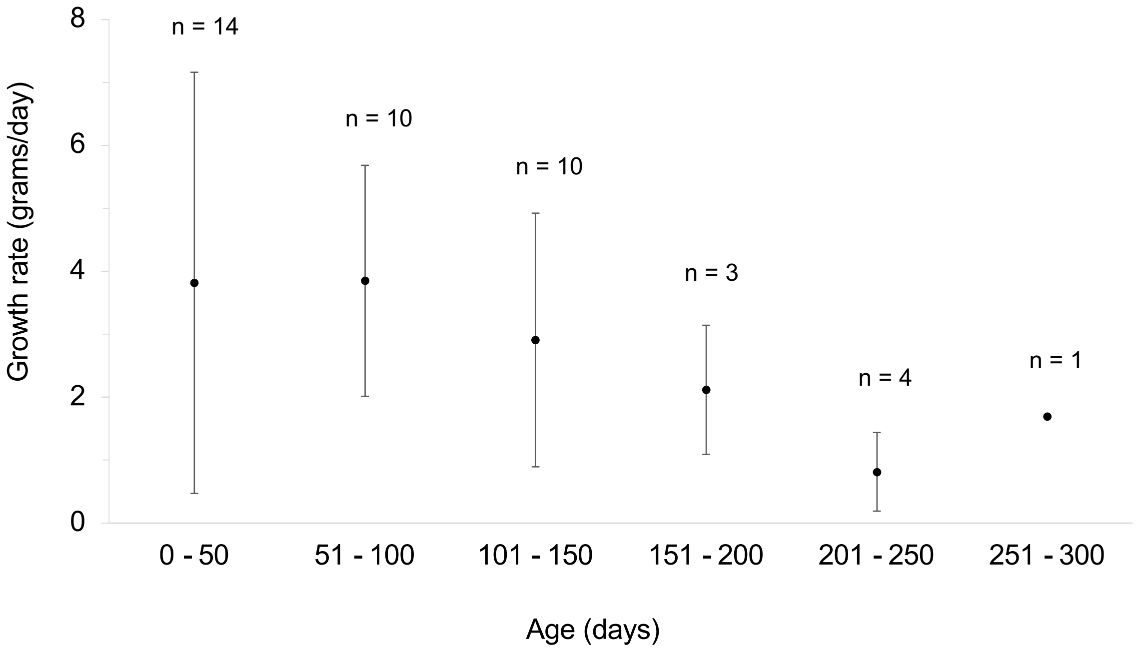


Figure 36. The growth rate (grams/day) of the nine Rakiura tokoeka chicks followed from age 0 to 300 days old, ± standard deviation.

The average growth rate appears to increase again between 251 – 300 days in Figure 36 above. However, there was only one sample for that age group. The highest variation is in the first three age groups, which also had the highest sample sizes.

Ulva Island chicks had both the maximum and minimum growth rates of all chicks, and the maximum was twice that of Kaipipi (Table 29). Both extremes of growth rate were for the same individual, a male chick that gained 280 g in 28 days (10 g day^{-1}), aged 21 to 39 days, then lost 40 g between 80 to 108 days of age (-1.43 g day^{-1}).

Table 29. The average (with standard deviation/SD), maximum and minimum growth rates (grams/day) for chicks from Kaipipi and Ulva Island.

	Growth rate (g/day)	SD	Max	Min
Kaipipi	2.76	1.32	5.19	0.00
Ulva Island	3.23	2.87	10.00	-1.43
Overall	2.97	2.15	10.00	-1.43

At Kaipipi the maximum weight gain was for a female chick aged 84 – 126 days that grew 218 g in 42 days (5.2 g day^{-1}). Another female did not gain any weight between 8 and 38 days old, giving her the minimum growth rate of 0 g day^{-1}. Importantly, the sample size was small, and it is unknown how common these growth values are in the growth rate distribution for the population.

The Kaipipi chicks appeared to have lower weights in the initial 100 days, but a more consistent growth rate overall. Limited weight gain between measurements could have been a result of a rat plague at Kaipipi (and mainland Rakiura) in the spring of 2019, increasing food competition for newly hatched chicks and reducing growth rates (Robertson & Colbourne, 2011; Shapiro, 2005) as rats desperately forage for food before declining sharply in early summer (Harper, 2005b). Furthermore, dry conditions could have reduced invertebrate abundance (which would likely adversely impact Kaipipi more than Ulva Island, which has a denser understorey and moss coverage to help retain moisture in soil) (Wilson, 2014), or there could consistently be less food available for chicks at Kaipipi due to the degraded forest. The growth rate of Kaipipi chicks increased after the initial 100 days, and weight gain was higher than for Ulva Island chicks during this latter period. It is possible that this was related to the drastic decline in rats, and that as the chicks grew larger, they could access food unavailable to rats. Reduced growth rates from food competition with rats could mean an extended period where chicks remain more vulnerable to predation because of their size (Robertson & Colbourne, 2011) and it is possible that rats could suppress the population growth of kiwi (Robertson & Colbourne, 2004).

Growth rates in general slowed over time, which is to be expected for most bird species (Ricklefs, 1968) and makes sense for kiwi which have an exceptionally slow growth rate (Robertson & Colbourne, 2004). The growth rates overall were variable, which was perhaps a reflection of flexible growth strategies tracking unpredictable food supplies (Wilson, 2014). Given that the surviving Ulva Island chicks gained weight rapidly to begin with, particularly when compared to Kaipipi chicks within the same period, something about the environment on Ulva Island appeared favourable for the growth of chicks within their first two to three months, or, unfavourable at Kaipipi. However, the single chick on Ulva Island with the maximum and then later minimum growth rate and the deceased chick with zero body fat reserves could imply a potential issue with food availability or competition in parts or all of the island.

Regarding the deceased chick in poor condition/starvation on Ulva Island, the evidence is as follows. Firstly, there were no abnormalities noticed during routine measurements of weight, bill, and tarsus on first (and only) capture. The other Rakiura tokoeka in the nest burrow included a juvenile, which was assumed to be a chick successfully recruited from the 2018 - 2019 breeding season. It can then be surmised that the deceased chick either (i) failed to successfully forage due to some anomaly not noted during capture or in the necropsy, (ii) failed to find food because there was a lack of suitable food in the areas where it was foraging, (iii) had some illness or condition that prevented foraging closer to its death or rendered the benefits of foraging void, or (iv) harassment by weka prevented adequate foraging. Unfortunately, evisceration prevented us from testing these possibilities. The chick's weight at first capture was the highest weight at that age on Ulva Island and the second highest overall from all transmitted chicks (Appendix D.1). The surviving Ulva Island chicks gained weight during this same period and the subsequent 30-day period between measurements. This indicates that at least for this sample of birds, the chick hatched at a normal to above-normal weight, that any issues with food availability must have been localised during this period, and the fact that it had zero fat reserves at the time of its death was unusual compared to the other chicks. However, it may not be unusual in a larger sample for growing kiwi, which have a slow metabolic rate and where growth can vary according to the resources available (Wilson, 2014).

Further research on Rakiura tokoeka diet, food availability, competition for resources (with natives and non-natives) and a larger sample of growth rates is required to determine if there is a true difference between the locations and what the reasons could be.

6.3.4.1.2 Dispersal

The movement of chicks away from their nest burrows could be monitored accurately via radio-telemetry. Chicks were mostly located within their natal territories, i.e., where transmitted adult and sub-adult birds from their nest had been found previously (Figure 37, Figure 38). They were found either alone, roosting with transmitted adults and sub-adults, or with UID birds. They were found in the same kinds of locations as adults, i.e., in burrows, on the surface under vegetation or actively foraging.

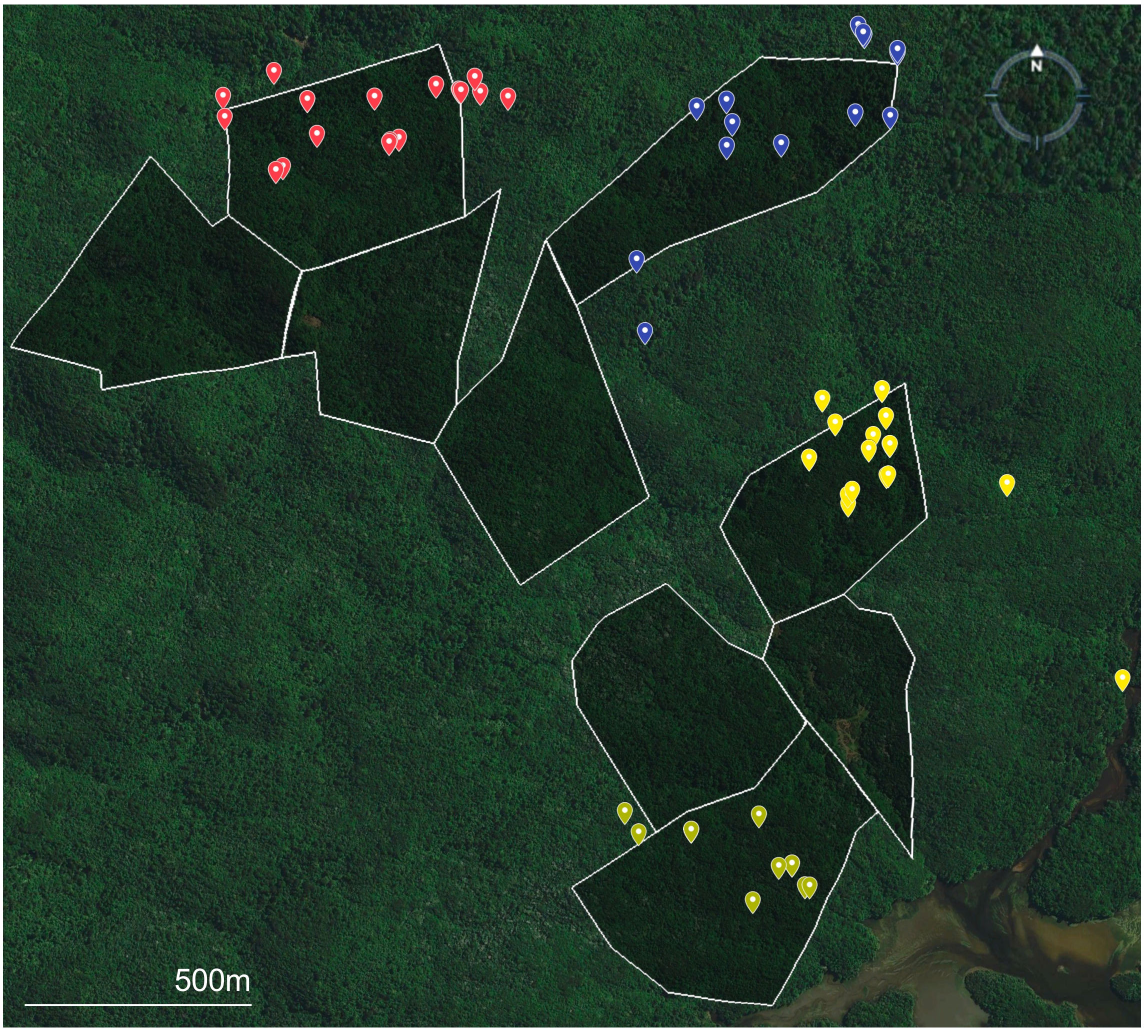


Figure 37. The locations of four chicks/juveniles (denoted by different coloured points) within and outside their natal territories at Kaipipi when tracked via radio-telemetry. Shaded areas with white boundaries represent known territories. The furthest yellow waypoint to the right is from the deceased chick, found 578 m from estimated natal territory boundaries.

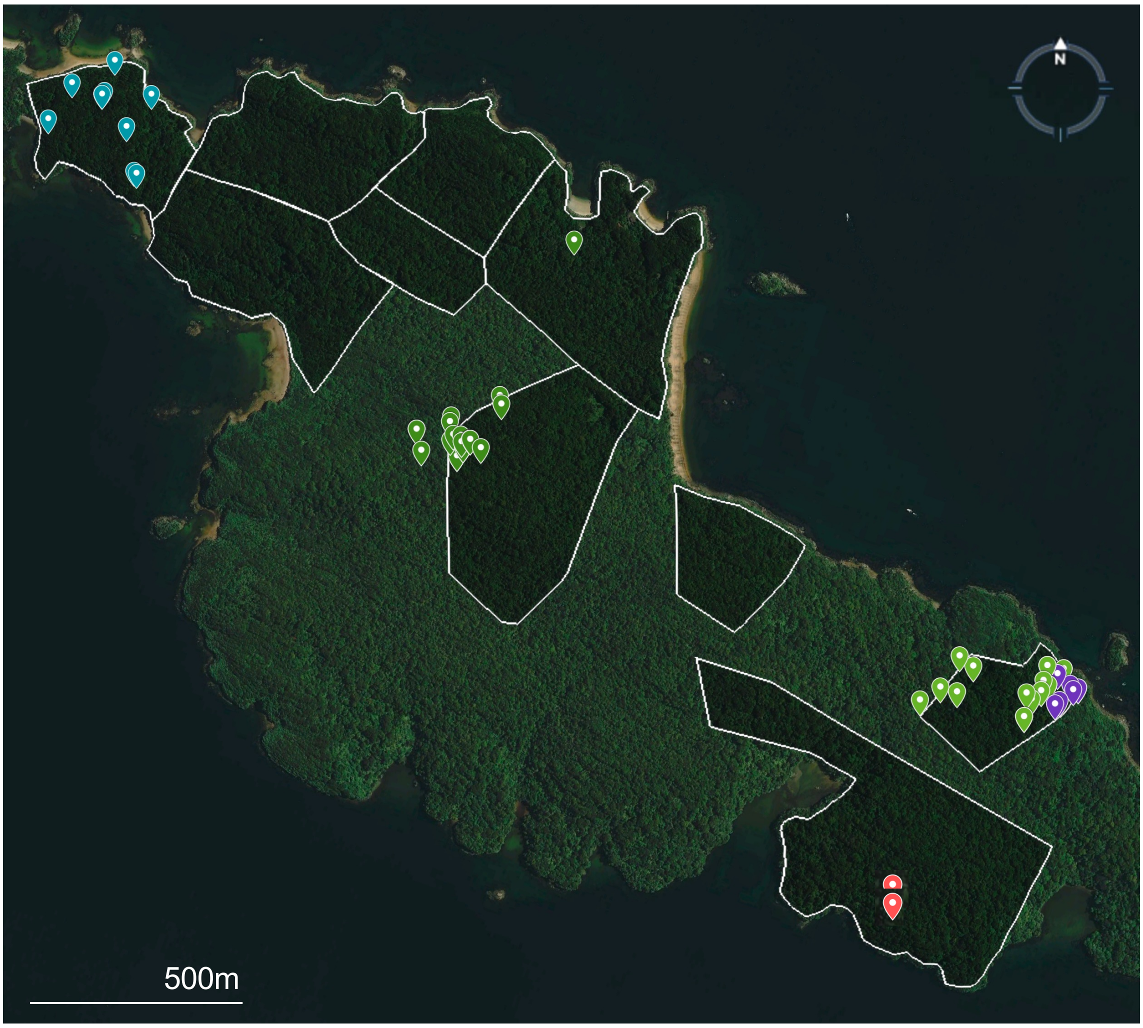


Figure 38. The locations of five chicks/juveniles (denoted by different coloured points) within and outside their natal territories on Ulva Island when tracked via radio-telemetry. Shaded areas with white boundaries represent known territories. Two chicks hatched in one territory in the lower right-hand corner (light green and purple waypoints). The red waypoints are from the deceased chick.

Movements outside the estimated territory boundaries were sporadic and temporary. From 132 total chick locations, there were eight (6.1%) that were more than 50 m from natal territory boundaries. Five of the eight locations came from the Kaipipi chicks, and the remaining locations were from one chick on Ulva Island. The average distance of movement outside territory boundaries was slightly higher at Kaipipi than on Ulva Island and the minimum age of movement outside territories was lower at Kaipipi (47 days old; 102m) than on Ulva Island (129 days old; 61m) (Table 30).

Table 30. The number of chick locations >50 m from natal territories, the average distance (m) moved away from the nest, range of distances moved, and the minimum and average age (days) of the chicks that moved >50 m.

	Locations	Avg. distance (m)	Range (m)	Min. age (days)	Avg. age (days)
Kaipipi	5	162	(51 - 578)	47	103
Ulva Is.	3	127	(61 - 246)	129	139

The furthest distance moved recorded for any of the chicks was for the deceased Kaipipi chick that was found 578 m from its natal territory. The longest distance detected on Ulva Island was 246 m, and this was the only occasion that it was possible to confirm that a chick was not within its natal territory, because it was within another known territory (Figure 38 above).

The minimal ‘dispersal’ of Rakiura tokoeka outside their natal territory is uncommon compared to other kiwi species at similar ages (Chan 1999, Forbes, 2009; Wilson, 2014), but not surprising given the assumption that most individuals in Rakiura tokoeka territory groups are related, and chicks are known to stay for years in their parent’s territory (Colbourne, 1991; Robertson & Colbourne, 2017; Robertson & Colbourne, 2022). For example, in 2018 a female was found in her natal territory at Mason Bay at the age of 10 years (Robertson et al., 2018). Importantly, radio-telemetry tracking is intermittent and, in this study, primarily diurnal. It was also interrupted by COVID lockdowns. Therefore, it is possible that there were more numerous and wider ranging movements that were not detected. Nevertheless, at the conclusion of the study no chicks/juveniles (age range 136 – 258 days, average 212) had dispersed beyond their natal territories permanently.

It is possible that the dispersal of kiwi is density dependent (Robertson & Colbourne, 2004). In a high-density population there is less available room for young kiwi to establish their own territories, and so they remain in the natal territory as ‘helpers’. In a high-density population of NIBK, Wilson (2014) suggested that low dispersal rates could be explained by decreased territoriality and an increased tolerance of young birds. There was very little territory overlap for Rakiura tokoeka at Kaipipi and Ulva Island during territory mapping (Section 3.3.1), and therefore no evidence of reduced territoriality, however, a larger sample size, longer tracking periods and genetic work on the relationships within territories is required to adequately investigate the dispersal of Rakiura tokoeka, and how many individuals establish their own territories and become part of the breeding population.

6.3.4.2 Inferences from burrow cameras

Burrow cameras helped identify the size and composition of nesting groups, including the number of unidentified birds (young and adult/subadult Rakiura tokoekoa). During the process of catching the adult/subadults for the purpose of attaching radio-transmitters, some birds were missed. However, burrow cameras detected the presence of unidentified (UID) Rakiura tokoeka adults, subadults, and young that had either not been found with other individuals that were tracked during telemetry work or had not been caught (Table 31). Four young Rakiura tokoeka at Kaipipi and two on Ulva Island that were not found during catching attempts for telemetry (Section 3.2.1) were detected by burrow cameras. These birds were probably juveniles (< 1800 g) and were likely chicks in 2017 or 2018.

Table 31. The number of burrows monitored with burrow cameras, with the number of resident Rakiura tokoeka with transmitters (TX Res.) or without (Unidentified [UID] Res.), and the number of UID transients detected, with the total proportion of UID birds.

	Burrows	TX Res.	UID Res.	UID transients	Proportion UID
Kaipipi	9	21	14	0	0.4
Ulva Island	8	18	7	3	0.3

Some of the UID birds were seen or heard during telemetry work, but regular or irregular footage of UID individuals on burrow cameras allowed confident allocation of these birds to territories as residents or transients respectively. This provided more accurate data on group size and could indicate the successful recruitment of chicks from previous years that were present at the nest burrow. This is important because young kiwi are notoriously difficult to detect, particularly without the use of a detection dog, and low detections can lead to concerning conclusions about population stability (Robertson & Colbourne, 2011 & 2022).

6.3.4.3 Inferences from a camera grid

The number of detections of young birds from the camera grid were low. From 4213 camera days spanning five surveys at four locations, there were 16 independent (> 30 minutes apart) captures of chicks/juveniles, which was 3% of the total captures of kiwi (adults = 543). Captures of young Rakiura tokoeka occurred during the night (n = 7), day (n = 2) and dawn (n = 7), with no captures at dusk. Most captures were of single birds (15/16), but in one case there was a young bird with an adult. The total number of camera stations that recorded young kiwi was 4/11 at Kaipipi, 1/7 on Ulva Island, 3/11 at Port Adventure and 0/11 at Mason Bay.

From 18 camera surveys (by season/location), there were seven where the presence of young kiwi within the study area was known (summer 2018: Mason Bay, summer & winter 2019, and summer 2020: Kaipipi and Ulva Island). Only 3/7 of these surveys detected any young birds (Table 32).

Table 32. The minimum number of young Rakiura tokoeka (< 1800 g) at each location per survey available for capture by the camera grid (Min.) and the number of independent captures by the grid (C). Minimum numbers of young were not always available for every survey (N/A). Zero captures are indicated by grey shading.

	Kaipipi		**Ulva Island**		**Mason Bay**		**Port Adventure**	
	Min.	C	Min.	C	Min.	C	Min.	C
Summer 2018	N/A	N/A	N/A	-	4	-	N/A	-
Winter 2018	N/A	-	N/A	-	N/A	-	N/A	-
Summer 2019	9	8	3	2	N/A	-	N/A	5
Winter 2019	4	1	2	-	N/A	-	N/A	N/A
Summer 2020	11	-	7	-	N/A	-	N/A	-

Chicks and juveniles were assumed to be present during at least some of the other surveys; there were 6 young birds at Port Adventure in 2017 (Robertson et al., 2017) and the age structure of the populations caught for territory mapping at Kaipipi and on Ulva Island in 2019 (Section 3.3) indicated there had been successful recruitment of chicks the previous year (2018). Therefore, the lack of detection does not necessarily signify a lack of chicks, but they were only detected during one additional survey (Summer 2019: Port Adventure).

For the summer 2019 survey, the minimum number of young Rakiura tokoeka known to be present at Kaipipi (n = 9) represented 20.9% of the minimum population (Section 3.3), the remainder being adults and subadults, while on Ulva Island young kiwi (n = 3) made up 9.1% of the total (Section 3.3). The number of independent detections by the camera trap grids of young kiwi for Kaipipi (n = 8) and Ulva Island (n = 2) during the summer 2019 surveys represented 6.6 and 11.8% of the total detections of Rakiura tokoeka respectively.

The number of adult/subadult Rakiura tokoeka detections during camera surveys was also low, but was still adequate to estimate total abundance (Section 5.3.3). Young kiwi made up a smaller proportion of the total population than adults/subadults (Section 3.3), and therefore fewer detections were expected. However, the percentage of known young kiwi recorded at Kaipipi (20.9%) and Ulva Island (9.1%) relative to adults/subadults during territory mapping surveys (Section 3.3) was not reflected in the percentages of independent captures by the camera grid in the summer 2019 surveys (which overlapped the territory mapping surveys) at these locations. Although the number of independent captures by cameras is not in itself an accurate reflection of the number of individuals at a site, this shows how the proportion of young to adult/subadult by camera surveys is also not a reliable metric for population structure.

It is not possible to say whether young kiwi passed in front of the cameras and were not detected, or if they did not encounter the cameras at all. Camera traps are often considered to be less successful at capturing small animals (Glen et al., 2013; Gompper et al., 2006; Pagnucco, Paszkowski, & Scrimgeour, 2011) because they have a reduced heat signature for triggering cameras and are less likely to encounter the zone of detection (Meek et al., 2015). However, there are an increasing number of studies that show their effectiveness for animals the size of Rakiura tokoeka chicks and smaller (De Bondi et al., 2010; Larrucea & Brussard, 2008; Mills et al., 2016; Thomas et al., 2020). Rakiura tokoeka chicks are less visible and probably do not range as widely as adults, particularly when they are very young, which is the case for NIBK (Wilson, 2014). Furthermore, when they do venture out, they may avoid open areas and therefore be less likely to be captured on cameras positioned there (Chan, 1999; Wilson, 2014). Dense vegetation cover has been shown to be important to small mammals and birds (Göth & Jones, 2001; Larrucea & Brussard, 2008). Alternatively, the presence of other species near cameras (i.e., weka on Ulva Island and possums/cats at Kaipipi) could cause a change in behaviour, such as avoidance, which could result in lower capture rates (Bischof, Ali, Kabir, Hameed, & Nawaz, 2014; Carpenter et al., 2021).

The season could have impacted the likelihood of capturing chicks versus juveniles on camera. Summer surveys (2018, 2019, and 2020) began at the end of January/start of February, which is the end of the breeding season for Rakiura tokoeka and, based on this study, new chicks captured on camera would be a few weeks to five months old. Winter surveys (2018, 2019) began in August and were therefore unlikely to capture new chicks, which were first seen emerging from burrows in September. Although the winter 2019 survey did continue into September, kiwi chicks at such a young age were unlikely to move far, recorded by Taborsky and Taborsky (1995) for NIBK chicks, and so probably wouldn't encounter a camera unless it happened to be very close to a nest. However, juveniles would have been available for detection in both summer and winter surveys and would have had a wider range than chicks (Section 6.3.4.1.2).

The most successful survey for detections of young Rakiura tokoeka was also the longest survey (summer 2019). Potentially, longer surveys are required to effectively survey for Rakiura tokoeka chicks and juveniles at these densities using a camera grid (of this grid density). Surveys of six nights or less have proved adequate in camera surveys for mammals smaller than young kiwi (Mills et al., 2016; Thomas et al., 2020), but in those studies bait was used in front of camera stations, and the target species could have been present in higher densities. Alternatively, the success of the summer 2019 survey could have been unrelated to duration and instead a consequence of unknown factors in the environment or population. For example, food availability, drought, or the presence of field workers could have influenced the numbers or movement patterns of young kiwi. More research is required on the best methods to monitor young kiwi successfully with a camera trap grid, including the number, spacing, and preferable location of cameras for capturing chicks, duration of survey, partitioning of space use with other species, the possibility of using bait, and whether the proportion of young in a population can be accurately captured.

6.4 Summary

6.4.1 Rakiura tokoeka chick survival

The information gained about young Rakiura tokoeka through using radio-transmitters and burrow cameras suggests there is no need for immediate concern or management intervention for this kiwi species, with the caveat that this study only provides a small sample size of limited duration.

Despite the concerns raised that feral cats could be affecting Rakiura tokoeka chick survival (Colbourne & Robertson, 2013; Robertson & Colbourne, 2011), no mortalities caused by feral cats were recorded in this study. Karl and Best (1982) noted that Rakiura tokoeka did not appear to be significantly preyed upon by cats. However, given the evidence of Rakiura tokoeka in cat scats (Appendix D.4) and regular footage of cats on burrow cameras, it is probable that some chicks are predated by cats, though this could be variable between years. Cats are flexible and opportunistic foragers (Bonnaud et al., 2010; Woinarski et al., 2017) and it is possible that there are sometimes easier prey alternatives for cats on Rakiura at the time that kiwi chicks are available, or they are cautious of the number of adults with the chicks when they are at the nest burrow (Harper, 2009), minimising the overall predation of chicks. At the time of transmitter removal, chicks were expected to still be vulnerable to cat predation, but as they continued to grow the risk would decrease as cats prefer smaller prey (Robertson et al., 2010; Strang, 2018). However, other pest species present could be having a negative impact on Rakiura tokoeka: rats could be limiting growth rates, and possum disturbance could be impacting nesting success. Though at current levels these are unlikely to cause large-scale population decline.

On Ulva Island there were no cats, rats, or possums, but weka were present in numbers not seen anywhere on mainland Rakiura. Weka are known to predate on the eggs and chicks of kiwi and other ground nesting birds (Carpenter et al., 2021; Jolly, 1989). For example, monitoring by the Department of Conservation of GSK over four years in the Kahurangi National Park showed an average of 30% of nest failures could be attributed to weka (A. McDonald pers. comm. 21/08/2020) and more than double that number of LSK nests at Te Kahuoterangi were believed to be lost to weka by Jolly (1989). Through the combination of burrow cameras recording weka disturbance to nests and radio-telemetry allowing necropsy of the deceased Ulva Island chick that identified weka as the primary cause of death (with starvation a possible contributor), weka could be identified as a threat to young Rakiura tokoeka on Ulva Island.

How much of a threat weka pose to kiwi at a population level is unknown (Carpenter et al., 2021). Weka and kiwi do coexist in other locations, for example, on Kapiti Island, where there is a high-density population of LSK. However, it is unclear whether the population of LSK could have increased during a period of decreased weka numbers (Robertson & Colbourne, 2004). The potential of Rakiura tokoeka to exist at high density with weka remains unclear, with weka largely absent from mainland Rakiura (Harper, 2009). There is no published research on the density of weka on Ulva Island, but it has been suggested that weka at high densities have a larger impact on prey (Carpenter et al., 2021). The importance of native predators is often overlooked (Carpenter et al., 2021), but will become more pertinent with New Zealand's conservation movement towards Predator Free 2050 and Predator Free Rakiura, which focus on eliminating introduced predators, potentially allowing the recovery of weka on mainland Rakiura.

Although two out of nine chicks died during the study, kiwi populations can suffer much higher rates of loss and still increase (Wilson, 2014) since these are long-lived birds that remain fertile for many years. However, further research on survival, resource (food) availability, competition (with natives and non-natives), growth rates, density-dependent dispersal, and breeding success would greatly add to current knowledge on this unique kiwi species.

6.4.2 Summary of methods

Monitoring methods should be related to project objectives, and it is helpful to consider implementing more than one method simultaneously (Thomas et al., 2020; Znidersic, 2017). The results of this chapter show that specific methods are better suited to certain research questions and different monitoring methods can provide complementary information, which is especially important in the establishment of new methods. Bassing et al. (2022) explains that integrating alternate methods can overcome the limitations of each by utilising their unique benefits to allow a more comprehensive interpretation. To monitor the survival, dispersal, and growth of young Rakiura tokoeka, radio-telemetry was essential. Cameras could not provide conclusive information on survival, but were useful for monitoring nest burrows, observing breeding behaviour, and determining nest fate (without the disturbance of manually checking burrows). Both methods helped with identifying probable nests and provided insight into recruitment and population structure through the number and proportion of young birds caught for telemetry and captured on burrow cameras.

While telemetry is currently the best option to monitor chick survival, burrow cameras add important information to the overall understanding of breeding and recruitment. Future development of the use of cameras for kiwi has great potential (see Chapters 4 and 5), including improving their use for population scale monitoring of young kiwi with camera grids. There are an increasing number of studies that focus on optimising the detection of small animals that could be trialled for young kiwi. For example, using two cameras side-by-side (Glen et al., 2013), comparing a horizontal versus vertical camera set-up (Smith & Coulson, 2012), obtaining specific models that perform better for small animals (Kelly et al., 2008; Meek et al., 2015) trialling the detection zone during camera placement (Glen et al., 2013; Meek et al., 2015; Palencia et al., 2021; Swann et al., 2004), and adjusting camera location, height and settings (Kelly et al., 2008; Palencia et al., 2021; Swann et al., 2004). Other options to increase detections would be to try extending the length of survey or density of cameras (Thomas et al., 2020).

When researchers prioritise the use of non-invasive monitoring methods, employing a selection of tools that complement each other is an excellent strategy (Ellis & Marsland, 2022), and the use of camera traps and radio-telemetry for monitoring young kiwi is a successful combination. Ultimately, increasing the ability and inclination to monitor remotely with a method that is more accessible to the many groups that conduct kiwi monitoring is highly appealing for the future of kiwi research, though the use of radio-telemetry is essential for certain objectives and to establish the validity of new methods.

Chapter 7: Synthesis

Preface: In this final chapter, I return to the research objectives to assess how I have addressed them and some of the limitations thereof, discuss the main themes that have been present throughout the thesis, and conclude with a discussion of the overall significance and wider implications of my research.

7.1 Addressing research objectives

This research was guided by the desire to estimate the population density of Rakiura tokoeka (*Apteryx australis australis*) by using a non-invasive monitoring method (camera trapping) and evaluate territory mapping with radio-telemetry while simultaneously evaluating evidence of decline or unmanaged threats. Each objective is addressed below.

Objective 1. Critically analyse territory mapping with radio-telemetry as the current gold standard for kiwi monitoring.

The monitoring methods currently used for kiwi (*Apteryx* spp.*)* are limited, and the use of telemetry for kiwi and its limitations and biases has not specifically been addressed until now. In Chapter 3 I analysed the use of radio-telemetry-based territory mapping for kiwi using Rakiura tokoeka as a case study.

I found that the duration of monitoring (accumulation of location fixes) and territory boundary method influenced density estimates by changes in territory and total study area size (Section 3.3.3). The duration of territory mapping survey and resulting accuracy in territory size is important for some monitoring objectives. For the Department of Conservation, which monitors kiwi populations with 5-yearly territory mapping surveys to look for overall trends, the length of survey is less likely to be relevant. If surveys are consistent in time of year, length of survey and amount of location data per individual and territory, then territory mapping surveys will still be effective. If the objective is to obtain the most accurate estimates of density possible, then extending the duration of the survey to collect a minimum of 40 location fixes per territory (equally spread amongst individuals) is preferable.

I determined that the method used for territory boundaries is important to consider regardless of project objectives, because consistency is key to any monitoring method. This is particularly critical for methods used to compare estimates spatially or temporally, and territory mapping with radio-telemetry is used to compare populations over time for kiwi. Field-workers-estimates for territory boundaries were difficult to apply in an objective and consistent manner, unlike convex polygons, which produced similar estimates but could be applied objectively. If radio-telemetry-based territory mapping methods cannot be replicated, then spatial and temporal comparisons are unreliable. Future territory mapping studies for kiwi should consider applying an objective boundary method such as the convex polygon.

As a result of field-workers-estimate boundaries and a few other subjective factors used previously for Rakiura tokoeka territory mapping (e.g., including projected call locations), it was difficult to replicate the methods of Robertson (2018) as intended (see Section 3.2). Consequently, the results obtained from the two novel study sites, Kaipipi and Ulva Island, may not provide a reliable basis for comparison or interpretation of past surveys. Nevertheless, this observation emphasizes the significance of maintaining objective consistency in monitoring methods.

Ideally, future territory mapping for kiwi would have consistent search effort between and within locations. While the amount of time and personnel put into finding birds on Ulva Island was consistent with that of Kaipipi, kiwi-detection dogs were not available for Ulva Island. Dogs were used at Kaipipi and the two historically monitored sites (Mason Bay and Port Adventure) to find kiwi that were not detected by broadcasting calls or found in burrows with radio-tagged birds. This means the minimum estimates of abundance for Ulva Island from Section 3.3 could have been different if dogs were also employed (Robertson & Fraser, 2009).

Future surveys would benefit from more systematic methodology across seasons, even if the focus of the study shifts (i.e., from tracking to nest burrow monitoring). I exerted uneven search effort recording locations throughout the breeding and non-breeding seasons, because I also conducted nest monitoring. Therefore, the comparison of territory size between these two seasons should be interpreted cautiously, and future studies should apply equal effort to gather the locations of all individuals throughout both seasons. Ideally, nocturnal locations would also be collected, so to accurately represent the full spectrum of movement and territory size and shape, which could be different at night, particularly for birds that were nesting during the day in the breeding season. However, given that the birds were nesting, a reduction in the extent of their territory is unsurprising.

For territory mapping surveys for kiwi it is important to attempt a consistent intensity of monitoring over the study period. During this study, the number of attempts to track the locations of individuals decreased from every 1 – 2 days during the initial two-week catch period to 1 – 3x per week in the following months. Although the territory estimates still accurately reflect how the duration of tracking and accumulation of location data can result in changes to territory size and shape over time, this also meant that changes could have been related to other variables such as the breeding/non-breeding seasons or environmental changes, as opposed to just the duration of monitoring.

Future studies should include the specific impact of transmitters on individuals as part of any critical analysis of the use of radio-telemetry. This is because they could have undesirable direct or indirect effects, and bias surveys in unknown ways (see Section 7.2.4).

Objective 2. Trial the use of a camera grid to establish population estimates of Rakiura tokoeka.

I trialled a new method for monitoring kiwi populations through camera trapping surveys. I used two methods for working with the post-survey camera data to (a) produce a relative abundance index using camera trap rates (Chapter 4), and (b) estimate point abundance per camera and density using abundance models (Chapter 5).

The CTR index was simple to apply and provided valuable information on Rakiura tokoeka. I found that there was no difference in CTR between the three mainland locations, Kaipipi, Mason Bay and Port Adventure, indicating the possibility that these populations could be similar densities and stable over the survey period (2018 – 2020). Ulva Island had a lower CTR due to less detections, which could be due to lower densities in part of the island or a number of other reasons affecting detection probability (Chapter 4). These results could be used to indicate where further research is warranted, for example, why was the detection rate on Ulva Island so much lower? Furthermore, CTR surveys could be applied in the future using consistent camera spacings, settings, and stations to detect potential changes in the population that need attention.

The results from the abundance models in Chapter 5 were exceptionally close to those from radio-telemetry-based territory mapping in Chapter 3. The potential to implement a camera trapping survey as opposed to undertake the significant effort involved in using radio-telemetry to obtain estimates of density is a significant contribution towards the future of monitoring kiwi populations. Camera traps are non-invasive, do not require catching or handling of individuals or accredited personnel, can monitor remotely, record behaviour and are easier to implement than radio-telemetry. Of particular importance is the wide applicability of camera trap surveys for the many conservation and community groups that may not have the resources required to implement radio-telemetry monitoring.

To explore the potential of camera surveys, future studies should trial their use on populations of different densities. This increases the reliability of the results and indicates that the method is reflecting true population change (Rovero & Marshall, 2009). This is an important process for indices like CTR (Chapter 4) and abundance models (Chapter 5). To ensure that estimates from camera surveys are reflecting the population, estimates should change in response to change in the population (Bengsen et al., 2011). For example, Duquette et al. (2014) and Bassing et al. (2022) used radio-telemetry and GPS-tracking respectively with camera surveys to monitor white-tailed deer (*Odocoileus virginianus*) populations and found that estimates from both methods tracked the same population growth trends. O'Brien and Kinnaird (2008) found that a traditional occupancy model, the RN model and the Binomial mixture-model all tracked the same decline in great argus pheasant (*Argusianus argus*). In this study, there was no significant difference in densities between the four locations (Section 3.4.3), or over the duration of monitoring, so this measure was not possible. Therefore, I was not able to correlate either the CTR or abundance model estimates to density estimates from territory mapping, which is the most reliable way to introduce the use of these methods for a species or population (Kafley et al., 2019; O'Brien et al., 2003; Palmer et al., 2018; Rovero & Marshall, 2009).

Future studies would benefit from consistent survey set-up when comparing results from camera trap surveys in different locations. In this study, the most significant limitation in the camera surveys was the inconsistency in survey set-up on Ulva Island compared to Kaipipi, Mason Bay, and Port Adventure. The size of Ulva Island dictated the area that seemed most appropriate for camera surveys, where the distance between both sides of the island was greatest. However, it was difficult to find enough individuals for radio-telemetry in this area, and so the area where kiwi were caught was extended towards the west beyond the camera grid. This meant that there was a discrepancy between the areas surveyed by each method. Furthermore, the grid had less cameras and was a different shape than the other locations (Section 4.2.2) due to the size and shape of the Island. For these reasons, it may not be reasonable to compare estimates from Ulva Island to the other locations.

It would also be worth attempting to identify useful covariates for abundance estimation models for kiwi populations in future research. If I had been able to find useful covariates for modelling the abundance of Rakiura tokoeka, these could have increased the precision of estimates, and provided valuable information on variables that affect the detection probability and abundance of Rakiura tokoeka for future population monitoring and management. I recommend applying additional and improved location-specific habitat or environmental measurements (i.e., location-based weather stations, measures of other species presence and abundance, invertebrate sampling, number of available burrows).

Objective 3. Compare the use of radio-telemetry and camera traps for monitoring young Rakiura tokoeka

I gathered information on the survival of chicks, causes of mortality, and their growth and dispersal using radio-telemetry, as well as unique data on the breeding behaviour and patterns of Rakiura tokoeka using both radio-telemetry and camera traps (Section 6.3). I also obtained snapshots of the age structure of the populations at Kaipipi and on Ulva Island through the use of radio-telemetry to estimate densities (Section 3.3.2) and trialled the use of a camera trap grid for detecting young (chicks and juveniles) kiwi (Section 6.3.4.3).

Although the sample size of chicks was small and the duration of the study short, my results offered some insights and provided direction for future research and monitoring of young kiwi. The most pertinent of these results was that cats may not be a significant threat to Rakiura tokoeka chicks and are unlikely to be having enough impact to cause a decline in the adult population. This is based on the age structure of the Kaipipi population showing a high proportion of young, as well as the lack of evidence of predation by cats (*Felis catus*), and low percentage of cat scats containing kiwi remains. However, a larger sample size over a longer time frame and consecutive breeding seasons would offer more conclusive information in this regard. Weka (*Gallirallus australis scotti*) are predating on Rakiura tokoeka eggs and chicks on Ulva Island, but recruitment was still shown to be occurring by the proportion of subadult, juveniles and chicks in the population. It would be interesting to investigate the dynamics between weka and Rakiura tokoeka further, in terms of competition for burrows, food, and space use. Specifically, future research could explore whether a division in space use could explain the patchy distribution of Rakiura tokoeka that seemed to occur on Ulva Island.

I showed how a combination of burrow cameras and radio-telemetry was an effective way to monitor breeding Rakiura tokoeka and young kiwi, with radio-telemetry providing direct data on individuals and camera traps offering remote, indirect monitoring. I found that a camera trap grid where the distances between camera stations was based on the average home range of Rakiura tokoeka was not an effective way to detect young birds. Future research on the use of cameras to detect young kiwi using a grid would benefit from reducing the distance between cameras from that used for adult/subadults to see if this improves detections.

Although I found that a combination of the two methods was most effective for monitoring young Rakiura tokoeka, it could be helpful for future studies to consider a cost-benefit analysis for each method to consider the resources required to obtain the desired output.

Objective 4. Report on the age structure, chick survival and density of Rakiura tokoeka for population management.

I contributed information towards the population management of Rakiura tokoeka using both monitoring methods. Firstly, I effectively doubled the number of locations where Rakiura tokoeka have been monitored, including the pest-free Ulva Island. Radio-telemetry and associated catch data (Section 3.3 and 6.3) provided data on chick survival and the age structure of the populations caught, while burrow cameras were important for identifying and clarifying the minimum number of unidentified individuals per territory, particularly young (Section 6.3.4.2). Radio-telemetry based territory mapping was used to estimate minimum densities (Section 3.3.2), and camera trapping was used to estimate absolute densities (Section 5.4.5). Cameras on burrows helped to identify factors that could affect chick survival (Section 6.3), and indices suggested the population on Ulva Island is worth investigating further due to low detections (Section 4.3.2).

This information is valuable because the location with the longest monitoring of Rakiura tokoeka, Mason Bay, is a unique environment not necessarily representative of the rest of Rakiura. Furthermore, the population at Mason Bay has only recently been considered stable, after a long period of decline (Robertson et al., 2018; Robertson & Colbourne, 2022). One of the reasons hypothesised to be driving this decline was the predation of chicks by feral cats, which has only been directly addressed in this study. The chicks monitored in this study were not predated by feral cats. I also found that although group sizes within territories were larger on average at Kaipipi, territory sizes on Ulva Island were smaller on average, and there was no significant difference in densities from territory mapping (Section 3.3). Ulva Island does not have feral cats, and if cats were having a significant effect on Rakiura tokoeka abundance on the mainland, we would have expected Ulva Island to have significantly higher densities than what were detected.

With recent reports of population recruitment and stability at Mason Bay and Port Adventure (Robertson et al., 2017, 2018), results from Kaipipi and Ulva Island in this study reflecting similar density estimates to the previous locations (Section 3.3), the Mason Bay decline possibly being localised as a result of unique habitat change (Robertson & Colbourne, 2022), the proportions of subadult and young birds detected (Section 3.3), and chick survival results (Section 6.3.3), there does not appear to be any reason for serious concern for the Rakiura tokoeka population.

Future studies should aim for a larger sample size of chicks so that wider inferences on growth, dispersal, survival, possible threats, and the impact of feral cats can be made about the population. Additionally, a longer sampling duration and multiple years of monitoring would provide more representative and reliable results reflecting population patterns.

7.2 Key themes

The key themes throughout this thesis have been (i) comparing radio-telemetry and camera trapping for monitoring an unmarked species, (ii) the difference between invasive and non-invasive monitoring, and (iii) the population health of Rakiura tokoeka.

7.2.1 What is a true comparison between methods?

It is difficult to truly compare two methods that collect inherently different data. Cameras collect detections at fixed locations at any time, while radio-telemetry obtains the precise location of the animal (assuming it can be found) at certain times. Consequently, post-monitoring data analyses should reflect this difference by being specific to each method, using the most appropriate approach as opposed to fitting one analysis for both (Bassing et al., 2022). For example, the use of an established method for estimating the effective sampling area from camera surveys to make density estimates (C Section 5.2), and a study area based on the locations of birds with radio-transmitters from radio-telemetry (Section 3.2).

The methods used in this thesis each have biases, assumptions, and limitations that differ, and this can complicate the comparison of results (Popescu et al., 2014). For instance, the population is assumed to be closed for camera trapping surveys and movements that violate this cannot be detected. Telemetry can detect movements outside the study area, but is more prone to sample bias than camera traps (which capture a random sample of the population), where the individuals with transmitters are not representative of the population (i.e., if catching methods are more likely to detect different ages/sex of birds). These inherent differences are common when using multiple methods for both field methodology and data analysis, but are rarely addressed.

Meeting the assumptions of each method and understanding the impact of violating those assumptions is essential (Keever et al., 2017; Link et al., 2018) and can influence the interpretation of estimates from different methods. For example, Rogan et al. (2019) used camera trap data to estimate leopard (*Panthera pardus*) densities using Spatial-Capture-Recapture (S-C-R) and the Royle-Nichols (RN) model.

However, S-C-R analysis requires camera spacing to detect individuals on multiple cameras, whereas the RN model assumes that individuals are only detected at a single camera. Unsurprisingly, Rogan et al. (2019) did not achieve reliable results from the RN model in this case.

Most comparisons of camera traps to other monitoring methods are similar to what this thesis offers, providing abundance or density estimates from two different methods for an unknown population (Gilbert et al., 2021; Linden et al., 2017; Palmer et al., 2018). In these study designs, where the true population is unknown, the validity of estimates is often at least partly judged by the researchers' own impressions of the population (Kafley et al., 2019; Suwanrat et al., 2015; Zou et al., 2019), which are valuable, but cannot be considered accurate without a true census. However, when estimates from both methods are similar, and authors conclude that the same management recommendations would have come from using either method independently (Linden et al., 2017), then there is more confidence that they are reflecting the true population. Realistically, these comparisons of methodology on an unknown population are better considered a comparison of the financial investment, effort required, necessary time, resources and personnel, and post-survey data requirements to implement each method independently for the same result.

Comparisons of methods are usually intended to validate a new or altered method, by using it alongside a method that is trusted or considered more robust or reliable (Rovero & Marshall, 2009). The only way to measure the accuracy of a monitoring method is to compare the estimates to a known population, i.e., with a true census. Keever et al. (2017) provides a rare example of achieving a study design close to this, by comparing abundance estimates from camera traps and a Binomial mixture-model on a contained and marked population of semi-wild, white-tailed deer. Most individuals were marked, and detections of unmarked deer were not included in the analysis. More commonly, established methods are used as a benchmark to compare estimates from other methods similarly to how I used territory-mapping results from Chapter 3 to evaluate camera trapping in Chapters 4 and 5. Importantly, the methods used to provide benchmark estimates are not necessarily close to the true population values but provide minimum estimates as a guide for new methods.

Ultimately, the use of different methods comes down to the project objectives. Bassing et al. (2022) describes some of the general aims of different types of monitoring methods. For example, tracking methods (e.g., GPS and telemetry) are good for drawing inference about very specific, wildlife-habitat relationships, working with species without pe-defined areas (i.e., prone to long range movements or dispersal), and collecting data on animal movement, survival, and reproduction (Bassing et al., 2022). Whereas methods like camera traps are useful for making decisions about species in pre-defined areas and to understand broad scale patterns (Bassing et al., 2022).

7.2.2 Combining methods

Despite the prevalence of comparisons of different field methodologies in the literature, using multiple methods in a *complementary* strategy enhances the knowledge captured during a survey. For example, the use of burrow cameras helped determine the proportion of individuals that were not detected during telemetry surveys, by the footage of marked and unmarked individuals present at a burrow (Section 6.3.4.2). This was particularly useful for capturing young Rakiura tokoeka, which can be harder to detect.

Linden et al. (2017) suggests that employing multiple methods within a project could be used to improve the reliability of less robust methods while keeping monitoring costs down. The authors suggest that more expensive and intensive methods could be used periodically to calibrate methods of lower cost and less effort that are used more frequently. For example, camera traps could be used to routinely monitor kiwi, with radio-telemetry surveys undertaken periodically to validate data from the cameras. This could also be an effective strategy if different methods varied in efficiency depending on the season or other factors inherent in the environment or target population (Vine et al., 2009). Incorporating various methods that fill different knowledge gaps maximises the power of a survey (Bassing et al., 2022; Thomas et al., 2020).

7.2.3 How representative are Rakiura tokoeka?

Rakiura tokoeka were used as a case study species to explore the use of territory mapping and camera trapping for kiwi monitoring. However, there are behavioural differences between kiwi species that could influence both the choice of methodology and most appropriate analyses. The most significant factors to consider that can vary among species and would impact surveys are the number of birds per territory, being predominantly nocturnal or diurnal, the degree of territoriality, and the size of an average territory/home range.

Probably the most important of these is that Rakiura tokoeka tend to live in groups, and the number of individuals in a group varies. This made it (i) difficult to determine if all the birds in a territory had been identified, (ii) harder to identify individuals from camera footage because there were multiple females and males in a territory/group, and (iii) impacted the choice of abundance model because detections of individuals might not have been independent (Martin et al., 2011). For other kiwi species, if there are only two or occasionally three adults in a territory, then estimates of total abundance in the study area will probably more reliable (because the variability in the number of individuals per territory is so much lower), the identification of individuals within a territory might be possible (as fully grown males and females can usually be distinguished through body and bill size), depending on the degree of territory overlap and camera placement within a territory, and other methods of analyses that incorporate individual identities might also be possible. The RN or Binomial mixture-model would still be applicable but might suffer from low detections given the lower number of kiwi present in territories. Although, in theory, if camera stations are spaced appropriately based on the assumption of independent detections, both models should be able to manage low detections (Kéry & Royle, 2015; Royle & Nichols, 2003).

Rakiura tokoeka are often active during daylight hours, whereas other kiwi species are predominantly nocturnal. It would be beneficial to determine whether some Rakiura tokoeka are consistently active during the day and others only at night, or if all individuals are active during the day routinely or at different times of year, i.e., breeding season. If this pattern changes throughout the year, it could influence temporal detection rates. If different individuals are available for detection from cameras during the day versus the night, then it is important to survey for the whole 24-hr period. However, if individuals are active during both periods, then they are more likely to be double counted and just nocturnal data should be used. The RN model is probably robust to double counting (Denes et al., 2015), but if this could be controlled by selective timing of surveys then it would mitigate the risk of affecting model estimates. Cameras were particularly well suited for monitoring Rakiura tokoeka because they could operate for 24 hours a day, which can otherwise be logistically challenging (O'Brien et al., 2010; O'Brien & Kinnaird, 2008). For other kiwi species that are more strictly nocturnal, camera surveys during the hours of darkness would be adequate to capture the activity of individuals.

The degree of territoriality in a population can impact the detectability of individuals, which is important to consider in camera trap surveys. For example, if territories were not strongly fixed and had substantial overlap then individuals would be more likely to be detected at multiple cameras (Linden et al., 2017), violating the model assumptions in this study. Rakiura tokoeka seem to be quite strongly territorial because they maintain territories over time that have little to no overlap (Robertson & Colbourne, 2022). However, territoriality among kiwi species and populations is inconsistent, and this should be considered when implementing field methodology and statistical models. The models used for Rakiura tokoeka may not be as appropriate for kiwi species that are less territorial. However, the RN model and the Binomial mixture-model have been used to make reasonable abundance estimates for species that have overlapping home ranges and are not strictly territorial, for example white-tail deer (Duquette et al., 2014) and fisher (*Pekania pennanti*) (Linden et al., 2017).

The size of an average territory/home range is important for camera trapping surveys. Information on Rakiura tokoeka average territory size (Robertson et al., 2017, 2018) was used to inform camera spacing, buffer size and total effective sampling area in this study and could be the reason estimates from the abundance models were not significantly different to estimates from territory mapping (Section 5.3.6). The key for surveying an unmarked population with cameras is to find the camera density that allows all the individuals in the study area the chance to be detected, but not at multiple camera stations (Gilbert et al., 2021). When establishing camera trapping for a new population it is possible to deploy more cameras than are expected to be required, and then discard the data from select points as required. Since territory size and movement patterns vary, camera trapping needs to be tailored to each population and species studied (Dillon & Kelly, 2008).

7.2.4 Does invasiveness matter?

In this study, I used radio-telemetry as an example of an invasive method because it requires the catching, handling, and tracking of individuals. However, there is little information available on the specific effects of these practices on kiwi.

Cunningham (2010) reported results from 1-3 years of tracking 43 adult and subadult NIBK (*Apteryx mantelli*) with radio-transmitters from a population on Ponui Island (that were being monitored for other purposes). The author reported that 30% of these birds had a direct injury from the transmitter, predominantly wounds from chafing, and the transmitter of one individual may have resulted in mortality due to entanglement. These direct effects are the simplest and most objective way to determine the impacts of invasive methods. Cunningham (2010) also used video footage of individuals (with and without transmitters) entering and exiting burrows and categorised certain behaviours that might be associated with wearing a transmitter as ‘discomfort behaviours’, such as picking up and extending the transmitter leg backwards. The author suggested this motion was only observed for birds with a transmitter on the leg in question (indicating it could be transmitter related). These more indirect effects are challenging to monitor and require assumptions to be made but can be more insidious and have longer-term impacts that cannot be measured in a short time frame.

Recent research has considered the effects of handling on NIBK on Ponui Island, through changes in call rates (De Rosa, 2021) and stress response measured by heart and breathing rates (Vattiato, 2021). De Rosa (2021) found no apparent change in the number of vocalisations before and after being caught and handled for a radio-transmitter change. Vattiato (2021) found that kiwi that had been caught more often appeared to be less stressed with subsequent capture (according to breathing rate), showing that there is a physiological response to being handled, although measures could only be taken once the birds were already in the hand. These efforts towards investigating the impact of using radio-transmitters for kiwi is promising.

In studies that consider the effects of transmitters, behaviours might be used as proxy for larger implications. For example, a reduction in feeding or foraging behaviour for individuals with transmitters could result in a long-term impact on fitness, reproduction or survival, which may not necessarily be measured (López-López, 2016). A change in defensive or protective behaviours such as flight or seeking cover could result in higher predation and a long-term decline in the population from reduced survival (Göth & Vogel, 2003). Studies that directly measure the impacts as opposed to making suppositions are more reliable, such as differences in breeding success, survival, parental care (leading to an impact on the survival or fitness of the young) (Göth & Jones, 2001). For kiwi, future research could build on the work by Cunningham (2010) and monitor individuals pre-and post-transmitter attachment for ‘disturbance behaviours’, but the most important outcome would be identifying what these behaviours mean for an individual’s fitness.

The impacts of any method on an individual are only explained with subjective conjecture unless the direct effects are measured. For example, Ellenberg, Mattern, Seddon, and Jorquera (2006) reported how Humbolt penguins (*Spheniscus humboldti*) on Damas Island showed no outward indication that they were disturbed by the presence of tourists, which could have been interpreted as there being no impact on the birds. However, the clever use of an egg-shaped dummy placed in nests recorded marked and prolonged increases in heart rate when the birds were exposed to people, even at a distance of 150 m (Ellenberg et al., 2006). The authors concluded that the breeding failure of these penguins was most likely related to the presence of people via eco-tourism. Although this was not a study based on invasive or non-invasive monitoring, it shows how the impact on wildlife of the mere presence of people cannot be underestimated, and that only specific measurements can truly describe the impacts we have on animals (Cockrem, Potter, Barrett, & Candy, 2008).

Studies that focus on an alternative to invasive monitoring to achieve the same outcomes are promising. For example, an excellent alternative for the invasive procedure of blood draws for marine mammals is the collection of exhaled respiratory condensate or ‘‘blow’’ to measure changes in stress hormones (Thompson et al., 2014), enabling sampling without restraint, capture or increased physiological stress. Gaglio et al. (2017) trialled a novel approach to investigating the diet of greater creased tern (*Thalasseus bergii*) by photo sampling as opposed to sampling by forced regurgitation and achieved similar results, successfully estimating prey composition and size while reducing observer-based biases and causing little to no disturbance to nesting birds. Although we do not know the indirect impacts of transmitters on kiwi, or the direct impacts for Rakiura tokoeka, the increased effort, cost and experienced personnel associated with more invasive methods alone are valid reasons to seek alternatives (Gaglio et al., 2017).

Camera traps are an appealing alternative because of their non-invasive nature. However, the effect of cameras on kiwi is also unknown. Cameras are constantly being improved to make them more discreet and less detectable in the environment, with sound and light being the most obvious triggers for an animal to respond to aside from the presence of a new object in the environment. Some animals are attracted to novel objects, and others will be wary. Rakiura tokoeka were recorded probing the cameras with their bills, showing no obvious signs they had noticed the camera, and showing a startle response. It is possible that there were individuals that were avoidant and therefore were not detected in the footage. Furthermore, the presence of burrow cameras on nests could be a possible attractant to predators of kiwi eggs and chicks. All these factors need more attention in the development of camera trapping for kiwi.

The information provided by invasive methods is in many cases vital. Therefore, justification for them is established by considering project objectives and if invasive methods are necessary to obtain them (Bassing et al., 2022), or if a less invasive alternative is available (Gaglio et al., 2017). Some species are more sensitive to invasive methods than others (Ellenberg et al., 2006), and invasive methods are not always suitable in every project or for every species (Gompper et al., 2006). Furthermore, the biases of invasive methods are usually poorly understood. For example, kiwi that have been caught or attempted to have been caught may have a subsequent avoidance of people (Cunningham, 2010). There are an increasing number of studies using less invasive methods for population monitoring, for example, (Long et al., 2012) used detection dogs, remote cameras, and hair snares (all with occupancy modelling) to survey black bears (*Ursus americanus*), fishers, and bobcats (*Lynx rufus*) throughout Vermont. Cunningham (2010) used bill length ratios from camera footage to sex NIBK on Ponui Island. The use of cameras represents a lower cost, more widely applicable method of monitoring for kiwi that does not require handling or catching, and this makes it worth pursuing even without knowing the direct or indirect impacts of telemetry.

7.3 Implementing territory mapping and camera trapping for kiwi

These suggestions have been made in previous chapters, but the most salient points are summarised below as a guide for kiwi practitioners.

Territory mapping with radio-telemetry

Current methods recommended by the Department of Conservation (Robertson, 2018) are reasonably sound except for some elements of inconsistency and subjectiveness that could be improved in the following ways.

a) Effort per survey needs to be consistent. The number of days spent territory mapping by Robertson et al. (2017) at Port Adventure in 2017 was higher than by Robertson & Colbourne (2011) in 2011, which makes the results difficult to compare. This was also an issue when I replicated these same territory mapping methods in Section 3.2, where I had teams with less experience (than participated during historical surveys) working with Rakiura tokoeka, and limited access to kiwi-detection dogs, which could have influenced the number of birds detected. In addition, the number of locations used for territory maps per individual or group should be as consistent as possible to capture territory shape and size while minimising bias.
b) Convex polygon boundaries are more objective and easier to replicate than field-workers-estimate boundaries. Although the latter allows incorporation of local knowledge and site experience, they are too subjective to apply consistently and repeat accurately.
c) The length of survey will influence the results and the decision of how long the survey should be depends on the project objectives. The longer the survey, the higher the likelihood that more birds will be caught (by detecting them in burrows when tracking birds with transmitters) and locations recorded, and that territory size and densities will change (Section 3.3.3). The degree of change might not be worth the extra investment in survey time and effort. For example, long-term (5-yearly) monitoring of Rakiura tokoeka using approximately 2-week surveys was adequate to identify trends in the data between surveys (Robertson et al., 2017, 2018). Longer surveys with a higher number of location fixes were necessary to capture the full extent of movement and territory boundaries to establish density estimates that were

as accurate as possible (Section 3.3.3) to judge the performance of camera trapping (Chapters 4 and 5). Once the length of survey (and associated number of fixes) has been established for a particular project it should remain consistent to allow temporal and spatial comparisons.

d) There will always be a proportion of birds that are not caught and remain unmarked (UID). Camera traps can help identify the minimum number of UID birds per territory (Chapters 4 and 6), which is valuable for better estimating the overall population density. Camera traps can be placed randomly in the study area or outside burrows where tracked birds are located. The latter is particularly useful for identifying young birds that also missed detection (Section 6.3).

Camera trapping for kiwi

The objectives of the project will dictate the use of an index like CTR (Chapter 4) or estimates of point abundance and density if the effective sampling area is known (Chapter 5). Practical knowledge of the species biology and behaviour should drive the design of camera trapping studies to best avoid possible biases (Suwanrat et al., 2015). Some general guidelines are as follows.

a) Camera spacing is key to the success of a survey and would be difficult to establish without knowledge of the average territory/home range size of the target population (Section 5.2) (Dillon & Kelly, 2008). The incorporation of radio-telemetry to initiate camera trapping for a new population is worth considering for this reason (Soisalo & Cavalcanti, 2006). If camera density is too high, total abundance estimates can be biased high, and if camera density is too low, individuals will be missed, and total population estimates biased low (Keever et al., 2017).
b) If a model is used for abundance estimates (e.g., Chapter 5), then the model assumptions and the reliability of estimates if those assumptions are violated must be considered (Link et al., 2018). Different models will be appropriate depending on the behaviour of the species, the resulting detections (high or low), and the project objectives, but the RN and Binomial mixture-models are likely to be applicable, at least as a starting point, for any kiwi species.
c) Point estimates of abundance are easier to compare than density estimates between studies and so should always be included when reporting results from abundance models (O'Brien & Kinnaird, 2008; Royle, 2004). This is

because the effective sampling area (ESA) and buffer of camera traps are difficult to estimate accurately, and can significantly impact density estimates (Section 5.3.6) (Dillon & Kelly, 2008).

d) There are multiple ways of deciding the ESA, and a lack of consensus around the best method (Sollmann, 2018). Different methods are preferred in separate studies and although an external polygon around the camera stations with a buffer was preferred in this study, this is the first use of these methods for kiwi monitoring and the exploration of various options should be continued. However, once a particular method is chosen within a project, it should be used consistently.

e) Trialling various possibilities for covariates that could be used to help explain the abundance and detection of kiwi is a worthwhile pursuit to help improve the precision of estimates, and to improve kiwi monitoring and management generally. Ideally, covariates would be measured at a local level, i.e., weather stations, habitat variables, food availability. Understanding how these factors relate to the detection and abundance of animals is important regardless of the monitoring methods used (Kafley et al., 2019).

7.4 Future research

In the previous chapters and earlier in this chapter I identified knowledge gaps as they arose, here I simply list the most significant points. I have used two categories; suggestions for future research that are Rakiura tokoeka specific, and others that concern the monitoring of any kiwi species.

Rakiura tokoeka research

1. Identifying whether there is a variable density of birds on Ulva Island and the reasons why would provide valuable insights into the habitat requirements of Rakiura tokoeka, and possibly the impact of native predators (weka), and dispersal following translocations (given all the original Rakiura tokoeka on Ulva Island were translocated, Section 1.2).
2. Food availability and competition for resources on Ulva Island versus mainland Rakiura is worth exploring. Rats (*Rattus norvegicus, Rattus rattus, Rattus exulans*) compete for food in the leaf litter, possums (*Trichosurus vulpecula*) and kiwi utilise the same burrows, and native birds in the absence of invasive predators (on Ulva Island) spend more time foraging on the ground. The difference in food availability and competition for food could be a significant difference between Ulva Island as a pest-free habitat, and mainland Rakiura. These differences seem pertinent as Rakiura moves ambitiously towards being predator free (Taylor, Russell, & Russell, 2020).
3. Chick survival and growth using a larger, multi-year sample would be valuable. My sample size was too small to comment on these aspects in the wider population, but suggested some interesting leads to pursue, including weka predation and the survival of Rakiura tokoeka eggs and chicks, and the impact of rat plagues on chick growth.
4. Rakiura tokoeka dispersal over longer time frames would potentially help explain the purpose and composition of groups, the likelihood of ‘drifter’ birds (i.e., not belonging to a territory) and the number of new unmarked birds captured in repeat territory napping surveys (Colbourne & Robertson, 2013; Robertson et al., 2018). None of the chicks/juveniles with radio-transmitters dispersed from their natal territories permanently by the conclusion of this study. We know that some of the extra birds in groups are chicks still present in their natal territories (Robertson & Colbourne, 2022). We also know

individual females make occasional long-distance forays (Section 3.3). But how dispersal, breeding opportunities, establishing territories, and relationships within groups works for Rakiura tokoeka is generally unknown.

5. The genetic relatedness of Rakiura tokoeka within groups and as a function of distance between groups would be an important component of any dispersal study and is a long-held question for this kiwi species. Genetic work could provide insights on the composure of groups, the relationship between the breeding behaviour of members of a group and their relatedness, and how Rakiura tokoeka disperse from these groups to find mates.

Kiwi monitoring research

1. The most valuable next step for camera trapping for kiwi is to correlate CTR indices or abundance estimates with different density populations or a population that goes through a known change over time.
2. Identifying whether there are covariates that explain the detection probability and abundance of different kiwi species would be valuable for their monitoring and management.
3. Trialling different ways to improve monitoring young kiwi with cameras so that camera grid surveys could be less biased towards adult and subadult birds (Section 6.3).
4. Experimenting with different methods of analysis for estimating the abundance of unmarked species, for example, a traditional occupancy model could be a good strategy to explore the distribution of Rakiura tokoeka on Ulva Island. Working with populations of partially marked birds could also enable methods that incorporate marked individuals if the sample size is big enough, i.e., Spatial-Capture-Recapture.

   Other models for unmarked species that are more statistically based than indices, account for detection probability, and provide abundance estimates are available, but require various assumptions to be met. These include the Random Encounter Model (REM) by Rowcliffe et al. (2008), Unmarked-spatial-capture-recapture (Chandler & Royle, 2013; Royle et al., 2014), Random-encounter-time-to-event and Space-to-event (Moeller, Lukacs, & Horne, 2018), the Random Encounter and Staying Time (REST) model (Nakashima et al., 2018), and Distance-sampling (Buckland, Rexstad, Marques, & Oedekoven, 2015). Gilbert et al. (2021) offers a thorough theoretical comparison of different models while Palencia, Rowcliffe, Vicente, and Acevedo (2021) compares the REM, REST and Distance-sampling models to estimate the density of three different terrestrial mammals. The difficulty of using these models is that they either (i) require prior knowledge of animal movement and density (and are sensitive to errors in these), (ii) have not been rigorously field tested, (iii) assume detection is perfect, or (iv) are challenging for nocturnal species (Denes et al., 2015; Gilbert et al., 2021; Palmer et al., 2018). However, their application for kiwi populations would be worthwhile to explore.

5. Exploring the idea of bait for kiwi to increase detections from camera trap grids would be worthwhile. Bait is used for this purpose for other species (Linden et al., 2017), and bait for kiwi could mean a camera is more likely to capture all the individuals present in a territory, which is particularly important for Rakiura tokoeka. However, bait could increase the likelihood of return visits of the same individual (Linden et al., 2017), and if there is no way to identify individuals, then detections would be inflated (Nakashima, 2020). Furthermore, a saturation of detections may result in poor performance of the RN model (Kéry & Royle, 2015), although baiting itself is not a problem for site-structed models like the RN (Gilbert et al., 2021). In these cases, count data and Binomial mixture-models could be a better option (Denes et al., 2015; Kéry & Royle, 2015), although Nakashima (2020) and Linden et al. (2017) achieved reasonable estimates with the RN model and multiple detections of the same individuals. If baited surveys were trialled for kiwi, shorter duration surveys would help reduce the amount of double counting of individuals.
6. Call counts using remote acoustic monitoring devices could be used to estimate the point abundance and density of kiwi using the RN, Binomial-mixture or potentially Beta-binomial model (if the calls of kiwi are correlated). The presence or absence of GSK (*Apteryx haastii*) calls was trialled in a traditional occupancy model (MacKenzie et al., 2002) by Jahn, Ross, et al. (2022) to estimate the distribution of birds within a translocated and source population over time. However, the distance over which calls could be detected was not measured and it was assumed each acoustic device recorded individuals in a single territory, which may not have been the case.

A significant challenge in monitoring a translocated or source population is that birds could make long distance exploratory forays into new territories, or expand home ranges, as opposed to persist in stable territories/home ranges, which could incorrectly inflate occupancy estimates. The spacing of devices needs to be carefully considered based on the distance that kiwi calls can be detected in the project environment. However, the development of effective acoustic surveys for kiwi that can estimate density and changes in the population is another promising monitoring method for the future of kiwi monitoring worth exploring further (De Rosa, 2021; Juodakis et al., 2021).

7.5 Conclusion

The specific knowledge gaps that this thesis has contributed to are (i) the use of camera trapping for population estimation of an unmarked, ground-dwelling bird with independent estimates of density, (ii) addressing the modern use of territory mapping using radio-telemetry, (iii) the use of camera traps to estimate the size of a kiwi population, and (iv) some of the varied and broad knowledge gaps that exist for Rakiura tokoeka, including chick survival, and age structure and densities outside Mason Bay and Port Adventure

Specifically, I evaluated the established (yet previously untested) method of monitoring kiwi by territory mapping with radio-telemetry for Rakiura tokoeka and offered suggestions for improvement (Chapter 3). In doing so, I expanded the areas in which Rakiura tokoeka have been monitored, with an additional mainland site (Kaipipi) and a pest-free island (Ulva Island), allowing more insight into the proposed causes of decline recorded at Mason Bay from either chick predation by feral cats or habitat change (Colbourne & Robertson, 2013; Robertson et al., 2018; Robertson & Colbourne, 2022). I introduced camera trapping as a novel method for monitoring kiwi using Rakiura tokoeka as a case study, presenting two different ways to interpret camera data (Chapters 4 and 5), which could suit different objectives, skill sets and species.

I showed that point abundance estimates using models for unmarked species were accurate, considering knowledge of group size from radio-telemetry territory mapping, and that density estimates using an ESA with a buffer width based on average territory size were not significantly different from minimum density estimates from radio-telemetry territory mapping (Section 5.3.6). I carried out a novel study on the breeding behaviour and chick survival of Rakiura tokoeka using a combination of radio-telemetry and camera traps (Chapter 6), which provides the first published information on incubation patterns, chick growth, movement, dispersal, threats to nesting success, and survival. In summary, I showed how radio-telemetry and camera traps can be effective methods for monitoring Rakiura tokoeka and can also be successfully used in combination depending on project objectives.

More broadly, I have provided a rare example of the successful population estimation of a ground-dwelling, unmarked bird species, contributing to the scarce literature on this topic. I have presented a novel approach to monitoring kiwi populations that can make similar estimates to the gold-standard method of radio-telemetry, but is easier to implement, requires less expertise, and hence can be more widely applied by the many independent groups monitoring kiwi across the country. I hope that I have encouraged kiwi practitioners to question established protocols, to keep testing methodology, and to incorporate their species and location specific knowledge while prioritising consistency and repeatability in surveys, and to question whether telemetry is essential for their objectives.

Population density is of fundamental importance to wildlife management. However, it is not always possible to obtain accurate estimates of density, and it may not be necessary depending on the project resources and objectives. In some instances, it is more important to compare relative abundance over time and space to identify population trends (Duquette et al., 2014; O'Brien & Kinnaird, 2008), and this can be achieved with an index like CTR (Bengsen et al., 2011). If resources are limited, indices or other low investment monitoring options can be used to identify specific population variables to target with more intensive monitoring that might require management intervention.

Catching animals for radio-telemetry or GPS tracking is the best way to obtain precise estimates of individuals (i.e., growth, vital rates, movement, survival), and spatial information of the population. However, the expense and labour requirements can limit the use of radio-telemetry, and ethical concerns on the use of invasive methods can be raised for species that are rare, particularly sensitive, or where the methods are being utilised for a purpose not in the best interest of the animals, for example, social media, ‘sexy data’, or other unjustifiable means. Camera traps are a non-invasive method that generally cause little disturbance to the target species, can monitor multiple species simultaneously, can be left to monitor remotely, require little specialised experience, and are appropriate for studying rare, elusive, and nocturnal/crepuscular animals that avoid humans. However, estimates from camera trapping are more reliable when compared to estimates from independent methods.

Estimating the abundance, density, and distribution of kiwi is challenging (Colbourne & Digby, 2016), and the development of new methods and honing of established methods is essential in the ongoing nationwide effort to increase or maintain kiwi populations (Germano et al., 2018). The available literature on monitoring unmarked species is valuable in this regard, and the statistical analysis of camera trap data for unmarked species is a growing field (Burton et al., 2015; Gilbert et al., 2021). The more successful we are at monitoring populations accurately, with methods that are consistent, can be widely applied and validated with independent estimates (Bengsen et al., 2011; O'Brien & Kinnaird, 2008; Rovero & Marshall, 2009), the more likely we are to successfully monitor, mitigate and manage kiwi populations into the future.

Appendices

Appendix A

1. Field methods

In early February 2019, two teams of kiwi practitioners were deployed, one to Kaipipi and one to Ulva Island. Night catching was undertaken following the methods of Robertson and Colbourne (2004) and Robertson et al. (2017, 2018) where a small team heads out after dusk, and uses pre-recorded kiwi calls or a shepherd's whistle to imitate a male kiwi in order to attract territorial birds close enough so they can be caught by hand or in long-handled fishing nets. Once a kiwi was in the hand, it was weighed, measured (tarsus depth, width, length and bill length), and body condition scored as per Kiwi Best Practice (Robertson & Colbourne, 2017). Three pin feathers and any naturally dropped feathers during handling were collected, to allow post-survey analysis of the sex of the individual using DNA methods. Field sexing was done by using size, weight, and bill length to separate males and females (females are larger than males with disproportionally longer bills). Every bird over 1800 g had a transmitter (18 – 22g Sitrack or Kiwitrack NIBK Chick Timer) attached to its tibiotarsus using a soft plastic hospital identification tag and Nitto electrical tape as per best practice (Robertson et al., 2017).

There is no accurate way to estimate age in kiwi, especially on first capture as it is not clear whether a bird is growing. In this study, birds were considered sub-adult birds if they were over 1800 g (could be close to an adult weight) and had young looking leg scales or a shorter than expected bill length for an adult, or measurements in subsequent catches had increased; sub-adult birds were estimated to be between 1 – 5 years old. A weight of 1800 g was decided on by analysing all the Rakiura tokoeka weights found by Robertson et al. (2017) and Robertson et al. (2018), as well as consultation of the Kiwi Best Practice manual (Robertson & Colbourne, 2017), to determine a safe size for transmitter attachment where growth rate within a year would be low. All birds over 1800 g were checked at 2 to 12-month intervals based on their likelihood of growth, which depended on their measurements at catch and results of sex testing. Individuals were classed as juveniles when they weighed between 800 – 1800g, and chicks when they were 800 g or less. Metal RA bands were initially attached to one female and one male bird over 1800 g, however, it was soon found that these bands (the largest available for kiwi), were not large enough for most of the adult females caught, and in other cases the birds age could not be determined and so a band was not attached. Birds were released at the catch site once the transmitter attachment had been checked and confirmed to be emitting a pulse, i.e., turned on.

Transmitters for kiwi each have a specific radio frequency so individual birds can be identified. During the day, birds that had a transmitter attached were detected using a Kiwitrack TR4 receiver (Telonics TM) or Sirtrack Ultra receiver (Sirtrack Ltd.) and three element yagi. Individuals were tracked to their locations, which were marked with a hand-held GPS (Garmin 62 or 64s), and flagging tape to enable a quicker, quieter approach to burrows/roosts on subsequent visits. Day tracking was initially done with a minimum of two people, to surround the location of individual birds and attempt to catch any untagged birds that could be in the same roost or burrow. Radio-tagged birds often led us to their mate or unidentified birds on subsequent days. These attempts were made as quietly as possible to avoid unnecessary disturbance to already transmitted birds. This was particularly challenging in the Rakiura context due to the birds often being active during the day or roosting on the surface, as opposed to in underground burrows. A single bird was found by randomly checking inside a promising looking burrow at Kaipipi. One kiwi-detection dog (See) and handler (Peter Kirkman) were also present for the first week of catching at Kaipipi and detected seven birds during the day by scent. Individuals found during the day without transmitters were processed according to the same methods as the birds caught at night. Obtaining a direct location for every bird with a transmitter was attempted every 1 – 2 days. Most location fixes were taken during daylight hours, while the birds were resting or active.

A second catching trip was held in April 2019, with one team at Kaipipi and one on Ulva Island for two weeks. A second trip was necessary to fulfil a similar outcome to Robertson et al. (2017, 2018) in terms of number of birds with a transmitter attached due to less experienced teams and less assistance from kiwi detection dogs. The methods of the second trip were a replication of the first, except for using smaller teams for night catching on Ulva Is, of 2 – 3 per team, and discarding pre-recorded calls for the sole use of a shepherd’s whistle to imitate a male kiwi call. Due to availability and budget restraints, there was no kiwi dog-handler team at either site for the second catching trip. Birds that were seen or heard but not caught were also recorded and labelled as unidentified (UID) to make as accurate a guess of local density as possible.

2. Kiwi catch results

Table 33. The number of adult/subadult (A/S), male/female (M/F) Rakiura tokoeka that had a radio-transmitter attached, and the single chick (C) caught (that did not have a transmitter attached) on Ulva Island, Rakiura in 2019. Including the location (Easting and Northing) and measurements taken on the date of capture, with body condition (scale of 1-4 with 1 being poor), and presence of a metal band (band), assigned territory number (territory), and time of capture (detection).

Location	Age	Sex	Date	E	N	Bill length	Tarsus depth	Tarsus length	Tarsus width	Weight (g)	Condition	Transmitter	Band	Territory	Detection
Ulva	A	F	11/02/19	1229177	4791488	145.7	20.3	98.7	14.5	3450	2	88	L/RA3115	7	Day
Ulva	S	F	10/02/19	1229177	4791488	120.2	19.1	99.1	13.5	1850	2	43		7	Night
Ulva	A	F	3/04/19	1228866	4791398	149.8	20.9	104.4	13.7	3100	2	39		1	Night
Ulva	A	F	6/04/19	1229138	4790848	136.6	21.5	102.1	14.8	3500	3	92		3	Day, tx bird
Ulva	S	M	13/02/19	1229869	4790642	NA	NA	NA	NA	1900	2	73		4	Day, tx bird
Ulva	A	M	5/02/19	1229269	4791562	110.8	20.9	104.1	14.9	2600	2	68	R/RA3118	7	Night
Ulva	A	M	3/04/19	1228866	4791398	111.0	20.4	101.9	12.6	2700	2-1	23	R/RA3119	1	Night
Ulva	S	F	6/04/19	1229138	4790848	107.3	19.1	91.5	12.8	1900	2	18		3	Day, tx bird
Ulva	A	M	6/04/19	1229208	4790689	112.2	19.0	96.1	12.6	2600	2-1	6		3	Night
Ulva	A	M	6/04/19	1228798	4791079	115.9	22.2	91.6	15.4	2600	3	46	L/RA3117	5	Night
Ulva	C	M	5/04/19	1230227	4790558	55.1	10.0	63.1	7.9	725	NA	NA		4	Day, tx bird
Ulva	A	M	6/02/19	1230613	4790617	109.9	20.9	97.4	13.8	2525	2	2		4	Night
Ulva	A	M	7/04/19	1229718	4790865	106.3	20.5	98.0	13.4	2700	2	96	R/RA3120	9	Night
Ulva	A	M	9/04/19	1228152	4791328	108.8	21.3	100.9	13.6	2850	3	54	R/RA3114	6	Night
Ulva	A	F	9/04/19	1228355	4791363	142.7	20.5	98.8	13.4	2900	2	27		10	Night
Ulva	A	M	9/04/19	1228705	4791411	108.4	19.2	98.6	14.0	2600	1	84		10	Night
Ulva	A	M	12/04/19	1230471	4790861	103.4	19.7	103.0	15.6	2800	2	56		2	Night
Ulva	A	F	12/04/19	1230114	4790695	145.3	21.4	107.4	16.3	3150	3	37		4	Night
Ulva	S	F	12/04/19	1229692	4790857	116.5	18.5	99.7	14.6	2150	2	48		9	Night
Ulva	A	M	10/04/19	1228997	4791206	116.4	19.8	98.5	13.6	2750	2	33		8	Night
Ulva	A	F	13/04/19	1230311	4790943	145.2	19.8	106.1	13.0	3800	3	20		2	Day, tx bird
Ulva	A	F	2/06/19	1229698	4991010	138.8	23.4	102.2	14.6	3150	2-3	59		9	Day, tx bird
Ulva	A	F	12/12/19	1228613	4791096	143.4	21.1	105.6	14.0	3150	3	14		5	Day

*Age described as adult (A), subadult (S), juvenile (J) or chick (C) and sex male (M) or female (F)

*All measurements are in millimeteres (mm) except weight in grams (g)

*Detection at night (usually in response to a conspecific call), day (foraging/roosting or in a marked or unmakred burrow, sometimes with a transmitted bird) or dog (kiwi scent detection dog)

Table 34. The number of adult/subadult (A/S), male/female (M/F) Rakiura tokoeka that had a radio-transmitter attached, and the number of chicks and juveniles (C/J) caught (that did not have a transmitter attached) at Kaipipi, Rakiura in 2019. Including the location (Easting and Northing) and measurements taken on the date of capture, with body condition (scale of 1-4 with 1 being poor), and presence of a metal band (band), assigned territory number (territory), and time of capture (detection).

Location	Age	Sex	Date	E	N	Bill length	Tarsus depth	Tarsus length	Tarsus width	Weight (g)	Condition	Transmitter	Territory	Detection
Kaipipi	S	F	5/02/19	1222779	4795706	109.0	20.5	99.38	14.7	2600	3	1	9	Night
Kaipipi	A	M	5/02/19	1222584	4795703	112.9	22.0	106.43	16.2	2900	3	4	2	Night
Kaipipi	A	F	6/02/19	1223523	4794637	144.7	24.8	108.56	15.8	3300	3	8	8	Night
Kaipipi	A	F	7/04/19	1223624	4795256	150.9	22.1	107.20	15.6	3700	3	10	3	Day, tx bird
Kaipipi	A	F	7/02/19	1222957	4795898	144.2	24.5	104.12	14.7	3550	3	13	4	Night
Kaipipi	S	F	4/02/19	1223881	4794875	109.1	19.5	85.50	13.8	2550	2	16	7	Night
Kaipipi	A	F	8/04/19	122274	47956725	151.3	24.8	108.10	14.9	3600	2	25	2	Day, tx bird
Kaipipi	A	M	6/02/19	1223523	4794637	143.8	21.9	100.54	15.7	3000	3	29	8	Night
Kaipipi	A	M	8/06/19	1223505	4796135	112.6	20.4	96.83	14.3	2900	3	31	1	Day, tx bird
Kaipipi	S	F	10/02/19	1222521	4795949	117.5	22.1	100.80	14.4	2350	3	35	4	Day, tx bird
Kaipipi	A	F	10/06/19	1222955	4795583	NA	20.1	115.97	15.5	3570	3	38	9	Day, tx bird
Kaipipi	A	F	7/02/19	1223268	4794855	99.6	23.0	103.92	15.2	2950	2	41	6	Night
Kaipipi	A	F	4/02/19	1223448	4795134	169.5	26.5	112.27	16.5	4000	3	45	6	Night
Kaipipi	J	M	24/12/19	NA	NA	85.3	16.4	86.30	86.3	1450	na	47	5	Day, tx bird
Kaipipi	A	M	9/02/19	1223880	4794793	106.2	20.6	98.20	14.0	2175	3	50	8	Night
Kaipipi	S	M	8/02/19	1223260	4795758	95.7	NA	NA	NA	1820	2	58	1	Night
Kaipipi	A	F	6/02/19	1223736	4794831	145.6	23.8	109.55	16.6	3300	3	62	7	Night
Kaipipi	A	F	12/02/19	1223379	4794374	102.0	21.5	106.47	14.9	3100	2	64	8	Day, tx bird
Kaipipi	A	F	7/02/19	1223057	4795592	158.4	24.9	106.24	16.0	3600	4	66	5	Night
Kaipipi	A	M	9/02/19	1223781	4795238	107.8	22.8	105.11	14.9	2350	3	70	3	Dog
Kaipipi	A	F	9/02/19	1223781	4795238	143.5	23.8	107.07	16.6	2950	2	75	3	Dog
Kaipipi	A	M	8/04/19	122274	47956725	106.5	19.7	100.27	12.9	2800	2-3	77	2	Day, tx bird
Kaipipi	A	M	6/02/19	1223123	4795422	114.0	NA	NA	NA	3150	4	80	5	Dog
Kaipipi	A	F	4/02/19	1223874	4794992	152.9	22.6	109.30	16.4	3300	2	86	7	Night
Kaipipi	A	F	8/02/19	1223579	4794399	114.8	20.9	108.40	18.0	3500	2	90	8	Day, tx bird
Kaipipi	A	M	9/02/19	1223781	4795238	113.4	21.1	105.63	14.6	3300	2	94	3	Dog
Kaipipi	S	M	13/02/19	1222913	5270	109.6	19.6	99.43	13.3	2250	2	99	10	Day
Kaipipi	S	F	14/01/20	1223881	4794636	105.3	19.6	NA	16.3	2400	na	29b	8	Day, tx bird
Kaipipi	NA	M	27/12/19	NA	NA	159.1	19.4	109.00	14.9	2595	na	86b	7	Day
Kaipipi	J	F	6/02/19	1222788	4795296	89.5	17.7	84.76	13.1	1360	2	NA	6	Night
Kaipipi	J	F	8/02/19	1223260	4795758	93.7	19.0	86.76	11.5	1600	2	NA	1	Night
Kaipipi	J	M	9/02/19	1223781	4795238	81.3	18.8	86.42	12.3	1440	3	NA	3	Dog
Kaipipi	C	F	12/02/19	1223379	4794374	60.7	11.7	66.93	10.2	780	2	NA	8	Day
Kaipipi	C	NA	9/02/19	1223781	4795238	NA	NA	NA	NA	500	NA	NA	3	Dog

*Age described as adult (A), subadult (S), juvenile (J) or chick (C) and sex male (M) or female (F)

*All measurements are in millimeteres (mm) except weight in grams (g)

*Detection at night (usually in response to a conspecific call), day (foraging/roosting or in a marked or unmakred burrow, sometimes with a transmitted bird) or dog (kiwi scent detection

Table 35. The total number of Rakiura tokoeka identified per territory at two locations on Rakiura. Adult/sub = adult and subadult (M = male, F = female), UID = unidentified/no transmitter. Juvenile and Chick = present during initial catching period in 2019. Total = all birds prior to the nesting season in 2020. Chick 2020 = chicks that hatched during the study period in 2020. *Two nesting attempts were made by this pair; it is believed the first egg and second egg or newly hatched chick were predated by weka just prior to emergence.

	Territory	Adult/sub M	Adult/sub F	Adult UID	Juvenile	Chick	Total	Chick 2020
Kaipipi	**1**	2	0	1	1	0	4	1
	2	2	1	1	0	0	4	ND
	3	2	2	1	1	1	7	1
	4	0	2	1	1	0	4	1
	5	2	1	0	0	1	4	1
	6	0	2	2	1	0	5	1
	7	0	3	1	0	0	4	ND
	8	2	3	1	1	1	8	1
	9	0	2	0	1	0	3	ND
	Total	**10**	**16**	**8**	**6**	**3**	**43**	**6**
Ulva Island	**1**	1	1	2	0	0	4	ND
	2	1	1	1	1	0	4	2
	3	1	2	1	1	0	5	1
	4	2	1	0	0	1	4	1
	5	1	1	1	0	0	3	ND
	6	1	0	2	0	0	3	1
	7	1	2	1	0	0	4	ND
	8	1	0	0	0	0	1	ND
	9	1	2	0	0	0	3	ND
	10	1	1	0	0	0	2	ND*
	Total	**11**	**11**	**8**	**2**	**1**	**33**	**5**

.

3. Incremental area analysis

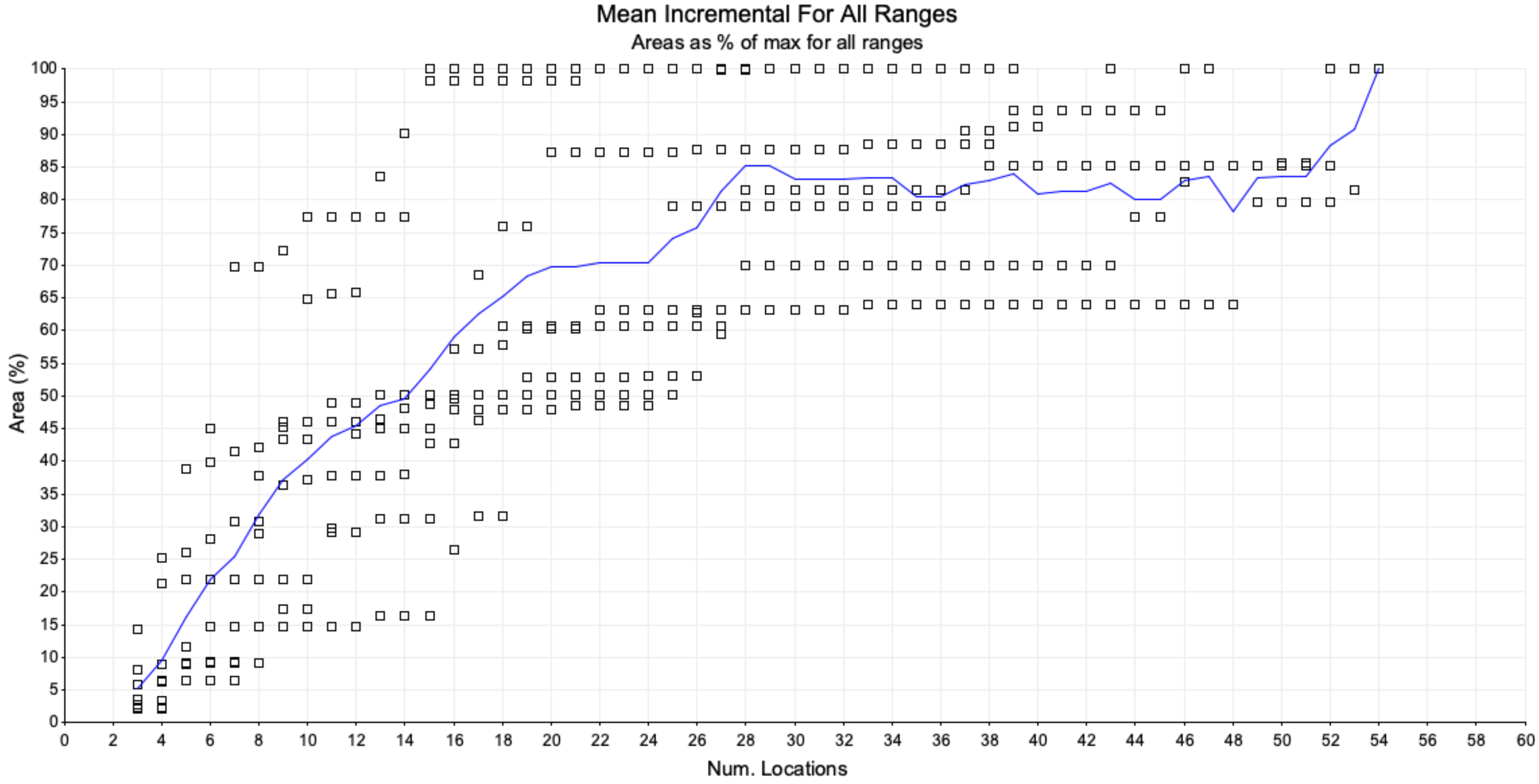


Figure 39. Incremental area analysis for convex polygon territories at Kaipipi, excluding territory 8. The curve flattens to approximately 85% with 28 location fixes.

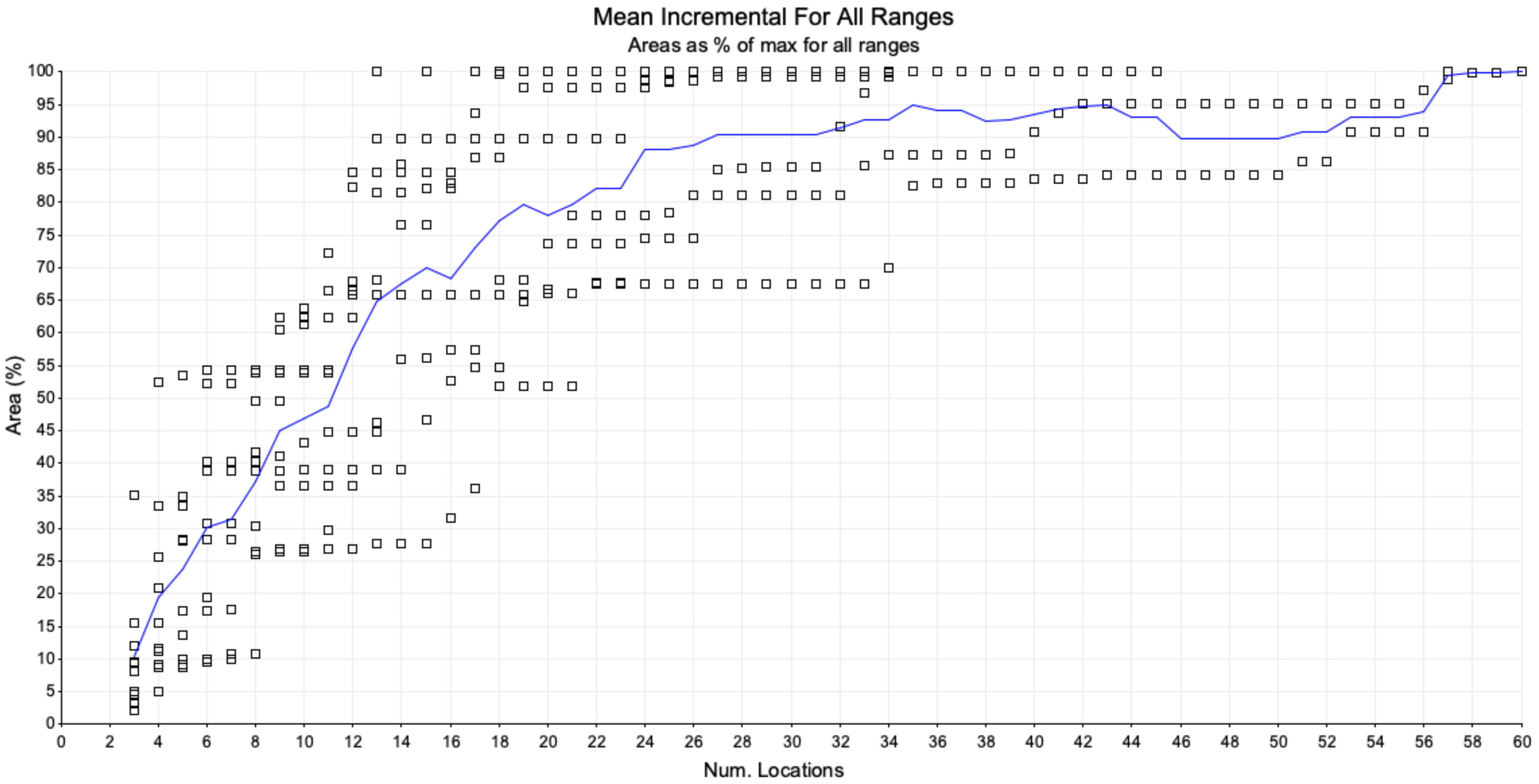


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Figure 40. Incremental area analysis for convex polygon territories on Ulva Island. The curve flattens to approximately 90% with 27 location fixes.

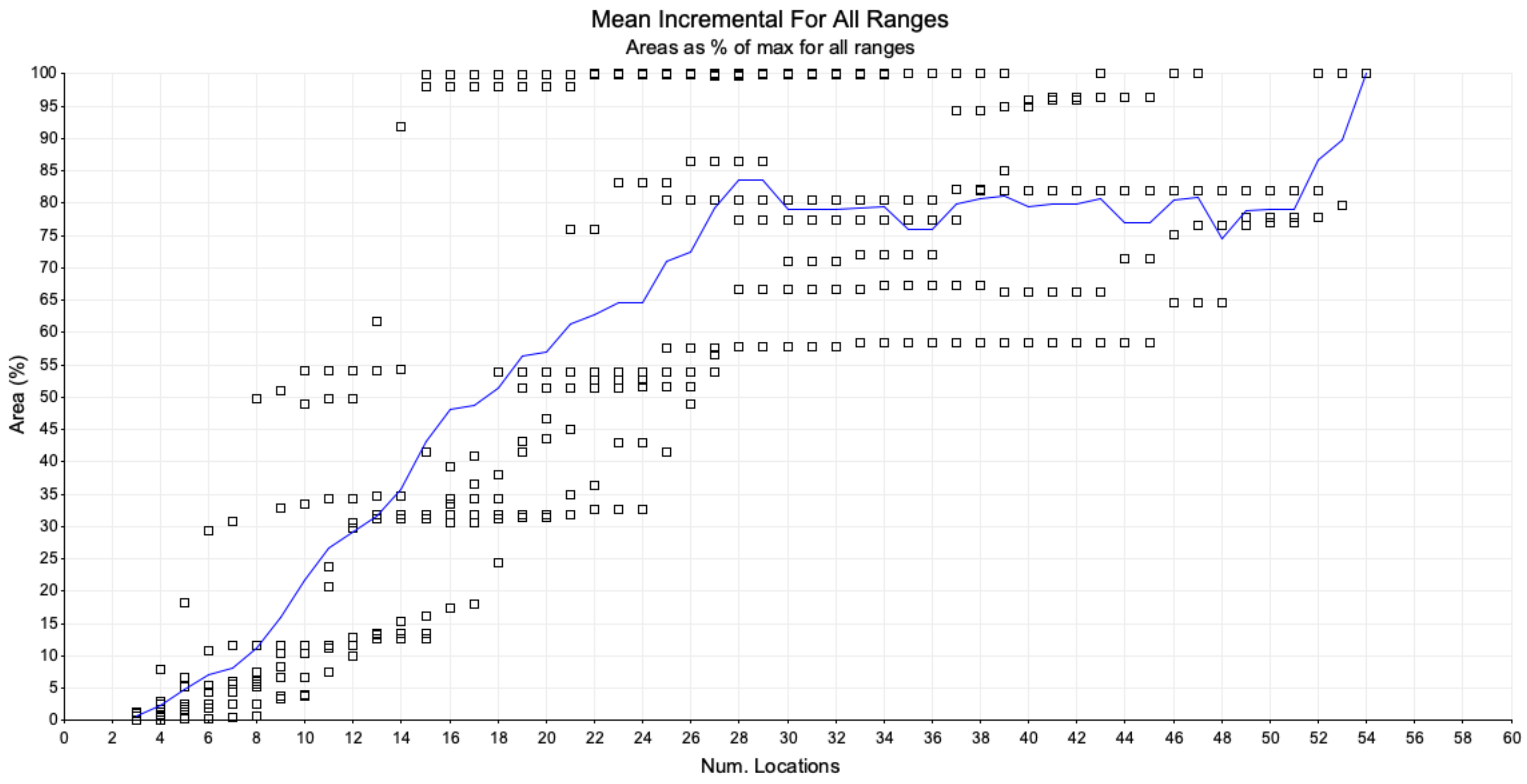


Figure 41. Incremental area analysis for concave polygon territories at Kaipipi, excluding territory 8. The curve flattens to approximately 84% with 28 location fixes.

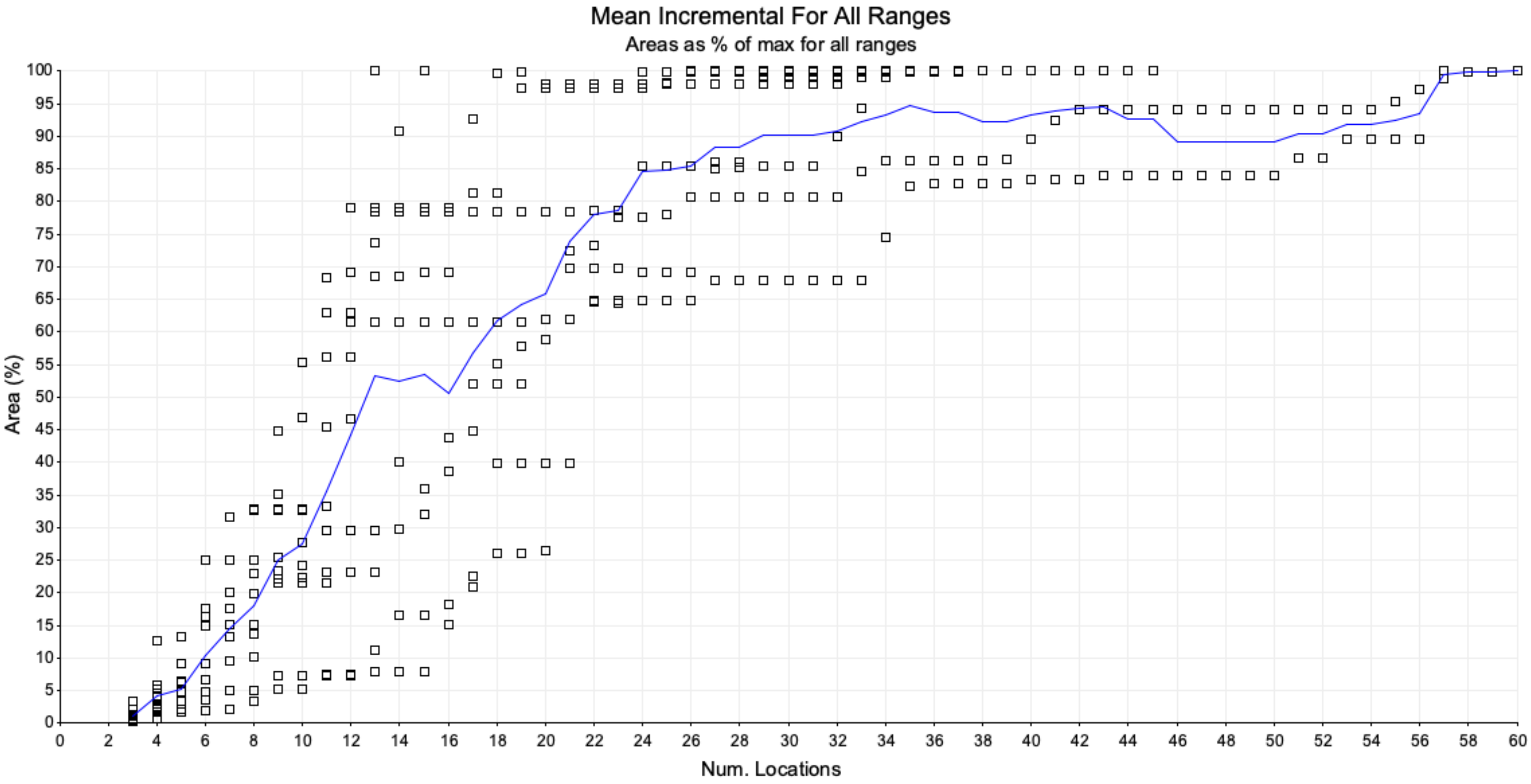


Figure 42. Incremental area analysis for concave polygon territories on Ulva Island. The curve flattens to approximately 87% with 28 location fixes.

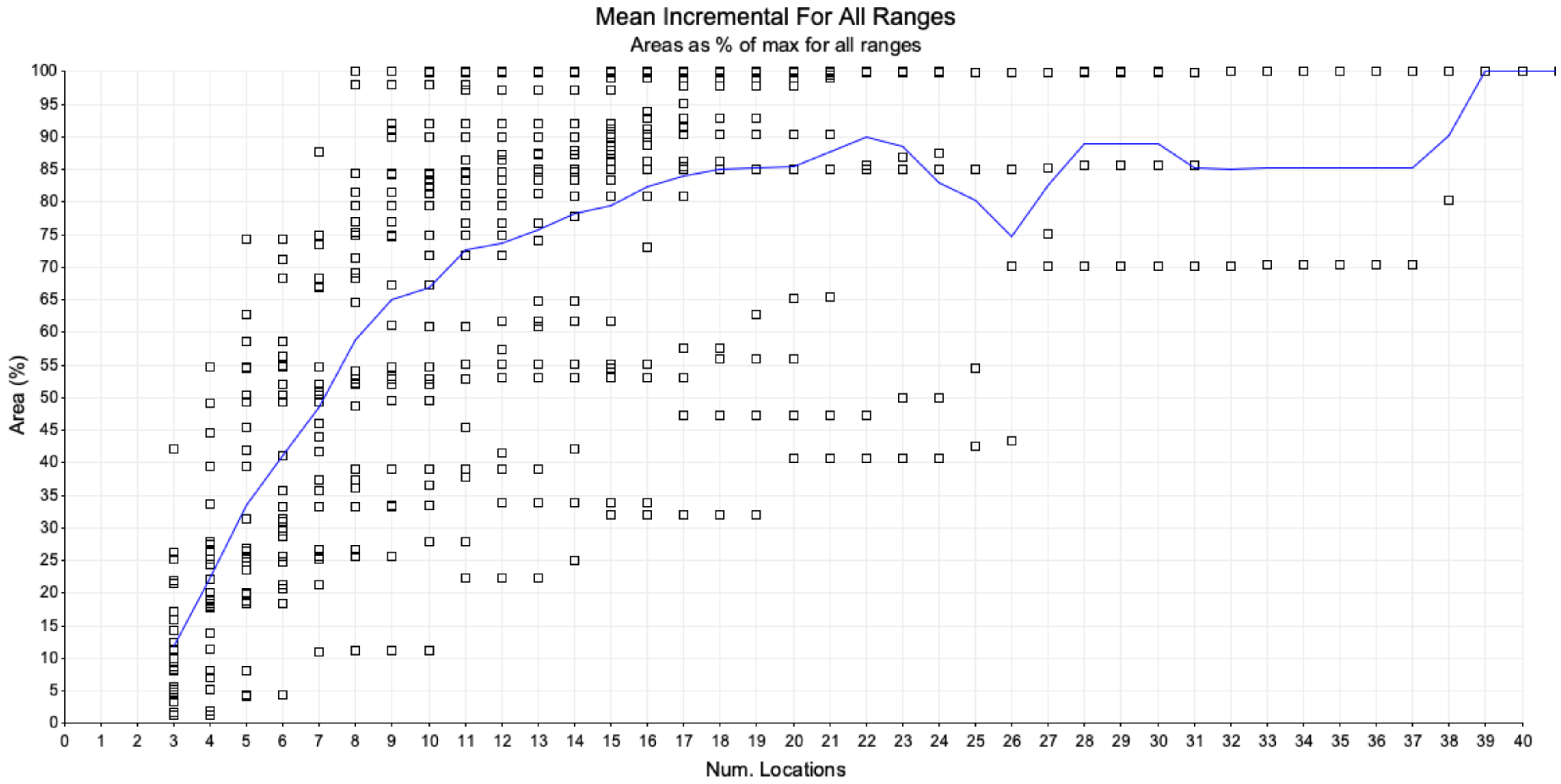


Figure 43. Incremental area analysis for convex polygon territories of individuals at Kaipipi. With 15 locations, the curve flattens to approximately 80% of the total territory size.

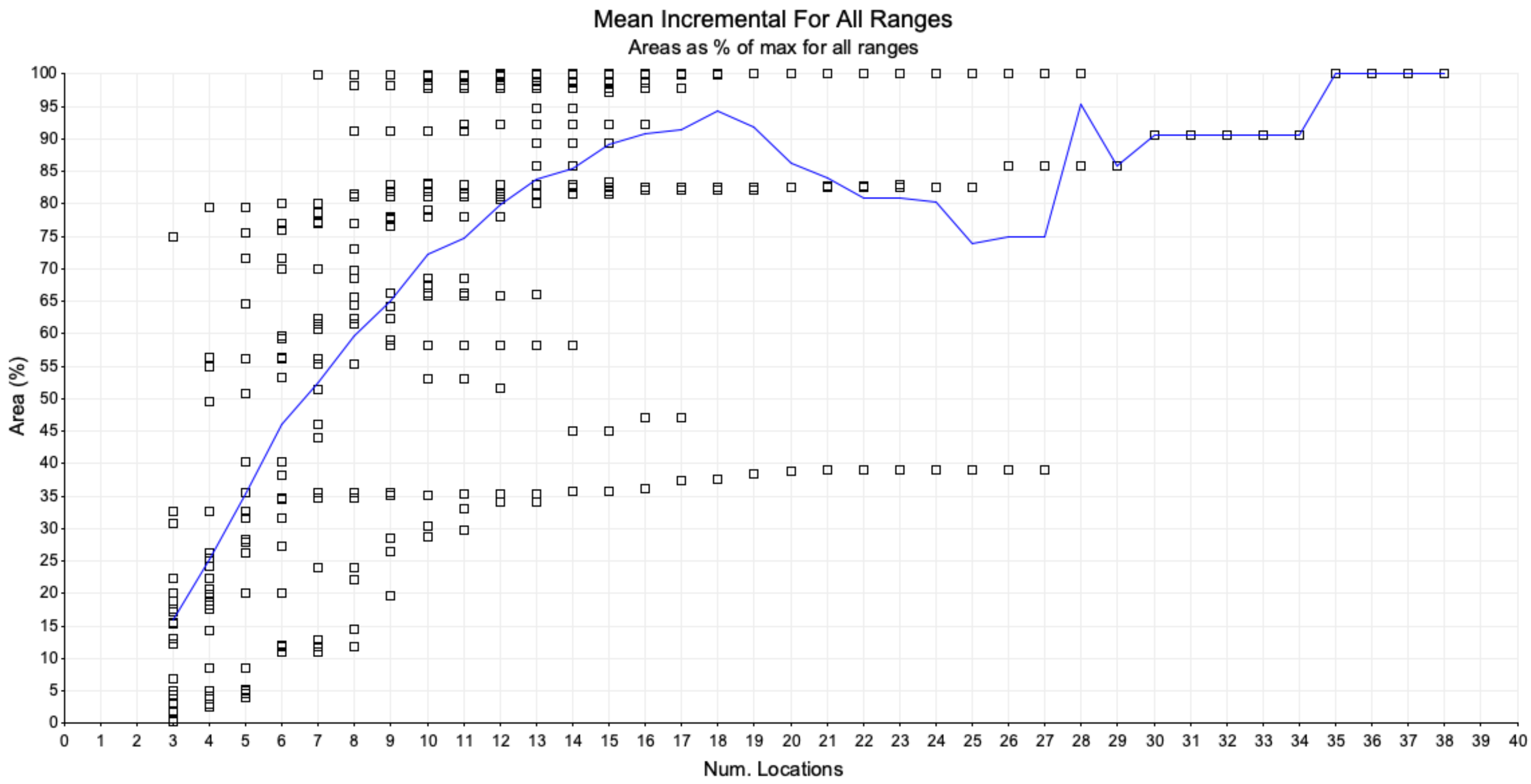


Figure 44. Incremental area analysis for convex polygon territories of individuals on Ulva Island. With 15 locations, the curve flattens to approximately 90% of the total territory size.

Appendix B

1. Significant camera trap rates per survey

Table 36. Comparisons between surveys of mean camera trap rates that were significant to the 5% level following Wilcoxon test and bootstrapping with 95% confidence intervals (CI) (MA = Mason Bay, UL = Ulva Island, KP = Kaipipi, PA = Port Adventure).

Comparisons	Estimate	test.stat	p.value	lower CI	upper CI
SUMMER19 MA - WINTER19 UL	7.36	52.5	0.0258	0	28.76
SUMMER19 UL - SUMMER20 MA	-15.37	7.5	0.0194	-26.67	-1.33
SUMMER20 MA - WINTER18 UL	15.88	34.5	0.0372	0	28
SUMMER20 MA -WINTER19 UL	16	48	0.0195	0	28
WINTER19 KP - WINTER19 UL	9.64	50	0.0465	0	22.73
PILOT18 PA - WINTER19 UL	7.14	45.5	0.042	0	21.43
SUMMER19 KP - WINTER19 UL	10.13	62.5	0.0301	0	19.23
PILOT18 UL - SUMMER20 MA	-12.264	5.5	0.045	-23.46	-2.36
SUMMER19 KP - SUMMER19 UL	7.766	41.5	0.0122	0.61	17.57

2. Marked (with transmitter or band) and unmarked Rakiura tokoeka detected during camera trap surveys

Table 37. The minimum number of marked and unmarked Rakiura tokoeka from camera trap surveys at four locations on Stewart Island, assuming individuals were not captured in more than one camera station.

	Marked	Unmarked	Unclear	Total
Kaipipi	14	18	0	32
Ulva Island	3	4	1	8
Mason Bay	11	9	4	24
Port Adventure	15	10	0	25

Marked birds were those wearing a transmitter or metal band, and could be identified as individuals by the colour of the transmitter, which leg it was on and sex/age (length of bill and body size). Unmarked birds were those with no visible transmitter or band and a view of both sides of the body, and if the view was not clear to determine if there was a mark birds were designated as unclear. Only one individual of each category was assigned per camera, for example, female/brown transmitter/left leg, or, unmarked/unidentified sex and age.

Appendix C

1. Description of the models used in chapter five

Royle Nichol Model

The model expresses the relationship between detection and abundance as below:

$$p_i = 1 - (1 - r)_i^N$$

where:

p_i is the probaility of detecting an occupancy at site i

N_i is the number of Kiwis present at sample unit i

r is binomial sampling probability that a particular Kiwi is detected.

Abundance is modelled by a Poisson distribution such that N_i ~ $Poisson(\lambda)$ so that:

$Pr(N = n) = \frac{e^{-\lambda}\lambda^n}{n!}$.

Abundance and detection can be affected by covariates. The relationship between abundance and such covariates is modelled by a generalized linear model with a log link (log linear model):

$$log(\lambda_i) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ldots + \beta_r X_{ir}$$

where; - $X_{i1} \ldots X_{ir}$ are the covariates, - λ_i is the estimated mean number of kiwi at site i, - $\beta_0 \ldots \beta_r$ are the estimates of covariate effects.

In a similar way the relationship between detection and covariates is modelled by a generalized linear model with a logit link (logistic regression model):

$$logit(p_i) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ldots + \beta_r X_{ir}$$

where; - $X_{i1} \ldots X_{ir}$ are the covariates, - p_i is the estimated kiwi detections on site i, - $\beta_0 \ldots \beta_r$ are the estimates of covariate effects.

Binomial N mixture models

The idea behind this model is that the number of individuals observed at site i at time t (day) follow a binomial distribution $n \sim (N_i, p)$

where:

N_i is the site Abundance

p is the detection probability

N_i is modeled with several distributions including;

Poisson, $N_i \sim Poisson(\lambda_i)$

Negative-binomial, $N_i \sim NegBinom(\lambda_i, \theta)$

Zero-Inflated Poisson distribution (ZIP), such that;

N_i =0 with probability ψ and $N_i \sim Poisson(\lambda_i)$ with probability $1 - \psi$

λ_i is the density on site i while θ is the overdispersion parameter.

Similar to the Royle and Nichol model (Royle & Nichols, 2003), the effect of covariates on abundance and detection were modelled by a general linear model with a log link and logit link respectively.

Beta-Binomial mixture model

With the previous models, detection probability (p_i) is assumed to be constant. This may not be a reasonable assumption given that Rakiura tokoeka tend to live in groups. The Beta-Binomial mixture model eases this assumption by allowing stochastic variation where p_i follows a beta distribution such that:

$p_i' \sim Beta\left(p_i \frac{1-\delta^2}{\delta^2}, (1-p_i)\frac{1-\delta^2}{\delta^2}\right)$ (Knape et al., 2018)

p_i is the mean detection probability and that the standard deviation of p_i' scales linearly with δ and is equal to $\delta\sqrt{p_i(1-p_i)}$, with $0 \leq \delta \leq 1$ (Knape et al., 2018)

Keeping in mind that the aim of this model is to change the p_i from constant to beta distribution, I repeated the previous three mixture methods (Poisson, Negative-binomial, ZIP), but now with a beta distributed detection probability.

Appendix D

1. Table 38. Rakiura tokoeka chick/juvenile records from each capture during 2019-2020 on Ulva Island and at Kaipipi. M = male, F = female, video cameo = date first seen on burrow camera, Est. age = estimated age based on first date of emergence (video cameo), body measurements (bill length, tarsus length, width and depth), weight in grams (g), found alone (A) or in company (C) and location found.

Location	Transmitter*	Sex	Video cameo	Date	Est. Age (days)	Bill length (mm)	Tarsus Length (mm)	Tarsus Width (mm)	Tarsus Depth (mm)	Weight (g)**	Alone (A)/Company	Location
Ulva Island	40	M	11/9/19	18/09/19	12	45.70	na	na	na	280	A	Active/nest burrow
Ulva Island	40	M	NA	17/10/19	42	53.50	55.8	7	8.5	405	A	Burrow small
Ulva Island	40	M	NA	10/12/19	87	56.50	66.9	9.2	12.2	693	A	Surface shelter
Ulva Island	40/85	M	NA	18/01/20	122	63.40	na	9.9	12.4	830	C	Nest burrow
Ulva Island	40/85	M	NA	21/2/20	150	64.20	na	10	12.7	860	A	Surface shelter
Ulva Island	40/85	M	NA	24/4/20	244	66.80	na	9.1	12.4	1025	C	Burrow
Ulva Island	61	M	26/9/19	14/10/19	21	44.1	53	8.1	8.8	340	C	Active/nest burrow
Ulva Island	61	M	NA	15/11/19	49	47.2	59.4	8.1	10	620	C	Surface shelter
Ulva Island	61	M	NA	11/12/19	80	51.40	63.1	8.8	12.3	690	A	Surface shelter
Ulva Island	61	M	NA	10/1/20	108	53.10	na	8.2	11.3	650	C	Surface shelter
Ulva Island	61/67	M	NA	21/2/20	147	55.40	na	8.2	12.4	680	A	Burrow small
Ulva Island	61/67	M	NA	25/4/20	228	57.00	na	8.7	11.1	720	A	Active
Ulva Island	95	M	24/9/19	16/10/19	21	46.9	54.8	7	8.4	355	C	Active/nest burrow
Ulva Island	95	M	NA	23/11/19	56	51.8	61.7	9.3	10.4	600	A	Hollow log
Ulva Island	95/57	M	NA	19/1/20	108	59.5	na	9.6	12	765	A	Surface shelter
Ulva Island	95/57	M	NA	22/2/20	140	61.7	na	9.5	13.6	890	C	Surface shelter
Ulva Island	95/57	M	NA	28/4/20	212	65.5	na	9.2	12	930	A	Surface shelter
Ulva Island	24	NA	24/10/19	30/10/19	10	45.2	52	7.2	8.2	300	A	Active
Ulva Island	44	F	6/1/20	18/1/20	14	45	na	6.6	8.3	285	C	Nest burrow
Ulva Island	44	F	NA	21/2/20	42	51	na	7	9	380	A	Hollow log
Ulva Island	44	F	NA	26/4/20	98	NA	na	7.7	10.1	620	A	Burrow
Kaipipi	5	F	05/10/19**	12/10/19	24	47.3	52.7	7.4	8.7	355	A	Nest burrow
Kaipipi	5	F	NA	12/11/19	52	52.3	54.5	7.2	8.3	385	C	Burrow
Kaipipi	5	F	NA	16/12/19	84	na	na	na	na	520	A	Burrow
Kaipipi	5/55	F	NA	3/2/20	126	59.7	na	8.1	12.8	738	A	Burrow
Kaipipi	5/55	F	NA	20/3/20	197	63.1	na	10	12.4	900	A	Burrow
Kaipipi	5/55	F	NA	17/5/20	258	69.6	71.1	10.1	13.7	1000	C	Surface shelter
Kaipipi	19	M	22/9/19	12/10/19	21	41.4	51.6	7	8	250	A	Active/nest burrow
Kaipipi	19	M	NA	24/11/19	49	47.6	54	7.5	8	335	NA	NA
Kaipipi	19	M	NA	27/12/19	77	50.6	53.6	7.4	9.8	452	A	Active
Kaipipi	19	M	NA	3/2/20	112	55.5	na	7.8	11.2	570	C	Burrow
Kaipipi	19	M	NA	11/3/20	167	57.7	na	8	11.1	655	C	Burrow
Kaipipi	19	M	NA	16/5/20	228	61	na	8.7	10.9	740	A	Surface shelter
Kaipipi	85	F	25/10/19	28/10/19	8	45.6	na	ns	na	330	A	Active/nest burrow
Kaipipi	85	F	NA	23/11/19	38	48.6	56.4	8.1	9.7	330	NA	NA
Kaipipi	85	F	NA	23/12/19	66	53.4	na	7.3	9.8	400	A	Burrow small
Kaipipi	85	F	NA	25/1/20	98	55.4	na	8	10.3	525	A	Burrow small
Kaipipi	85	F	NA	29/2/20	136	58.5	na	8.1	10.2	630	A	Burrow
Kaipipi	9	M	7/11/19	12/11/19	10	41.5	50.9	7.7	8.1	275	C	Active/nest burrow
Kaipipi	9	M	NA	26/12/19	49	47.7	53.5	7	7.1	365	A	Burrow small
Kaipipi	9	M	NA	24/1/20	77	48.6	na	7.9	9.5	440	A	Surface shelter
Kaipipi	9	M	NA	11/3/20	119	54.8	na	9.1	10.5	630	A	Burrow
Kaipipi	9	M	NA	9/5/20	175	59	na	9.1	12.7	830	A	Burrow small
Kaipipi	NA	M	31/10/19	31/10/19	NA	NA	NA	NA	NA	NA	NA	NA
Kaipipi	NA	M	4/11/19	4/11/19	NA	NA	NA	NA	NA	NA	NA	NA

*Two numbers indicates a change from chick to juvenile transmitter

**Weights include a transmitter (5.5g chick, 11g juvenile)

***Camera was set up on this date on a new burrow and immediately captured a chick so age was an estimate based on size as opposed to first recordered emergence from burrow

2. The post-mortem report from the deceased chick on Ulva Island (Wildbase Pathology, School of Veterinary Science, Massey University)

School of Veterinary Science

Pathology Report

Submitter Ref.:	Date Sent: 11/12/2019	Accession No.: **58258**

To:
Emma Feenstra / I Castro
Massey University School of Agriculture and Environment
Private Bag 11222
Palmerston North
Manawatu-Wanganui

Email: emmafeenstra@gmail.com

Report Sent: 11/12/2019
Copy To: emmafeenstra@gmail.com
I.C.Castro@massey.ac.nz

Species: Avian-Wildlife		Breed: Kiwi (Haast Tokoeka)	
Age: Juvenile - 7 weeks		Sex: Unknown	
Owner: Department of Conservation, Rakiura			Type: Post Mortem
ID: #24			Prev. Accn.:
Submitted: 1	At Risk:	Affected:	Dead:

History

Caught for the first and only time on 30/10/19 and transmitter attached. Still in and out of the natal nest with adult and sub-adult kiwi present,. Found dead approx 10m from nest when tracked for a 1-month transmitter change. Found in the open on leaf litter 18:30. There had been significant rainfall in the previous few days before body found. Temperature of the environment relatively cool, usually 8-14C. Two weka nearby, presumably targeting the body just before we arrived.

No toxins on the Island. Island pest-free, with occasional rat incursions

Gross Findings

Weight = 291gms (minus viscera). Body condition score = 2/9. No body fat reserves were present. The right eye had been removed without haemorrhage (postmortem scavenging). The cloaca and surrounding tissue had been removed leaving a 25 x 30mm hole with very little haemorrhage. Numerous (20-30), 5mm long blowfly maggots were present in the abdomen. Similar maggots were present in the oral cavity, right orbit and within the cranium having consumed most of the brain.

The dorsal skin covering the lumbar region and distal thorax was severely reddened and showed occasional short linear abrasions.The underlying subcutaneous tissues of the dorsal thorax and left flank showed severe irregular subcutaneouus haemorrhage which in some places extended through to the pleural surface of the thoracic cavity. The lungs were severely congested and partially collapsed (sank in water). The abdominal cavity had been largely eviscerated. The GI tract, ventral liver, kidneys and spleen were no longer present.

Morphological Diagnosis

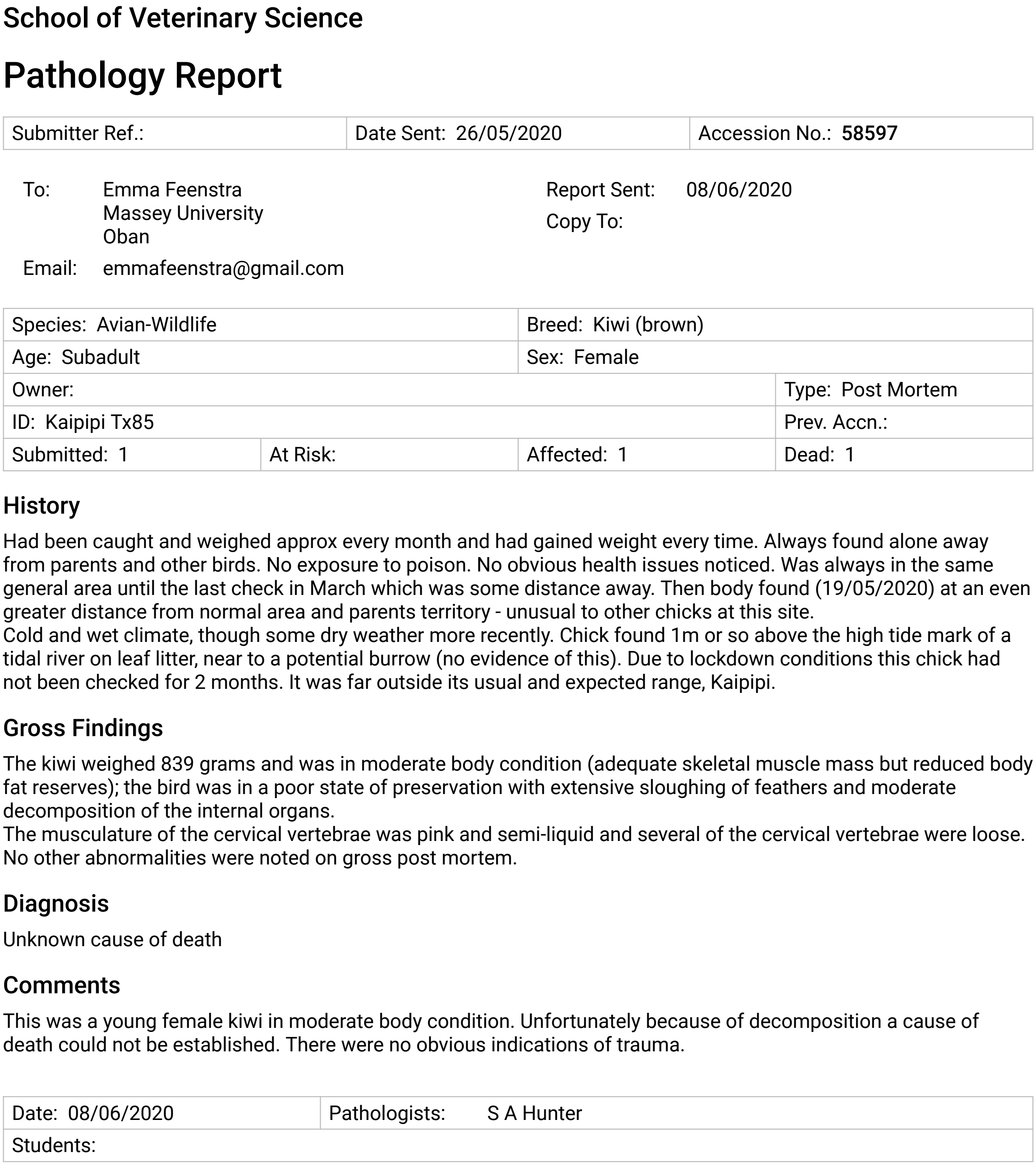
1.Severe dorsal lumbar and thoracic trauma with subcutaneous and pleural haemorrhage
2. Evisceration of abdomen via the cloaca
3. Starvation.

Provisional Diagnosis

Predation by weka

Date: 11/12/2019	Pathologists: M R Alley
Students:	

3. The post-mortem report from the deceased chick at Kaipipi (Wildbase Pathology, School of Veterinary Science, Massey University)



School of Veterinary Science

Pathology Report

Submitter Ref.:	Date Sent: 26/05/2020	Accession No.: **58597**

To: Emma Feenstra
Massey University
Oban
Email: emmafeenstra@gmail.com

Report Sent: 08/06/2020
Copy To:

Species: Avian-Wildlife		Breed: Kiwi (brown)	
Age: Subadult		Sex: Female	
Owner:			Type: Post Mortem
ID: Kaipipi Tx85			Prev. Accn.:
Submitted: 1	At Risk:	Affected: 1	Dead: 1

History

Had been caught and weighed approx every month and had gained weight every time. Always found alone away from parents and other birds. No exposure to poison. No obvious health issues noticed. Was always in the same general area until the last check in March which was some distance away. Then body found (19/05/2020) at an even greater distance from normal area and parents territory - unusual to other chicks at this site.

Cold and wet climate, though some dry weather more recently. Chick found 1m or so above the high tide mark of a tidal river on leaf litter, near to a potential burrow (no evidence of this). Due to lockdown conditions this chick had not been checked for 2 months. It was far outside its usual and expected range, Kaipipi.

Gross Findings

The kiwi weighed 839 grams and was in moderate body condition (adequate skeletal muscle mass but reduced body fat reserves); the bird was in a poor state of preservation with extensive sloughing of feathers and moderate decomposition of the internal organs.

The musculature of the cervical vertebrae was pink and semi-liquid and several of the cervical vertebrae were loose. No other abnormalities were noted on gross post mortem.

Diagnosis

Unknown cause of death

Comments

This was a young female kiwi in moderate body condition. Unfortunately because of decomposition a cause of death could not be established. There were no obvious indications of trauma.

Date: 08/06/2020	Pathologists: S A Hunter
Students:	

4. Cat scat prey species identification analysis, Rakiura

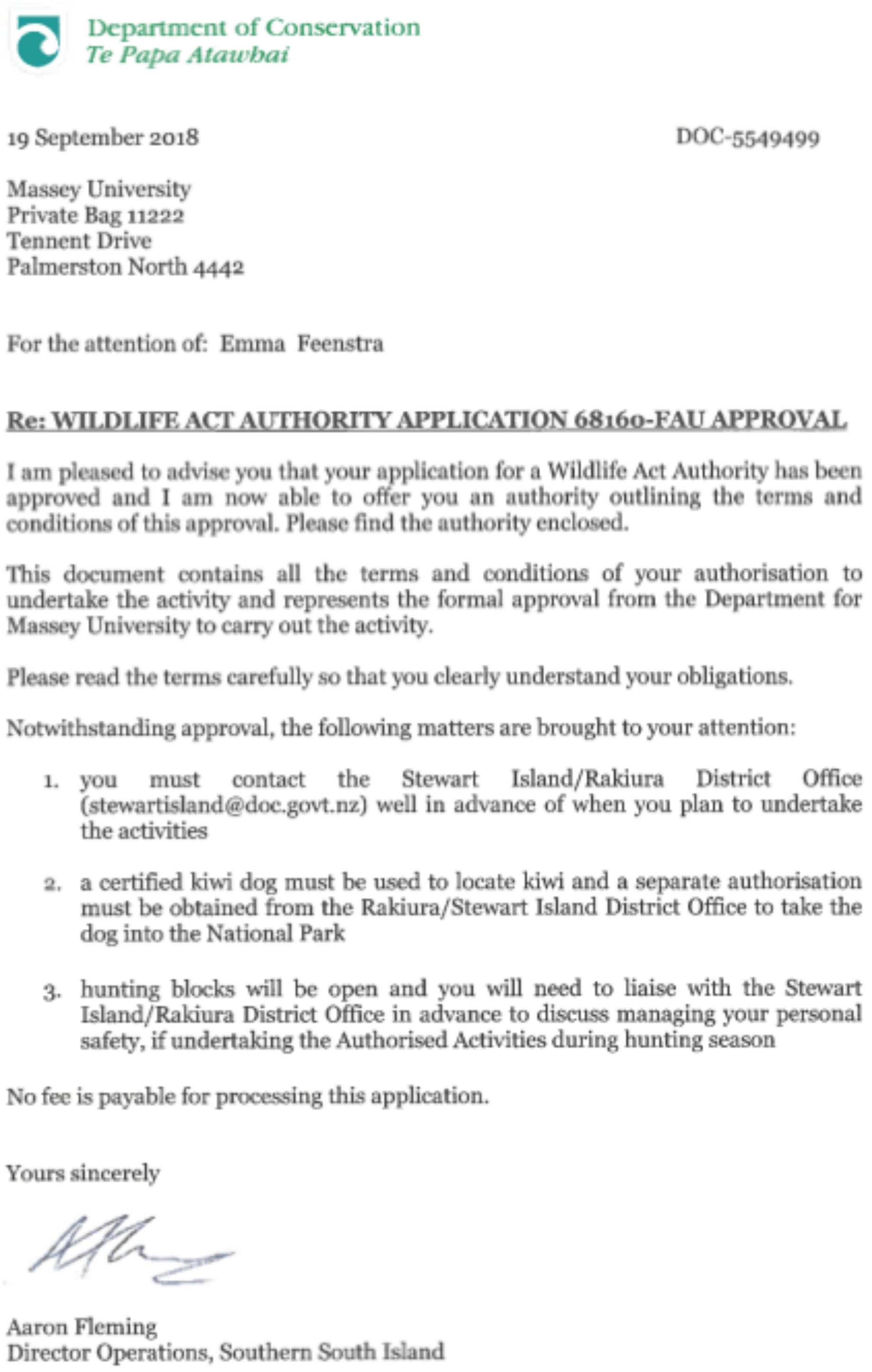
The Rakiura Department of Conservation (DOC) submitted feral cat scats for diet analysis to EcoGene/DNA based diagnostics for prey species identification and genetic profiling over 2016 to 2020. Scats were also collected and submitted to EcoGene over the course of this project (2018 – 2020). The cat scats were collected by DOC from locations that are important for breeding Southern NZ Dotterel (*Charadrius obscurus obscurus*) and I collected scats from the locations used in this study, Kaipipi, Mason Bay and Port Adventure. Ulva Island does not have cats. From 158 cat scats that were analysed between 2016 and 2020, six tested 99% positive for Rakiura tokoeka remains (Table 39).

Table 39. Feral cat scat prey identification records from scats collected at different locations by the Department of Conservation (DOC) and this Rakiura tokoeka project (RTP) between 2016 and 2020. No.scats = the number of scats analysed, RT present = the number of scats with Rakiura tokoeka remains present.

Year	Source	No. Scats	RT present	Location
2016	DOC	6	0	NA
2017	DOC	53	2	Table hill
2018	RTP	27	2	Mason Bay, Garden Mound
2018	DOC	10	0	NA
2019	RTP	14	1	Kaipipi
2020	RTP	22	0	NA
2019 - 2020	DOC	26	1	Blakies Hill
Total:		**158**	**6**	
Percentage with Rakiura Tokoeka			**3.80%**	

Appendix E

1. Wildlife Act Authority Permit



Department of Conservation
Te Papa Atawhai

19 September 2018 DOC-5549499

Massey University
Private Bag 11222
Tennent Drive
Palmerston North 4442

For the attention of: Emma Feenstra

Re: WILDLIFE ACT AUTHORITY APPLICATION 68160-FAU APPROVAL

I am pleased to advise you that your application for a Wildlife Act Authority has been approved and I am now able to offer you an authority outlining the terms and conditions of this approval. Please find the authority enclosed.

This document contains all the terms and conditions of your authorisation to undertake the activity and represents the formal approval from the Department for Massey University to carry out the activity.

Please read the terms carefully so that you clearly understand your obligations.

Notwithstanding approval, the following matters are brought to your attention:

1. you must contact the Stewart Island/Rakiura District Office (stewartisland@doc.govt.nz) well in advance of when you plan to undertake the activities

2. a certified kiwi dog must be used to locate kiwi and a separate authorisation must be obtained from the Rakiura/Stewart Island District Office to take the dog into the National Park

3. hunting blocks will be open and you will need to liaise with the Stewart Island/Rakiura District Office in advance to discuss managing your personal safety, if undertaking the Authorised Activities during hunting season

No fee is payable for processing this application.

Yours sincerely

Aaron Fleming
Director Operations, Southern South Island

2. Research and Collection Permit

Department of Conservation
Te Papa Atawhai

5 July 2018

Emma Feenstra,
200 Huia Rd
Titirangi
Auckland
New Zealand

Dear Emma

Re: RESEARCH & COLLECTION AUTHORISATION 67843-RES APPROVAL

I am pleased to advise you that your application for a Research and Collection authorisation has been approved and I am now able to offer you an authority outlining the terms and conditions of this approval. Please find the authority enclosed.

This document contains all the terms and conditions of your authorisation to undertake the activity and represents the formal approval from the Department for Emma Frances Feenstra, to carry out the activity.

Please read the terms carefully so that you clearly understand your obligations.

Yours sincerely

Ren Leppens
Operations Manager
Rakiura

References

Allen, L., Engeman, R., & Krupa, H. (1996). Evaluation of three relative abundance indices for assessing dingo populations. *Wildlife Research, 23*(2), 197-205.

Alves, F., López-Iborra, G. M., & Silveira, L. F. (2015). Population size assessment of the Endangered red-billed curassowCrax blumenbachii: accounting for variation in detectability and sex-biased estimates. *Oryx, 51*(1), 137-145. doi:10.1017/s0030605315000721

Anich, N. M., Benson, T. J., & Bednarz, J. C. (2009). Estimating territory and home-range sizes: do singing locations alone provide an accurate estimate of space use? *The Auk, 126*(3), 626-634.

Anile, S., Ragni, B., Randi, E., Mattucci, F., & Rovero, F. (2014). Wildcat population density on the Etna volcano, Italy: a comparison of density estimation methods. *Journal of Zoology, 293*(4), 252-261. doi:10.1111/jzo.12141

Barg, J. J., Jones, J., & Robertson, R. J. (2005). Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. *Journal of Animal Ecology*, 139-149.

Barron, D. G., Brawn, J. D., & Weatherhead, P. J. (2010). Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution, 1*(2), 180-187.

Bassing, S. B., DeVivo, M., Ganz, T. R., Kertson, B. N., Prugh, L. R., Roussin, T., Gardner, B. (2022). Are we telling the same story? Comparing inferences made from camera trap and telemetry data for wildlife monitoring. *Ecological Applications, n/a*(n/a), e2745. doi:https://doi.org/10.1002/eap.2745.

Bengsen, A., Algar, D., Ballard, G., Buckmaster, T., Comer, S., Fleming, P. J., Moseby, K. (2016). Feral cat home-range size varies predictably with landscape productivity and population density. *Journal of Zoology, 298*(2), 112-120.

Bengsen, A., Butler, J., & Masters, P. (2011). Estimating and indexing feral cat population abundances using camera traps. *Wildlife Research, 38*(8). doi:10.1071/wr11134.

Bibby, C. J., Burgess, N. D., Hillis, D. M., Hill, D. A., & Mustoe, S. (2000). *Bird census techniques*: Elsevier.

Bischof, R., Ali, H., Kabir, M., Hameed, S., & Nawaz, M. A. (2014). Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology, 293*(1), 40-48.

Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Maisels, F. (2007). Forest elephant crisis in the Congo Basin. *PLoS Biol, 5*(4), e111. doi:10.1371/journal.pbio.0050111.

Block, W. M., Franklin, A. B., Ward Jr, J. P., Ganey, J. L., & White, G. C. (2001). Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology, 9*(3), 293-303.

Bocca, M., Carisio, L., & Rolando, A. (2007). Habitat use, home ranges and census techniques in the black woodpecker *Dryocopus martius* in the Alps. *Ardea, 95*(1), 17-29. doi:10.5253/078.095.0103.

Bonnaud, E., Medina, F. M., Vidal, E., Nogales, M., Tershy, B., Zavaleta, E., Horwath, S. V. (2010). The diet of feral cats on islands: a review and a call for more studies. *Biological Invasions, 13*(3), 581-603. doi:10.1007/s10530-010-9851-3.

Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology letters, 11*(6), 637-650.

Broadley, K., Burton, A. C., Avgar, T., & Boutin, S. (2019). Density-dependent space use affects interpretation of camera trap detection rates. *Ecol Evol, 9*(24), 14031-14041. doi:10.1002/ece3.5840.

Brodie, J. F., & Pangau-Adam, M. (2015). Human impacts on two endemic cassowary species in Indonesian New Guinea. *Oryx, 51*(02), 354-360. doi:10.1017/s0030605315001039.

Brook, L. A., Johnson, C. N., & Ritchie, E. G. (2012). Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology, 49*, 1278-1286.

Buckland, S. (2006). Point-transect surveys for songbirds: robust methodologies. *The Auk, 123*(2), 345-357.

Buckland, S., Marsden, S. J., & Green, R. E. (2008). Estimating bird abundance: making methods work. *Bird Conservation International, 18*(S1). doi:10.1017/s0959270908000294.

Buckland, S., Rexstad, E. A., Marques, T. A., & Oedekoven, C. S. (2015). *Distance sampling: methods and applications* (Vol. 431): Springer.

Burbidge, M. L., Colbourne, R. M., Robertson, H., & Baker, A. J. (2003). Molecular and other biological evidence supports the recognition of at least three species of brown kiwi. *Conservation Genetics, 4*(2), 167-177.

Burgos, G., & Zuberogoitia, I. (2020). A telemetry study to discriminate between home range and territory size in Tawny Owls. *Bioacoustics, 29*(1), 109-121.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy, 24*(3), 346-352.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Stephens, P. (2015). REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology, 52*(3), 675-685. doi:10.1111/1365-2664.12432.

Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M., Haswell, P. M., Hayward, M. W.,Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation, 3*(3), 109-122.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Kinnaird, M. (2001). *The use of photographic rates to estimate densities of tigers and other cryptic mammals.* Paper presented at the Animal Conservation forum.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J. R., Wan Shahruddin, W. N. (2002). The use of photographic rates to estimate densities of cryptic mammals: response to Jennelle et al. *Animal Conservation, 5*(2), 121-123. doi:10.1017/s1367943002002172.

Carpenter, J., Innes, J., Wood, J., & Lyver, P. (2021). Good predators: the roles of weka (Gallirallus australis) in New Zealand's past and present ecosystems. *New Zealand Journal of Ecology*. doi:10.20417/nzjecol.45.15.

Caughley, G. (1977). Analysis of vertebrate populations. *Analysis of vertebrate populations.*

Caughley, G., & Sinclair, A. R. E. (1994). *Wildlife ecology and management*: Blackwell Science.

Chan, T. (1999). Habitat selection by brown kiwi chicks (Apteryx mantelli) in Trounson Kauri Park, Northland. *Unpublished MSc. thesis (Environmental Science), University of Auckland*.

Chandler, R. B., & Royle, J. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics, 7*(2), 936-954.

Chapple, T. K., Gleiss, A. C., Jewell, O. J. D., Wikelski, M., & Block, B. A. (2015). Tracking sharks without teeth: a non-invasive rigid tag attachment for large predatory sharks. *Animal Biotelemetry, 3*(1). doi:10.1186/s40317-015-0044-9.

Cochran, W. W., & Lord Jr, R. D. (1963). A radio-tracking system for wild animals. *The Journal of Wildlife Management*, 9-24.

Cockrem, J. F. (1995). Timing of seasonal breeding in birds, with particular reference to New Zealand birds. 7: 1-9. *Reproduction, Fertility and Development, 7*, 1-9.

Cockrem, J. F., Potter, M. A., Barrett, D. P., & Candy, E. J. (2008). Corticosterone responses to capture and restraint in emperor and Adélie penguins in Antarctica. *Zoological science, 25*(3), 291-298.

Colbourne, R. (1991). Further evidence of female incubation and family grouping in brown kiwis. *Notornis, 38*(3), 248-249.

Colbourne, R. (1992). Little spotted kiwi (Apteryx owenii): recruitment and behaviour of juveniles on Kapiti Island, New Zealand 22(4), 321-328. *Journal of the Royal Society of New Zealand, 22*(4), 321-328.

Colbourne, R. (2002). Incubation behaviour and egg physiology of kiwi (Apteryx spp.) in natural habitats Author(s): Rogan Colbourne. *New Zealand Journal of Ecology, 26*(2), 129-138.

Colbourne, R., & Digby, A. P. (2016). *Call rate behaviour of brown kiwi (Apteryx mantelli) and great spotted kiwi (A. haastii) in relation to temporal and environmental parameters*: Publishing Team, Department of Conservation.

Colbourne, R., & Kleinpaste, R. (1983). A banding study of North Island brown kiwis in an exotic forest. *Notornis, 30*(2), 109-124.

Colbourne, R., & Powlesland, R. G. (1988). Diet of the Stewart Island brown kiwi (Apteryx australis lawryi) at Scollay's flat, Southern Stewart Island. *New Zealand Journal of Ecology, 11*, 99-104.

Colbourne, R., & Robertson, H. (2013). *Status of Stewart Island Tokoeka (Apteryx australis lawryi) at Mason Bay, Stewart Island, February 2013*. Retrieved from Science & Technical Group, Department of Conservation, PO Box 10-420 Wellington.

Cristescu, R. H., Foley, E., Markula, A., Jackson, G., Jones, D., & Frere, C. (2015). Accuracy and efficiency of detection dogs: a powerful new tool for koala conservation and management. *Sci Rep, 5*, 8349. doi:10.1038/srep08349.

Cunningham, S. J. (2010). *Tactile senses and foraging in birds, with emphasis on kiwi: a thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Ecology at Massey University, Manawatu, New Zealand.* Massey University.

De Bondi, N., White, J. G., Stevens, M., & Cooke, R. (2010). A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. *Wildlife Research, 37*(6). doi:10.1071/wr10046.

De Rosa, A. (2021). *On kiwi (Apteryx mantelli) vocal behaviour and activity: relations to population densities and applications to conservation: a dissertation presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Zoology at Massey University, Manawatū, Aotearoa New Zealand.* Massey University.

Denes, F. V., Silveira, L. F., & Beissinger, S. R. (2015). Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. *Methods in Ecology and Evolution, 6*(5), 543-556. doi:10.1111/2041-210x.12333.

Denes, F. V., Tella, J. L., & Beissinger, S. R. (2018). Revisiting methods for estimating parrot abundance and population size. *Emu, 118*(1), 67-79. doi:10.1080/01584197.2017.1401903.

Dent, J. M., & Molles, L. E. (2016). Call-based identification as a potential tool for monitoring Great Spotted Kiwi. *Emu-Austral Ornithology, 116*(4), 315-322.

Dice, L. R. (1938). Some census methods for mammals. *The Journal of Wildlife Management, 2*(3), 119-130.

Dillon, A., & Kelly, M. J. (2008). Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *Journal of Zoology, 275*(4), 391-398. doi:10.1111/j.1469-7998.2008.00452.x.

Dinata, Y., Nugroho, A., Haidir, I. A., & Linkie, M. (2008). Camera trapping rare and threatened avifauna in west-central Sumatra. *Bird Conservation International, 18*(1), 30-37.

Dixon, T. (2015). *What they do in the shadows : habitat utilisation and diet of brown kiwi (Apteryx mantelli) adults within a high-density island population : a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in Ecology, Massey University, Palmerston North, New Zealand.* (Master of Science (MSc) Masters). Massey University, Retrieved from http://hdl.handle.net/10179/10991.

Duquette, J. F., Belant, J. L., Svoboda, N. J., Beyer, D. E., & Albright, C. A. (2014). Comparison of occupancy modeling and radio-telemetry to estimate ungulate population dynamics. *Population Ecology, 56*(3), 481-492.

Efford, M. G. (2004). Density estimation in live-trapping studies. *Oikos, 106*(3), 598-610.

Efford, M. G. (2019). Non-circular home ranges and the estimation of population density. *Ecology, 100*(2), e02580.

Ekman, J., & Ericson, P. G. (2006). Out of Gondwanaland; the evolutionary history of cooperative breeding and social behaviour among crows, magpies, jays and allies. *Proceedings of the Royal Society B: Biological Sciences, 273*(1590), 1117-1125.

Ellenberg, U., Mattern, T., Seddon, P. J., & Jorquera, G. L. (2006). Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. *Biological Conservation, 133*(1), 95-106. doi:10.1016/j.biocon.2006.05.019.

Ellis, S., & Marsland, S. (2022). Sounding out the nest. *New Zealand Journal of Ecology, 46*(1), 1-11.

Elzinga, C. L., Salzer, D. W., & Willoughby, J. W. (1998). *Measuring and monitoring plant populations*. Retrieved from Bureau of Land Management, National Business Center, Denver, CO.

Engeman, R. M. (2005). Indexing principles and a widely applicable paradigm for indexing animal populations. *Wildlife Research, 32*, 203-210.

Enoksson, B., & Nilsson, S. G. (1983). Territory size and population density in relation to food supply in the nuthatch Sitta europaea (Aves). *The Journal of Animal Ecology*, 927-935.

Evans, K. (2021). The mystery kiwi. *Geo news.* 169. Retrieved from https://www.nzgeo.com/stories/the-mystery-kiwi/.

Ewing, D. E., Clark, W. R., & Vohls, P. A. (1994). Evaluation of implanted radio transmitters in pheasant chicks. *Journal of the Iowa Academy of Science: JIAS, 101*(3-4), 86-90.

Fancourt, B. A., Sweaney, M., & Fletcher, D. B. (2018). More haste, less speed: pilot study suggests camera trap detection zone could be more important than trigger speed to maximise species detections. *Australian Mammalogy, 40*(1). doi:10.1071/am17004.

Farris, Z. J., Golden, C. D., Karpanty, S., Murphy, A., Stauffer, D., Ratelolahy, F., Kelly, M. J. (2015). Hunting, exotic carnivores, and habitat loss: anthropogenic effects on a native carnivore community, Madagascar. *PLoS One, 10*(9), e0136456.

Forbes, Y. (2009). *Natal dispersal, habitat selection and mortality of North Island Brown Kiwi (Apteryx mantelli) at the Moehau Kiwi Sanctuary, Coromandel.* (Doctoral dissertation). Auckland University of Technology.

Foster, R. J., & Harmsen, B. J. (2012). A critique of density estimation from camera-trap data. *The Journal of Wildlife Management, 76*(2), 224-236. doi:10.1002/jwmg.275.

Foster, R. J., Harmsen, B. J., & Doncaster, C. P. (2010). Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica, 42*(6), 724-731.

Fuller, M. R., Levanon, N., Strikwerda, T., Seegar, W., Wall, J., Black, H., . . . Partelow, J. (1984). Feasibility of a bird-borne transmitter for tracking via satellite.

Fuller, T. K., York, E. C., Powell, S. M., Decker, T. A., & DeGraaf, R. M. (2001). An evaluation of territory mapping to estimate fisher density. *Canadian Journal of Zoology, 79*(9), 1691-1696. doi:10.1139/cjz-79-9-1691.

Furnas, B. J., Landers, R. H., Callas, R. L., & Matthews, S. M. (2017). Estimating population size of fishers (Pekania pennanti) using camera stations and auxiliary data on home range size. *Ecosphere, 8*(3), e01747. doi:https://doi.org/10.1002/ecs2.1747.

Gaglio, D., Cook, T. R., Connan, M., Ryan, P. G., Sherley, R. B., & Kurle, C. (2017). Dietary studies in birds: testing a non-invasive method using digital photography in seabirds. *Methods in Ecology and Evolution, 8*(2), 214-222. doi:10.1111/2041-210x.12643.

Gasson, P. (2005). *Translocation of great spotted kiwi/roa (Apteryx haasti) to Rotoiti Nature Recovery Project*: [Nelson/Marlborough Conservancy], Department of Conservation.

Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (1995). *Bayesian data analysis*: Chapman and Hall/CRC.

Gelman, A., & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*: Cambridge university press.

Germano, J., Barlow, S., Castro, I., Colbourne, R., Cox, M., Gillies, C.,Yong, S. (2018). *Kiwi Recovery Plan 2018–2028 / Mahere Whakaora Kiwi 2018–2028*. (Threatened Species Recovery Plan 64). Wellington, New Zealand. 60p.

Gibbs, J. P., Eagle, P., & Droege, S. (1998). Monitoring populations of plants and animals. *BioScience, 48*(11), 935-940. doi:10.2307/1313297.

Gibbs, S. (2000). *Distribution, habitat use and survival of immature North Island brown kiwi (Apteryx australis mantelli) at Trounson Kauri Park.* University of Auckland.

Gilbert, N. A., Clare, J. D. J., Stenglein, J. L., & Zuckerberg, B. (2021). Abundance estimation of unmarked animals based on camera-trap data. *Conserv Biol, 35*(1), 88-100. doi:10.1111/cobi.13517.

Girard, I., Ouellet, J.-P., Courtois, R., Dussault, C., & Breton, L. (2002). Effects of sampling effort based on GPS telemetry on home-range size estimations. *The Journal of Wildlife Management*, 1290-1300.

Glen, A. S., Cockburn, S., Nichols, M., Ekanayake, J., & Warburton, B. (2013). Optimising camera traps for monitoring small mammals. *PLoS One, 8*(6), e67940. doi:10.1371/journal.pone.0067940.

Glenn, E. M., Lesmeister, D. B., Davis, R. J., Hollen, B., & Poopatanapong, A. (2016). Estimating density of a territorial species in a dynamic landscape. *Landscape Ecology, 32*(3), 563-579. doi:10.1007/s10980-016-0467-6.

Gliwicz, J. (1980). Island populations of rodents: their organization and functioning. *Biological Reviews, 55*(1), 109-138.

Goldstein, H., & Healy, M. J. (1995). The graphical presentation of a collection of means. *Journal of the Royal Statistical Society: Series A (Statistics in Society), 158*(1), 175-177.

Gompper, M. E., Kays, R. W., Ray, J. C., Lapoint, S. D., Bogan, D. A., & Cryan, J. R. (2006). A comparison of noninvasive techniques to survey carnivore communities in Northeastern North America. *Wildlife Society Bulletin, 34*(4), 1142-1151.

Gonzalez, L. F., Montes, G. A., Puig, E., Johnson, S., Mengersen, K., & Gaston, K. J. (2016). Unmanned Aerial Vehicles (UAVs) and Artificial Intelligence Revolutionizing Wildlife Monitoring and Conservation. *Sensors (Basel), 16*(1). doi:10.3390/s16010097.

Göth, A., & Jones, D. N. (2001). Transmitter attachment and its effects on Australian brush-turkey hatchlings. *Wildlife Research, 28*(1), 73-78.

Göth, A., & Vogel, U. (2003). Juvenile dispersal and habitat selectivity in the megapode Alectura lathami (Australian brush-turkey). *Wildlife Research, 30*(1), 69-74.

Gottschalk, T. K., & Huettmann, F. (2011). Comparison of distance sampling and territory mapping methods for birds in four different habitats. *Journal of Ornithology, 152*(2), 421-429.

Greene, T. C., & Pryde, M. A. (2012). Three population estimation methods compared for a known South Island robin population in Fiordland, New Zealand. *New Zealand Journal of Ecology, 36*(3), 1.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour, 28*(4), 1140-1162.

Gregg, M. A., & Crawford, J. A. (2009). Survival of greater sage-grouse chicks and broods in the northern Great Basin. *The Journal of Wildlife Management, 73*(6), 904-913.

Gregory, R. D., Gibbons, D. W., & Donald, P. F. (2004). Bird census and survey techniques. In W. J. Sutherland, I. Newton, & G. Rhys (Eds.), *Bird Ecology and ConservationA Handbook of Techniques*. Oxford Scholarship Online.

Harper, G. A. (2004). *Feral cats on Stewart Island/Rakiura: Population regulation, home range size and habitat use*. Retrieved from Department of Conservation PO Box 10-420 Wellington, New Zealand.

Harper, G. A. (2005a). Heavy rimu (Dacrydium cupressinum) mast seeding and rat (Rattusspp.) population eruptions on Stewart Island/Rakiura. *New Zealand Journal of Zoology, 32*(3), 155-162. doi:10.1080/03014223.2005.9518408.

Harper, G. A. (2005b). Numerical and functional response of feral cats (Felis catus) to variations in abundance of primary prey on Stewart Island (Rakiura), New Zealand. *Wildlife Research, 32*(7). doi:10.1071/wr04057.

Harper, G. A. (2009). The native forest birds of Stewart Island/Rakiura: patterns of recent declines and extinctions. *Notornis, 56*, 63-81.

Harris, S., Cresswell, W., Forde, P., Trewhella, W., Woollard, T., & Wray, S. (1990). Home-range analysis using radio-tracking data–a review of problems and techniques particularly as applied to the study of mammals. *Mammal review, 20*(2-3), 97-123.

He, F., & Gaston, K. J. (2000). Estimating Species Abundance from Occurence. *The American Naturalist, 156*(5), 553-559. Retrieved from https://www.journals.uchicago.edu/doi/10.1086/303403.

Heather, B., & Robertson, H. (2005). The Field Guide to the Birds of New Zealand, revised edn.(Penguin NZ: Auckland).

Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philos Trans R Soc Lond B Biol Sci, 365*(1550), 2303-2312. doi:10.1098/rstb.2010.0087.

Hinsch, M., & Komdeur, J. (2017). What do territory owners defend against? *Proceedings of the Royal Society B: Biological Sciences, 284*(1849), 20162356.

Holzapfel, S. A., Robertson, H., McLennan, J. A., Sporle, W., Hackwell, K., & Impey, M. (2008). *Kiwi (Apteryx spp.) recovery plan 2008–2018*. Retrieved from Department of Conservation, Wellington, New Zealand.

Innes, J., Eppink, F. V., & Robertson, H. (2015). *Saving a national icon: Preliminary estimation of the additional cost of achieving kiwi population stability or 2% growth* (LC2136). Landcare Research Manaaki Whenua.

IUCN. (2019). The IUCN Red List of Threatened Species. Version 2018-2. Retrieved from https://www.iucnredlist.org/.

Ivan, J. S. (2011). *Density, demography, and seasonal movements of snowshoe hares in central Colorado*: Colorado State University.

Jahn, P., Cagua, F., Molles, L., Ross, J., & Germano, J. (2022). Kiwi translocation review: are we releasing enough birds and to the right places? *New Zealand Journal of Ecology*. doi:10.20417/nzjecol.46.1.

Jahn, P., Harper, G. A., & Gilchrist, J. (2013). Home range sharing in family units of great spotted kiwi (Apteryx haastii) at Nelson Lakes National Park. *Notornis, 60*, 201-209.

Jahn, P., Ross, J. G., MacKenzie, D. I., & Molles, L. E. (2022). Acoustic monitoring and occupancy analysis: Cost-effective tools in reintroduction programmes for roroa-great spotted kiwi. *New Zealand Journal of Ecology, 46*(1), 3466.

Jakob, C., Ponce-Boutin, F., & Besnard, A. (2014). Coping with heterogeneity to detect species on a large scale: N-mixture modeling applied to red-legged partridge abundance. *The Journal of Wildlife Management, 78*(3), 540-549.

Jean-Pierre, A., Loranger-Merciris, G., & Cézilly, F. (2022). Spatial Occupancy, Local Abundance and Activity Rhythm of Three Ground Dwelling Columbid Species in the Forests of Guadeloupe in Relation to Environmental Factors. *Diversity, 14*(6), 480.

Jenkins, D., & Burrows, G. (1980). Ecology of otters in northern Scotland. III. The use of faeces as indicators of otter (Lutra lutra) density and distribution. *The Journal of Animal Ecology*, 755-774.

Johnson, D. D., Macdonald, D. W., Newman, C., & Morecroft, M. D. (2001). Group size versus territory size in group-living badgers: a large-sample field test of the Resource Dispersion Hypothesis. *Oikos, 95*(2), 265-274.

Jolly, J. N. (1989). A field study of the breeding biology of the little spotted kiwi (Apteryx owenii) with emphasis on the causes of nest failures. *Journal of the Royal Society of New Zealand, 19*(4), 433-448. doi:10.1080/03036758.1989.10421846.

Joseph, L. N., Field, S. A., Wilcox, C., & Possingham, H. P. (2006). Presence-absence versus abundance data for monitoring threatened species. *Conserv Biol, 20*(6), 1679-1687. doi:10.1111/j.1523-1739.2006.00529.x.

Jouventin, P., & Dobson, F. S. (2002). Why breed every other year? The case of albatrosses. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 269*(1503), 1955-1961. Retrieved from https://www. ncbi.nlm.nih. gov/pmc/articles /PMC1691107/pdf/12350259.pdf.

Juodakis, J., Castro, I., & Marsland, S. (2021). Precision as a metric for acoustic survey design using occupancy or spatial capture-recapture. *Environmental and Ecological Statistics, 28*, 587-608.

Kafley, H., Lamichhane, B. R., Maharjan, R., Thapaliya, B., Bhattarai, N., Khadka, M., & Gompper, M. E. (2019). Estimating prey abundance and distribution from camera trap data using binomial mixture models. *European Journal of Wildlife Research, 65*(5), 1-14.

Karanth, K. U. (1995). Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. *Biological Conservation, 71*(3), 333-338.

Karanth, K. U., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology, 79*(8), 2852-2862.

Karanth, K. U., & Nichols, J. D. (2002). *Monitoring tigers and their prey: a manual for researchers, managers, and conservationists in tropical Asia*: Centre for Wildlife Studies.

Karanth, K. U., & Nichols, J. D. (2011). Estimating tiger abundance from camera trap data: field surveys and analytical issues. *Camera traps in animal ecology: methods and analyses*, 97-117.

Karl, B. J., & Best, H. A. (1982). Feral cats on Stewart Island; their foods, and their effects on kakapo. *New Zealand Journal of Zoology, 9*(2), 287-293. doi:10.1080/03014223.1982.10423857

Karl, B. J., & Clout, M. N. (1987). An improved radio transmitter harness with a weak link to prevent snagging (nuevo arnés para colocar radiotransmisores en aves). *Journal of Field Ornithology*, 73-77.

Kasper, C. B., Schneider, A., & Oliveira, T. G. (2016). Home range and density of three sympatric felids in the Southern Atlantic Forest, Brazil. *Braz J Biol, 76*(1), 228-232. doi:10.1590/1519-6984.19414.

Kays, R., Arbogast, B. S., Baker-Whatton, M., Beirne, C., Boone, H. M., Bowler, M., . . . Espinosa, S. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution, 11*(6), 700-713.

Kays, R., & Slauson, K. M. (2008). Remote cameras. *Noninvasive survey methods for carnivores*, 110-140.

Keever, A. C., McGowan, C. P., Ditchkoff, S. S., Acker, P. K., Grand, J. B., & Newbolt, C. H. (2017). Efficacy of N-mixture models for surveying and monitoring white-tailed deer populations. *Mammal Research, 62*(4), 413-422.

Kelly, M. J., Noss, A. J., Di Bitetti, M. S., Maffei, L., Arispe, R., Paviolo, A., . . . Blanco, E. D. (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Beliize. *Journal of Mammalogy, 89*(2), 408-418.

Kenward, R. E. (2000). *A manual for wildlife radio tagging*: Academic press.

Kery, M., Gardner, B., Stoeckle, T., Weber, D., & Royle, J. (2010). Use of Spatial Capture-Recapture Modeling and DNA Data to Estimate Densities of Elusive Animals. *Conservation Biology*, no-no. doi:10.1111/j.1523-1739.2010.01616.x.

Kéry, M., & Royle, J. (2015). Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS.

Kéry, M., Royle, J., & Schmid, H. (2005). Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications, 15*(4), 1450-1461.

Keye, C. (2008). *A study of home ranges, movement and activity patterns of Great Spotted Kiwi (Ateryx haastii) in the Hurunui Region, South Island, New Zealand.* Masters thesis, Lincoln University, New Zealand. Retireved from https://hdl.handle.net/10182/1195.

Keye, C., Roschak, C., & Ross, J. (2011). Summer home range size and population density of great spotted kiwi (Apteryx haastii) in the North Branch of the Hurunui River, New Zealand. *Notornis, 58*, 22-30.

Kochanny, C. O., Delgiudice, G. D., & Fieberg, J. (2009). Comparing Global Positioning System and Very High Frequency Telemetry Home Ranges of White-Tailed Deer. *Journal of Wildlife Management, 73*(5), 779-787. doi:10.2193/2008-394.

Kolowski, J. M., Oley, J., & McShea, W. J. (2021). High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. *Ecosphere, 12*(2), e03350.

Kross, S. M., & Nelson, X. J. (2011). A portable low-cost remote videography system for monitoring wildlife. *Methods in Ecology and Evolution, 2*(2), 191-196. doi:10.1111/j.2041-210X.2010.00064.x.

Kruschke, J. (2014). Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan.

Larrucea, E. S., & Brussard, P. F. (2008). Habitat selection and current distribution of the pygmy rabbit in Nevada and California, USA. *Journal of Mammalogy, 89*(3), 691-699.

Laver, P. N., & Kelly, M. J. (2008). A critical review of home range studies. *The Journal of Wildlife Management, 72*(1), 290-298.

Lees, D., Sherman, C., Maguire, G., Dann, P., & Weston, M. (2017). Implications of radio-tracking for the survival of Masked Lapwing chicks.

Lin, C.-W., Hsu, F.-H., & Ding, T.-S. (2011). Applying a territory mapping method to census the breeding bird community composition in a montane forest of Taiwan. *Journal of Forest Science, 26*(3), 267-285.

Linden, D. W., Fuller, A. K., Royle, J., & Hare, M. P. (2017). Examining the occupancy–density relationship for a low-density carnivore. *Journal of Applied Ecology, 54*(6), 2043-2052.

Link, W. A., Schofield, M. R., Barker, R. J., & Sauer, J. R. (2018). On the robustness of N-mixture models. *Ecology, 99*(7), 1547-1551. doi:https://doi.org /10.1002/ecy.2362.

Long, R. A., MacKay, P., Ray, J., & Zielinski, W. (2012). *Noninvasive survey methods for carnivores*: Island Press.

López-López, P. (2016). Individual-Based Tracking Systems in Ornithology: Welcome to the Era of Big Data. *Ardeola, 63*(1). doi:10.13157/arla.63.1.2016.rp5.

Lyons, J. E., Royle, J., Thomas, S. M., Elliott-Smith, E., Evenson, J. R., Kelly, E. G., Andres, B. A. (2012). Large-scale monitoring of shorebird populations using count data and N-mixture models: Black Oystercatcher (Haematopus bachmani) surveys by land and sea. *The Auk, 129*(4), 645-652.

MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology, 53*(2), 330-342.

Macdonald, D., Ball, F., & Hough, N. (1980). The evaluation of home range size and configuration using radio tracking data. In *A handbook on biotelemetry and radio tracking* (pp. 405-424): Elsevier.

MacKenzie, D. I., & Nichols, J. D. (2004). Occupancy as a surrogate for abundance estimation. *Animal biodiversity and conservation, 27*(1), 461-467.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology, 83*(8), 2248-2255.

MacKenzie, D. I., Nichols, J. D., Royle, J., Pollock, K. H., Bailey, L., & Hines, J. E. (2006). *Occupancy modeling and estimation*. San Diego, California, USA: Academic Press.

Mander, V. (2016). *How translocation affects the activity, home range and pair-bonds of great spotted kiwi (Apteryx haastii).* Lincoln University, New Zealand.

Marsh, D. M., & Trenham, P. C. (2008). Current trends in plant and animal population monitoring. *Conservation Biology, 22*(3), 647-655. Retrieved from https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/j.1523-1739.2008.00927.x.

Martin, J., Royle, J., Mackenzie, D. I., Edwards, H. H., Kery, M., & Gardner, B. (2011). Accounting for non-independent detection when estimating abundance of organisms with a Bayesian approach. *Methods in Ecology and Evolution, 2*(6), 595-601.

Mattsson, B. J., Meyers, J. M., & Cooper, R. J. (2006). Detrimental impacts of radiotransmitters on juvenile Louisiana Waterthrushes. *Journal of Field Ornithology, 77*(2), 173-177.

McComb, B. C., Zuckerberg, B., Vesely, D., & Jordan, C. (2010). *Monitoring animal populations and their habitats: a practitioner's guide*: CRC Press.

McKelvey, K. S., & Pearson, D. E. (2001). Population estimation with sparse data: the role of estimators versus indices revisited. *Canadian Journal of Zoology, 79*(10), 1754-1765. doi:10.1139/z01-139

McLennan, J., Dew, L., Miles, J., Gillingham, N., & Waiwai, R. (2004). Size matters: predation risk and juvenile growth in North Island brown kiwi (Apteryx mantelli). *New Zealand Journal of Ecology*, 241-250.

McLennan, J., & McCann, A. (1991). *Ecology of great spotted kiwi, Apteryx haastii*: DSIR Land Resources.

McLennan, J., Potter, M. A., Robertson, H., Wake, G. C., Colbourne, R., Dew, L., . . . Reid, J. (1996). Role of predation in the decline of kiwi, Apteryx spp., in New Zealand. *New Zealand Journal of Ecology, 20*(1), 27-35.

McLennan, J., Rudge, M. R. H., & Potter, M. A. (1987). Range size and denning behaviour of brown kiwi, Apteryx australis mantelli, in Hawke's Bay, New Zealand. *New Zealand Journal of Ecology, 10*, 97-107.

Meek, P. D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., Townsend, S. (2014). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation, 23*(9), 2321-2343. doi: 10.1007/s10531-014-0712-8.

Meek, P. D., Ballard, G.-A., & Fleming, P. J. S. (2015). The pitfalls of wildlife camera trapping as a survey tool in Australia. *Australian Mammalogy, 37*(1). doi:10.1071/am14023.

Mere Roncal, C., Middendorf, E., Forsyth, A., Cáceres, A., Blake, J. G., Almeyda Zambrano, A. M., & Broadbent, E. N. (2019). Assemblage structure and dynamics of terrestrial birds in the southwest Amazon: a camera-trap case study. *Journal of Field Ornithology, 90*(3), 203-214. doi:https: //doi.org/10.1111/jofo.12299.

Mills, C. A., Godley, B. J., & Hodgson, D. J. (2016). Take Only Photographs, Leave Only Footprints: Novel Applications of Non-Invasive Survey Methods for Rapid Detection of Small, Arboreal Animals. *PLoS One, 11*(1), e0146142. doi:10.1371/journal.pone.0146142.

Moeller, A. K., Lukacs, P. M., & Horne, J. S. (2018). Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere, 9*(8), e02331.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *The American Midland Naturalist, 37*(1), 223-249.

Morrin, P. (1989). Possum in a kiwi burrow. *Notornis, 36*, 148-149.

Murphy, A. J., Farris, Z. J., Karpanty, S., Kelly, M. J., Miles, K. A., Ratelolahy, F., Golden, C. D. (2017). Using camera traps to examine distribution and occupancy trends of ground-dwelling rainforest birds in north-eastern Madagascar. *Bird Conservation International, 28*(4), 567-580. doi:10.1017/s0959270917000107.

Nakashima, Y. (2020). Potentiality and limitations of N-mixture and Royle-Nichols models to estimate animal abundance based on noninstantaneous point surveys. *Population Ecology, 62*(1), 151-157.

Nakashima, Y., Fukasawa, K., & Samejima, H. (2018). Estimating animal density without individual recognition using information derivable exclusively from camera traps. *Journal of Applied Ecology, 55*(2), 735-744. doi:10.1111/1365-2664.13059.

Newell, F. L., Sheehan, J., Wood, P. B., Rodewald, A. D., Buehler, D. A., Keyser, P. D., Wigley, T. B. (2013). Comparison of point counts and territory mapping for detecting effects of forest management on songbirds. *Journal of Field Ornithology, 84*(3), 270-286. doi:10.1111/jofo.12026.

Newsome, T. M., Ballard, G. A., Dickman, C. R., Fleming, P. J., & van de Ven, R. (2013). Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. *Ecography, 36*(8), 914-925.

Newton, P., Nguyen, T. V., Roberton, S., & Bell, D. (2008). Pangolins in peril: using local hunters knowledge to conserve elusive species in Vietnam. *Endangered Species Research, 6*, 41-53. doi:10.3354/esr00127.

Nichols, M., Ross, J., Glen, A. S., & Paterson, A. M. (2019). An evaluation of systematic versus strategically-placed camera traps for monitoring feral cats in New Zealand. *Animals, 9*(9), 687.

Nisbet, I. C. T. (2000). Disturbance, Habituation, and Management of Waterbird Colonies. *Waterbirds, 23*(2), 312-332.

Noss, A., Cuéllar, R., Barrientos, J., Maffei, L., Cuéllar, E., Arispe, R., Rivero, K. (2003). A camera trapping and radio telemetry study of lowland tapir (Tapirus terrestris) in Bolivian dry forests. *Plant Divers, 229*, 44-45.

Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology, 4*(4), 355-364.

O'Brien, T. G., Baillie, J. E. M., Krueger, L., & Cuke, M. (2010). The Wildlife Picture Index: monitoring top trophic levels. *Animal Conservation, 13*(4), 335-343. doi:10.1111/j.1469-1795.2010.00357.x.

O'Brien, T. G., & Kinnaird, M. F. (2008). A picture is worth a thousand words: the application of camera trapping to the study of birds. *Bird Conservation International, 18*(S1). doi:10.1017/s0959270908000348.

O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation, 6*(2), 131-139. doi:10.1017/s1367943003003172.

O'Connell, A. F., Nichols, J. D., & Karanth, K. U. (2011). *Camera traps in animal ecology: methods and analyses* (Vol. 271): Springer.

O’Brien, T. G. (2011). Abundance, density and relative abundance: a conceptual framework. *Camera traps in animal ecology: methods and analyses*, 71-96.

Oliveira-Santos, L. G. R., Tortato, M. A., & Graipel, M. E. (2008). Activity pattern of Atlantic Forest small arboreal mammals as revealed by camera traps. *Journal of Tropical Ecology, 24*(5), 563-567.

Pagnucco, K. S., Paszkowski, C. A., & Scrimgeour, G. J. (2011). Using cameras to monitor tunnel use by long-toed salamanders (Ambystoma macrodactylum): an informative, cost-efficient technique. *Herpetological Conservation and Biology, 6*(2), 277-286.

Palencia, P., Rowcliffe, J., Vicente, J., & Acevedo, P. (2021). Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology, 58*(8), 1583-1592. doi:10.1111/1365-2664.13913.

Palmer, M. S., Swanson, A., Kosmala, M., Arnold, T., & Packer, C. (2018). Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African Journal of Ecology, 56*(4), 791-803.

Paredes, R., Jones, I. L., & Boness, D. J. (2005). Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Animal Behaviour, 69*(1), 197-208.

Peele, A. M., Marra, P. M., Sillett, T. S., & Sherry, T. W. (2015). Combining survey methods to estimate abundance and transience of migratory birds among tropical nonbreeding habitats. *The Auk: Ornithological Advances, 132*(4), 926-937.

Perera, P., Karawita, H., & Jayasinghe, C. (2022). The applicability of camera trap data to monitor the cryptic Indian pangolin (Manus crassicaudata) populations: A survey from a tropical lowland rainforest in Southwest Sri Lanka. *Global Ecology and Conservation, 34*, e02046.

Pérez-Irineo, G., & Santos-Moreno, A. (2017). Occupancy, relative abundance, and activity patterns of Great Curassow (Crax rubra) in southeastern Mexico. *Ornitol. Neotrop, 28*, 313-320.

Pimm, S. L., Russell, G. J., Gittleman, J. L., & Brooks, T. M. (1995). The future of biodiversity. *Science, 269*, 347-350. Retrieved from https://science.sciencemag.org/content/269/5222/347.long.

Plummer, M., Stukalov, A., & Denwood, M. (2016). rjags: Bayesian graphical models using MCMC. *R package version, 4*(6).

Pollock, K. H., Nichols, J. D., Simons, T. R., Farnsworth, G. L., Bailey, L. L., & Sauer, J. R. (2002). Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics: The official journal of the International Environmetrics Society, 13*(2), 105-119.

Popescu, V. D., Valpine, P., & Sweitzer, R. A. (2014). Testing the consistency of wildlife data types before combining them: the case of camera traps and telemetry. *Ecol Evol, 4*(7), 933-943. doi:10.1002/ece3.997.

Potter, M. (1989). *Ecology and reproductive biology of the North Island brown kiwi (Apteryx australis mantelli).* (Ph.D. thesis). Massey University, Palmerston Nort.

Powell, L., & Gale, G. (2015). Estimation of parameters for animal populations. *Lincoln: Caught Napping Publications*.

Powell, R. (2000). Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences, 442*, 65-110.

Powell, R., & Mitchell, M. (2012). What is a home range? *Journal of Mammalogy, 93*(4), 948-958. doi:10.1644/11-mamm-s-177.1

Powlesland, R. G. (1988). Kiwi Research and Conservation: an acocunt of a NZ Wildlife Service Workshop 20-21 MAY 1986.

Quaglietta, L., Hájková, P., Mira, A., & Boitani, L. (2015). Eurasian otter (Lutra lutra) density estimate based on radio tracking and other data sources. *Mammal Research, 60*(2), 127-137. doi:10.1007/s13364-015-0216-2.

R Development Core Team, R. (2021). R: A language and environment for statistical computing. In: R foundation for statistical computing Vienna, Austria.

Randler, C., & Kalb, N. (2018). Distance and size matters: A comparison of six wildlife camera traps and their usefulness for wild birds. *Ecology and Evolution, 8*(14), 7151-7163.

Ricklefs, R. E. (1968). Patterns of growth in birds. *Ibis, 110*(4), 419-451.

Robertson, H. (2018). Birds: kiwi territory mapping Version 1.0. *Inventory and monitoring toolbox: birds.* DOCCM- 5597576. Retrieved from https://www.doc.govt.nz/globalassets/documents/science-and-technical/inventory-monitoring/im-toolbox-birds-kiwi-territory-mapping.pdf.

Robertson, H., & Colbourne, R. (2004). Survival of little spotted kiwi (Apteryx owenii) on Kapiti Island. *Notornis, 51*, 161-163.

Robertson, H., & Colbourne, R. (2017). *Kiwi Best Practice manual*. Department of Conservation, PO Box 10420, The Terrace, Wellington 6143, New Zealand.

Robertson, H., & Westbrooke, I. M. (2005). *A practical guide to the management and analysis of survivorship data from radio-tracking studies*. Retrieved from Science & Technical Publishing Department of Conservation PO Box 10–420, Wellington, New Zealand.

Robertson, H., Baird, K. A., Elliott, G. P., Hitchmough, R. A., McArthur, N. J., Makan, T. D., & Michel, P. (2021). *Conservation status of birds in Aotearoa New Zealand, 2021.* Wellington, New Zealand: Department of Conservation, Te Papa Atawhai.

Robertson, H., Coad, N., Colbourne, R., & Fraser, J. (2017). *Status of Rakiura tokoeka (Apteryx australis lawryi) near Port Adventure Hut in 2017*. Retrieved from Terrestrial Ecosystem Unit, Biodiversity Group, Department of Conservation, PO Box 10-420, Wellington 6143.

Robertson, H., Coad, N., Colbourne, R., & Fraser, J. (2018). *Status of Rakiura tokoeka (Apteryx australis lawryi) at Mason Bay, Stewart Island/Rakiura, February 2018*. Retrieved from Biodiversity Group, Department of Conservation, PO Box 10-420, Wellington.

Robertson, H., Coad, N., Colbourne, R., & Fraser, J. (2019a). *Status of little spotted kiwi (Apteryx owenii) on Red Mercury Island (Whakau) in March 2016*: Publishing Team, Department of Conservation.

Robertson, H., Coad, N., Colbourne, R., & Fraser, J. (2019b). *Status of little spotted kiwi (Apteryx owenii) on Tiritiri Matangi Island in April 2017*: Publishing Team, Department of Conservation.

Robertson, H., & Colbourne, R. (2001). Survival of little spotted kiwi exposed to the rodenticide brodifacoum. *The Journal of Wildlife Management*, 29-34.

Robertson, H., & Colbourne, R. (2005). Population status of great spotted kiwi Apteryx haastii near saxon hut, Heaphy Track, New Zealand. *Notornis, 52*, 27-33.

Robertson, H., & Colbourne, R. (2011). *Status of Rakiura tokoeka (Apteryx australis lawryi) near Port Adventure Hut, Rakiura National Park, Stewart Island, in 2011*. Department of Conservation. Department of Conservation.

Robertson, H., & Colbourne, R. (2022). Habitat loss drives population decline and reduced mass of Rakiura tokoeka (Apteryx australis australis, Stewart Island brown kiwi,) at Mason Bay, Stewart Island/Rakiura. *Notornis, 69*, 147-157.

Robertson, H., Colbourne, R., Graham, P., Miller, P., & Pierce, R. (2010). Experimental management of Brown Kiwi Apteryx mantelli in central Northland, New Zealand. *Bird Conservation International, 21*(02), 207-220. doi:10.1017/s0959270910000444.

Robertson, H., Colbourne, R., Graham, P., Miller, P., & Pierce, R. (2011). Experimental management of brown kiwi Apteryx mantelli in central Northland, New Zealand. *Bird Conservation International, 21*(2), 207-220.

Robertson, H., Craig, E., Gardiner, C., & Graham, P. (2016). Short pulse of 1080 improves the survival of brown kiwi chicks in an area subjected to long-term stoat trapping. *New Zealand Journal of Zoology, 43*(4), 351-362.

Robertson, H., & Fraser, J. R. (2009). Use of trained dogs to determine the age structure and conservation status of kiwi Apteryx spp. populations. *Bird Conservation International, 19*(2), 121-129.

Robley, A., Gormley, A., Woodford, L., Lindeman, M., Whitehead, B., Albert, R., & Smith, A. (2010). *Evaluation of camera trap sampling designs used to determine change in occupancy rate and abundance of feral cats*: Arthur Rylah Institute for Environmental Research in partnership with Australian Government Department of the Environment, Water, Heritage and the Arts.

Rogan, M. S., Balme, G. A., Distiller, G., Pitman, R. T., Broadfield, J., Mann, G. K. H., & O'Riain, M. J. (2019). The influence of movement on the occupancy–density relationship at small spatial scales. *Ecosphere, 10*(8), e02807. doi:https://doi.org/10.1002/ecs2.2807.

Rogers, K. B., & White, G. C. (2007). Analysis of movement and habitat use from telemetry data. *Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland*, 625-676.

Rosenstock, S. S., Anderson, D. R., Giesen, K. M., Leukering, T., Carter, M. F., & Thompson, F. (2002). Landbird counting techniques: Current practices and an alternative. *The Auk, 119*, 46-53.

Rovero, F., & Marshall, A. R. (2009). Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology, 46*(5), 1011-1017. doi:10.1111/j.1365-2664.2009.01705.x.

Rovero, F., Tobler, M., & Sanderson, J. (2010). Camera trapping for inventorying terrestrial vertebrates. *Manual on field recording techniques and protocols for all taxa biodiversity inventories and monitoring. The Belgian National Focal Point to the Global Taxonomy Initiative, 8*, 100-128.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). “Which camera trap type and how many do I need?” A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy*. doi:10.4404/hystrix-24.2-6316.

Rowcliffe, J., & Carbone, C. (2008). Surveys using camera traps: are we looking to a brighter future? *Animal Conservation, 11*(3), 185-186. doi:10.1111/j.1469-1795.2008.00180.x.

Rowcliffe, J., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology, 45*(4), 1228-1236. doi:10.1111/j.1365-2664.2008.01473.x.

Royle, J. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics, 60*(1), 108-115.

Royle, J., Chandler, R., Sollmann, R., & Gardner, B. (2014). Spatial capture-recapture. Waltham, Massachusetts. In: Elsevier, Academic Press.

Royle, J., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*: Elsevier.

Royle, J., & Nichols, J. D. (2003). Estimating abundance from repeated presence–absence data or point counts. *Ecology, 84*(3), 777-790.

Sales, J. (2005). The endangered kiwi: A review. *Folia Zoologica, 54*(1-2), 1-20.

Samejima, H., Ong, R., Lagan, P., & Kitayama, K. (2012). Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management. *Forest Ecology and Management, 270*, 248-256. doi:10.1016/j.foreco.2012.01.013.

Samuel, M. D., Pierce, D., & Garton, E. O. (1985). Identifying areas of concentrated use within the home range. *The Journal of Animal Ecology*, 711-719.

Sauer, J. R., Link, W. A., Fallon, J. E., Pardieck, K. L., & David J. Ziolkowski, J. (2013). The North American Breeding Bird Survey 1966–2011: Summary Analysis and Species Accounts. *North American Fauna*, 1-32. doi:10.3996/nafa.79.0001.

Scofield, R., Wood, J., de Nascimento, L., Robertson, H., Colbourne, R., De Pietri, V., & Weir, J. (2021). Identification of the type locality of the South Island Brown Kiwi Apteryx australis. *Conservation Genetics, 22*(4), 645-652.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., & Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, 739-747.

Seber, G. A. (1986). A review of estimating animal abundance. *Biometrics*, 267-292.

Shapiro, L. M. (2005). *Diet overlap and potential competition between North Island brown kiwi chicks (Apteryx mantelli) and ship rats (Rattus rattus) for limited resources on Ponui Island, New Zealand.* (Master of Science in Ecology). Massey University, Palmerston North, New Zealand.

Silveira, L., Jácomo, A. T., & Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation, 114*(3), 351-355.

Silvy, N. J. (2020). *The Wildlife Techniques Manual: Volume 1: Research. Volume 2: Management* (Vol. 1): Johns Hopkins University Press.

Skirrow, M. J. A. (2018). *Estimating the population size of two critically endangered South Pacific parakeets: the Tasman Parakeet and Malherbe's Parakeet: a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in Conservation Biology, Massey University, New Zealand.* Massey University.

Smith, D. H. V., & Weston, K. A. (2017). Capturing the cryptic: a comparison of detection methods for stoats (Mustela erminea) in alpine habitats. *Wildlife Research, 44*(5). doi:10.1071/wr16159.

Smith, J. K., & Coulson, G. (2012). A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. *Australian Mammalogy, 34*(2), 196-201.

Sodhi, N. S., Brook, B. W., & Bradshaw, C. J. (2009). Causes and consequences of species extinctions. *The Princeton guide to ecology, 1*, 514-520.

Soisalo, M. K., & Cavalcanti, S. M. C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation, 129*(4), 487-496. doi:10.1016/j.biocon.2005.11.023.

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology, 56*(4), 740-749. doi:10.1111/aje.12557.

Sollmann, R., Gardner, B., Parsons, A. W., Stocking, J. J., McClintock, B. T., Simons, T. R., . . . O'Connell, A. F. (2013). A spatial mark–resight model augmented with telemetry data. *Ecology, 94*(3), 553-559.

South, A. (1999). Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal. *Ecological Modelling, 117*(2-3), 343-360.

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the royal statistical society: Series b (statistical methodology), 64*(4), 583-639.

Strang, K. E. (2018). *The ecology of feral cats (Felis catus) on a New Zealand offshore island : considerations for management : a thesis presented in partial fulfilment of the requirements for the degree of Doctor of Pholosophy in Zoology at Massey University, Manawatu, New Zealand.* (Doctor of Philosophy (PhD) Doctoral). Massey University, Retrieved from http://hdl.handle.net/10179/14952.

Streby, H. M., Loegering, J. P., & Andersen, D. E. (2012). Spot-mapping underestimates song-territory size and use of mature forest by breeding golden-winged warblers in Minnesota, USA. *Wildlife Society Bulletin, 36*(1), 40-46.

Street, P. A., Riecke, T. V., Williams, P. J., Behnke, T. L., & Sedinger, J. S. (2022). Estimating survival and adoption rates of dependent juveniles. *Ecology and Evolution, 12*(6), e9005.

Sunde, P., Zuberogoitia, I., & Martínez, J. (2011). What do we know about territorial behaviour and its consequences in Tawny Owls. *Ecology and Conservation of European forest dwelling raptors (eds. Zuberogoitia, I. & Martínez, IG)*, 253-260.

Sutherland, G. D., Harestad, A. S., Price, K., & Lertzman, K. P. (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation ecology, 4*(1).

Sutherland, W. J. (2006). *Ecological census techniques: a handbook*: Cambridge university press.

Sutherland, W. J., Newton, I., & Green, R. E. (2004). *Bird ecology and conservation, A handbook of techniques*. New York, United States: Oxford University Press.

Suwanrat, S. (2013). *Habitatselection and abundanceestimates of siamese fireback lophura diardi at Sakaerat Environmental Research Station.* School of Biology Institute of Science Suranaree University of Technology.

Suwanrat, S., Ngoprasert, D., Sutherland, C., Suwanwaree, P., & Savini, T. (2015). Estimating density of secretive terrestrial birds (Siamese Fireback) in pristine and degraded forest using camera traps and distance sampling. *Global Ecology and Conservation, 3*, 596-606. doi:10.1016/j.gecco.2015.01.010.

Svenson, S., & Williamson, K. (1969). Recommendations for an international standard for a mapping method in bird census work. *Bird Study, 16*(4), 249-255.

Svensson, S. (1979). Census efficiency and number of visits to a study plot when estimating bird densities by the territory mapping method. *Journal of Applied Ecology*, 61-68.

Swann, D. E., Hass, C. C., Dalton, D. C., & Wolf, S. A. (2004). Infrared-triggered cameras for detecting wildlife: an evaluation and review. *Wildlife Society Bulletin, 32*(2), 357-365.

Taborsky, B., & Taborsky, M. (1995). Habitat use and selectivity by the brown kiwi (Apteryx australis mantelli) in a patchy environment. *The Auk, 112*(3), 680-689.

Taborsky, B., & Taborsky, M. (1999). The Mating System and Stability of Pairs in Kiwi Apteryx spp. *Journal of Avian Biology, 30*(2), 143-151.

Taylor, C. N., Russell, J. C., & Russell, K. J. (2020). A strategic social impact assessment for Predator-Free Rakiura, New Zealand, with a human–ecological approach. *Socio-Ecological Practice Research, 2*(2), 161-174. doi:10.1007/s42532-020-00049-0.

Taylor, H. R., Nelson, N. J., & Ramstad, K. M. (2014). Chick Timer™ software proves an accurate disturbance minimising tool for monitoring hatching success in little spotted kiwi (Apteryx owenii). *New Zealand Journal of Zoology, 41*(2), 139-146. doi:10.1080/03014223.2014.886600.

Teunissen, W., Schekkerman, H., Willems, F., & Majoor, F. (2008). Identifying predators of eggs and chicks of Lapwing Vanellus vanellus and Black-tailed Godwit Limosa limosa in the Netherlands and the importance of predation on wader reproductive output. *Ibis, 150*, 74-85.

Thomas, M. L., Baker, L., Beattie, J. R., & Baker, A. M. (2020). Determining the efficacy of camera traps, live capture traps, and detection dogs for locating cryptic small mammal species. *Ecology and Evolution, 10*(2), 1054-1068.

Thompson, C. M., Royle, J., & Garner, J. D. (2012). A framework for inference about carnivore density from unstructured spatial sampling of scat using detector dogs. *The Journal of Wildlife Management, 76*(4), 863-871. doi:10.1002/jwmg.317.

Thompson, L. A., Spoon, T. R., Goertz, C. E., Hobbs, R. C., & Romano, T. A. (2014). Blow collection as a non-invasive method for measuring cortisol in the beluga (Delphinapterus leucas). *PLoS One, 9*(12), e114062. doi:10.1371/journal.pone.0114062.

Thunhikorn, S., Grainger, M. J., McGowan, P. J., & Savini, T. (2016). Methods used to survey avian species and their potential for surveying ground-dwelling birds in Asia. *Forktail*.

Tobler, M. W., Carrillo-Percastegui, S. E., Leite Pitman, R., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation, 11*(3), 169-178. doi:10.1111/j.1469-1795.2008.00169.x.

Tomiałojć, L. (2004). Accuracy of the Mapping Technique for a Dense Breeding Population of the HawfinchCoccothraustes coccothraustesin a Deciduous Forest. *Acta Ornithologica, 39*(1), 67-74. doi:10.3161/068.039.0101.

Toy, R., & Toy, S. (2020). Post-translocation dispersal and home range establishment of roroa (great spotted kiwi, Apteryx haastii): need for long-term monitoring and a flexible management strategy. *Notornis, 67*, 511-525.

Vattiato, G. (2021). Modelling individual heterogeneity in behaviour for wildlife management and conservation.

Verner, J. (1985). Assessment of counting techniques. In *Current ornithology* (pp. 247-302): Springer.

Vine, S. J., Crowther, M. S., Lapidge, S. J., Dickman, C. R., Mooney, N., Piggott, M. P., & English, A. W. (2009). Comparison of methods to detect rare and cryptic species: a case study using the red fox (Vulpes vulpes). *Wildlife Research, 36*(5). doi:10.1071/wr08069.

Warburton, B., Barker, R., & Coleman, M. (2004). Evaluation of two relative-abundance indices to monitor brushtail possums in New Zealand. *Wildlife Research, 31*(4), 397-401.

Weir, J. T., Haddrath, O., Robertson, H., Colbourne, R. M., & Baker, A. J. (2016). Explosive ice age diversification of kiwi. *Proc Natl Acad Sci U S A, 113*(38), E5580-5587. doi:10.1073/pnas.1603795113.

White, G. C., & Garrott, R. A. (1990). *Analysis of wildlife radio-tracking data*. Academic Press Ic, Academic Press Limited.

White, G. C., Franklin, A. B., & Shenk, T. M. (2002). Estimating parameters of PVA models from data on marked animals. *Population viability analysis. University of Chicago Press, Chicago, Illinois, USA*, 169-190.

Whittington, J., Hebblewhite, M., Chandler, R. B., & Lentini, P. (2018). Generalized spatial mark-resight models with an application to grizzly bears. *Journal of Applied Ecology, 55*(1), 157-168. doi:10.1111/1365-2664.12954.

Williams, A. B. (1936). The composition and dynamics of a beech-maple climax community. *Ecological monographs, 6*(3), 317-408.

Williams, E. M. (2016). Developing monitoring methods for cryptic species: A case study of the Australasian bittern, Botaurus poiciloptilus. *Ecology Doctorate thesis, Massey University, Palmerston North, New Zealand. Massey University*.

Williams, P. J., Schroeder, C., & Jackson, P. (2020). Estimating Reproduction and Survival of Unmarked Juveniles Using Aerial Images and Marked Adults. *Journal of Agricultural, Biological and Environmental Statistics, 25*(2), 133-147. doi:10.1007/s13253-020-00384-5.

Wilson, A. (2014). *The triumphs, challenges and failures of young North Island brown kiwi (Apteryx mantelli): a study of behaviour, growth, dispersal and mortality.* (Master of Science in Zoology). Massey University, Palmerston North, New Zealand.

Wilson, G., & Delahay, R. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research, 28*, 151-164.

Wilson, H. (1987). Plant communities of Stewart Island (New Zealand). Vegetation of Stewart Island, New Zealand. *New Zealand Journal of Botany*, 1-80.

Wilson, K., & Anderson, D. (1985). Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy, 66*(1), 13-21.

Witmer, G. W. (2005). Wildlife population monitoring: some practical considerations. *Wildlife Research, 32*(3), 259-263.

Woinarski, J. C. Z., Murphy, B. P., Legge, S. M., Garnett, S. T., Lawes, M. J., Comer, S.,Woolley, L. A. (2017). How many birds are killed by cats in Australia? *Biological Conservation, 214*, 76-87. doi:10.1016/j.biocon.2017.08.006.

Worton, B. J. (1989) Kernel methods for estimatinng the utulization distribution in home-range studies. *Ecology*, 70(1), 164-168.

Ziesemann, B. (2011). *The social organisation and mating system of the brown kiwi (Apteryx mantelli).* (Doctor of Philosophy in Ecology). Massey University, Albany, New Zealand.

Znidersic, E. (2017). Camera traps are an effective tool for monitoring Lewin's Rail (Lewinia pectoralis brachipus). *Waterbirds, 40*(4), 417-422. doi:10.1675/063.040.0414.

Zou, F., Zhang, Q., Zhang, M., Lee, M.-B., Wang, X., Gong, Y., & Yang, C. (2019). Temporal patterns of three sympatric pheasant species in the Nanling Mountains: N-mixture modeling applied to detect abundance. *Avian Research, 10*(1), 1-10.

Zwerts, J. A., Stephenson, P., Maisels, F., Rowcliffe, J., Astaras, C., Jansen, P. A., & Bruce, T. (2021). Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps, and passive acoustic sensors. *Conservation Science and Practice, 3*(12), e568.