Measuring abundance and monitoring behaviour of invasive rats around control devices using camera traps

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Biological Sciences, University of Auckland, 2019.

Taumaha ki runga,
Taumaha ki raro,
Ki taku matua wahine,
I ti ai taku kiore,
Ma te reke taumaha taumaha,
E taka te po,
E taka ki tuhua,
E taka te ao,
E taka ki Karewa,
I tutu ai, he kiore.

Give thanks above,
Give thanks below,
To my mother,
My rat squeaks (it is caught),
For thy coming thanks, thanks,
Night suitable falls,
Inland it falls,
Day falls,
At Karewa it falls,
What is that standing up? It is a rat.

Karakia sung by Māori before placing rat traps in the forest.

(Taylor, 1855)

Abstract

Invasive rats are one of the major threats to native species and ecosystems worldwide. Reliable rat detection is essential to evaluate management, confirm eradication success or detect invaders. Detection relies on interactions between rats and detection devices. Therefore, it is important to understand rat behaviour around detection devices, particularly changes in response to ongoing control. I used camera traps alongside traditional detection devices to answer i) how camera traps can be used to estimate abundance of invasive rats and ii) which factors affect the behaviour, and hence detectability, of invasive rats.

On Goat Island, New Zealand, self-resetting Goodnature A24 rat traps were monitored with camera traps. Counting the number of rat videos was the preferred method when measuring relative abundance and did not result in loss of information compared to the more laboriously counting of individual rats. Estimating density requires identification of individuals. I tested three novel statistical models to estimate density of unmarked animals using camera traps and compared the results to spatially explicit capture-recapture (SECR) estimates from live trapping data in French Polynesia. The spatially explicit Chandler model underestimated density and the estimates were confounded by low precision, presumably due to an insufficient density of detection devices. The random encounter and staying time model had a similar density to SECR in one session but underestimated density in another session. Differences in rat activity and behaviour have influenced density estimates. The random encounter model failed to provide realistic density estimates. The model needs information about rat movement speed and day range, which were not available and difficult to measure. A different random encounter model (REST) obtained information about rat movement speed from the time an individual stays in the field of view, resulting in more precise density estimates. Camera traps were shown to be useful to measure rat relative abundance even when A24s failed to detect the remaining individuals after sustained control.

To understand the behaviour of rats around detection devices, both live traps and Goodnature A24s were monitored with camera traps. Detection probability using live traps for Pacific rats differed between sites and was lower where ship rats were present, and Pacific rat detection was delayed where both species coexisted. Rat density and detection probability varied between times, presumably due to seasonality in food abundance and rat reproduction. Higher rat abundance resulted in more trap encounters and interactions. However, the trapping rate remained low throughout the study. Detectability was influenced by season, abundance and interspecific competition. To improve rat detection from devices that require interaction with a trigger mechanism either the threshold for rats to interact with the trigger must be lowered or attractiveness of the bait must be improved to overcome trigger avoidance.

Acknowledgements

First of all, I want to thank Michael Horton. Without Michael’s passion for birds and their protection and his generosity I would not have been able to conduct this study. Secondly, I thank my main supervisor James Russell for giving me the opportunity to do valuable research on the most beautiful islands. Big thanks go to my co-supervisor Ben Stevenson for being a teacher and collaborator. Ben has been incredibly helpful in developing a project, helping with statistical analysis of the data, writing, and patiently answering all my questions.

I want to thank Araceli Samaniego for being the best friend, teacher, mentor, colleague, and collaborator one could wish for. Araceli has giving me insights into how good research can produce applicable results. I have learned a lot about how impactful the work of good eradication scientists can be. During our time in the field, I received a huge amount of help and support from numerous fantastic people of the Tetiaroa Society and Te Mana O Te Moana, with extra thanks to my colleagues and friends Margaux Touron and Quentin Genet.

Special thanks to Judy Gilbert for inviting me to Windy Hill Sanctuary on Aotea and giving me the best support. Judy is one of the most passionate and inspiring people I have met in my life. I feel privileged that I got the chance to meet Judy and look back on many interesting conversations over a cup of tea. Judy is a rolemodel for what a strong will and persistence can achieve in conservation. I also thank the Windy Hill Rosalie Bay Catchment Trust and residents at Windy Hill for letting me live and work on their properties. Thanks to Scott Sambell and Auckland Council for inviting me to Glenfern Sanctuary and supporting my work on site. The on-site support was incredible. A general “thank you” goes to the Aotea communities. I have met the most

welcoming and helpful people all over the island who made sure I would leave this place with great memories despite the long and exhausting field trips. Local iwi, the Department of Conservation and Auckland Council were always very helpful on Aotea, Rakiura and Te Hāwere-a-Maki.

Besides fieldwork and data collection, office time became very enjoyable thanks to Souad Boudjelas and Zachery Carter. A very special thanks to Jo Peace for always being helpful, knowledgeable, kind and approachable. Without Jo there would have been much less fun throughout the PhD.

I am very grateful for help in the field in New Zealand by great and nice people, Hayley Ricardo, Carlos Abrahão, Lea Stolpmann, Edin Whitehead, Henry Cookson, Kevin Parson, Abi Wittmeyer-Hill and Michael Kinahan. Clive Gregory on Aotea deserves special mention for his unconditional helpfulness at all times.

My very special thanks go to Wenyi. Her distraction and positivity were invaluable. Without her this journey would have been much harder.

Finally, many thanks to Mayasa, my favourite field assistant, who was not helpful at all, but encouraged me to keep on walking through rough terrain. She cheered me up every day we spent together with her unconditional love and contagious happiness. I hope she finally found infinite joy.

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1 Introduction

1.1 Management of invasive species

Biological invasions are one of the main causes of biodiversity loss (Clavero & García-Berthou, 2005). Invasive species can have direct and indirect effects on native ecosystems. The impacts can involve predation on and competition with native species as well as modification of ecosystems (Simberloff et al., 2013). Human colonisation has caused the spread of invasive species of various taxonomic groups to previously inaccessible ecosystems (Lowe et al., 2000). Invasive predators have caused extinction of birds (Blackburn et al., 2004), mammals (Burbidge & Manly, 2002), fish (Dextrase & Mandrak, 2006), reptiles (Medina et al., 2011), invertebrates (St Clair, 2011), amphibians and plants (Bellard et al., 2016).

Invasive species have been successfully eradicated across various taxa, including vertebrates and invertebrates, terrestrial as well as marine organisms (Myers et al., 2000). Native species on islands have benefitted from the removal of invasive mammals (Jones et al., 2016). Considering ecosystem changes and extinctions, invasive rodents have probably the biggest impact on island ecosystems worldwide (Towns et al., 2006). In response to invasions, the control of invasive species is important for the protection of the endemic fauna and flora. However, for all invasive mammal eradication attempts from islands, rodent eradications have the highest failure rate. Globally 10% of the documented more than 650 rat eradication attempts have failed (Russell & Holmes, 2015). Eradication failure rate within the genus *Rattus* is highest for Pacific rats and lowest for Norway rats (*R. norvegicus*) (Table 1.1). New Zealand takes a leading role in island eradications and rodents have been successfully removed from one third of the islands, but only 10% of the offshore island area (Russell & Broome, 2016). The eradication of rodents from Aotea/Great Barrier Island and Rakiura/Stewart Island would increase the rodent free offshore island area to 50%. The ecological and economic benefits of rodent free islands are undeniable (Russell et al., 2015). The planning phase for a predator free Rakiura was already initiated (Sage, 2019). However, both Aotea and Rakiura face the challenge of eradicating multiple invasive rat species, which is complicated and expensive (Springer, 2016).

Table 1.1. Number of island rat eradication attempts and failures for the three commonest invasive rat species. Data received from the Database of Island Invasive Species Eradication

	Island eradications		
	Attempts	**Failures**	
***Rattus* spp**	**837**	**89**	**10.63%**
R. rattus	426	49	11.50%
R. norvegicus	253	10	3.95%
R. exulans	158	30	18.99%

The success of eradications is affected by numerous factors, including the size of the island or if the island is inhabited (Harper et al., 2020; Holmes et al., 2015; Howald et al., 2007). When eradication is not possible, suppression to low levels is a widely used management strategy (Armstrong et al., 2014; Bomford & O'Brien, 1995; Duron et al., 2017). Even though rodent control might not be as effective as eradication in achieving conservation goals (Ruffell & Didham, 2017), it may be necessary to protect native species from further decline or extinction (Innes et al., 1999). Rodent control was shown to have positive effects on native flora (Pender et al., 2013) and fauna (Buckle & Fenn, 1992; Vanderwerf & Smith, 2002).

1.2 Invasive rats in New Zealand

Lowe et al. (2000) listed species from the genus *Rattus* among the world's worst invasive species. Worldwide more than 80% of island groups are inhabited by at least one of the three invasive rat species, ship rat (*R. rattus*), Norway rat and Pacific rat (*R. exulans*) (Atkinson, 1985). Unlike many other invasive species, the damage done by ship rats can be detected soon after the invasion, especially when they have access to manmade structures (Bell et al., 2016). Rats are omnivorous and opportunistic, having an impact on both plants and animals either by direct predation or competition (Campbell & Atkinson, 1999; Crook, 1973; Lovegrove, 1996; Meyer & Butaud, 2009; Penloup et al., 1997). The impact on plant communities can be masked by a temporal delay between seed predation and the according change of forest community structure (Shiels et al., 2014). In contrast, the damage to vertebrates can lead to rapid extinction on islands. On Lord Howe Island the extinction of several bird species occurred after rats had arrived from a shipwreck (Hindwood, 1938).

All three invasive rat species are present in New Zealand. The Pacific rat was the first species to arrive in New Zealand approximately 1280 A.D. with the first Polynesian colonists (Wilmshurst et al., 2008). Since it was seen as a delicacy (Wishart, 2010), it was probably brought on ships deliberately as a food source. This is supported by Māori knowledge about Pacific rats in New Zealand (Haami, 1994). The second species that established in New Zealand was the Norway rat. It arrived on ships from Europe or North America in the late 18th century (Atkinson, 1973). In mid to late 19th century the ship rat, was able to successfully spread in New Zealand. Ship rats have repeatedly invaded New Zealand and are presently the most common species whereas Pacific rats have been replaced from most of New Zealand's main islands (Russell et al., 2019). All three rat species cause damage to New Zealand's ecosystems on various levels. The negative impacts include predation on vertebrates (Brown et al., 1998), invertebrates, and seeds, as well as indirect effects by influencing the habitat structure or abundance of ecosystem drivers (Campbell & Atkinson, 1999; Crook, 1973; Fukami et al., 2006; Grant-Hoffman et al., 2010; Thoresen et al., 2017; Towns, 2009). The absence of mammal predators has left the native species without defence mechanisms against them (Dowding & Murphy, 2001).

1.3 Monitoring animal abundance and behaviour using camera traps

Early detection of invaders as well as invasive species control and eradication programmes require reliable monitoring (Bomford & O'Brien, 1995). Monitoring tools must be able to detect individuals at low population density and species that are reluctant to interact with detection devices or are elusive. A dominant species limiting access of a subordinate species to detection devices may further complicate monitoring. On Wake Atoll asymmetric competition between Pacific rats and *R. tanezumi* may have been one reason for eradication failure (Griffiths et al., 2014). While *R. tanezumi* was successfully removed from the atoll, Pacific rats were still present in very low density. However, the commonly used method for rodent monitoring, i.e. chew blocks, did not detect Pacific rats at low population density (Griffiths et al., 2014). In New Zealand, tracking tunnels with ink cards are a widely used method for monitoring relative abundance of rodents and mustelids and tracking tunnels are perceived as the better monitoring method relative to snap traps (Gillies & Williams, 2013). However, ship rats showed hesitation in stepping on the ink pads in a pen trial, a behavioural response that can potentially affect monitoring rats at low population density (Cooper et al., 2018). Camera traps are alternative detection devices that can optimize detectability at low population density or of species with reluctance to interact with detection devices.

Remotely triggered camera systems in wildlife monitoring have been used increasingly since the second half of the 20th century (Kucera & Barrett, 2011). A key technology for remote triggering is the passive infrared sensors (PIR) which has been used since the 1990s and is part of nearly every motion sensored camera nowadays (Shapira et al., 2013). Mace et al. (1994) have successfully used cameras with PIR to monitor grizzly bears (*Ursus arctos horribilis*) which were difficult to observe due to a densely forested and remote habitat and aggressiveness of the species. Camera traps have been used in different contexts in animal ecology, behaviour and conservation (Nichols et al., 2011). They were successful in confirming the presence of rare species (Kucera & Barrett, 2011) and even led to the detection of a previously unknown rabbit species in Southeast Asia (Surridge et al., 1999). Population density estimates using established capture-recapture models can be used when individuals can be distinguished, e.g. tigers (*Panthera tigris*) (Karanth & Nichols, 1998).

Many species cannot be identified to the individual level using camera traps. Therefore, many studies state an index of relative abundance (Güthlin et al., 2014; Rovero & Marshall, 2009). Many studies focused on medium to large target species (Karanth & Nichols, 1998; Mace et al., 1994; Rovero & Marshall, 2009; Wang & Macdonald, 2009). However, recent studies have shown the potential of camera traps for monitoring small animals (Austin et al., 2017; Glen et al., 2013; Gronwald et al., 2019; Mills et al., 2016; Thomas et al., 2020; Yamada et al., 2016). Meek et al. (2013) have surveyed experience in camera trap use among wildlife managers and more than half of the respondents have used camera traps for surveying small mammals. Recently, camera traps have also been successfully used to monitor abundance of small mammals (Dundas et al., 2019; Rendall et al., 2014; Welbourne et al., 2015). However, an index of relative abundance from camera traps needs calibration with independent estimates of abundance (O'Brien, 2011), which is rarely done.

In addition to monitoring abundance, camera traps are a valuable tool for documenting and analysing behaviour and activity patterns. One third of the studies using camera traps analysed behaviour of the target animal, mostly mammals (Burton et al., 2015). Camera traps have been used to analyse circadian rhythms, nest predation, foraging, niche partitioning, habitat use and reproduction (Bridges & Noss, 2011). Most behavioural studies have focused on the identification and behaviour of predators at bird nests (Bridges & Noss, 2011), but also resulted in direct evidence of predation for other taxa. Camera trap data have revealed introduced tegu lizards (*Tupinambis merianae*) preying upon American alligator (*Alligator mississippiensis*) nests in Florida, USA (Mazzotti et al., 2015), and have shown how invasive ship rats prey upon hatchlings of endangered green sea turtles (*Chelonia mydas*) in French Polynesia (Gronwald et al., 2019). Further studies have used camera traps to analyse the behaviour of rats in their natural habitat, e.g. the behavioural response of Australian native rodents to odour of competitors (Heavener et al., 2014) and predators (Carthey & Banks, 2016; Hayes et al., 2006) or the effect of predator presence on the behaviour of rats in an urban habitat (Parsons et al., 2018). However, behavioural observation mostly focussed on predator impacts on their environment.

Behaviour was traditionally documented by an observer in the field. The use of cameras has both advantages and disadvantages in data collection as well as analysis over the traditional method. The presence of humans can alter the behaviour of the target species and observation of natural behaviour without disturbance is hardly possible (Martin & Bateson, 1993). While binoculars may be a suitable tool to observe large, diurnal animals from a great distance, observing small, cautious, and nocturnal animals like rodents is challenging. Using camera traps removes disturbance by the observer and allows the target individuals to behave naturally in their environment. However, using a traditional flash can disturb the target animal and cause trap avoidance behaviour (Schipper, 2007). The obvious advantage of video analysis over traditional observance is that important behaviour can be watched repeatedly and in slow motion for a more detailed analysis. In addition, motion sensored cameras document behaviour while long times of inactivity can be skipped which is of value when the target species is elusive or at very low density. Camera traps allow for monitoring different sites at the same time. Another advantage of using camera traps can be reduced costs. Welbourne et al. (2015) calculated lower costs of camera traps compared to live trapping when surveying terrestrial squamata and mammals in Australia. Even though initial costs for camera equipment may be high, the follow-up costs can be lower than for conducting traditional surveys (Lyra-Jorge et al., 2008). The analysis of the camera data can be laborious, but labour can be reduced by public participation using citizen science (Anton et al., 2018a) or automated software (Falzon et al., 2020). However, the use of camera traps also involves a variety of potential problems that must be considered when planning the study. These problems include trap avoidance induced by flash use (Schipper, 2007), infrared illumination and trigger sound that may be perceptible for the target species (Meek et al., 2014), difficulties in identifying animals on pictures (Meek et al., 2013), and production of biased indices of abundance (Sollmann et al., 2013). Furthermore, technical and operational limitations when using camera have to be acknowledged (Meek et al., 2015; Newey et al., 2015).

1.4 Study aims and predictions

Detecting rats that have persisted in areas of sustained control effort and understanding their behaviour around control devices will help to inform management. This thesis sets out to determine how camera traps can be used to establish a rat relative abundance index and if a more informative estimate for true density can be obtained. My study also sets out to understand behaviour of rats around detection devices.

My major thesis aims are to:

1. **Determine how camera traps can be used to measure rat abundance**

   There is evidence that ship rats meet and forage together (Dowding & Murphy, 1994). Video footage from Aotea has shown rat couples foraging together around detection devices (pers. obs.) and groups of up to three individuals were observed foraging around green sea turtle nests in French Polynesia (Gronwald et al., 2019). Therefore, I predict that counting individual rats in videos will result in a higher rat relative abundance index than counting the number of videos that show rats.

   Individual rats can only be detected once by a kill trap and are then removed from the population. However, a single rat can trigger a camera multiple times. Therefore, a camera trap index is expected to be higher than a kill trap index. Camera traps may detect more rats than live traps (De Bondi et al., 2010). I predict that during times of high abundance both indices will show similar results and that, once abundance is reduced due to sustained trapping, the camera traps will be better in detecting the remaining rats, including trap shy individuals.

Recent studies have estimated density of unmarked mammals using camera traps (Chandler & Royle, 2013; Manzo et al., 2012; Nakashima et al., 2020). I will test three novel statistical models using camera trap data from high density rats and compare the results to estimates from a capture-recapture study, an established method to estimate density. I predict that the tested models will confirm high rat density. If results from the new models are comparable to the capture-recapture density estimates, camera traps can become the preferred method over live trapping due to simplified data collection.

2. **Determine factors that affect rat behaviour around control devices, and hence detectability?**

Rats can avoid a new device in a familiar environment for an extended period of time (Barnett, 1988; Wallace & Barnett, 1990). However, the use of tracking tunnels for rat monitoring is a common method that relies on rat-device interactions in the first night after deployment. I predict that ship rats will interact with newly deployed self-resetting kill traps in the first night.

Sustained trapping is expected to remove naïve and explorative individuals first. Once abundance is reduced the population is likely to mainly consist of cautious rats and individuals that are not attracted by the kill traps. Therefore, I expect that, after a peak of interactions and kills at the beginning of a control operation, the number of rat-trap interactions will decrease over time.

Asymmetric interspecific competition between Pacific rats and *R. tanezumi* may be one reason for failed Pacific rat detections (Griffiths et al., 2014). I predict that dominant ship rats can restrict the access of Pacific rats to live traps, which would lead to a lower detection probability.

The main factor controlling population density is food availability, which differs among seasons (Wilmshurst et al., 2021). I predict that at times when rat abundance is seasonally high and food abundance low, more trap encounters, interactions, and triggers will be observed than at times with lower rat abundance.

1.5 Thesis structure

This thesis is presented in six chapters. A general introduction (chapter 1) gives contextual information about invasive species management and the use of cameras in ecology to form a background knowledge to understand the context of and the link between the following research chapters. The main research is presented in four independent chapters (2, 3, 4 and 5). These four chapters can be read and understood by themselves. The reader should be aware that this involves a low degree of repetition in the introductions in each chapter. The final chapter (6) summarises and discusses the key findings of the main research chapters. References for all chapters can be found after the final chapter. A summary of the chapters is given below:

Chapter 2: Measuring rat relative abundance using camera traps and digital strike counters for Goodnature A24 self-resetting traps

Invasive ship rats pose a threat to the biota of Goat Island (9.3 ha), New Zealand. In June 2016 I installed 10 Goodnature A24 CO2 powered self-resetting rat and stoat traps equipped with digital strike counters (Goodnature Ltd., Wellington, NZ) to control rat numbers on the island. The self-resetting traps were monitored with motion-activated cameras to develop a measure of rat abundance from camera traps. All devices were checked on 10 occasions from August 2016 to October 2017. The videos revealed high rat activity on the island, which reduced over time. Counting only the number of videos that showed rats did not result in any loss of information when compared to more laboriously counting individual rats in videos and was therefore the preferred method for obtaining an index of relative rat abundance. I also found that digital strike counters designed to record the number of times an A24 is triggered, accurately reflected the number of individuals killed by A24s. However, measuring rat abundance in number of rat videos per 100 camera nights was shown to be of greater value when rat abundance was low and A24s failed to detect the remaining individuals.

Chapter 3: Estimating small mammal density using camera traps: testing theory in the field

Knowledge about animal population density is essential for ecologists and wildlife managers. A common method to estimate small mammal population density is capture-recapture analysis, but this is labour intensive and requires individual marking and handling. Camera traps are a new popular alternative monitoring tool, but individual distinction of small mammals is typically not possible. I tested three proposed methods to estimate population density from unmarked animal detections using camera traps. A capture-mark-recapture study using 50 live traps estimated population density of Pacific rats on Reiono, a 22 ha islet of Tetiaroa atoll. Eight camera traps were also operated within the trapping grid. Video data were used to estimate population density of Pacific rats with three different novel statistical methods. I compared these estimates to the results of the commonly used spatially explicit capture-recapture model SECR (Efford et al., 2009a). The random encounter model (Rowcliffe et al., 2008) failed to provide biologically realistic density estimates due to difficulties in estimating animal movement speed. The spatial model after Chandler and Royle (2013) estimated a population density lower than the capture-recapture analysis. Low precision was identified as problematic when using the model after Chandler and Royle (2013), presumably due to an insufficient number of cameras. The random encounter and staying time model (Nakashima et al., 2018) appeared to be sensitive to different staying times and provided a similar estimate to the SECR model for May 2018, but underestimated density for June 2018. Parameterisation of the models was difficult, because the information needed, e.g. rat movement speed, day range, activity times, were not available or difficult to obtain. Further field trials are needed to evaluate model performance in different densities and with different target species.

Chapter 4: Trappability of low density invasive rats

On Aotea/Great Barrier Island, New Zealand, two invasive rat species, Pacific rats and ship rats pose risks to the ecosystems and challenge the management in two sanctuaries. At Glenfern Sanctuary (83 ha) an eradication has successfully removed ship rats and a predator proof fence prevents reinvasion. However, Pacific rats persist in low numbers. At Windy Hill Sanctuary (770 ha) intensive rodent control maintains both species at low abundance despite ongoing reinvasion. A capture-mark-recapture study was conducted between February and April in 2016 and repeated between July and September 2017 to determine population densities, confirm species composition and analyse the effects of time, population density and interspecific competition on rat behaviour. Live traps were monitored with camera traps to analyse behaviour of rats around traps. Population density and detection probability of Pacific rats varied between times reflecting seasonality in food abundance and rat reproduction. The detection probability of Pacific rats also differed between sites, being higher at

Glenfern Sanctuary than at Windy Hill Sanctuary, presumably due to interspecific competition with ship rats. Where Pacific rats were the sole species they were captured in traps in the first night. However, in coexistence with ship rats Pacific rat detection was delayed by at least ten days. Population density influenced the number of trap encounters and interactions but did not significantly influence the capture rate. Interspecific competition was identified as problematic for monitoring, controlling and eradicating Pacific rats.

Chapter 5: Behaviour of invasive ship rats, *Rattus rattus*, around Goodnature A24 self-resetting traps

Invasive ship rats are a major threat to the native species and ecosystems of islands. I used 10 self-resetting traps (A24 rat and stoat traps, Goodnature Ltd., Wellington, NZ), along with existing single kill DOC200 traps at two devices per hectare on a 9.3 hectare island in New Zealand to reduce rat numbers and ideally achieve eradication. Each self-resetting trap was monitored with motion-activated cameras to analyse rat behaviour and A24 kill numbers were documented using Goodnature digital strike counters. The traps were checked on 10 occasions from August 2016 to October 2017. The videos documented initial high rat activity on the island, which reduced over time following initial trapping success. An immediately obvious neophobic response towards the A24 traps was not observed. Rats interacted with the A24 traps within hours after initial deployment and 60% of the traps were triggered in the first night. After three nights, all traps were triggered at least once. While rats interacted with the traps at all times of the year the number of observed trap-triggers was relatively low. High number of interactions resulted in high kill numbers in late spring when population size was increasing and seasonal food abundance had not yet reached its peak. A second peak was observed in late autumn when rat abundance was presumably high. Recruitment of naïve individuals was a probable cause for high kill numbers during the breeding season. In winter, when rat abundance was presumably lower, a few individuals were the likely cause for a high number of interactions while kill numbers were low. A knock-down (i.e. suppression from high to low abundance) of rats using both trap types was achieved in the first 100 days. However, kill numbers of A24s declined over time. After the initial suppression, the number of rats killed was insufficient to offset intrinsic population growth and reinvasion from the adjacent coast, thereby preventing eradication.

2

Measuring rat relative abundance using camera traps and digital strike counters for Goodnature A24 self-resetting traps

2.1 Introduction

Early detection of invaders as well as invasive species control and eradication programmes require reliable monitoring (Pichlmueller & Russell, 2018). In particular, monitoring tools must be able to detect individuals at low population densities and species which are reluctant to interact with detection devices or are elusive. In New Zealand, tracking tunnels are a widely used method for monitoring relative abundance of rodents and mustelids. Interaction is minimised to walking through the tunnel and the tunnels are perceived as the better alternative to snap traps (Gillies & Williams, 2013). However, ship rats (*Rattus rattus*) showed hesitation in stepping on the ink pads in a pen trial, a behavioural response that can potentially affect monitoring rats at low population density (Cooper et al., 2018). The standard protocol advises a distance of 50 m between tunnels and using multiple lines (Gillies & Williams, 2013); however, at small sites the number of tracking tunnels would be low or the distance between the tunnels would be too small. Various studies have shown that ship rats have an average travel distance of more than 100 m (Dowding & Murphy, 1994; Harper & Rutherford, 2016; Hooker & Innes, 1995).

Motion-activated trail cameras are alternative detection devices which can optimize detectability at low population density or of species or individuals with reluctance to interact with detection devices (Karanth & Nichols, 1998; Larrucea et al., 2007; Mace et al., 1994; Zimmermann et al., 2013). The majority of studies which have used camera traps targeted large mammals (Burton et al., 2015). The detection of small, fast moving animals can be technically challenging and is influenced by the sensor and flash type used (Glen et al., 2013). However, camera traps have been successfully used to detect presence, measure activity, and document behaviour of small rodents (Gronwald et al., 2019; Mills et al., 2016; Rendall et al., 2014). Camera traps have even been more successful in detecting small mammals than traditional live or kill trapping (De Bondi et al., 2010; Glen et al., 2014; Welbourne et al., 2015). The ongoing technological improvement of trail cameras, including sensors, trigger speed, and resolution, increases their suitability for surveys of small species.

Obtaining an estimate for the number of target animals in the study area is important for both scientific studies as well as conservation projects. Motion-activated game trail cameras extend the tool set for monitoring animal abundance. Population density estimates using established capture-recapture models can be used when individuals can be identified on a picture. Camera data were used to estimate the population density of tiger (*Panthera tigris*) in India, a secretive species which only occurs at low population densities (Karanth & Nichols, 1998). However, many species cannot be identified to the individual on a photo. Therefore, many studies state an index of relative abundance (Güthlin et al., 2014; Rovero & Marshall, 2009). An index of abundance is easier and cheaper to obtain than performing a capture-recapture study for robust population density estimates (O’Brien, 2011). However, cameras have high initial costs to purchase and the unautomated analysis of videos is labour intensive (Anton et al., 2018b). The development of software which uses artificial intelligence to identify the target species in a photo can significantly reduce data processing time (Falzon et al., 2020).

Here we evaluate two different methods for obtaining an index of abundance from camera footage for invasive rats based on 1) the number of videos showing rats per time unit, and 2) the number of rats in videos per time unit. Rat population density at the study site was unknown. The comparison of the two methods sets out to determine if the obtained indices of rat relative abundance differ and if the difference changes when rat numbers are reduced due to ongoing kill trapping. We then also evaluate the reliability of a digital strike counter for characterising killed individuals at Goodnature A24 CO_2 powered self-resetting rat and stoat traps (Goodnature Ltd., Wellington, NZ, subsequently referred to as A24s) where carcasses do not necessarily remain at the trap and therefore cannot be counted. Finally, we compare indices of abundance from digital strike counters and camera traps to assess if camera traps are a suitable tool for monitoring rat abundance and trends in it.

2.2 Methods

2.2.1 Study site

Goat Island (Te Hāwere-a-Maki; 36°15′54.8″S, 174°47′51.1″E) is a small island of approximately 9.3 ha. It lies in the Cape Rodney-Okakari Point Marine Reserve in Leigh on the east coast 70 km north of Auckland (Fig. 2.1). The island has small breeding colonies of seabirds: grey-faced petrels (*Pterodroma gouldi*) and little penguins (*Eudyptula minor*). Ship rats are the only invasive mammal permanently present on the island. During low tide rocks are exposed along the coastline and reduce the distance between the mainland and the island to less than 100 m. This enables ship rats to swim across and imposes a risk of an incursion. Maintaining Goat Island rat-free has proven difficult and ship rats remain abundant (Pichlmueller & Russell, 2018).

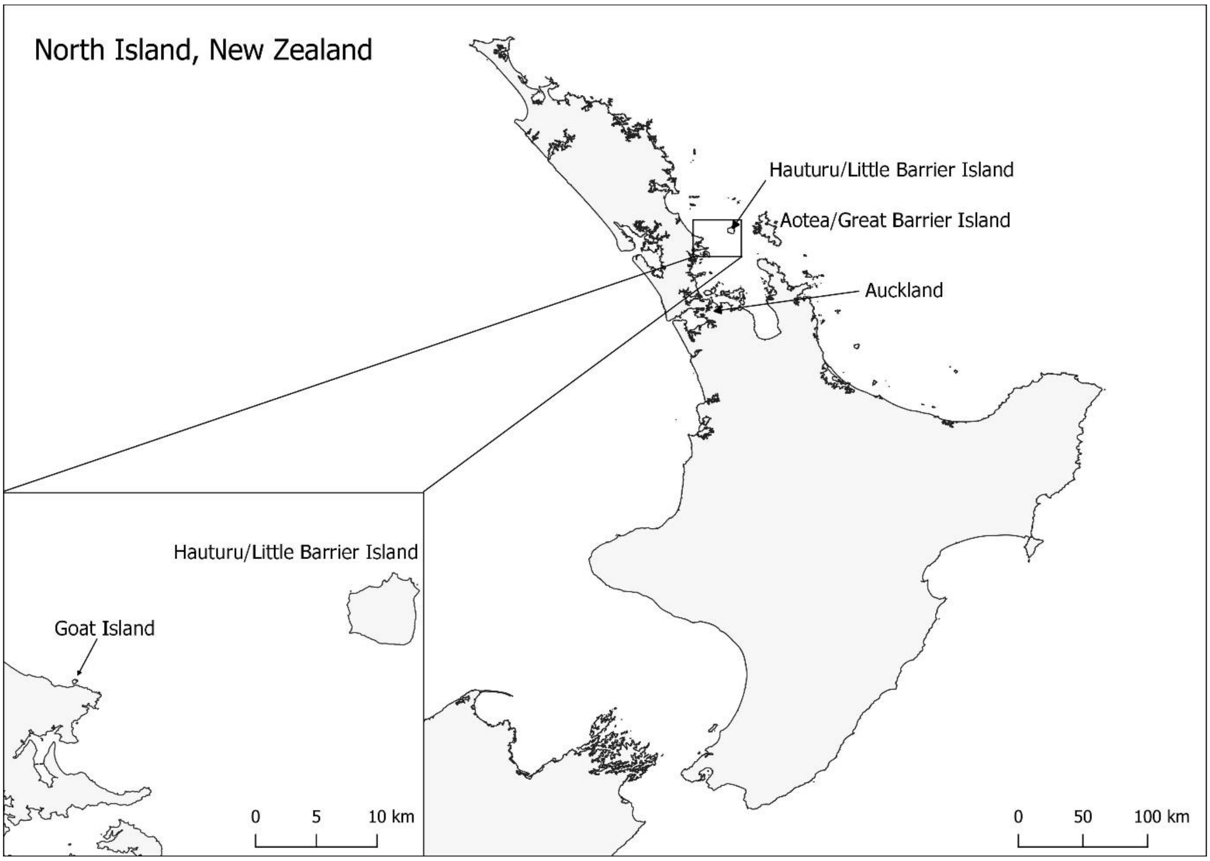

Figure 2.1. Goat Island and adjacent mainland sites. Leigh Marine Laboratory buildings indicated. Rectangle indicates the location of Goat Island in the North Island of New Zealand.

2.2.2 Cameras and A24s

Ten A24s were placed across the island in July 2016 at an average distance of 75 m (range 45–89 m). Each trap was equipped with a digital strike counter. The strike counters sense the vibration of the triggering of the trap and briefly displays the number on a digital LED display and records the number of times the trap fires. The traps were baited with Goodnature Automatic Lure Pumps (ALP)-chocolate formula for rats. An ALP contains 55 g of non-toxic bait slowly dispensed continuously over 6 months. The traps were placed vertically on large tree trunks approximately 12 cm above the ground following the manufacturer's guidelines. During the 15-month field trial, from August 2016 to October 2017, the ALPs were replaced after 6 months in January and July 2017. Gas cartridges were replaced when the strike counter showed 20 or more. The traps were on average checked every 49 days (range 27–63 days).

Each A24 was monitored with a trail camera with PIR motion-activated sensor (Bushnell Trophy Cam HD 8MP; Bushnell, Cody, USA) to record rat activity around the devices. The cameras were attached to a tree, using adjustable mounts (Slate River EZ Aim Game Camera Mount), pointing to the trap at a 45°-angle from a height of 145 cm and a distance of c. 1.5 m. Slight variations were caused by the difficulty of the terrain, e.g. slopes, dense vegetation, and the availability of trees suitable for mounting. This set-up was chosen to limit the sensor field to approximately 1 m to each side of the trap to avoid the cameras being triggered by rats or movements which are too far from the trap, and to keep the camera at a height suitable for regular checks. The detection rate when using cameras with PIR sensors is related to the body mass of the detected animal (Lyra-Jorge et al., 2008). Small and fast or very slow-moving animals might not be detected (Glen et al., 2013). Therefore, the highest sensor sensitivity was used for all cameras. Cameras were set to record a 60-second video when triggered with a one second interval between videos.

2.2.3 Measuring rat abundance

An index of abundance is commonly stated as captures per 100 corrected trap-nights (Nelson & Clark, 1973). In this study the equation was simplified. Camera traps and A24s do not produce lost trap-nights because they always retain the ability to detect individuals. The trap-nights were extended to trap-days which cover 24 hours. Even though the main activity time of rats is during the night they can be and are active during the day (M. Gronwald pers. obs.). The resulting equation is:

$$\text{Index of abundance} = \frac{\text{Captures} \times 100}{\text{Trap-days}} \qquad (1)$$

2.2.3.1 A24 index

Digital strike counters on the A24s register when the trap is triggered and the counts are assumed to equal the number of rats killed. These data can be used to calculate an index of abundance that is comparable to an index of abundance based on kill trap data with the advantage that the A24s do not have to be checked as frequently as single kill traps. The display of the digital strike counter blinks when the A24 is triggered. This makes a trigger count visible in the video. Only videos showing the moment when a rat triggers the A24 were analysed. Records were made if the rat was hit and/or if the strike counter was triggered to evaluate the reliability of the digital strike counts. Even though the 'capture' rate for predators are higher with cameras than kill traps (Glen et al., 2014), the strike counters have the potential to be a reliable and relatively cheap monitoring tool for Goodnature A24s.

2.2.3.2 Video index and rat index

Two different ways of counting can be used to determine an index of rat relative abundance from camera footage, either the number of rat videos (i.e. a video where one or more rat is present at any time) per 100 camera-days (video index) or the number of rats (i.e. the maximum number of rats observed at once in a video) per 100 camera-days (rat index). A video can show more than one rat. The maximum number of rats was documented for each video. If there was a rat at the beginning of a video leaving the field of view and a rat entering the video later in the same video it was counted as one animal unless they were obviously two different rats. Individuals within one video could be distinguished from each other when they were visible at the same time or when distinct characteristics were identifiable, e.g. adult/juvenile, tail/no tail. Determining the rat index is much more labour intensive than the video index. Therefore, an evaluation of the difference between the two indices will determine how much workload is needed for future video analyses.

2.2.4 Statistical analysis

The rat index and the video index were compared with a paired *t*-test to answer the question if the rat index differs significantly from video index. A Pearson's product-moment correlation test was run to analyse the relationship between the index of abundance from the video analysis and the A24 index based on the digital strike counts. All analyses were conducted in R (R Core Team, 2019).

2.3 Results

A total of 7155 videos, more than 119 hours of footage, from 2161 camera days were analysed. Seventy-four percent of the videos recorded rats.

2.3.1 Comparison between rat index and video index

There were only minor differences in the index values between rat index and video index. The maximum number of rats in a video was four. The average number of rats per session that could be seen in a video with rats was 1.03 rats video^{-1} (range 1–1.18) (Table 2.1). The two indices did not differ significantly from each other ($t = 1.403$, df= 9, $p = 0.19$). Since usually only one rat was ever seen in a video, the video index is close enough to the rat index to be chosen as a measure of abundance without losing information but easier to obtain.

Table 2.1. Number of rats and rat videos per 100 camera days from August 2016 to October 2017 on Goat Island.

Recording period	**Rats**	**Rat videos**
August 2016	1282	1182
September 2016	156	156
November 2016	465	450
January 2017	164	159
March 2017	131	129
May 2017	204	195
June 2017	153	152
July 2017	219	219
August 2017	183	181
October 2017	189	188

2.3.2 Reliability of the digital strike counts

The moment of a rat triggering an A24 was visible and audible in 70 videos, in further 24 videos the activation of the strike counter was missed due to delayed recording. In 60 videos the rat was obviously hit lethally. The strike counters recorded 92% of the kills correctly (i.e. were triggered when a rat was killed), slightly underestimating the actual number of kills confirmed by the video footage. In the remaining 10 videos where the rat was not obviously hit lethally, the strike counters still recorded the triggering 30% of the time, resulting in overestimated kill counts, although these cases were few. However, the overall counts correlated with the actual kill numbers well, as these two opposing errors of count tended to balance each other out. Ultimately, there was a slight underestimation from the strike counters with 97% of all kills being reflected in the strike counts (Table 2.2), i.e. 58 strikes for 60 kills. Taking the small margin into account, the strike counter numbers were an appropriate equivalent to the number of rats killed by the A24s.

Table 2.2. Number of Goodnature digital strike counts on A24s. False negatives (top row) are observed kills which were not registered by the digital counters. False positives (bottom row) were observed strikes which did not kill the individual but were counted by the digital counter.

	Visible in video	**Digital strike counts**	**Digital strike as a % of recorded strikes**
Kill	60	55	91.67
No kill	10	3	30.00

2.3.3 Comparison of indices of abundance

The video index was the highest in the first month after trap deployment (Figure 2.2) and after three months it remained relatively constant for the rest of the study. The A24 index showed a similar pattern in the first three months but then fell to almost zero at the end of the study, 0.7 kills per 100 trapping days in October 2017. Unlike the A24 index, the number of rat videos stayed at a constant high level (Figure 2.2).

There was no significant evidence of a correlation between the two indices (r = 0.36, n = 9, *p* = 0.34) (Figure 2.3)

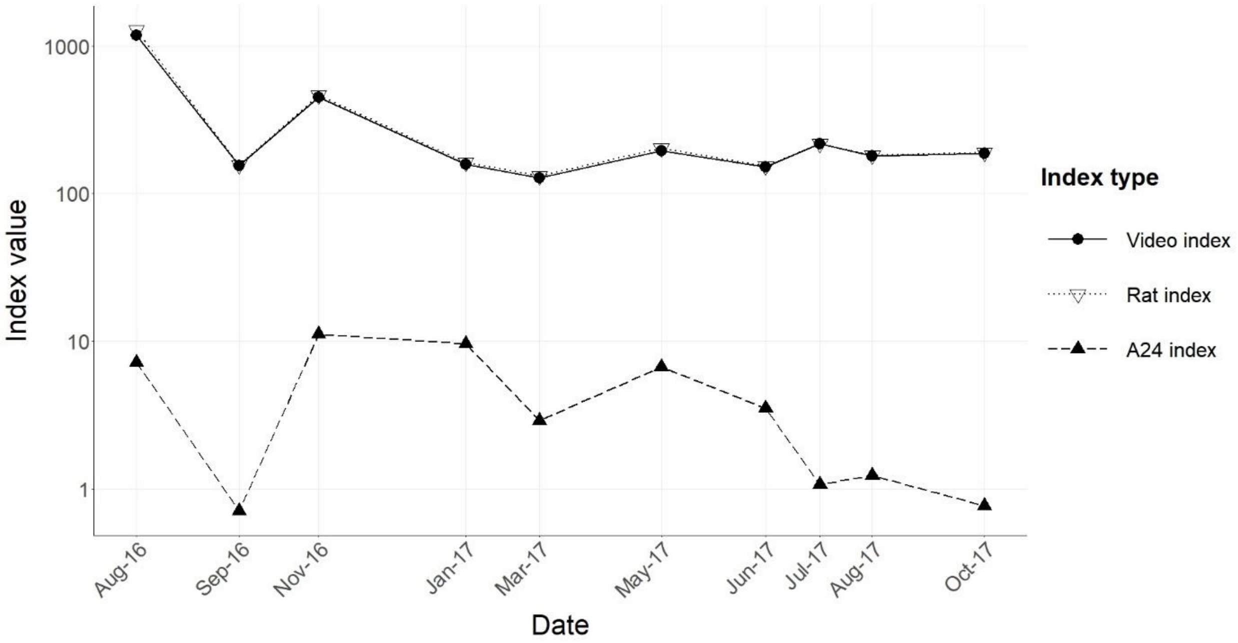

Figure 2.2. Indices of ship rat relative abundance on Goat Island plotted against time from August 2016 to October 2017. A24 index represents Goodnature digital strike counts per 100 trap days and video index represents number of rat videos per 100 camera days.

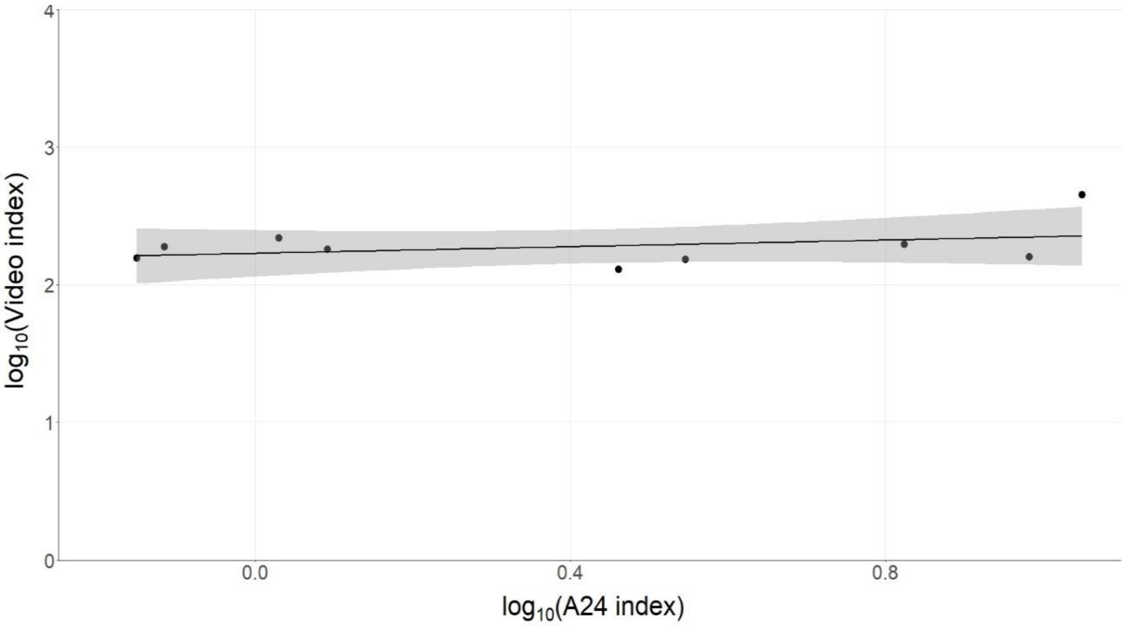

Figure 2.3. Correlation between A24 index based on digital strike counts and video index for Goodnature A24s monitored by cameras on Goat Island, Sep 2016–Oct 2017, both log10-transformed to remove high leverage effects of large values. Pearson's product-moment correlation: $r = 0.36$, $n = 9$, $p = 0.34$.

2.4 Discussion

When measuring the abundance of rats on Goat Island the video index and the rat index differed only to a small margin. However, obtaining the rat index involved more work. The whole video had to be watched to count all possible rats and the identification of individuals costed extra time and would always contain an element of subjectivity. The time used for the analysis went beyond the actual footage time and increased the work nearly ten-fold. The difference between the indices could be larger when the population density is higher, i.e. many more than one rat seen per video. A comparison with other temperate ecosystems with similar densities as well as studies in tropical environments where densities can be many times higher than in New Zealand are needed to confirm the widespread suitability of a video index for rat abundance.

Regarding labour costs in research, as well as limited human resources in community projects, reducing the work time can be crucial. Categorising the videos into rat presence and absence was a quick and useful approach and did not lose essential information compared to distinguishing individuals in the videos. Besides time saving, video categorising can be undertaken by any person who is capable of identifying a rat. This enables the involvement of non-professionals in the analysis of huge data sets in academic research (Citizen Science) which is already in use, e.g. in monitoring biodiversity, abundance or pest detection (Anton et al., 2018a; Chandler et al., 2017). Furthermore, automated identification technology in development (e.g. Thermal Imaging: https://cacophony.org.nz/) has the potential to even further increase the number of recordings that can be processed.

While a kill by a single kill trap can be confirmed by the presence of a carcass or parts of it, the only consistent evidence at an A24 is the strike counter number. The numbers acquired from the digital strike counters were generally a suitable representation of the actual number of individuals killed. When a rat is killed by the self-resetting A24 its body drops to the ground. However, the rats can still move a few metres away from the trap and roll out of the field of view in spasms. In addition, rats, ruru (*Ninox novaseelandiae*), and kāhu (*Circus approximans*) are potential scavengers (M. Gronwald pers. obs.) and were present on or nearby Goat Island. The strike count numbers have shown to slightly underestimate but approximately match the real number of kills closely enough to be seen as a reliable source of information. Ogden (2018) has described an underestimation by the counters of 19% on Aotea/Great Barrier Island. However, the data were based on counting carcasses around the trap and data from a malfunctioning strike counter might also have been included. It should be noted that the strike counts can only be used to estimate relative abundance in areas with only one target species and when it is unlikely that non-target species can trigger the trap. A general advantage of the strike counters is that they provide information suggesting when the gas cartridge has to be replaced. In high population density of the target animals the traps might be triggered more than 24 times within 6 months, which is the maximum trigger number advised for the cartridges per manufacturer. Video data and kill numbers on Goat Island have given different information about rat abundance. The correlation between rodent relative abundance indices from different devices are influenced by population density and behaviour (Blackwell et al., 2002; Nathan et al., 2013). Relative abundance estimates from camera traps strongly correlated with indices obtained from traditional methods for a range of large herbivores (Palmer et al., 2018; Rovero & Marshall, 2009). On Aotea/Great Barrier Island true density estimates for invasive rats from live trapping data also strongly correlated with an index of relative abundance from camera traps

(M. Gronwald, unpubl. data). The population density on Goat Island was expected to decline over time during this study due to the sustained trapping effort. With rat trapping ongoing at the coastline of the adjacent mainland the rate of incursions was assumed to be low. Even before the trapping along the mainland coast was started, incursions to Goat Island were not the driving factor in population growth (Pichlmueller & Russell, 2018). The A24s failed to detect remaining individuals on Goat Island towards the end of this study. The camera traps revealed that the rat removal rate was too low to sufficiently reduce rat activity. Long term trials have shown a reduced kill rate for A24s when initially successful trapping reduced abundance to low levels (Carter et al., 2016; Carter et al., 2019; Gilbert, 2018). Therefore, camera traps were a valuable tool to gain information about rat abundance on Goat Island.

Motion-activated cameras, as a non–invasive detection tool, circumvent the need for device interactions. At the moment the most common method in New Zealand is the use of tracking tunnels with ink cards which require interaction between the individual and the tunnel. The animal has to enter the tunnel and can show reluctance in the first night (Cooper et al., 2018). Cameras don’t intervene with the natural behaviour of the rats. The distance between detector and individual can be several metres, while animals may sense cameras through audible and visual cues (Meek et al., 2014), it does not necessarily influence the detection rate (Henrich et al., 2020; Taggart et al., 2019). Ball et al. (2005) have described the probability of detection as the product of the probability of encountering a device and the probability of interacting with the device. When using cameras, the probability of interaction can be removed from this equation. However, technological imperfection cause error. Camera specifications, e.g. different types of sensors or trigger speed influences the detectability in a negative way (Glen et al., 2013). Standardising the field of view, sample size and trapping distance in a best practice protocol for the use of cameras in monitoring the abundance of invasive mammals is needed to enable the comparison of results across study sites and ecosystems. In a conservation context a reduced probability of detection due to the lack of interaction with devices is problematic. Not detecting individuals during ongoing control as well as missing invaders in a predator-free ecosystem can lead to wrong decision making in the management of the area, e.g. reducing control effort or not responding to incursions In addition, simplifying the camera monitoring methodology allows the involvement of groups without a specific knowledge background, e.g. community groups, schools, etc.

We showed that for an index of abundance based on video data the number of rat videos can be used instead of the number of individuals visible in the videos without significant loss of information. The video index is preferred to the rat index because it is easier and cheaper to obtain. Although videos were used here the results are expected to hold true for photos as well. Digital strike counters were proven to be a reliable source of information for the number of individuals killed by A24s in our study, where ship rats were the only target species and interactions of non-target species with the traps were unlikely. However, the cameras were better than A24s in detecting rats once abundance was reduced after sustained trapping. The camera traps were a suitable tool for monitoring invasive rats at different abundances on Goat Island.

2.5 Acknowledgements

We thank Edin Whitehead, Carlos Abrahão, Lea Stolpmann and Araceli Samaniego for help with data collection in the field. Thanks to Ngāti Manuhiri and the Department of Conservation for supporting the work on Goat Island. This study was conducted under animal ethics permit R1677 from the University of Auckland. This study was funded by the Avian Research Scholarship from the University of Auckland to MG and the Rutherford Discovery Fellowship RDF-UOA1404 to JCR.

3

Estimating small mammal density using camera traps: testing theory in the field

3.1 Introduction

Knowledge about population size is important for understanding population processes and answering ecological questions and crucial for managing wildlife populations. Population abundance can be of importance when a population size needs to be maintained or increased, e.g. in the fishery (Botsford et al., 1997), game industry (Bleier et al., 2012), and the protection of endangered wildlife or when population size needs to be decreased, like in management of pest populations. When removing invasive species, population density helps determine what effort is needed to meet management targets. In the planning of invasive mammal eradications population density is useful to determine the best time for the operation and to detect risks, e.g. density dependent behaviour (Keitt et al., 2015). From a planning perspective it is desirable to obtain these data with a simple, cost efficient method.

However, it is usually not possible to count every individual of a population. A robust tool when estimating population abundance in animals is capture-mark-recapture (Borchers et al., 2002; Seber, 1982). Population density, the number of individuals per unit area, can be derived when the sampling area is known, but the spatial component when live-trapping animals has been neglected in earlier models. Borchers and Efford (2008) developed a spatially explicit maximum likelihood method for estimating population densities in capture-mark-recapture studies, which is now a benchmark of studies of small mammal population density .

Camera traps have more recently been used to answer questions in animal ecology, behaviour and conservation (Gilbert et al., 2020; Nichols et al., 2011). Camera traps are mostly used to monitor presence or abundance (Burton et al., 2015), especially if a species has a large home range, is rare, elusive or difficult to trap and handle. Data from camera traps can be used for spatially explicit models when individuals can be identified on the camera footage. Mace et al. (1994) have used sightings of grizzly bears (*Ursus arctos horribilis*) from camera traps to estimate the population size. Some large feline predators, e.g. tigers (*Panthera tigris*) (Karanth & Nichols, 1998), leopards (*Panthera pardus fusca*) (Wang & Macdonald, 2009), jaguars (*Panthera once*) (Borchers et al., 2014; Sollmann et al., 2011), and ocelots (*Leopardus pardalis*) (Trolle & Kéry, 2003) can be individually identified by distinct natural markings on pictures and population density can be estimated from camera trap data alone using capture-recapture models. However smaller animals cannot be reliably identified to the individual without artificial marking, e.g. ear tags, dyed or clipped fur.

When individual identification is not possible, an index of abundance is a typical measure that allows one to monitor changes within a population over time (O'Brien et al., 2003). Camera traps were used alongside the traditional method of faeces counts to monitor relative abundance of red fox (*Vulpes vulpes*) in Germany. Both methods resulted in similar indices of relative abundance (Güthlin et al., 2014). Carbone et al. (2001) analysed 19 different studies of tiger abundance and found the capture rate of camera traps to correlate with an independent population density estimate. But indices of abundance from trap capture rates are controversial because they do not account for variations in detection probabilities and are strongly affected by the study design, e.g. camera placement (Sollmann et al., 2013). Therefore, population density cannot be estimated from camera data in a simple way (Jennelle et al., 2002). Different approaches have been developed to estimate population density using stationary camera traps without the need of individual identification, and two of these have the potential for widespread application. Rowcliffe et al. (2008) have adopted a two-dimensional random encounter model from physics which describes the contact rate between gas molecules and fitted it to describe the contact rate between animals and traps. Nakashima et al. (2018) developed a model that estimates density from the mean number of detections by a camera trap and staying time of individual animals in a predetermined detection zone. Chandler and Royle (2013) use spatial detections of animals and utilise the correlation between counts to estimate population density.

On Tetiaroa Atoll, French Polynesia invasive rats pose a risk to the native ecosystem and mediate an ongoing decline in seabird fauna (Russell et al., 2011). To counteract the impacts, the atoll managers plan to eradicate rats from the whole atoll (Russell et al., 2016). The first phase involved the eradication of Pacific rats (*Rattus exulans*) from one of the twelve islets, Reiono, in 2018. As part of the eradication, a capture-mark-recapture study was conducted in conjunction with my study to estimate population density (Samaniego et al., 2020a). My study sets out to employ the methods for population density estimation for unmarked animals by Rowcliffe et al. (2008), Nakashima et al. (2018), and Chandler and Royle (2013) and test them against density estimates from a spatially explicit capture recapture (SECR) analysis. With SECR being a standard method for estimating population density, SECR results are used as the benchmark for methodological comparison, although the estimates can also contain bias (Efford, 2014). My study is the first to compare the four methods with data from the field and the first test for small mammals and high densities. By doing so, my study determines if camera traps can be used as a substitute for live trapping of small mammals in high population densities.

3.2 Methods

3.2.1 Study Area

Tetiaroa is a tropical coral atoll 50 km north of Tahiti, French Polynesia (Figure 3.1). The atoll consists of 12 forested coral islets. Two invasive rat species inhabit islets of Tetiaroa: ship rat (*R. rattus*) and Pacific rat. While Pacific rats have been present for more than a hundred years, ship rats were introduced in the 1970s when modern development on Tetiaroa started (Russell et al., 2011). Islets are in close proximity to each other from Onetahi in the west through Tiaraunu in the northwest to Oroatera in the northeast (Figure 3.1). On all of these islets ship rats and Pacific rats coexist, while the more isolated islets Rimatuu, Tahuna Rahi, Reiono and Aie are only inhabited by Pacific rats (Russell et al., 2011).

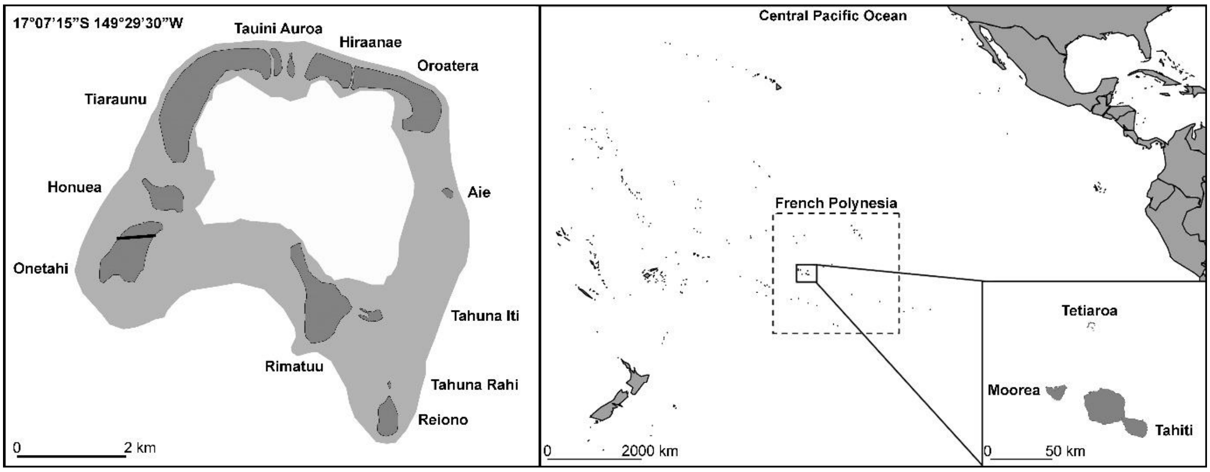

Figure 3.1. Map of Tetiaroa atoll, Society Islands, French Polynesia (Russell et al., 2011)

Reiono (22 ha) is a flat, uninhabited islet at the southern end of the atoll. The forest on Reiono is dominated by native Pisonia grandis. Introduced coconut palms

(*Cocos nucifera*) can be found on most parts of the islet. It is an important nesting site for native seabirds, with breeding colonies of black noddy (*Anous minutus*), white tern (*Gygis alba*), brown noddy (*Anous stolidus*), and red footed booby (*Sula sula*) (Russell et al., 2011).

3.2.2 Live Trapping

The population density of Pacific rats on Reiono was estimated as part of a rat eradication programme (Samaniego et al., 2020a). Rats were captured in two sessions with 5 trap nights using cage traps from 2 - 7 December in 2017 and 4 trap nights using Sherman traps from 16 - 20 June in 2018. Traps were baited with pieces of fresh coconut and placed on top of an upturned 5 litre bucket to reduce interference by abundant land crabs. A total of 50 traps were arranged in a grid of 5 lines with 10 traps per line (Figure 3.2). The distance between traps was 10 m and the grid covered 0.36 ha. Captured rats were weighed, sexed and fitted with a metal ear tag carrying a unique number.

A total of 70 adult rats were fitted with radio collars in August 2018 as part of the rat monitoring for the eradication (Samaniego et al., 2020a). Three female and one male rat were located multiple times using radio telemetry between 12 - 18 August 2018. Time and coordinates of multiple consecutive bearings where the collared rat was seen were noted for each rat.

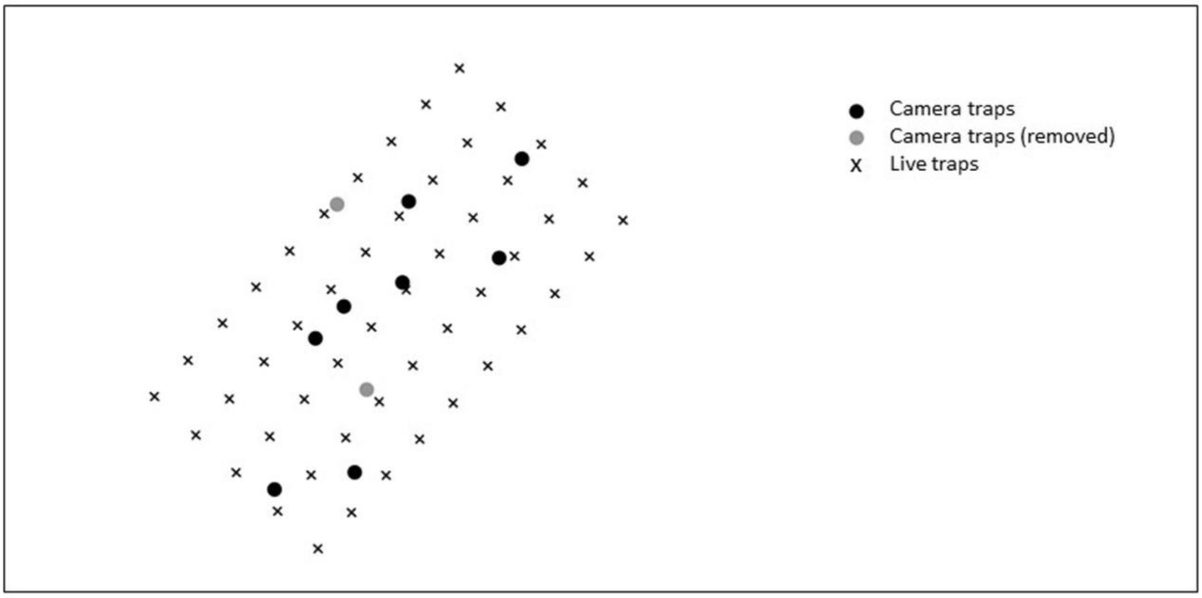

Figure 3.2. North-oriented schematic map of camera trap locations within the live trapping grid on Reiono. Grey dots mark cameras which were later removed from the analysis due to malfunction. Distance between live traps is 10 m.

3.2.3 Camera Traps

Ten Browning Spec Ops Advantage trail cameras were set within the live trapping grid (Figure 3.2). A previous study using the random encounter model (see below) successfully used as few as 5 cameras per site (Rovero & Marshall, 2009). Density estimates from the random encounter and staying time model (see below) were unbiased even when research effort was small (Nakashima et al., 2018). The exact camera position was determined by the availability of a tree suitable for camera mounting. The camera mounts were screwed into trees approximately 145 cm above ground facing straight downwards. The vertical view installation has the highest detection rate for small mammals (Smith & Coulson, 2012). The dimensions of the detection zone were measured by triggering the camera and taking a picture of two measure tapes showing width and height of the recorded rectangular picture. The cameras were set to record a 20 second video with the highest available resolution when triggered and 1 second delay between videos. Contact between a rat and the camera were defined as independent when the time difference between two videos was more than 25 seconds. A time difference less than 25 seconds only occurred when a rat did not leave the detection zone thereby triggering the camera several times consecutively. Also, two cameras malfunctioned and repeatedly recorded three videos in a row resulting in 22 seconds time difference between the videos. These two cameras were subsequently excluded from further analysis. The cameras were equipped with 8 GB SD cards. Cameras were operated from 3 - 10 May 2018 and from 13 - 16 June 2018.

3.2.4 Statistical Analysis

Population density estimation for Pacific rats on Reiono from three different models were compared. All analyses were carried out in R Version 3.4.0 (R Core Team, 2019).

Spatially explicit capture-recapture model (SECR)

Population density was estimated using a spatially explicit capture recapture model from the live-trapping data. The half normal detection function in SECR models is shaped by the two parameters *g0* (detection probability at home range centre) and σ (distance of detector to home range centre). Age (adult/juvenile), sex and session were considered as possible covariates for *g0* and σ. All possible models were fitted with conditional likelihood and the best model was chosen by comparison of the Akaike Information Criterion. All population density and detection probability estimates were obtained using the R package secr (Efford, 2019).

Spatially explicit model after R. B. Chandler and Royle, 2013

Efford et al. (2009b) developed a SECR model for scenarios where a single individual could be detected by multiple detectors within a single occasion, for example if camera traps or microphones are used to detect animals. Chandler and Royle (2013) developed a Bayesian version of this model that does not require individuals to be identified. However, the spacing between detectors must allow for an individual to be detected by more than one detector. The correlation between counts is then utilized as information about animal distribution and population size.

Like other Bayesian SECR models, estimation of abundance relies on a data augmentation approach, which involves specifying a maximum possible population size (M) and estimating the proportion of these hypothetical animals that actually exist (ψ) (Royle et al., 2013). The estimate for abundance is the product of these two values. I specified M = 750, which, given the extent of the survey area, is equivalent to a density of approximately 750 rats per hectare, about seven times larger than the SECR estimates. To fit the Bayesian model, priors for the parameters must be specified. As per the recommendation of Chandler and Royle (2013), an informative prior for sigma was used, which in this case was based on the SECR model consistency of invasive rat home range size on islands around the world (Samaniego-Herrera et al., 2013). This was parameterized as a lognormal distribution for which the associated normal distribution has mean log(15) and variance 5. This is consistent with a prior belief that the sigma parameter is between 5 and 30 m. An uninformative uniform prior between 0 and 50 was used for the expected number of detections by a camera at the activity centre $\lambda 0$ and an uninformative $\beta(1, 1)$ prior was used for ψ. Furthermore, number of traps (J) and number of occasions (K) are required for this method. In May occasions were K = 8, in June K = 4. In both sessions the number of functioning (camera) traps was *J* = 8. The model was run using the R package rjags (Plummer, 2018). I tested for convergence using the Gelman-Rubin convergence diagnostic (Gelman & Rubin, 1992), increasing the length of the Markov chains when lack of convergence was detected.

Random encounter model (REM)

Rowcliffe et al. (2008) proposed using the random encounter model for gas particles to estimate animal population density using camera traps by modelling the contact rate between animals and cameras. They describe density *D* as a function of trapping rate *y*/*t* (*y* = number of videos, *t* = time unit), animal movement speed *v* and the dimensions of the camera detection zone, which is assumed to be a circular sector with angle *ϴ* and radial distance *r* (Rowcliffe et al., 2008: equation 4):

$$D = \frac{y}{t} * \frac{\pi}{v * r(2 + \theta)}$$

The cameras in the study of Rowcliffe et al. (2008) were installed with a horizontal view. In my study, the view was vertical resulting in a rectangular detection zone with width *a* = 0.6 m and length *b* = 1.15 m. The equation above can be modified for use with a rectangular detection zone (Appendix B), which provides:

$$D = \frac{y}{t} * \frac{\pi}{v * 2(a + b)}$$

REM requires a separate estimate of animal speed that is representative of the time the cameras are in operation. To estimate animal movement speed, *v*, the distance between subsequent observed locations of radio collared rats was divided by the time between the bearings for five radio-tracked rats. Average rat movement speeds vary throughout the day because they are typically more active at night. The locations of radio-collared rats were taken between 6pm and 12am. Only camera detection data collected during between this period were retained for analysis, during which time rat movement speeds can be considered consistent with those calculated from the radio telemetry data.

The REM counts a detection of a group by a camera trap as one detection and estimates the number of groups per unit area. To estimate population density, REM results have to be multiplied by the average group size. A nonparametric bootstrap was performed for v, y and D with 10,000 samples each.

Random encounter and staying time (REST)

Nakashima et al. (2018) use a likelihood-based model to describe the relationship between population density, mean number of detections by a camera trap during a survey period, and the time individual animals stay in the focal area of the camera. They derive density D from the the expected cumulative staying time of all individuals in a detection zone within a research period DsH (s = detection zone, H = survey period) as function of expected encounters $E(Y)$ and expected staying time $E(T)$, with Y being the number of detections and T the staying time after detection (Nakashima et al., 2018, equation 1):

$$D = \frac{E(Y) * E(T)}{sH}$$

The same detection zone was used for both the REM and the REST model (see above). Staying times were measured for May and June 2018 using a random sample of 51 videos for each session.

3.3 Results

Spatially Explicit Capture-Recapture (SECR) model

To estimate population density a total of 116 individual Pacific rats were trapped in 450 trap nights over two sessions from 2 - 7 December 2017 and 16 - 20 June 2018 on Reiono (Table 3.1).

Table 3.1. Live trapping results for Pacific rats from Reiono in December 2017 and June 2018.

Session	Individuals	Total Captures	Recaptures	Occasions
December 2017	44	63	19	5
June 2018	72	107	35	4

Table 3.2 shows the 17 most supported models (ΔAICc ≤ 3) of the model comparison with age, sex and session as covariates on the detection probability at the home range centre g0 and the spatial parameter σ, the distance of the trap to the home range centre. The most strongly supported model (8.4%) included age as an effect on g0 and age, sex and session as effects on σ. Estimated rat density was 97 rats/ha (95% CI: 60 – 156) for December 2017 and 100 rats/ha (95% CI: 65 – 153) for June 2018. However, the estimated densities were similar for most of the 17 models

and between sessions. The effective sampling area was estimated as 0.47 ha (SE = 0.09) for December and 0.7 ha (SE = 0.12) for June.

Table 3.2. Results of model comparison with session, age and sex as covariates on *g0* (detection probability at home range centre) and *σ* (distance of detector to home range centre). Shown are models with ΔAICc ≤ 3. D.1 is rat population density in rats/ha for the December trapping session, **D.2** for the trapping session in June 2018. (Samaniego et al., 2019).

g0	σ	npar	AICc	ΔAICc	AICcwt	D.1	D.2
age	age+sex+session	6	1111.508	0	0.084	96.88	99.69
1	age+sex+session	5	1112.298	0.79	0.0566	100.12	110.70
age	age+age:sex+session	6	1112.686	1.178	0.0466	96.27	97.27
1	age+age:sex+session	5	1112.931	1.423	0.0412	98.28	105.17
age+age:sex	age+sex+session	7	1113.384	1.876	0.0329	100.03	98.59
age+sex	age+sex+session	7	1113.587	2.079	0.0297	99.17	99.50
age+session	age+sex+session	7	1113.692	2.184	0.0282	98.17	99.91
age	age*sex+session	7	1113.758	2.25	0.0273	96.97	99.99
age+ age:sex	age+session	6	1114.065	2.557	0.0234	97.38	86.95
age+sex	age+session	6	1114.226	2.718	0.0216	96.86	87.40
1+session	age+sex+session	6	1114.229	2.721	0.0215	102.80	110.38
sex	age+sex+session	6	1114.287	2.779	0.0209	102.82	110.47
age+session	age+sex	6	1114.331	2.823	0.0205	80.51	111.53
age+sex	age+age:sex+session	7	1114.455	2.947	0.0192	99.51	96.35
age+ age:sex	age+age:sex+session	7	1114.473	2.965	0.0191	99.78	96.26
1+session	age+sex	5	1114.483	2.975	0.019	85.45	120.18
1	age*sex+session	6	1114.508	3	0.0187	100.58	111.91

Camera Traps

A total 2966 videos from the 8 functioning cameras were used for the analysis: 2024 videos from 64 trap days for May 2018, and 942 from 32 trap days for June 2018. Two additional cameras were removed from both data sets due to malfunctioning.

Spatially Explicit Model after Chandler and Royle (2013)

Population density estimates using the model after Chandler and Royle (2013) require individuals to be detected by multiple detectors. Average minimum distance between two cameras was 14 m (range 8 – 20 m). The mean maximum distance moved by individuals during the live trapping in June 2018 was 26.5 m (SE = 4.15, n = 22).

Initially I ran five MCMC chains, retaining 50,000 iterations from each after discarding 2,000 iterations for burn-in. However, I observed slow mixing, and the Gelman-Rubin convergence diagnostic indicated a lack of convergence. I increased the scale of my MCMC procedure by running 25 MCMC chains, retaining 75,000 iterations from each after discarding 2,000 for burn-in. The Gelman-Rubin convergence diagnostic no longer indicated a lack of convergence; upper limits of 95% CIs for the parameters' potential scale reduction factors were all 1.06 or lower. Population density estimates were 136 rats/ha (95% CI: 25 – 403) for May 2018 and 122 rats/ha (95% CI: 22 – 362) for June 2018.

Random Encounter Model

Figure 3.3 shows the number of videos showing rats for each hour of the day. Rat activity was high between 4pm and 12am and did not differ hourly between May and June (paired t-test, t = 0.79, df = 23, p = 0.44). To estimate the movement speed of rats for the random encounter model four free-roaming individuals, three females and one male, were located using radio telemetry on 12, 13, 17 and 18 August 2018 (when no trapping was occurring). Bearings of individuals which remained stationary (e.g. denning) were removed from the calculation. An average of 5 bearings (range 2-10) were taken for each individual every 61 minutes (range 15-104), and most (95%) bearings were taken after sunset between 6pm and 12am. The average linear (i.e. minimum) movement speed was 18 m/h (11 - 22).

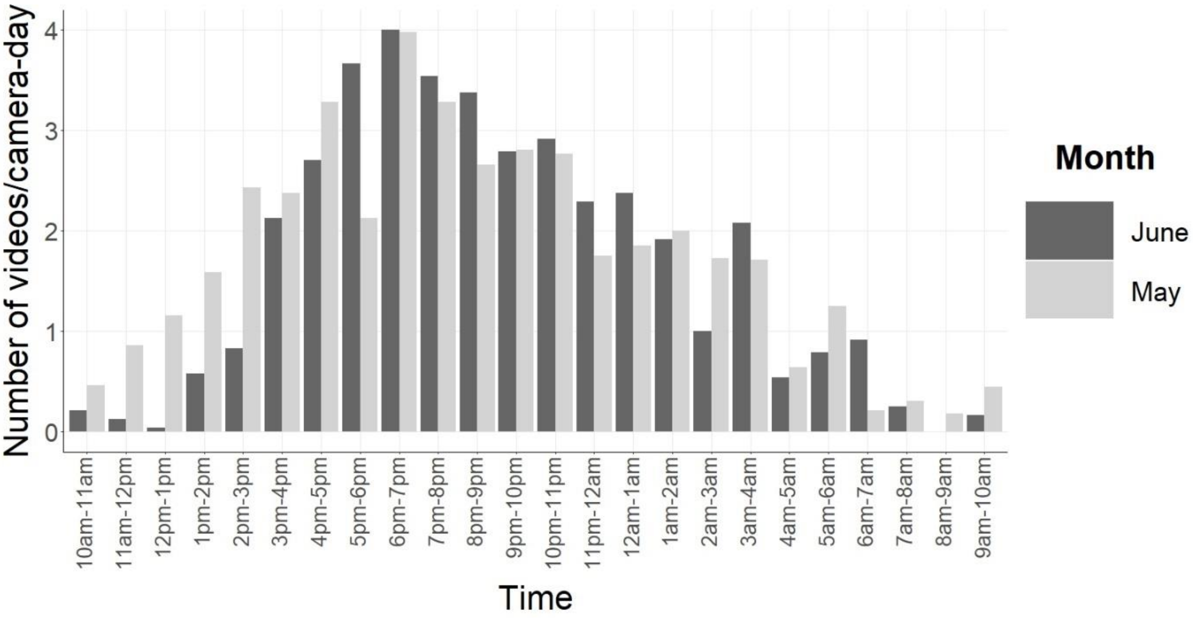

Figure 3.3. Rat activity times from Reiono, Tetiaroa. Shown is the number of videos showing Pacific rats per day from 3 – 10 May and 17 – 20 June 2018 plotted against time.

REM density estimates were 693 groups/ha (95% CI: 384 – 1224) for May 2018 and 815 groups/ha (95% CI: 433 – 1484) for June 2018. The average group size observed in 2966 videos was 1.06 individuals in May (2024 videos, range 1 to 5) and 1.06 individuals in June (942 videos, range 1 to 3). Therefore, the estimated group size was treated as 1 individual/group.

Random encounter and staying time (REST)

Population estimates were 134 rats/ha (95% CI: 68 – 265) for May 2018 and 53 rats/ha (95% CI: 30 – 97). The average staying time was 6.9 s (range 1 – 20) in May and 5.06 s (range 1 – 20) in June.

The REM model failed to provide realistic density estimates. The model after Chandler and Royle (2013) resulted in population density point estimates similar to the benchmark of SECR estimates. The REST model underestimated density in June.

SECR resulted in more precise estimates than the Chandler method which had very wide confidence intervals (Table 3.3).

Table 3.3. Population density estimates for Pacific rats on Reiono for December 2017, May 2018 and June 2018 from four statistical models: **SECR**: spatially explicit capture recapture (SECR), **Chandler**: model after Chandler and Royale (2013), **REM**: Random encounter model (Rowcliffe et al., 2008), **REST**: Random encounter and staying time model (Nakashima, 2018).

			Confidence interval	
Model	**Date**	**D in rats/ha**	**2.5%**	**97.5%**
SECR	December 2017	97	65	153
	June 2018	100	60	156
Chandler	May 2018	54	12	339
	June 2018	87	7	219
REM	May 2018	693	384	1224
	June 2018	815	433	1484
REST	May 2018	134	68	265
	June 2018	53	30	97

3.4 Discussion

Point estimates from the model after Chandler and Royle (2013) were lower than that of the spatially explicit capture recapture model. Estimates from the REST model differed between sessions and the REM failed to produce realistic results. SECR estimates were used as the benchmark in my study because it is a standard method to estimate population density. Although only the second SECR estimate coincides with the second camera trapping session (June 2018), there was no evidence to suggest density varied between sessions, and so it can be reasonably assumed that rat density would have been about the same in the first camera trapping session (May 2018) when no SECR estimate was available.

Group size and animal movement speed are essential parameters for the REM to estimate population density. The group size for Pacific rats on Reiono was previously unknown, but most rats observed during the stay on the island were solitary. However, groups with up to 15 individuals could be seen foraging (pers. obs). They were observed gathering around food sources together. When moving on to the next food source, often piles of coconuts, they often separated or ran in a loose band with up to several metres between individuals. Additionally, individuals were observed moving as members of a group before leaving the group again and moving on solitarily. Therefore, the number of rats visible in a video may not reflect the group size properly and estimated group size in my study has to be considered with caution. Previous studies have used the REM to estimate population density for species which were solitary, e.g. Harvey’s duiker (*Cephalophus harveyi*) or pine marten (*Martes martes*) and could therefore use a group size of one (Manzo et al., 2012; Rovero & Marshall, 2009). For Pacific rats it is probably not possible to provide reliable group size estimates without additional independent data.

The REM also requires the estimation of the animal movement speed. However, neither the day range nor the activity time of Pacific rats were previously known anywhere. On Reiono, most rats were nocturnal, but rats were also observed during the day. How many hours the rats were active and how much time they spent moving remains unknown. Continuous tracking of Pacific rats, e.g. using GPS collars, is required to obtain such information about day range or movement speed. The requirement of this parameter is problematic for the application of the REM because it often is not available or not even possible to obtain. When testing the model to estimate population density of Harvey’s duiker, a small forest ungulate in Tanzania, Rovero and Marshall (2009) used data from a different species, black-backed duiker (*Cephalophus dorsalis*), and scaled it to their smaller target species. For a study on lions (*Panthera leo*) in Tanzania thirty year old movement data were used for animal speed estimation (Cusack et al., 2015) and Manzo et al. (2012) used movement data from Poland for a study on pine martens in Italy. These examples show the difficulty in obtaining data required for the REM.

Rowcliffe et al. (2008) suggest a set-up with 20 camera locations and a minimum of 10 photos per camera may be needed to obtain enough detections from monitoring animals at low density with a low trapping rate. In my study, the first requirement was violated due to limited field equipment at the remote site. However, rat density was high leading to high detection numbers. Two possible reasons that the REM failed to produce realistic estimates were an insufficient number of cameras and too many detections due to high rat density.

The REST model has successfully been used to estimate density of forest ungulates (Nakashima et al., 2020). In my study, the REST density estimate from the first session was comparable to the SECR estimates. However, the REST estimate from the second session was lower. The difference between the two data sets was the estimate of time an animal stays in the focal area. The model is sensitive to differences in staying times. The REST model was easy to parameterize. The time needed during video analysis to obtain the staying time does usually not exceed the actual footage time. This makes the model attractive for management and may become an alternative to traditional survey techniques. The work in the field is reduced to Camera trap installation and maintenance.

The precision of estimates from the model after Chandler and Royle (2013) was too low to make meaningful inference about population density. Chandler and Royle (2013) suggest expanding the trapping grid and marking subsets of the population to improve performance of the model. However, both suggestions can be difficult to realise. The use of more camera traps can result in large amounts of footage. Material as well as labour costs are a prohibiting factor for studies using camera traps and defeat the purpose of trying to use a method more labour efficient than capture-recapture. Chandler and Royle (2013) performed a simulation that used 225 detection devices, an unrealistic number of cameras for most projects. Partially marking the population can improve estimate precision (Chandler & Royle, 2013). However, marking animals to enable individual identification in a monochrome night video can be problematic and is usually not done for rats. (Nathan, 2016) used dye to create patterns in the fur of ship rats which were visible in monochrome videos, but the procedure was effortful including anaesthetising each individual twice. In addition, identification success on videos did not reach 100% as required by Chandler and Royle (2013). Camera placement posed a potential problem for this model. The distance between cameras on Reiono may have been too large to allow individuals to encounter multiple camera traps. Even though distances were smaller than the expected SECR home range of the rats, individuals may have moved in the spacing between cameras.

A focussed study is needed to obtain better data on activity and movement of Pacific rats. However, for many species obtaining group size and movement speed will be the limiting factor. For testing the method after Chandler and Royle (2013), I advise to test a set-up of an increased number of cameras with reduced distances between cameras to increase precision of the estimate. The REST model needs more test with data from the field to evaluate if it can provide reliable density estimates across different population densities and target animal movement speeds.

In my study, the statistical models were not tested with an experimental design which perfectly met all requirements, but to answer the question if this method can be used as a substitute for a capture-mark-recapture study of invasive rats in high population densities to inform wildlife management. Capture-mark-recapture studies involve high costs because a trained scientist or veterinarian has to be on site to handle the animals. Documentation and set-up must be precise to obtain reliable estimates. Camera traps have the potential to automate parts of the work by automatically documenting time, position and additional environmental information, e.g. temperature. The camera set-up in my study was easy and standardised and could be done by any person. Video analysis only required the skill to identify a rat but was very time intensive. However, this process might be accelerated in the future with emerging smart software which can sort out pictures not showing an animal (Falzon et al., 2020). Statistical expertise was mainly needed for the analysis, although this is also true for capture-mark-recapture studies. Additionally, existing data from studies using camera traps may be reused to estimate population densities with a reliable model. The REST model and the model after Chandler and Royle (2013) showed promising results in this and other studies. For eradication science, estimates of population density help understand population biology to inform eradications. Even though estimates differed from the benchmark obtained from SECR, two models showed that population density was high (>50 rats/ha), which was key information for a successful eradication (Samaniego et al., 2020b).

3.5 Acknowledgements

I thank Tetiaroa Society for local support and Araceli Samaniego for help with data collection. The study was funded through the Avian Research Scholarship of the University of Auckland.

4

Trappability of low density invasive rats

4.1 Introduction

The negative impact of invasive species can involve modification of ecosystems, competition and predation and are well studied (Simberloff et al., 2013). It is widely accepted that introduced predators are one of the main causes of extinction and has been demonstrated for numerous vertebrate taxa including reptiles, mammals and birds (Doherty et al., 2016). Eight out of 14 mammals listed in the 100 of the world's worst invasive alien species (Lowe et al., 2000) are present in New Zealand, including brushtail possum (*Trichosurus vulpecula*), domestic cat (*Felis catus*), goat (*Capra hircus*), mouse (*Mus musculus*), pig (*Sus scrofa*), rabbit (*Oryctolagus cuniculus*), red deer (*Cervus elaphus*), ship rat (*Rattus rattus*) and stoat (*Mustela erminea*). Being an island nation and given its biogeographic history, New Zealand is vulnerable to biological invasions and the threat to its unique ecosystems with a great number of endemic species is high.

The damage done by invasive rats has been recognized early and New Zealand has performed rat eradications on offshore islands for more than 50 years (Russell & Broome, 2016). Rats are omnivorous and opportunistic, having an impact on both plants and animals either by direct predation or competition (Campbell & Atkinson, 1999; Crook, 1973; Lovegrove, 1996; Meyer & Butaud, 2009); (Penloup et al., 1997). However, while the preferred goal is eradication, the commonest management strategy for invasive rats in New Zealand involves reducing population densities.

Monitoring or control of invasive species is conducted on 45% of New Zealand's mainland, but intensive management is confined to less than 0.2% of the mainland area (Russell et al., 2015). Controlling rats to very low numbers is a desired goal where eradications are not viable at the time (Duron et al., 2017). Particularly endemic bird species have benefitted from high intensity of mammal control in New Zealand (Fea et al., 2020). The reduction of population densities of ship rats and brushtail possum to very low levels has resulted in an increased breeding success in the endangered North Island kokako (*Callaeas cinerea wilsoni*) (Innes et al., 1999) and Starling-Windhof et al. (2011) have shown that predator control increased nesting success for New Zealand fantail (*Rhipidura fuliginosa*), grey warbler (*Gerygone igata*), bellbird (*Anthornis melanura*) and South Island robin (*Petroica australis*). Organized predator control in New Zealand is conducted by the Department of Conservation, councils and local community projects in a system of regional and national pest management. Beside public projects, private sanctuaries are playing an important role in restoring ecosystems and now play a key role in conservation and reintroduction of wildlife Innes (Innes et al., 2015).

While densities can be reduced with control devices (traps, bait stations), even if immigration is (nearly) zero rats can persist throughout the landscape at low population densities. The reason could be an insufficient number of control devices, inefficient control devices, density dependent behaviour, differences in individual behaviour or a potential selection for cautiousness. If a reduction of population density causes a shift in behaviour it will result in a lower detectability. Two parameters affecting detection probability are the probability of a rat encountering a device, and the probability of the rat interacting with the device. The probability of encounter is determined by the home range and the distance between an individual's activity centre and the detection device (Efford et al., 2016). The probability of an individual interacting with a device can be affected by numerous factors. Nathan (2016) found that the probability of interaction differed significantly between different devices for ship rats. Studies on mice found the encounter probability affected by moon phases (Shapira et al., 2013) and interaction probability affected by sex (Davis et al., 2003). The variation in individual behaviour also plays a significant role in probability of both encountering and interacting with a device (Nathan, 2016).

Another factor affecting detectability and therefore the successful control and monitoring of invasive rats is interspecific competition. The main mechanisms of interspecific competition are exploitation and interference. Direct interference was the most likely mechanism of interspecific competition between invasive ship rats and native rats in both Australia and Ecuador (Harris & Macdonald, 2007; Stokes et al., 2009). Harper et al. (2005) suggest that invasive Pacific rats (*R. exulans*) are affected by interspecific competition with ship rats and Norway rats (*R. norvegicus*) on Rakiura, New Zealand, leading to micro-habitat partitioning.

Ongoing rodent control at two sanctuaries on Aotea -Windy Hill Sanctuary and Glenfern Sanctuary- has reduced rat population densities of Pacific rats and ship rats to low levels. Both sanctuaries are important breeding sites for endemic birds, e.g. kaka (*Nestor meridionalis*), black petrel (*Procellaria parkinsoni*), pateke (*Anas chlorotis*) and reptiles, e.g. Chevron skink (*Oligosoma homalonotum*), and forest gecko (*Hoplodactylus granulatus*). Trapping results after a rat eradication attempt at the fenced Glenfern Sanctuary suggested that ship rats had been successfully removed but Pacific rats persisted. A capture-mark-recapture study was conducted to determine species composition and population densities at all study sites. Live traps were monitored with motion sensored trail cameras to analyse rat behaviour around devices. This study aimed to understand the behaviour of invasive rats at low population densities. It set out to determine i) how *R. exulans* population density and detection probability is affected by interspecific competition with *R. rattus* or season, ii) if the behaviour of *R. exulans* around detection devices is affected by population density.

4.2 Methods

4.2.1 Study site

Aotea/Great Barrier Island lies in the Hauraki Gulf 100 km north-east of Auckland (Figure 4.1). Pacific rats and ship rats are present on the island, but Norway rats (*R. norvegicus*) are absent. Glenfern Sanctuary is situated in the North-West of the island. It covers 83 ha of the Kotuku peninsula. When founded in 1992 it consisted mainly of farmland and has been reforested in the following years. It has developed into a mixed broadleaf forest retaining old puriri (*Vitex lucens*), kauri (*Agathis australis*) and kanuka (*Knightia excelsa*) present. Some forest patches are dominated by tree-ferns (*Cyathea dealbata*). The sanctuary is protected by a 2.1 km predator proof fence, isolating Kotuku peninsular. In 2009 an eradication attempt by aerial application of brodifacoum successfully reduced rat numbers. Following the eradication attempt ground based pulsed control using diphacinone and continuous snap trapping has been ongoing. Until today Pacific rats persist in the sanctuary. Outside the fence more than 90% of the rats captured by the Department of Conservation between January and March 2012 near Glenfern Sanctuary were ship rats (J. Russell, unpubl. data).

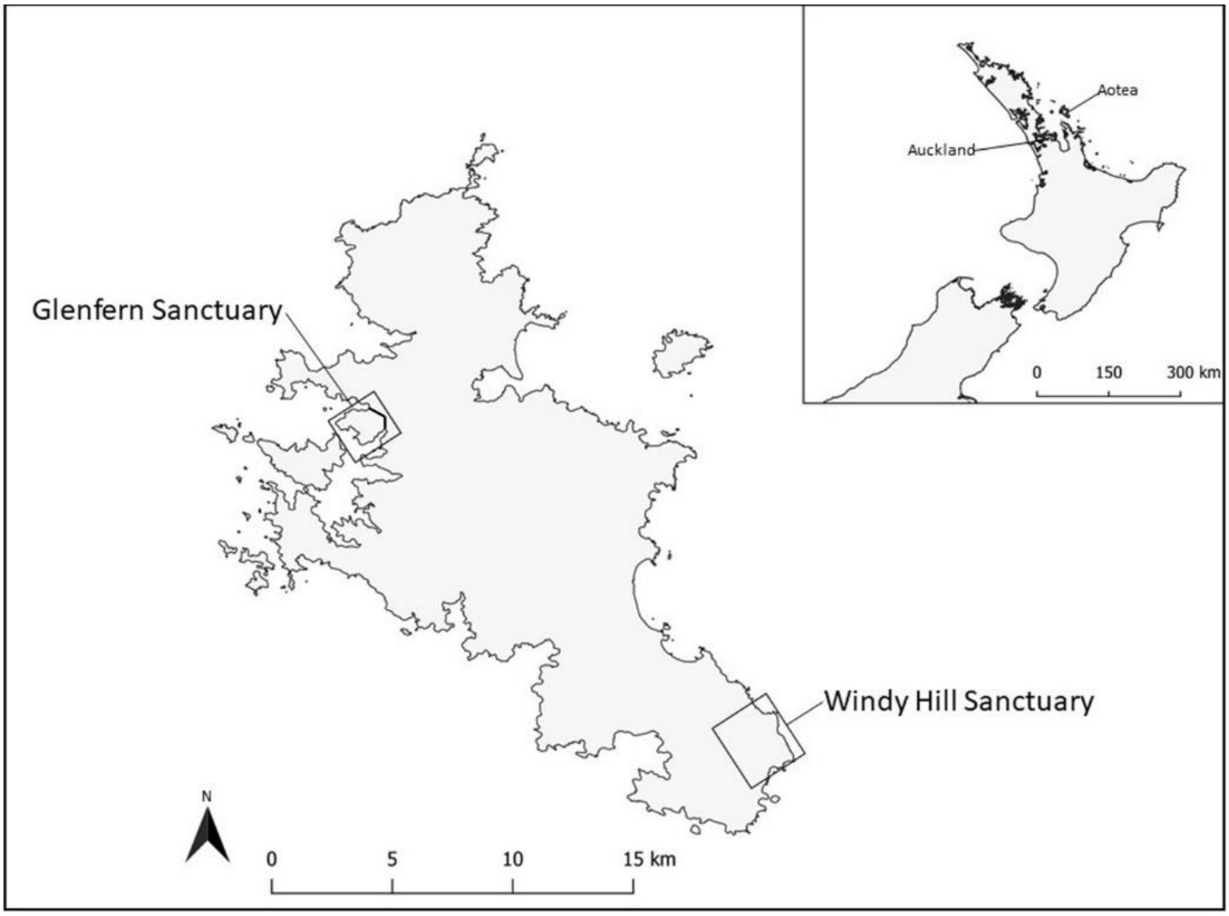

Figure 4.1. Map of Aotea/Great Barrier Island with the two study sites Glenfern Sanctuary and Windy Hill Sanctuary. Bold line indicates the predator proof fence.

The Windy Hill Sanctuary is an area of 770 ha in the South of the island. The land was used as farmland and was allowed to regenerate from the 1970s on. It is now a mix of mature and rejuvenating coastal podocarp broad leaf forest and kanuka (*Kunzea ericoides*) scrub. Rodent control started in 1999 and has grown over the following years and now covers nearly the whole sanctuary. Both ship rats and Pacific rats are present in low numbers. Vegetation for Windy Hill Sanctuary and Glenfern Sanctuary was described in detail by (Perry et al., 2010).

4.2.2 Population density

Live trapping was conducted using live cage traps (Model 201, Tomahawk) baited with peanut butter and oats. A total of 49 traps were arranged in a grid of seven lines with seven traps per line. The distance between traps was 25 m and the grid covered an area of 2.25 ha. Each set trap was checked every morning. Captured rats were transferred into a clear plastic bag and anaesthetised using isoflurane gas to improve recapture rates (Prout & King, 2006). The rats were identified to species, weighed, sexed and fitted with a metal ear tag carrying a unique number.

Rats were trapped at Glenfern Sanctuary (Glenfern) and at Windy Hill and Benthorn which are two different sites within the Windy Hill Sanctuary. Live trapping was conducted at Glenfern and Windy Hill in winter 2016 and at Glenfern, Windy Hill and Benthorn in autumn 2017 (Table 4.1). Rodent control around the trapping grids was halted during the live trapping with a minimum buffer of 100 m around the trapping grid.

Table 4.1. Dates of rat capture-mark-recapture sessions on Aotea.

Site	Year	Season	Date	Nights
Glenfern	2016	Autumn	Feb 24 – Mar 9	12
	2017	Winter	Jul 10 – Jul 30	20
Windy Hill	2016	Autumn	Apr 4 – Apr 19	15
	2017	Winter	Aug 10 – Aug 26	16
Benthorn	2017	Winter	Sep 12 – Oct 1	19

4.2.3 Video monitoring

In the centre of the trapping grid a total of 25 cage traps were monitored with motion activated trail cameras (Bushnell Trophy Cam 119437, Moultrie M-990i). They were arranged in a 5 x 5 camera grid (Figure 4.2). The cameras were installed 1.45 m above ground and 2 m away from the trap and were pointing to the trap in a 45°-angle. All cameras were set to 60 second video length, one second interval between videos, highest sensor sensitivity and lowest LED intensity.

	1	2	3	4	5	6	7
1	X	X	X	X	X	X	X
2	X	O	O	O	O	O	X
3	X	O	O	O	O	O	X
4	X	O	O	O	O	O	X
5	X	O	O	O	O	O	X
6	X	O	O	O	O	O	X
7	X	X	X	X	X	X	X

Figure 4.2. Trapping grid and camera set-up on Aotea. Distance between devices is 25 m. “x” – cage trap, “O” – cage trap with trail camera.

The behaviour of the rats was distinguished into four escalating categories:

No Interest

A rat is fully visible in the video but does not show any interest in the device, passes it or moves away from it.

Interest

The rat shows interest in or acknowledgement of the device. This is defined as turning its head towards the device and sniffing.

Interaction

The rat interacts with the device in the form of touching it, chewing on it, jumping on it, and sniffing on the device so close that it cannot be determined in the video if it touches the device or not.

Trigger

The rat triggers the device and consequently gets captured in the cage.

Each video was assigned to one category only, i.e. if an interaction was observed the video was categorised as Interaction but was not counted as Interest which must have preceded the interaction.

4.2.4 Statistical analysis

Two data sets were used for the analysis containing i) only Pacific rat captures and ii) both Pacific rat and ship rat captures. All analyses were conducted in R Version 3.4.0 (R Core Team, 2019).

To analyse the effects of site and year on population density and detection probability of Pacific rats the capture-mark-recapture data containing Pacific rats only was used to estimate population density D using a spatially explicit capture recapture (SECR) model. The covariate time confounds year and season since data was acquired in autumn 2016 and winter in 2017. The detection function in SECR models is shaped by the two parameters *g0* (detection probability at home range centre) and σ (distance of detector to home range centre). Site and time were the covariates for density *D* and *g0*, while σ was assumed to be constant across sites to avoid overparameterization given the low number of recaptures. Analysis was done with the R package secr Version 3.1.3 (Efford, 2019).

To analyse the effect of population density on rat behaviour around traps recorded by video cameras, the capture data set combining both species was used to estimate combined species rat population densities for all five trapping sessions, without distinguishing rat species. This was because the rat species cannot be identified in a video without uncertainty, and so required pairing with equivalent trapping data that did not distinguish species. Session (each unique trapping grid in space and time) was used as the only covariate for *D* and *g0*. As expected for a capture-mark-recapture study of rats at low population density data were sparse. Fitting basic models was preferred over complex model comparisons because the focus lied on obtaining reliable parameter estimates. Sigma was assumed to be constant between species because the number of ship rat recaptures was low and did not allow for a more detailed analysis. The effect of population density on the behaviour of rats around live traps was analysed with the R package lme4 (Bates et al., 2015) using a generalised linear mixed model with the R code:

$$Count \sim Behaviour * Population\ density + (1 \mid Trap)$$

The response variable was the number of videos counted per behavioural category (*Count*). Fixed effects were the behavioural categories (*Behaviour*) and rat population density (*Population density*). The random effect was the trap number (*Trap*).

4.3 Results

A combined total of 39 individual *R. exulans* and 12 individual *R. rattus* were trapped over five trapping sessions in 4,067 trap nights (Table 4.2) on the three trapping sites Glenfern, Windy Hill and Benthorn.

While Pacific rats were present at all sites no evidence for the presence of ship rats at Glenfern sanctuary was found. Even though no ship rat was caught at Windy Hill in 2017 their presence in low abundance was likely. Ship rats were present in the wider sanctuary during the time of the study and were caught in snap traps in the area surrounding the study site.

Table 4.2. Live trapping results from Aotea from August 2016 to October 2017 for the two invasive species *Rattus exulans* (R.ex.) and *R. rattus* (R.rat.). Notes: "I" – Number of individual rats trapped; "C" – Total number of captures; "R" – Number of recaptures; "Sess." – Session length in nights; "*" – individuals were euthanised.

		R.ex.			*R.rat.*				Night of 1st capture	
Site	Year	I	C	R	I	C	R	Sess.	*R.ex.*	*R.rat.*
Glenfern	2016	6	9	3	0	0	0	13	2	NA
	2017	6	32	26	0	0	0	20	1	NA
Windy Hill	2016	3	3	0	8	9	1	15	10	1
	2017	6	20	14	0	0	0	16	10	NA
Benthorn	2017	10	21	11	4	4*	0	19	11	1

The number of trap nights until the first Pacific rat was captured differed between sites (Table 4.2). It was higher on sites with ship rat coexistence, Windy Hill and Benthorn, than at Glenfern where ship rats were not present ($t = 3.123$, $df = 4$, $p = 0.04$). At Glenfern the first Pacific rat was captured in the second night in 2016 and in the first night in 2017. At Windy Hill the first Pacific rat was captured in the 10th night in both years and at Benthorn in the 11th night in 2017. Ship rats were caught in the first night at Windy Hill in 2016 and at Benthorn in 2017.

Site and time had effects on population density *D* and detection probability *g0* of Pacific rats. In autumn 2016 the population density estimate for Pacific rats was 2.9 ± 1.7 rats/ha at Glenfern and 4.1 ± 3.4 rats/ha at Windy Hill. In winter 2017 it was 1.1 ± 0.5 rats/ha at Glenfern and 1.6 ± 0.6 rats/ha at Windy Hill. In winter 2017 population density at Benthorn was higher than at Glenfern with 3.1 ± 1.0 rats/ha.

The detection probability of Pacific rats differed between sites and times (Figure 4.3). Compared to Glenfern it was lower at Windy Hill and Benthorn. In 2016 it was 0.050 ± 0.035 at Glenfern and 0.007 ± 0.001 at Windy Hill. In 2017 it was 0.727 ± 0.131 at Glenfern, 0.252 ± 0.020 at Windy Hill and 0.064 ± 0.035 at Benthorn.

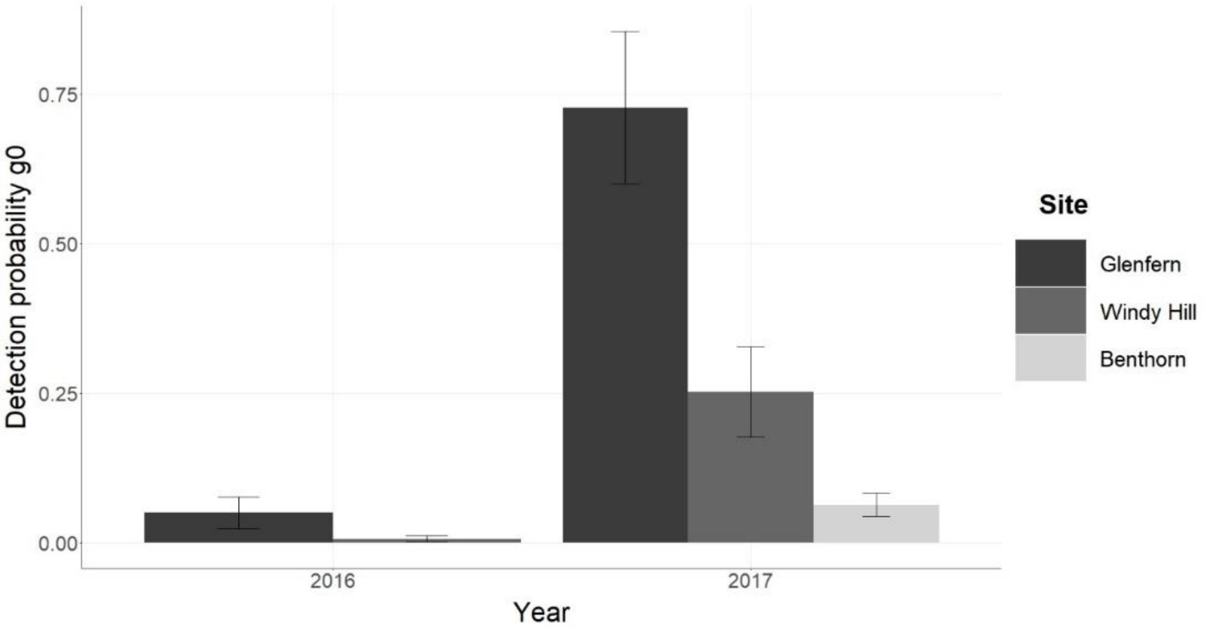

Figure 4.3. Detection probability at home range centre *g0* estimates and standard errors for *Rattus exulans* from three sites on Aotea in 2016 and 2017.

4.3.1 Population density dependent behaviour

To analyse the effect of population density on rat behaviour around live traps the combined species rat population density without distinguishing between Pacific rats and ship rats was estimated. The most strongly supported model had 100% support and included the effects of session for both *D* and *g0*. Population densities differed between sites and times. In autumn 2016 the combined species rat population density estimate was 2.5 ± 1.4 rats/ha at Glenfern and 12.3 ± 8.1 rats/ha at Windy Hill. A lower population density was observed in winter 2017 with 1.2 ± 0.5 rats/ha at Glenfern and 1.4 ± 0.6 rats/ha at Windy Hill. In 2017 the population density was highest at Benthorn with 4.9 ± 1.5 rats/ha.

A total of 11,941 videos, more than 190 hours of footage, were examined. Approximately 30% of the videos could be used for the behavioural analysis. The other 70% of the videos were triggered by rabbits, birds, humans, dogs or cats or did not show anything at all.

The regression model showed that the number of videos was affected by population density (Figure 4.4). Significant interactions between population density and behaviour (essentially non-linear density-dependent behavioural effects) could be observed (Table 4.3). The number of camera records expectedly increased with population density for all categories of behaviour, but records of *Interest* ($p = 0.003$) and *Interaction* ($p < 0.001$) occurred significantly more often when population density was high. The number of videos showing rats triggering a trap remained constant and was unaffected by population density. However, the overall count of camera records of a rat triggering a trap was significantly lower than for the other behavioural categories ($p < 0.001$) reflecting that not every encounter leads to a rat being captured.

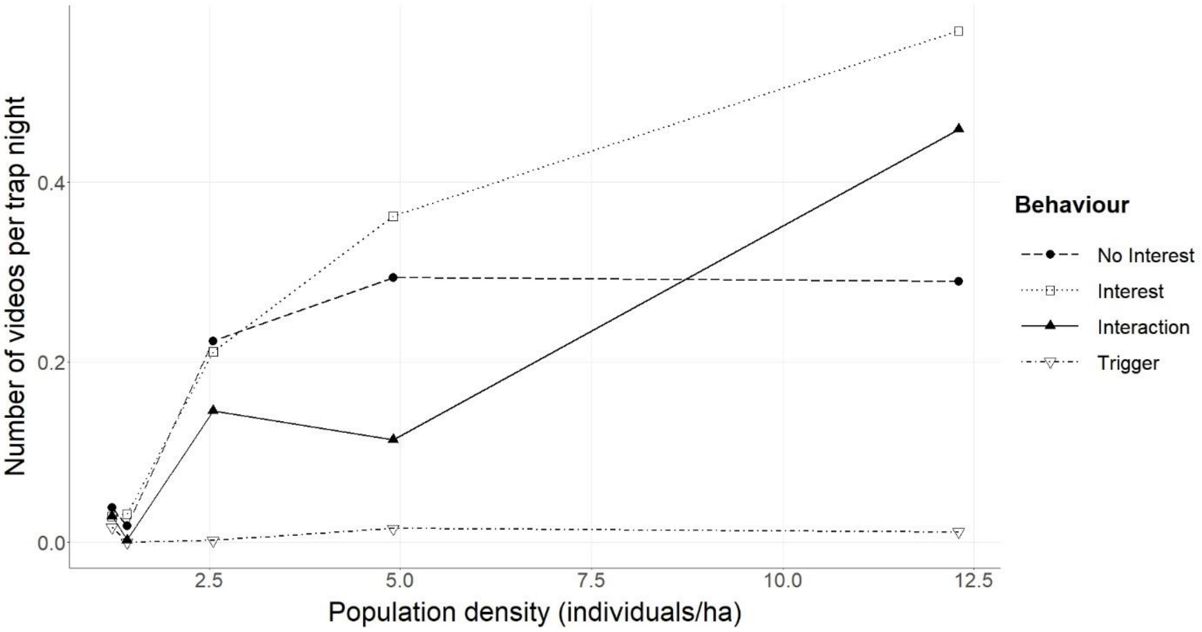

Figure 4.4. Number of videos per trap night plotted against population density across four categories of behaviour of invasive rats around live traps (combined *Rattus exulans* and *R. rattus*) monitored on Aotea in 2016 and 2017.

Table 4.3. Results of the generalised mixed model analysing the effect of population density on the behaviour of invasive rats (combined *Rattus exulans* and *R. rattus*) around live traps on Aotea in 2016 and 2017. Response variable was the number of videos recorded. Notes: "B" – Behaviour.

	Estimate	**SE**	**Z**	**p**
Intercept/(No Interest)	-1.02	0.22	-4.59	<0.001
Behaviour (Interest)	-0.06	0.13	-0.51	0.610
Behaviour (Interaction)	0.09	0.12	0.74	0.460
Behaviour (Trigger)	-2.43	0.38	-6.41	<0.001
Density	0.29	0.02	13.17	<0.001
B (Interest) x Density	0.05	0.02	2.99	0.003
B (Interaction) x Density	0.05	0.01	3.62	<0.001
B (Trigger) x Density	-0.10	0.06	-1.62	0.105

4.4 Discussion

Rat population density in this capture-mark-recapture study was low due to active rodent control at three sites in two different sanctuaries on Aotea. Pacific rats were present at all sites, but at only two sites ship rats were coexisting at low density with them. This allowed for analysing the effect of presence of a dominant interspecific competitor on population density and detection probability of a subdominant species. Correlative evidence was found for the presence of ship rats to be the cause of a behavioural change in Pacific rats. A temporal delay in interacting with devices as well as a lower detection probability for Pacific rats occurred when there was coexistence with ship rats, probably due to some form of interspecific competition.

Our results suggest that the presence of ship rats seemed to affect the trappability of Pacific rats on Aotea/Great Barrier Island. Pacific rats needed longer to be caught in a trap than ship rats, which were captured immediately at the same sites. Interspecific competition is a probable explanation for the differences in the behaviour at Windy Hill and Benthorn compared to Glenfern. The live traps on Aotea represented an additional food source. Avoiding potential encounters with the larger ship rats could have limited the opportunities to interact with the traps for Pacific rats or even exclude access to several traps. In a predator-prey system a predator can scare the prey away from food patches (Brown et al., 1999). Wirsing et al. (2007) have studied the foraging behaviour of dugongs (*Dugong dugon*) in Australia. The threat of predation by tiger sharks (*Galeocerdo cuvier*) altered the behaviour of dugongs and resulted in a shift of habitat use. Tiger sharks had the same effect on sea turtles even though predation on adult turtles is rare (Heithaus et al., 2008). Laundré et al. (2010) suggest that animals can learn to avoid predation by learning to evaluate risk in a “landscape of fear”. Parsons et al. (2018) have studied the behaviour of Norway rats in New York City. The presence of cats affected the movement behaviour of the rats even though actual predation was rare. When cats were sighted at the study site rats moved more often towards shelter and exhibited slow locomotion, probably to avoid sudden cat encounters.

The competition between these Pacific rats and ship rats in New Zealand is understudied. Coexistence with ship rats had a negative effect on skull size and weight of Pacific rats on Rakiura/Stewart Island and other Pacific islands, but the mechanism of competition remained unknown (Yom-Tov et al., 1999). Harper et al. (2005) have shown that dominant ship rats have displaced Pacific rats from habitats on Stewart Island and interference by aggressive encounter has been identified as the mechanism of interspecific competition between invasive ship rats and native rats in the Galapagos Islands (Harris & Macdonald, 2007) and Australia (Stokes et al., 2009). Russell et al. (2014) found interference competition as the cause for ship rat domination over Pacific rats on a tropical island where exploitative competition could be excluded. Ship rats from New Zealand's North Island have shown predatory aggressive behaviour towards mice Bridgman et al. (2013). Ship rat predation on Pacific rats has not been reported yet but is conceivable due to the differences in size between the two species.

The differences in detection probability of Pacific rats over time were most likely based on a seasonal effect. Trapping sessions in 2017 were conducted in winter when abundance of natural food was lower compared to autumn 2016. The availability of alternative food may influence the interaction probability and hence, the detection probability. Weerakoon and Banks (2011) have shown that decreased availability of alternative food sources increased the bait uptake of less favourable bait by invasive ship rats in Australia. A low probability of detection or a temporally delayed detection is problematic for predator control in areas infested with invasive species. It can lead to an underestimation of the population size or misinterpretation of species composition when monitoring infested areas with indices. Wilson et al. (2007) developed a protocol for population density studies of ship rats in New Zealand using capture-mark-recapture and suggest that five trap nights with 64 traps result in an acceptable precision of the density estimate. Five trap nights is also commonly used in capture-mark-recapture studies of *Rattus* spp.. Following this protocol, in this study subdominant Pacific rats would not have been detected at Windy Hill Sanctuary where ship rats were present. Therefore, rat monitoring in ecosystems where both rats could be present must be planned carefully to avoid underestimating abundance and incorrectly assessing species composition.

Both Windy Hill Sanctuary and Glenfern Sanctuary have successfully reduced invasive rats to low population densities and were able to maintain this status with extensive ongoing rodent control. However, at Glenfern Sanctuary eradication has not been achieved. At Windy Hill Sanctuary, the management goal was to reduce population densities as much as possible to limit the impact on the ecosystem by rats to a minimum and enable potential bird relocation programmes in the area. It was originally hypothesized that a change in the behaviour of the rats once low numbers are reached could lead to avoiding control devices. Even though the regression model showed an effect of population density on the quantity of rat interactions with traps the hypothesis of a trap avoidance causing difficulties in catching rats in low densities was not supported. Fewer rats naturally lead to fewer videos. The constancy of the number of videos still showing rats getting captured in the trap shows that low population density alone is not the driving factor for low trapping success.

While rat behaviour in different population densities was compared, further studies of rat behaviour within populations before, during and after control are necessary to detect a change in behaviour around control devices when rat density gets reduced. The identification of a behavioural change within a population may enable a management or technological response to improve control of invasive rats in very low density.

4.5 Acknowledgements

We thank Judy Gilbert (Windy Hill Sanctuary), Scott Sambell and Auckland Council (Glenfern Sanctuary) for giving access to the study area and on-site support. This study was conducted under animal ethics permit R1677 from the University of Auckland. This study was funded by the Avian Research Scholarship from the University of Auckland to MG and the Rutherford Discovery Fellowship RDF-UOA1404 to JCR.

5

Behaviour of invasive ship rats, *Rattus rattus*, around Goodnature A24 self-resetting traps

5.1 Introduction

Invasive species are one of the main drivers for biodiversity loss on islands (Jones et al., 2008; Kurle et al., 2008; Reaser et al., 2007). Rats from the genus *Rattus* are among the world's 100 worst invasive alien species (Lowe et al., 2000). Ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), and Pacific rats (*R. exulans*) are present in New Zealand (Atkinson, 1985). The damage done by invasive rats was recognized early and New Zealand has undertaken rat eradications on offshore islands for more than 50 years. However, some islands are a challenge for rat eradications due to their large size, human residents, or vulnerability to reinvasion from the mainland (Russell & Broome, 2016). Eradication using traps only is rarely successful (DIISE, 2020). An obvious limitation for the use of traps for eradications is island size and the labour required. The largest island in the list of successful eradications using only traps is Motuhoropapa, New Zealand (12.9 ha) (DIISE, 2020).

World-wide, on only nine small islands have rodent eradications been successful with trapping as sole method (DIISE, 2020). One approach to extend the tool box for rodent eradications is to improve present mechanical devices for rodent control, or develop entirely new ones. Often, the success or even the feasibility of predator control is influenced and limited by the availability of human and financial resources. Toxin-free devices like single-set traps demand a high amount of time for maintenance and, after an individual is killed, the area around the trap is left without any control until the trap is reset. Self-resetting traps can perpetuate more effective predator control. Mechanisms have been developed for existing traps, e.g. a battery powered motor attached to single-set traps to reset the bar (www.nzautotraps.com). Goodnature has chosen a different approach for a self-resetting trap (A24 rat and stoat trap, Goodnature Ltd., Wellington, NZ) that uses pressurised gas to operate a piston to kill the rat and then resets itself.

The success of rat control is defined by the expected outcome. Self-resetting A24s suppressed invasive rats on a large scale (>140 ha), but rarely resulted in tracking tunnel detections at acceptably low levels (Gillies et al., 2013). In a trial of A24s over two and a half years in a 100 ha area on Aotea/Great Barrier Island, New Zealand, the traps also failed to fulfil conservation requirements (Gilbert, 2018). On Oahu, Hawaii, A24s were more effective in controlling rats than single-kill traps but failed to meet requirements for the successful protection of the native tree *Cyanea superba* (Franklin, 2013). Shiels et al. (2019) successfully used A24s to suppress rat relative abundance in Hawaii, but the A24s were used in combination with snap traps and the acceptable tracking tunnel index of 20% for the area was high compared to previous studies (Gilbert, 2018; Gillies et al., 2014). While traps are usually used only to suppress numbers of invasive rats, an eradication using A24s was successful on a 6 ha cay in Puerto Rico (Zaluski & Soanes, 2016). However, the rat eradication using A24s on nearshore 62 ha Native Island, New Zealand, was first reported successful (DOC, 2015) but later described as a suppression operation (Carter et al., 2016; Carter et al., 2019). It remains unclear if the eradication failed or the island was reinvaded.

Camera traps are a valuable tool for documenting and analysing animal behaviour and activity patterns. Remotely triggered camera systems in wildlife monitoring have been used increasingly since the second half of the 20th century in different contexts in animal ecology, behaviour, and conservation (Kucera & Barrett, 2011; Nichols et al., 2011). Recent studies have shown the potential of camera traps for monitoring small animals including rodents (Austin et al., 2017; Glen et al., 2013; Gronwald et al., 2019; Gronwald & Russell, 2021; Mills et al., 2016; Yamada et al., 2016). Camera trapping for behavioural studies allows deeper investigation into how animals interact with devices prior to their final recovery as corpses. Understanding the behaviour around devices helps to identify the optimal deployment of these devices. Various contextual factors need to be considered when analysing behaviour of animals around devices in the wild including biogeography, seasonality, animal abundance, food abundance or competition. Important behaviours influencing interactions between animals and devices may include foraging strategies, intraspecific aggression or neophobia. Neophobia is the avoidance of a new object for an extended period of time. For example, animals may take some time after first encountering a device to interact with it. Wallace and Barnett (1990) reported avoidance behaviour of *R. rattus* lasting up to 12 days when being confronted with a new object. If a general cautious response towards a new device affects trapping success then the installation of a new device will result in a temporally delayed interaction between rats and devices. Cameras can measure the extent of this delayed response in the wild and help interpreting trapping and monitoring results. Minimising the time and number of behavioural steps required to kill an animal ultimately maximises the efficiency of a control tool.

This study was conducted on a small island with ship rats as the only rat species present and sets out to determine i) if self-resetting Goodnature A24 rat traps along with single-kill traps can suppress rat numbers and ideally achieve eradication on a small island, ii) if the rats show cautiousness towards new deployed A24s, and iii) if season or population abundance affect the behaviour of rats around A24s. We used motion sensored camera traps to measure rat relative abundance and to monitor the behaviour of ship rats around A24s. Our study design allowed a non-invasive observation of the behaviour towards an unknown device within a familiar environment. Food abundance determined by season and intra-specific competition in the system might alter the behaviour of rats. The interaction rate between rats and traps might change disproportionately if novel behaviours emerge at low abundance after successful trapping. Analysing the behaviour of the rats around A24s will help to evaluate their suitability as a control tool.

5.2 Methods

5.2.1 Study site

Te Hāwere-a-Maki, or Goat Island, is a small island (9.3 ha) north of Auckland at the east coast of North Island, New Zealand. The island is a nesting site for grey-faced petrels (*Pterodroma gouldi*), little penguins (*Eudyptula minor*), and variable oystercatcher (*Haematopus unicolor*). The island is used by numerous native and introduced bird species. Ship rats and stoats (*Mustela erminea*) can swim to Goat Island and pose a risk to the seabird colonies. The risk of incursions is particularly high during low tide when rocks are exposed and the distance to the adjacent mainland is reduced to less than 100 m. Ship rats have established a population on the island (MacKay & Russell, 2005) while stoats are occasional visitors (Pichlmueller and

Russell, 2018, M. Gronwald pers. obs.). Eradication attempts using a combination of Victor traps and brodifacoum took place on the island in 1994 and 2005. In both cases rats were detected on the island two years later (MacKay & Russell, 2005). From 2011 an intensive rat trapping campaign was conducted initially using only Victor snap-traps (Pichlmueller & Russell, 2018). Pichlmueller and Russell (2018) suggest that, even though reinvasion occurred in 2012 and 2013, the main reason for not achieving eradication was that resident rats were not being removed fast enough and recolonisation further facilitated the reestablishment of the rat population. Control of invasive rats and stoats on Goat Island using eight DOC200 single-set kill traps baited with eggs started in June 2015 following the detection of a stoat incursion on the island (Pichlmueller & Russell, 2018). The distance between traps was approximately 100 m and trap density one device per hectare. The traps were checked and rebaited approximately once a month from June 2015 to February 2016. After that, they were not serviced until the beginning of our study in July 2016.

5.2.2 Self-resetting traps

In July 2016 the existing trapping grid was expanded by 10 Goodnature A24s, thereby increasing the overall trap density on the island to about two devices per hectare. The A24 is a self-resetting kill trap targeting rats and stoats. The rats fall underneath the trap after being killed leaving them open to scavenging by other rats, ruru (*Ninox novaeseelandiae*) or harriers (*Circus approximans*). The traps were equipped with Goodnature Digital Strike Counters and Automatic Lure Pumps – Chocolate Formula for rats. The strike counters sense the vibration of the triggering of the trap and show the illuminated number on a digital display. Automatic Lure Pumps (ALP) continuously deliver fresh lure for about six months (Carter et al., 2019). Installation and maintenance followed the manufacturer’s guidelines. The traps were placed on large tree trunks approximately 12 cm above the ground. The traps were on average checked for strike counter numbers every 49 days (median = 53 days). During the 16 month field trial, from July 2016 to October 2017, the ALPs were replaced after six months in January and July 2017. Gas cartridges were replaced when the strike counter showed 20 or more. Dates in this manuscript represent dates of trap checks.

5.2.3 Video monitoring

Each of the A24s was monitored with a Bushnell Trophy Cam HD 8MP, a trail camera with passive infrared-based motion sensor. The cameras were pointing to the trap at a 45°-angle from a height of 145 cm and a distance around 1.5 m (Figure 5.1). The cameras were attached to a tree using adjustable mounts (Slate River EZ Aim Game Camera Mount). This set-up was chosen to limit the sensor field to approximately 1 m to each side of the trap. It avoided unwanted triggering of the cameras but kept the field of view large enough to analyse the behaviour. No cameras were placed at the DOC200 traps. All cameras were set to highest sensor sensitivity, lowest LED brightness, 1-minute video length and 5-second interval between videos. The cameras were equipped with 8GB SD cards fitting up to 240 videos.

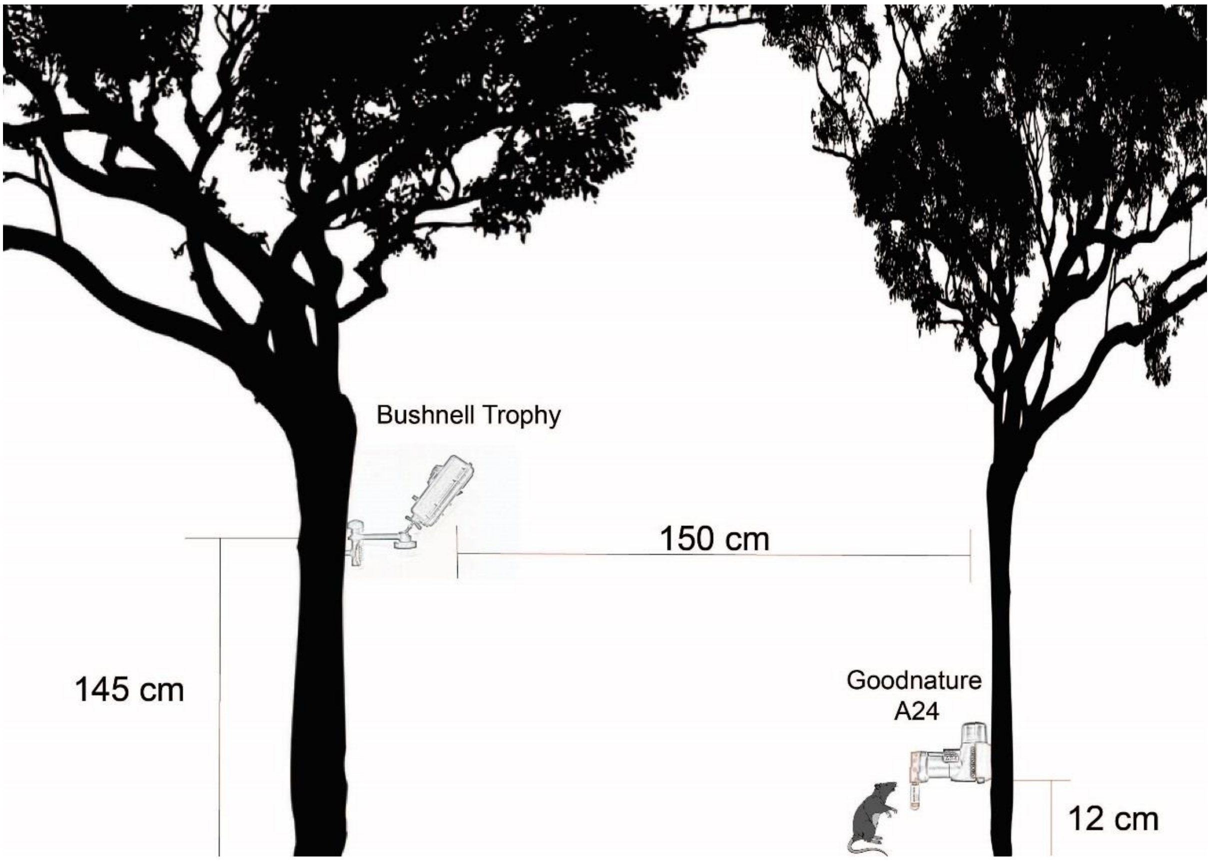

Figure 5.1. Schematic of equipment layout at each Goodnature A24

Video footage was used to estimate rat relative abundance (see Gronwald and Russell, 2021) and observe rat behaviour around the self-resetting traps. Because rats could not be identified to individuals in the footage and we cannot distinguish changes in absolute abundance from detection, our video measure is only one of relative abundance, or here after “rat activity”. Two consecutive videos may have been triggered by the same rat. In only 16 videos (0.2% of all videos) a rat was visible in two consecutive videos with maximum 15s between videos. Therefore, we defined each video as a separate event. Observed behaviour was categorised into No Interest, Interest, Interaction (touching the trap), and Trigger, following the methods of (Gronwald & Russell, 2020b).

5.2.4 Season and abundance effects on behaviour

Rat activity was reported as the island-wide number of detections (videos showing a rat) per 100 camera days (Gronwald & Russell, 2021). The effects of season and rat activity on rat behaviour were analysed using a generalised linear mixed model. Response variable was the number of videos counted per behaviour (Count). Fixed effects were season (spring, summer, autumn, winter), rat activity, and behaviour observed in the videos, which included No Interest, Interest, Interaction, and Trigger. The random effect in the model was the site which was represented by the trap number.

Count ~ Season * Behaviour + Rat activity * Behaviour + (1|Trap)

The number of Trigger videos may differ from the number of individuals killed due to imperfect detection. Therefore, digital strike counts, which accurately reflect the number of rat kills (Gronwald & Russell, 2021), were the preferred measure. The effects of time and rat activity on the number of kills were analysed using a generalised linear mixed model. Response variable was the number of kills (Kills). Fixed effects were the number of days after A24 trap deployment (Days) and rat activity. The random effect was site which was represented by the trap number.

Kills ~ Days + Rat activity + (1|Trap)

The models were fitted using the R package lme4 (Bates et al., 2015). Data from August 2016 (the first session) was excluded from the generalised mixed models to exclude potential neophobic or neophilic behavioural responses in the rat population towards the A24s that could have biased the results. Therefore, the data used for this analysis of behaviour were from September 2016 (the second session), i.e. starting 53 days after the initial trap deployment once the devices would have become familiar to the rats in their environment. Video data from only nine cameras were analysed. A broken mount led to a different setup of one camera using a horizontal recording angle instead of the 45° used for the other cameras. This caused problems in the categorisation of the observed behaviour. Depending on the position of the rat in the video it was difficult to determine if the rat had touched the trap. This camera was subsequently excluded from any further analyses. All analyses were carried out in R Version 3.4.0 (R Core Team, 2019).

5.2.5 Behavioural response to new devices

Video footage from nine cameras was used to document the time to the first encounter (either no interest or interest), interaction, and trigger at each trap after the initial installation on the island. One trap was excluded from the examination of the behavioural response because it was installed close to the base for the field staff and was disturbed throughout the day. However, data from all ten cameras could be used to determine the first night a rat was killed at each trap.

5.3 Results

A total of 7155 videos from more than 119 hours of footage over 2161 camera days were analysed. Seventy-four percent (n = 5270) of the videos showed rats and could be included in the analysis of behaviour. The number of rat videos was the highest in August, the first month after installing the traps (1182/100 camera days). A second peak of activity appeared four months following deployment, in November 2016

(450/100 camera days); from then on, rat activity stayed consistently at a lower level (128-219 videos/100 camera days) (Figure 5.2). The A24s were able to remove more rats than the single-kill traps in the first three months of the study and at peak times in November 2016, January and May 2017 (Figure 5.2). The total number of rats killed throughout the study was 242 by A24s and 27 by DOC200s (Gronwald & Russell, 2020a).

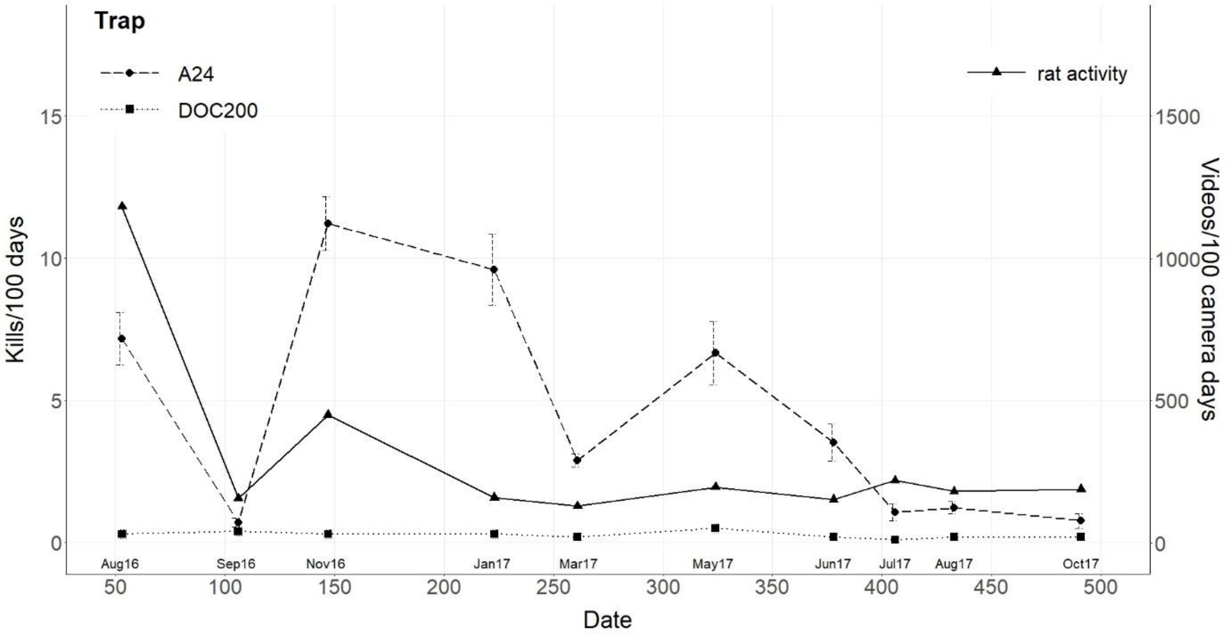

Figure 5.2. Kills per 100 days by eight DOC200 single-kill and ten Goodnature A24 self-resetting traps (left hand axis) and rat activity (videos per 100 camera days right hand axis) between July 2016 and October 2017 on Goat Island. DOC200s were installed one year before A24s but were not set for 6 months prior to our study. Dates represent trap and camera servicing dates. Numbers on the x-axis are number of days after camera/trap installation. Error bars represent standard error.

Table 5.1. Results of the Generalised Linear Mixed Model analysing the effects of rat activity and seasonality on the number of kills by Goodnature A24 self-resetting traps on Goat Island from September 2016 to October 2017. Intercept is Spring and No Interest. Significance codes are '***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$

	Estimate	SE
Intercept	1.150**	0.231
Days	-0.002**	0.001
Rat activity	0.139***	0.025

The kill rate of A24s decreased with increasing time of deployment in the field (Table 5.1, Figure 5.2) despite rat activity remaining relatively constant throughout 2017. More rats were killed when rat activity was high (Table 5.1, Figure 5.2). It should be noted that the DOC200s had been on the island for more than a year before the A24s were installed and thus trap efficacy could not be directly compared. Rats interacted with the A24s throughout the study but juveniles were not observed to be killed. An unexpected behaviour observed was rats feeding underneath the traps on what was assumed to be lure that had dropped from the automatic lure pumps. The moment of a rat triggering the trap was visible in 70 videos but was never preceded by a rat feeding under the trap.

5.3.1 Season and activity effects on behaviour

The regression model showed seasonal differences in the behaviour of the rats around the self-resetting traps. The behaviours of Interest, Interaction, and Trigger followed a similar pattern, with the lowest counts all being in early autumn (Figure 5.3). The interaction rate was relatively high throughout the study while the number of trigger events stayed low. The number of videos showing No Interest, however, was lowest in summer and autumn before going up again in winter.

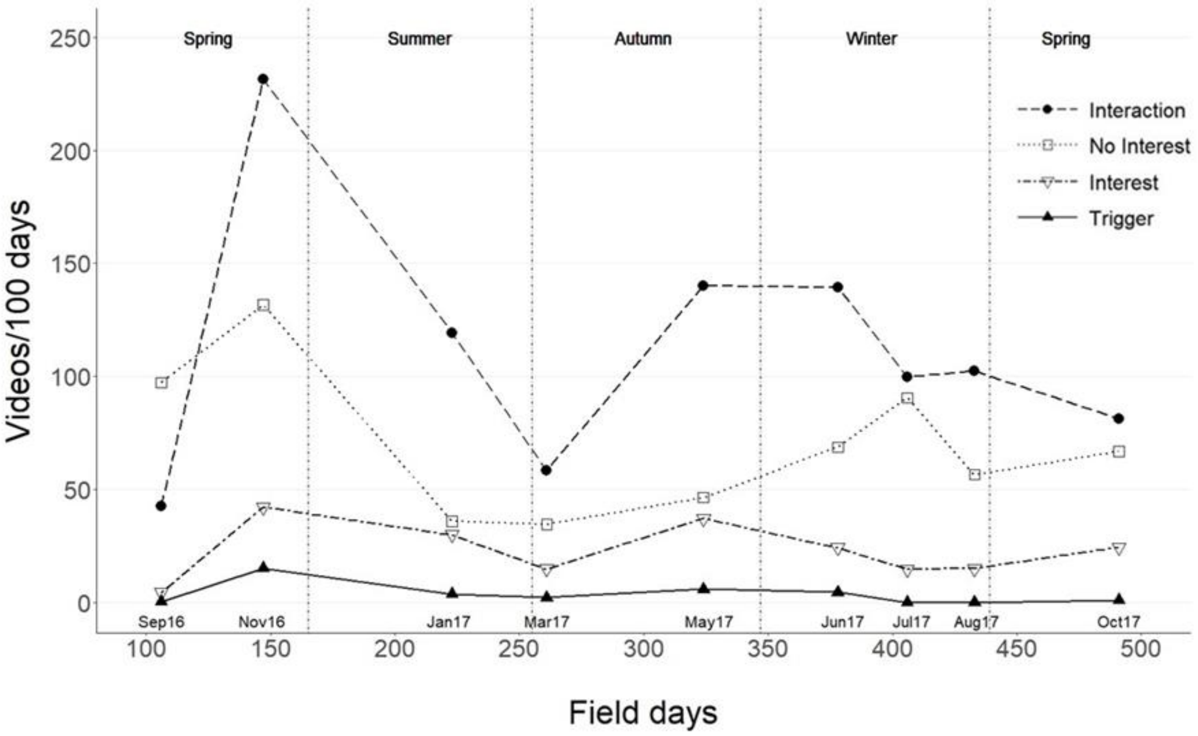

Figure 5.3. Number of videos per camera day plotted against time for the four behavioural categories observed by cameras around Goodnature A24 self-resetting traps on Goat Island from September 2016 to October 2017. Field days are the number of days after A24 deployment. Note the first 100 days of knock-down (i.e. suppression from high to low abundance) are excluded.

Interaction and No Interest were the most frequent behaviours observed at all levels of rat activity. The number of camera records increased linearly with rat activity for all behaviour types, although the number of Interactions was significantly higher than expected at higher rat activity (Table 5.2).

Table 5.2. Results of the Generalised Linear Mixed Model analysing the effects of rat activity and seasonality on rat behaviour around Goodnature A24 self-resetting traps on Goat Island from September 2016 to October 2017. Intercept is Spring and No Interest. Significance codes are '***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$

	Estimate	SE
Intercept	2.902***	0.110
Interest	-1.113***	0.151
Interaction	0.031	0.097
Trigger	-2.976***	0.343
Summer	-0.467***	0.113
Autumn	-0.440***	0.092
Winter	0.004	0.075
Rat activity	0.086***	0.013
Summer : Interest	0.880***	0.187
Summer : Interaction	0.690***	0.138
Summer : Trigger	0.765	0.396
Autumn : Interest	0.676***	0.163
Autumn : Interaction	0.602***	0.115
Autumn : Trigger	0.633	0.347
Winter : Interest	-0.501**	0.157
Winter : Interaction	-0.240*	0.098
Winter : Trigger	-0.934*	0.387
Rat activity : Interest	0.006	0.026
Rat activity : Interaction	0.073***	0.016
Rat activity : Trigger	0.030	0.063

5.3.2 Behavioural response to new devices

Any cautiousness in the first monitoring session towards the newly-installed A24s was not observed. The rats visited the traps within hours after they had been installed. The cameras were all activated in the afternoon and the first interactions with a trap occurred just over an hour later around dusk. Times to the first interaction at each trap ranged from 63-199 min (median = 139 min, n = 9). It took no more than five visits at each trap until the first interaction occurred and in 50% of the first visits the rats immediately interacted with the traps. At 6 out of 10 traps we observed a rat getting killed in the first night. After three nights all ten A24 traps on the island had killed at least one rat.

5.4 Discussion

Understanding animal behaviour around control devices, particularly new-to-market devices, helps understand optimal ways to deploy these devices and determine the appropriate pest control contexts in which they should be deployed. While the self-resetting traps were useful for population suppression on Goat Island, eradication could not be achieved with one A24 per hectare in combination with DOC200s. Previous population estimates from exhaustive trapping of rats on Goat Island fluctuate between 28 – 33 individuals (Pichlmueller & Russell, 2018; Russell et al., 2009). During our study the removal rate of rats on the island must not have been higher than the population growth rate, inclusive of recruitment within the population and immigration from the nearby mainland, both of which have plagued previous eradications (Pichlmueller & Russell, 2018). Most kills by A24s happened during the breeding season in 2016 in the first third of the study and in May 2017 when food may have been scarce at the end of autumn. The substantial difference in rat activity and kill numbers between August and September 2016 shows the initial success in reducing rat numbers on the island. Kill numbers then continued to decline over time but never reached zero (i.e. eradication). These kills possibly comprised the ongoing removal of naïve individuals, such as recently recruited adults and immigrants, while a small number of cautious adults remained on the island. Such an effect has also been seen in stoat trapping operations on islands within swimming distance (McMurtrie et al., 2011). A long term trial of self-resetting traps on Aotea/Great Barrier Island showed a similar pattern of decline in A24 kills over time. A reduction in tracking tunnel indices in an area without previous rat control was achieved with A24s as the sole control tool with 3-5 traps/ha, but very low levels of rat abundance (< 20% tracking tunnel index) could not be maintained (Gilbert, 2018). At Ark in the Park in the Waitakere Ranges near Auckland City, A24s were installed and reduced the tracking tunnel index after two months but also failed to maintain a very low level of rat abundance (Gilbert, 2018). A recent trial of a bait delivery system for A24s on Native Island, which also has a high incursion risk, has shown a relatively high rat abundance (37% tracking tunnel index) when using A24 as a biosecurity tool at a density of three A24s/ha (Carter et al., 2019). A very high device density of 10 A24s/ha in combination with single-kill snap-traps (25 traps/ha) was able to maintain lower rat abundance than in an unmanaged area in Hawaii (Shiels et al., 2019). In addition to the relatively low device density, a potential issue for achieving eradication in our study was size selectivity, as small rats were not observed being killed by A24s and the DOC200s were not expected to kill juveniles with a trigger weight of approximately 96g (Warburton, 2016).

The observed number of trigger events was low compared to the interaction rate throughout the study. Our footage showed that rats did not avoid contact with the A24 itself but were hesitant in entering it. A key aspect in improving the capture rate of A24s may be the automatic lure pumps (Gilbert, 2018; Ogden, 2018). The number of rats showing no interest in the trap was high throughout the study. Generally, a food lure is less effective when food abundance is high and competition is low (Jackson et al., 2016). However, a lure which is more attractive than the food available in the habitat will likely increase interaction and capture rate. The exact composition of the Goodnature chocolate formula is unknown but it has a sweet chocolate-like smell. In a comparison of different food lures, milk chocolate and a hazelnut cocoa spread were more attractive to rats than peanut butter, which is a standard lure for rats worldwide (Jackson et al., 2016). However, the nutritional value of the lure also determines its attractiveness with fat being a preferred energy source for rats (Kasper et al., 2014). A comparative test of different lures in A24s is needed to evaluate the attractiveness of the Goodnature chocolate formula. The trap design may also influence the capture rate. Norway rats on Motukorea, New Zealand, were more likely to enter traps covered with clear plastic or wire netting than traps covered with solid iron (Weihong et al., 1999). A clear housing for A24s may have the potential to increase the number of rats entering and triggering the trap.

5.4.1 Season and activity effects on behaviour

Seasonal effects on the behaviour of ship rats around the self-resetting traps were evident. Interaction peaks appeared in spring and late autumn. The high interaction rate consequently led to high kill numbers in November 2016 and May 2017. Ship rats follow a seasonal breeding pattern and reproduction starts in spring and peaks in late summer with rat numbers being the highest in autumn (Wilmshurst et al., 2021). The high kill rate in late spring was likely due to increasing population size and recruitment of naïve individuals while food abundance had not reached its peak. The main factor controlling population density is food availability, which differs among seasons (Wilmshurst et al., 2021). Russell et al. (2009) found rat stomachs in autumn and winter on Goat Island to be almost empty, suggesting that food availability is very low in these seasons. Even though not measured in our study, we assumed that that seasonal food availability does not differ significantly between years. Therefore, the combination of increased rat abundance and decreased food availability likely led to a high number of observed interactions between rats and traps in autumn, which consequently resulted in high kill numbers in May 2017. On Goat Island, an expected higher interest in A24s as an additional food source in winter may have been offset by generally lower population density. The relatively high interaction rate in winter may have been caused by a few individuals repeatedly interacting with A24s. The lure, however, was then not attractive enough that these cautious surviving rats would enter the trap.

Rat activity appeared to influence the behaviour of the rats on Goat Island. The rats were more likely to interact with the traps when rat activity was high. A higher rat activity was assumed to lead to more interactions with the A24s which presented a food source in an environment with relatively low food productivity. Population density is often positively correlated to competition (Adler & Levins, 1994). Increasing intraspecific competition due to growing rat numbers may have been the driving factor for the higher observed activity and interaction rate with the A24s in November 2016, the end of austral spring. However, in July 2017 increased rat activity did not result in increased numbers of kills. The reason for the low kill numbers could have been that the rats were able to access the lure without entering the trap. The automatic lure pumps released the lure steadily over time. Excess lure dropped underneath the trap and video footage showed that the rats were feeding on it. Preventing the lure from dripping down the trap could be a key improvement to the design of automatic lure pumps for A24s, since it can also cause mechanical issues with the trigger mechanism leading to trap failures (Gilbert, 2018).

5.4.2 Behavioural response to new devices

The rats on Goat Island did not show any reluctance in interacting with the Goodnature A24s and trapping success was immediately high at the beginning of the study. At all trap locations first encounters occurred around dusk when rats became active and it took only few visits before rat-trap interactions were observed. The first kills occurred in the first night at most traps. The rat population on Goat Island was not naïve towards kill trapping. Predator control with DOC200s had been conducted for more than a year prior to the installation of Goodnature A24s. The time between deployment of A24s and the rats showing interest in and interacting with the traps was short enough to exclude neophobia. In addition, after three nights kills had been observed at each of the ten A24s. On Aotea, A24s have also been most effective in the first week after deployment (Ogden, 2018). In contrast, the highest capture rate for DOC200s during our study, which was in May 2017 (two years after first activating DOC200s), was only five rats in eight traps.

Previous research suggested that new objects in the environment cause avoidance behaviour in rats that lasted up to 12 days (Barnett, 1988; Wallace & Barnett, 1990). The context in which rats encounter unknown objects influences their behaviour. Ship rats showed a neophobic response when they encountered new objects in their familiar environment (Cowan, 1976) but new food in a familiar container did not induce a neophobic response (Inglis et al., 1996). However, it can be assumed that rats in these studies were either stressed or habituated to disturbance and artificial environments since they were either bred for laboratory experiments or caught in the wild and laboratorized (Boice, 1971). Therefore, one must be cautious to make inferences to the behaviour of wild rats in their natural habitat. While the presentation of a new object can influence rat behaviour in the laboratory it does not mean that it will affect the behaviour of free-living rats (Martin & Bateson, 1993). In an observation of two A24 traps on Aotea/Great Barrier Island rats were also killed in the first night (Ogden, 2018). Most of the rats in our study possibly avoided the newly-installed A24s while a small proportion of the population did not. The bold behaviour of a few individuals interacting with the traps might have concealed any cautious response by most other rats. However, by the time the bold rats are removed the remaining individuals are probably habituated to the presence of the new devices. As additional context, Goat Island is small and does not have a very diverse and productive forest (Russell et al., 2009). Therefore, the population is probably strongly regulated by food availability and hunger may have been a driving factor for prompt interactions with the traps.

Our study showed that environmental seasonality and rat activity influenced the behaviour of ship rats around self-resetting traps on Goat Island and no neophobic response towards the new devices was found. After initial knock-down rats killed subsequently may have been naïve invaders and young adults while a certain number of cautious island residents avoided the traps. On Frégate Island, Seychelles, mainly juvenile Norway rats were killed in a trapping operation while adults avoided the traps (Thorsen et al., 2000). Studies of home range and behaviour of individuals that survive control efforts are needed to identify if trap avoidance or lack of device encounters are the reason for their survival (Garvey et al., 2020). Given the seasonality in rat activity on Goat Island, intensifying rat control in autumn when interaction rates between rats and traps are high may increase A24 trapping success. The self-resetting Goodnature A24 traps were useful in reducing rat numbers and required relatively low maintenance effort. However, at one per hectare the self-resetting traps were not able to offset population growth and achieve eradication on the island, which requires additional investments in the system, e.g. a more attractive lure, higher device density, or a combination of tools including toxins. Video monitoring a combination of different control devices could identify if the low A24 kill rate following knock-down is unique to the A24s or simply an outcome of low abundance due to ongoing control.

6 General Discussion

6.1 Summary of findings

In my thesis, I have used several case studies to improve invasive rat monitoring and control. I used camera traps to gather a large dataset of behavioural observations of invasive rats around detection devices in the wild. The study was conducted on islands in temperate New Zealand and tropical French Polynesia. Additionally, capture-mark-recapture data was used to get robust estimations of rat population density at the study sites. I used these data to evaluate the reliability of indices of rat relative abundance obtained from camera traps and digital strike counters on self-resetting traps. I also tested recently developed statistical models for their suitability to inform management about rat population density. I found that camera traps can be used to estimate rat relative abundance even when kill traps failed to detect individuals. However, estimating true density of unmarked animals remains challenging. The novel statistical models to estimate population density of unmarked animals using camera traps were not suitable for the management scenario they were tested in. They were difficult to parameterise and may need a large number of cameras to achieve desirable precision for the density estimates. I showed that detection probability and population density differed between times, presumably affected by season. Population density influenced the number of live trap encounters and interactions but did not significantly influence the capture rate. The presence of a dominant competitor had a significant negative effect on the detection of the subordinate species. My findings will give management confidence when using camera traps as monitoring devices for invasive rats, particularly when abundance is low due to ongoing control or when interspecific competition may affect the detection probability of the target species. I found that triggering a trap is a critical part of interaction behaviour and independent from general trap encounters and interactions.

6.1.1 Measuring rat relative abundance using camera traps and digital strike counters for Goodnature A24 self-resetting traps

In Chapter 2, the aim was to evaluate two different methods for obtaining an index of rat relative abundance based on video footage from camera traps. I showed that counting only the number of videos that showed rats did not result in any loss of information when compared to more laboriously counting individual rats in videos and was therefore the preferred method for obtaining an index of rat relative abundance. Based on observations from the video footage I then evaluated the reliability of Goodnature digital strike counters for measuring the number of killed individuals at Goodnature A24 traps. The digital strike counters were found to accurately reflect the number of individuals killed. However, once rat abundance was reduced after sustained trapping, cameras were better in detecting the remaining individuals than Goodnature A24 traps.

6.1.2 Estimating small mammal density using camera traps: testing theory in the field

In Chapter 3 I tested three different novel statistical methods to estimate abundance of unmarked invasive rats using camera traps and compared them to the results of the commonly used spatially explicit capture-recapture model SECR (Efford et al., 2009a). The random encounter model (Rowcliffe et al., 2008) failed to provide biologically realistic density estimates due to difficulties in estimating animal movement speed. The spatial model after Chandler and Royle (2013) estimated a population density lower than the capture-recapture analysis. Low precision was identified as problematic when using the model after Chandler and Royle (2013), presumably due to an insufficient number of cameras. The random encounter and staying time (REST) model (Nakashima et al., 2018) appeared to be sensitive to different staying times and provided a similar estimate to the SECR model for May 2018, but underestimated density for June 2018. However, the REST models showed that population density was high and therefore, was informative.

6.1.3 Trappability of low density invasive rats

In Chapter 4 I aimed on analysing the effects of time and interspecific competition on population density and detection probability of Pacific rats at low population densities after sustained control. I showed that population density and detection probability of Pacific rats varied between times reflecting seasonality in food abundance and rat reproduction. The detection probability of Pacific rats also differed between sites, being higher where Pacific rats were the only rat species, presumably due to absence of interspecific competition with ship rats. Where Pacific rats were the sole species, they were captured in traps in the first night. However, in coexistence with ship rats Pacific rat detection was delayed by at least ten days. Population density influenced the number of trap encounters and interactions but did not significantly influence the capture rate.

6.1.4 Behaviour of invasive ship rats, *Rattus rattus*, around Goodnature A24 self-resetting traps

In Chapter 5 my principal aim was to analyse the behaviour of ship rats around A24s over time and evaluate the suitability of A24s for effective rat control on Goat Island. An immediately obvious neophobic response towards the A24 traps after initial deployment was not observed. I found that the behaviour was influenced by environmental seasonality and rat activity. However, while rat activity remained relatively constant after 3 months of sustained trapping, the number of rats killed by A24s declined over time. A24s were suitable to suppress the rats from high to low abundance but eradication was not achieved.

6.2 Discussion of key findings

The use of camera traps to answer various ecological questions has consistently increased over the past two decades (Burton et al., 2015). In my thesis, camera traps were used to determine how camera traps can be used to measure rat abundance and to understand behaviour of rats around detection devices.

6.2.1 The use of camera traps to measure rat abundance

I showed that camera traps are a valuable addition to traditional tools for measuring rat abundance. I have used a standardised camera set-up and most of the data collection could be done by field staff. Measuring rat abundance in number of rat videos per 100 camera nights was of greater value than A24 kill numbers. My prediction that camera traps will be better in detecting rats than A24s was correct. Camera traps detected rats even when rat abundance was low after sustained kill trapping and A24s failed to detect the remaining individuals on Goat Island. I predicted that counting individual rats in videos will result in a higher rat relative abundance index than counting the number of videos that show rats. However, when using video footage, just confirming rat presence did not lose information compared to counting individual rats. Results from the latest statistical models to estimate density from unmarked animal detections were confounded by a high level of uncertainty in the estimates and one model (random encounter model) failed in delivering biologically realistic estimates. I assumed that the novel statistical models would provide informative density estimates and may be a valuable alternative to the established capture-recapture models due to a simplified data collection. However, complicated model parameterisation and the potential need for a large number of cameras, hence increased costs, to achieve a desirable precision of estimates may outweigh the benefits of simplified data collection.

When camera traps were used to estimate abundance the target species were often slow moving large herbivores or large predators (Carbone et al., 2001; Karanth & Nichols, 1998; Mace et al., 1994; O'Brien et al., 2003; Rovero & Marshall, 2009). Monitoring small mammals can be challenging due to imperfect detection by cameras (DeSa et al., 2012; Tobler et al., 2008). Differences in detection probability between devices may depend on the density of the target species, De Bondi et al. (2010) showed that cameras were better in detecting rare and elusive species than live traps. Detection rates for cats, hedgehogs, rabbits, and possums were higher for camera traps than kill traps in areas where predator management was present (Glen et al., 2014). On Goat Island, cameras were also better in detecting rats than mechanical traps (A24), once rat abundance was reduced after sustained kill trapping, leading to only weak correlation between the index from camera footage and kill numbers. Even though rat density was very low on Aotea, an index of rat relative abundance strongly correlated with density estimates from capture-mark-recapture data (Figure 6.1). Success in the detection of small mammals may be influenced by the camera model (Apps & McNutt, 2018). However, I used the same cameras models on Aotea and Goat Island. The Tomahawk live traps used on Aotea may be better in detecting rats than A24s. On Aotea, A24s also performed worse in controlling rats than a combination of snap traps and toxins (Gilbert, 2018). The A24s on Goat Island may not have detected the remaining rats because the threshold to trigger the trap was too high for cautious individuals or the lure was not attractive enough compared to naturally occurring food. However, while individuality can influence trappability in some taxa (Biro, 2013; Carter et al., 2012), numerous studies could not confirm such a correlation between personality and trappability in rodents (Brehm & Mortelliti, 2018; Broecke et al., 2021; Jolly et al., 2019).

An index of relative abundance may identify temporal trends within one study population but inferring changes over space must be seen with caution (O'Brien et al., 2003). Therefore, proper population estimation studies should be conducted when possible. While camera trap data can be used to estimate true density when individuals can be identified (Borchers et al., 2014; Karanth & Nichols, 1998; Mace et al., 1994; Wang & Macdonald, 2009), new statistical approaches were needed for unmarked animals. Testing these new statistical methods in the field, outside the controlled environment of simulations, is valuable and necessary to evaluate their use. Simulations of the models used up to 225 detection devices (Chandler & Royle, 2013). The initial purchase costs of 225 trail cameras, including batteries and SD card, as well as labour costs when analysing a vast amount of camera footage would most likely be the biggest barrier for use in management.

Density estimates using the random encounter model developed by (Rowcliffe et al., 2008) were higher than from consensus data for Harvey’s duiker (Rovero & Marshall, 2009) and lions (Cusack et al., 2015). My density estimates for Pacific rats from the random encounter model were biologically unrealistic, most likely due to lack of information about rat movement speed and day range. The information that is needed to inform the random encounter model is rarely available for any species and difficult to obtain. Previous studies using the random encounter model had to use estimates of day range from different sites (Manzo et al., 2012) and even different species (Rovero & Marshall, 2009). I assumed that using only a small number of camera traps caused the high level of uncertainty in the estimates. However, Rovero and Marshall (2009) used even fewer cameras per site but density estimates did not result in the low precision observed in my study.

An index of relative abundance from camera traps reflects animal activity but may not necessarily allow inference to abundance. To evaluate the reliability of an index of relative abundance from camera traps, more studies need to calibrate the index, preferably with capture-recapture data. Long term studies could then explore the effects of season and population density on the index.

A comparison between A24s and other detection devices using the same lure could reveal differences in interaction rates and detection probabilities that may be caused by the device design. Using different lures, including standard lures like peanut butter and coconut, in A24s. More knowledge about the effects of device design and lure efficacy on detection probability can improve rat management and future product design.

More knowledge is needed about activity times and movement speed of the target animals to inform the random encounter model. These data are not easy are not available yet and hard to obtain. Radio telemetry did not deliver the desired outcome. It cannot be determined how much distance on the ground was covered by the individual between two bearings. Especially fast moving animals with small home ranges require constant tracking to estimate day range. Day range estimates then need to be compared between different habitats, seasons, abundances, and other influencing factors, e.g. interspecific competition, predation etc.. Once the necessary data for model parametrization is available, an extended study using more cameras over a larger area for a longer time would provide a valuable data set to determine the effects of trapping effort on estimate precision.

6.2.2 Behaviour of invasive rats around detection devices

The behaviour of target animals between encountering and triggering a control device has previously neither been described nor analysed. I showed that, abundance influenced the number of trap encounters and interactions but did not significantly influence the capture rate. I predicted to observe a high number of encounters, interactions, and triggers when rat abundance is high. However, I did not expect that the observed rat activity around control devices stays high when abundance is lower and that rats interact with control devices but not trigger them. I correctly predicted that rat activity and detection probability differed between seasons, supposedly being linked to seasonal differences in food availability and rat reproduction. The detection probability of Pacific rats on Aotea also differed between sites, presumably due to interspecific competition with ship rats. In coexistence with ship rats, Pacific rat detection was delayed. I predicted lower detection probabilities for Pacific rats in coexistence with ship rats. However, the delay of Pacific rat detection was surprisingly long. As assumed, at all sites, rats were detected in the first night by newly deployed devices.

Detectability of animals in trapping studies is influenced by numerous factors, including device type (Harkins et al., 2019; Wilson et al., 2007), bait type (Paull et al., 2011; Shafi et al., 1990), alternative food availability (Weerakoon & Banks, 2011), habitat type (Bacheler et al., 2014; Harper et al., 2015), and season (Bukombe et al., 2016; Harper et al., 2015). Detection probability involves the probability that an individual encounters a control device and the probability that this individual then interacts with the device in a way that leads to a detection. Differences in detection probability between seasons can be explained with rat reproduction and food abundance. Rat abundance in New Zealand is highest in late autumn at the end of the breeding season (Innes et al., 2001; Wilmshurst et al., 2021). Low detection rates in winter were based on low rat abundance and activity. Whereas trapping success was high in autumn when high rat abundance coincides with a decreasing food availability.

Population density can be positively correlated to competition (Adler & Levins, 1994). An increased intraspecific competition for food may explain the higher rat activity around detection devices when abundance was high. However, it was hypothesized that releasing rats from competition at low abundance may lead to trap avoidance and the number of encounters and interactions with the trap would decrease accordingly. On Goat Island, a flaw of the automatic lure pump allowed the rats to access bait without entering the trap, may explain why the rats were still interacting with the trap at low abundance, but not triggering it. However, when using live traps on Aotea, the rats could not access the bait without triggering the trap. Therefore, it is not low rat density alone that leads to low trapping success. The constant interaction rate shows that rats did not avoid the detection device in general but the trigger mechanism. Technological responses to improve control devices should include either design changes to lower the threshold for rats to interact with the trigger mechanism or to improve the attractiveness of the bait to overcome trigger avoidance.

The differences in detection probabilities between sites where Pacific rats coexisted with ship rats and sites where Pacific rats were the sole species may indicate an effect of interspecific competition. Asymmetric competition between dominant puma (*Puma concolor*) and subordinate bobcats (*Lynx rufus*) has shown to reduce the detection probability of the subordinate species (Lewis et al., 2015). Ship rats on Aotea were captured at the beginning of the trapping session and removed from the population. The delayed capture of Pacific rats may have been caused by trap avoidance to prevent potentially aggressive encounters with ship rats. Cheetahs (*Acinonyx jubatus*) exhibited local avoidance behaviour with dominant lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). If Pacific rats avoided encounters with ship rats, they may have been excluded from the detection device during the first days of my study. Excluding Pacific rats from accessing control devices by dominant *R. tanezumi* is also one possible reason for the rat eradication failure on Wake Atoll (Griffiths et al., 2014; Hanson et al., 2019). While a reduced detection probability of Pacific rats in coexistence with ship rats was anticipated, the delay of 10 days to the first Pacific rat detection was unexpectedly long. Pacific rats may have remained undetected in previous studies where interspecific competition was present.

Another reason for animals being undetected can be a neophobic response, i.e. the target animal avoids the newly deployed detection device. Ship rats have avoided new objects for up to 12 days in the laboratory (Wallace & Barnett, 1990). Norway rats have shown reduced interactions with a new food container in their home range (Inglis et al., 1996). Invasive ship rats on Goat Island were under ongoing control with kill traps (DOC200) and therefore, not naïve toward detection devices. However, installation of a new device type (A24) did not invoke a neophobic response in all rats on Goat Island. Rats were also caught in the first night of trapping on Aotea using cage traps that were unknown to the individuals at the site. Confirming the presence of neophobia requires the measurement of baseline behaviour (Barnett, 1988) and would not have been possible in my study. Confirming the absence of neophobia in many individuals, however, was possible. Rats interacted with detection devices shortly after deployment, which, by definition, excludes the presence of neophobia. The prompt rat-trap interactions at all sites suggest that neophobic responses to new detection devices do not impede monitoring of ship rats and Pacific rats.

6.3 Implications for management

6.3.1 Using camera traps to monitor wildlife

This thesis has demonstrated the advantages of camera traps for monitoring invasive rats on islands compared to mechanical detection devices, i.e. live or kill traps. For management costs and benefits must be considered when planning the monitoring of a target species. The use of camera traps can be divided into initial costs for camera purchase, maintenance costs, and costs for data analysis.

Literature comparing different camera models is available and the body of literature is growing due to ongoing technological development (Dixon et al., 2009; Driessen et al., 2017; Randler & Kalb, 2018; Urlus et al., 2014; Weingarth et al., 2013). While certain technological specifications (e.g. trigger speed) are important when choosing the right camera model, available funding may often decides which model to purchase. However, financial savings during camera purchase may be nullified by consequential costs due to practical issues with deployment and operation of the cameras or data management (Newey et al., 2015). In my study, maintenance costs were not evaluated. Cameras were checked regularly during kill trap servicing or daily within the live trapping grid. Therefore, additional visits to replace batteries or SD card were not necessary.

Data analysis can be the costliest part when using camera traps. In my study, the main issue with footage from all camera models (Bushnell, Moultrie, Browning) was overexposure due to the short distance between camera and target area.

Overexposure was corrected using the video adjustment settings for the VLC media player (v3.0.7). However, the video settings had to be adjusted for each camera and overexposure could even differ between nights, leading to extended viewing times. Furthermore, cameras can be triggered by non-target animals or by vegetation movement. When only confirmation for the presence of a target species in a picture is needed, the use of artificial intelligence (Falzon et al., 2020), citizen science (Anton et al., 2018a; Chandler et al., 2017) or a combination of both (Green et al., 2020) can increase efficiency in the data analysis. Therefore, an optimised data analysis process combined with high data quality will outweigh initial purchase costs.

6.3.2 Site specific comments

I provided the first rat density estimates for two sanctuaries on Aotea and for Reiono, Tetiaroa. Additionally, I estimated an index of rat relative abundance for Goat Island. At all sites little was known about rat abundance before my study. Therefore, I will provide a brief review of the rat management at the study sites. These suggestions will help managers to make use of the abundance estimates from this thesis.

6.3.3 Control of invasive ship rats, *Rattus rattus*, on Goat Island, New Zealand (Gronwald & Russell, 2020a)

Invasive ship rats (*Rattus rattus*) are the major threat to the native species and ecosystem of Goat Island (9.3 ha), New Zealand. The island is only 100 m away from the mainland, which imposes a risk of incursions by rats swimming over. Accessibility depends on weather and tide times which makes regular trap servicing complicated. In 2016 we extended an existing trapping grid of 8 kill traps (DOC200; Department of Conservation, New Zealand) with 10 self-resetting traps (Goodnature A24s; Goodnature Limited, Wellington, New Zealand) to improve current management and ideally achieve eradication. Before our study started, DOC200s on the island had not been serviced for six months. Rats were active even during the day and rat numbers were assumed to be high. The DOC200 kill traps were lured with an egg and A24s were lured with Goodnature automatic lure pumps (ALP) baited with chocolate formula for rats. The A24s were equipped with Goodnature digital strike counters to document the number of rats killed by the self-resetting traps. All devices were on average checked every 49 days from August 2016 to October 2017. DOC200s were reset after triggering or after three months, whichever occurred first. ALPs were replaced in January and July 2017. Gas cartridges of the A24s were replaced when the strike counter showed 20 or more.

Table 6.1. Numbers of ship rats killed by eight DOC200 and ten Goodnature A24s and days between trap servicing from August 2016 to October 2017 on Goat Island, New Zealand.

Date	A24	DOC200	Days
Aug-16	38	3	53
Sep-16	3	4	53
Nov-16	46	3	41
Jan-17	73	3	76
Mar-17	11	2	38
May-17	42	5	63
Jun-17	19	2	54
Jul-17	3	1	28
Aug-17	3	2	27
Oct-17	4	2	58
Total	**242**	**27**	**491**

A substantial number of rats were killed on the island (242 by A24s and 27 by DOC200s) in 8,838 uncorrected trap nights between August 2016 to October 2017 (Table 6.1). The initial number of individuals killed by A24s in the first month after deployment in August 2016 was high. The number of rats removed by A24s remained at a high level from November 2016 until June 2017. The number of A24 kills varied widely between the beginnings of the breeding seasons across the two years, with 46 individuals killed between September and November 2016 but only 4 kills between August and October 2017. Even though initial trapping success was high, eradication could not be achieved, and the self-resetting traps did not perform better than traditional kill traps once rat abundance was low. The Goodnature A24 has shown the potential to work effectively for initial knock-down when rat numbers and activity were high. The advantage over traditional single kill traps, like the DOC200, was the low need for servicing. However, once the population density was reduced to a lower level, this advantage vanished. Most kills by A24s happened during the breeding season in 2016 in the first third of the study. In the last three months of the project the kill numbers did not differ meaningfully from the DOC200 kill numbers. Even though trapping numbers were low, rat abundance was still assumed to be high. After our study had finished rat control on the island using these devices was continued by local community volunteers. A further 357 rats were caught between June 2018 and March 2020, indicating no decline in rat captures. On 1 September 2019 and 1 March 2020 tracking tunnel indices were 100% (K. Tricklebank pers. commun.).

In March 2020 initial cost for a DOC200 was NZD$145.00. The purchase costs for a Goodnature A24 with lure and gas for 6 months was NZD$169.00 (excluding digital strike counter). For the first six months the differences in costs were moderate. However, after six months, the material costs for servicing a DOC200 was NZD$0.55 (one free-range egg), or less when using peanut butter. The servicing cost for a Goodnature A24 is NZD$19.00 (gas cartridge + ALP). On Goat Island, servicing costs for a six months period were approximately NZD$9.00 for eight DOC200s and NZD$190.00 for ten A24s. Higher costs for A24 purchase and servicing compared to

DOC200 were not compensated by noteworthy higher kill numbers once rat numbers were reduced. However, A24s performed well during peak times and labour costs were not considered in our study. Self-resetting devices at one per hectare did moderately reduce rat numbers in an area where kill trap maintenance was time and cost intensive but suppressing to very low rat numbers or achieving eradication requires additional investment in the system (e.g., a combination of different tools including toxins or a higher density of devices).

6.3.4 Windy Hill Sanctuary, Aotea

Windy Hill Sanctuary has shown the potential to maintain very low population densities of invasive rats with a well organised control strategy despite ongoing reinvasion. The use of a more potent second generation anticoagulant, e.g. brodifacoum, should be considered to further suppress rat numbers. A major concern is the risk for pets. The use of bait stations reduces the risk to almost zero. More important is an appropriate storage and handling protocol for the toxin to avoid dogs accessing the bait. Properties upon which owners oppose the use of brodifacoum can be alternatively controlled with the already established method. However, reinvasion of rats into the sanctuary is currently thwarting any attempt to achieve rat abundance close to zero. Currently, a single line of alternate toxin and trap devices along the perimeter with a distance of 12.5 m between devices is the only barrier between the sanctuary and unmanaged areas. Bell et al. (2019) tested a virtual barrier to prevent reinvasion of rats onto Bottleneck peninsula in the South Island, New Zealand. The barrier consisted of six lines 100 m apart with 10 m distance between detection devices on each line. Each detection device consisted of two DOC150 kill traps. The barrier prevented 95% of reinvasion. At the perimeter of Windy Hill Sanctuary needs to be improved to further reduce reinvasion into the sanctuary.

6.3.5 Glenfern Sanctuary, Aotea

The rat eradication attempt in 2009 has successfully removed ship rats from Glenfern Sanctuary. The rat proof fence has since successfully prevented the reestablishment of ship rats in the sanctuary. Even though outside the sanctuary most rats trapped are ship rats (J. Russell, unpubl. data), they could not be detected within the fenced area. The current management strategy is not sufficient to eradicate rats from the sanctuary but only to control rat numbers to low abundance. A further eradication attempt is highly recommended to fully utilise the advantage of having a rat proof fence as a physical barrier against reinvasions. A possible reason for the eradication failure may have been interspecific competition between ship rats and Pacific rats. Reduced bait availability to the subordinate competitor may have been one reason contributing to the failure of Wake Atoll rat eradication (Hanson et al., 2019). Even though eradication of low density rats is considered difficult when food is abundant (Kappes et al., 2019), in my study, rats did interact with the peanut butter lure provided in live traps, resulting in a high detectability in winter. An eradication can reduce long term costs for the management of the sanctuary compared to ongoing control (Pascal et al., 2008), but monitoring and incursion response can also be very resource intensive (Maitland, 2011). However, Glenfern Sanctuary is open to the public and therefore, is a key site for environmental education, where endemic species like Chevron skink (*Oligosoma homalonotum*) and black petrel (*Procellaria parkinsoni*) can be found and eradication benefits would outweigh the costs.

Both Glenfern Sanctuary and Windy Hill Sanctuary are promising conservation projects. Not only are they valuable for promoting the idea of a Predator Free Aotea, but they can also be an important step towards in achieving that goal. Further improving rat management and utilising the sanctuaries for research will extend their impact as role models for conservation projects on Aotea.

6.3.6 Tetiaroa

During the eradication of Pacific rats from Reiono various risks were identified which could have led to eradication failure: rats were reproductive, high natural food abundance, high abundance of land crabs which consumed bait, short period of bait availability (two nights) and short period of only seven days between bait applications. Despite these risks the operation successfully removed all rats from the island(Samaniego et al., 2020b). The long term goal is to eradicate invasive rats from the whole atoll (Russell et al., 2016). In 2020, an eradication attempt was undertaken for the main motu Onetahi and adjacent Honuea. However, in 2021 a rat was detected on Onetahi, intensive trapping and monitoring is currently in progress. The next eradication unit should be Rimatuu (88 ha), an islet northwest of Reiono. Rimatuu is the second islet of the atoll where only Pacific rats have been present at high population density. Bird Island, Tahuna Iti, an important bird nesting site in the atoll, is less than 10 m offshore from Rimatuu. Therefore, the risk of rat incursion on Tahuna Iti is high. The geography on Rimatuu is more complex than on Reiono. A lake is situated in the north of the island and vegetation can be dense in parts of the island. Given the size of the island, the terrain an aerial bait application may be preferred. The aerial application of bait using drones is under development (Island Conservation, 2019 January 24) and may be a practical solution for Rimatuu.

Rimatuu is isolated enough that the risk of incursions by swimming rats after a successful eradication are considered low. However, the island is easy to access and is a popular destination for visitors. This led to a cat incursion on the island in 2018. Therefore, an effective biosecurity strategy must be developed including information for visitors as well as a response plan for incursions. To detect incursions camera traps should be used in regular monitoring operations across the island to detect incursions. A cost efficient way to detect rats would be to utilise current surveys of coconut crabs (*Birgus latro*). During these surveys, coconut crabs are lured with opened coconuts which are set along transects. During previous surveys Pacific rats were attracted by the coconuts and approached them minutes after they had been placed (pers. obs.). Camera traps used to monitor the coconuts along transects would be a valuable biosecurity tool to detect incursions.

6.4 Future research recommendations

Interspecific competition with ship rats was a probable cause for reduced detectability at low density Pacific rats. Further research could investigate the underlying mechanisms. A study in which the dominant competitor is selectively removed from the study area could answer questions about behavioural response to interspecific competition. After interspecific competition is removed possible immediate and long term changes in behaviour of the subordinate species could involve a shift in activity times, foraging time around detection devices or changes in home range. The delay in the behavioural change after competitor removal would give valuable information about the persistence of a landscape of fear. The temporal information is of high value when informing management of invasive species, e.g. interval between bait applications in a multi species eradication.

A more standardised experimental set-up across all seasons, preferably at various sites simultaneously, is needed to obtain more detailed information about behavioural differences between seasons but was beyond the scope of this project. Knowledge about seasonal effects on the probability of interaction could help determine the best timing for control operations beyond the argument that lure is most attractive when natural food abundance is low, i.e. usually winter. This would be particularly important in the tropics when food resources are not necessarily that limited.

The high rat trapping success in very low density in this thesis showed that trapping effort is a crucial factor. Detectability of Pacific rats at Glenfern Sanctuary was very high despite very low population density. This raises the question why conventional poison bait stations failed to remove the remaining individuals. Further studies should determine whether it is the trapping effort, i.e. distance between devices, or a behavioural response to the device. A possible study could involve live trapping and marking every individual in an area and then switching devices to kill traps. Differences in recapture rates between live and kill traps can reveal a device related response. A grid of bait stations filled with either poison or the same lure as used during live trapping could identify bait related issues when analysing the uptake.

The statistical methods for estimating population density of unmarked wildlife tested in this thesis provided promising results. Extended studies with a higher device density will allow for a more precise evaluation for the application of these models with data from the field. Further research is also needed to evaluate their performance for low population density rats. Studies should also extend to other species. In the context of Predator Free New Zealand 2050 and considering the positive results using the random encounter model (Rowcliffe et al., 2008) to estimate population density of pine martens (Manzo et al., 2012), studies should include mustelids in New Zealand.

Finally, cultural knowledge about Pacific rats should find its way into research. Māori were successful hunters and their knowledge about the ecology of Pacific rats will present a valuable addition to current knowledge. Māori have gained knowledge about food preference as well as movement of rats in their habitat. However, this knowledge is often difficult to access due to a language barrier or lack of written documentation.

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Appendix A. GPS locations of detection devices from a) Goat Island, New Zealand b) Aotea, New Zealand and c) Reiono, French Polynesia

a) Goat Island

Trap ID	Device type	lat	lon
G1	DOC150	-36.2673	174.7966167
G2	DOC150	-36.26643333	174.79645
G3	DOC150	-36.2661	174.7971167
G4	DOC150	-36.2655	174.7972833
G5	DOC150	-36.26473333	174.7967667
G6	DOC150	-36.2641	174.7976
G7	DOC150	-36.26498333	174.7985
G8	DOC150	-36.26753901	174.79881
GN01	Goodnature A24	-36.26684496	174.796632
GN02	Goodnature A24	-36.26693197	174.797325
GN03	Goodnature A24	-36.26638203	174.798259
GN04	Goodnature A24	-36.26553001	174.798527
GN05	Goodnature A24	-36.26448202	174.799113
GN06	Goodnature A24	-36.26439996	174.798116
GN07	Goodnature A24	-36.26504201	174.797098
GN08	Goodnature A24	-36.26528802	174.797876
GN09	Goodnature A24	-36.26554702	174.796503
GN10	Goodnature A24	-36.26504998	174.799563

b) Aotea/Great Barrier Island

	Glenfern		Windy Hill		Benthorn	
Trap ID	lat	lon	lat	lon	lat	lon
1.1	-36.158417	175.353464	-36.296059	175.521995	-36.30237099	175.519899
1.2	-36.15845103	175.353736	-36.29588951	175.5222722	-36.30260501	175.51988
1.3	-36.15847902	175.354018	-36.29577301	175.522481	-36.30278296	175.519925
1.4	-36.15842203	175.354268	-36.29568801	175.522637	-36.30305202	175.519899
1.5	-36.15836402	175.354539	-36.29558902	175.522879	-36.30325997	175.519878
1.6	-36.15824098	175.354757	-36.29550797	175.523033	-36.30344597	175.519837
1.7	-36.15814199	175.354989	-36.29539004	175.523274	-36.30370103	175.519771

2.1	-36.15821701	175.353405	-36.29638103	175.522325	-36.30243201	175.519521
2.2	-36.15826	175.35366	-36.296232	175.522529	-36.30266201	175.519424
	Glenfern		Windy Hill		Benthorn	
Trap ID	**lat**	**lon**	**lat**	**lon**	**lat**	**lon**
2.3	-36.15826	175.353947	-36.29602899	175.522699	-36.30288798	175.5195
2.4	-36.15819999	175.354211	-36.29594802	175.522942	-36.30308102	175.51945
2.5	-36.15815104	175.354454	-36.29581198	175.5231	-36.30325503	175.519501
2.6	-36.15803202	175.3547	-36.29558299	175.523245	-36.30347698	175.51949
2.7	-36.15794602	175.354965	-36.29550504	175.52342	-36.30369298	175.51959
3.1	-36.15806001	175.353237	-36.29653299	175.522457	-36.30244601	175.51922
3.2	-36.15807996	175.353534	-36.29645403	175.522702	-36.30269	175.519229
3.3	-36.15809002	175.353806	-36.29628799	175.522846	-36.30291296	175.519214
3.4	-36.15802397	175.354052	-36.29618598	175.523115	-36.30315604	175.519093
3.5	-36.15795298	175.35432	-36.29605799	175.523312	-36.30335603	175.519183
3.6	-36.15781702	175.354522	-36.295987	175.523478	-36.303638	175.519241
3.7	-36.15786203	175.354777	-36.29582497	175.523749	-36.30380002	175.519244
4.1	-36.15784401	175.353128	-36.296794	175.522594	-36.30250803	175.518888
4.2	-36.157929	175.35338	-36.29660399	175.522847	-36.302732	175.518927
4.3	-36.15789204	175.353683	-36.29651397	175.52303	-36.302934	175.518918
4.4	-36.15783697	175.353961	-36.29636896	175.523223	-36.30316903	175.518992
4.5	-36.15773798	175.354223	-36.29624499	175.523466	-36.303365	175.51907
4.6	-36.15764804	175.354345	-36.29610099	175.52367	-36.30351998	175.518971
4.7	-36.15764402	175.354612	-36.29597803	175.523892	-36.30377898	175.518945
5.1	-36.15764997	175.353032	-36.29696701	175.522746	-36.30250099	175.51864
5.2	-36.157699	175.353324	-36.296808	175.522957	-36.30264197	175.518622
5.3	-36.15767503	175.353598	-36.29671496	175.523197	-36.30291397	175.518681
5.4	-36.15761301	175.353866	-36.29656903	175.523388	-36.30307901	175.518586
5.5	-36.15753598	175.35413	-36.29648698	175.523564	-36.30325503	175.518545
5.6	-36.15743296	175.354398	-36.296304	175.523804	-36.30355602	175.518528
5.7	-36.15747001	175.354707	-36.29616704	175.524002	-36.30370698	175.518585
6.1	-36.15747596	175.352933	-36.29718804	175.522958	-36.302603	175.518312
6.2	-36.15750798	175.353269	-36.29710003	175.523146	-36.30270601	175.518385
6.3	-36.15747102	175.353499	-36.296909	175.523292	-36.30295596	175.518371
6.4	-36.15741603	175.353763	-36.29685	175.523555	-36.30314799	175.518311
6.5	-36.15735903	175.353968	-36.29663902	175.523782	-36.30332996	175.518297
6.6	-36.15728502	175.354204	-36.29651598	175.523895	-36.30357698	175.518352
6.7	-36.15728703	175.354518	-36.29648798	175.524167	-36.30376004	175.51838
7.1	-36.15727203	175.352786	-36.29736699	175.523092	-36.30256897	175.517961
7.2	-36.15724001	175.353068	-36.29724696	175.523347	-36.30276393	175.5180322
7.3	-36.15718997	175.353347	-36.29719097	175.523533	-36.30297298	175.518047
7.4	-36.15717899	175.353626	-36.29697497	175.523787	-36.30315201	175.51799
7.5	-36.15719299	175.353823	-36.29691596	175.523957	-36.30336399	175.518009
7.6	-36.15717304	175.354038	-36.29681597	175.524162	-36.30355803	175.517927
7.7	-36.15713197	175.35435	-36.29678906	175.5243385	-36.30382902	175.517949

c) Reiono

Camera ID	lat	lon
CAM1	-17.046136	-149.544817
CAM2	-17.04621102	-149.545016
CAM3	-17.04621596	-149.545142
CAM4	-17.04635301	-149.545027
CAM5	-17.04654101	-149.54509
CAM6	-17.04668602	-149.545111
CAM7	-17.04671603	-149.545252
CAM8	-17.04645099	-149.54518
CAM9	-17.04631001	-149.544857
CAM10	-17.046395	-149.54513

Trap ID	lat	lon
A1	-17.04610004	-149.544723
A2	-17.04622099	-149.544734
A3	-17.04627003	-149.544767
A4	-17.04633599	-149.544852
A5	-17.04648997	-149.544816
A6	-17.04653699	-149.544938
A7	-17.04666004	-149.544901
A8	-17.04668803	-149.544907
A9	-17.04685098	-149.544925
A10	-17.04691702	-149.544992
B1	-17.04608697	-149.544832
B2	-17.046151	-149.544808
B3	-17.04622803	-149.544916
B4	-17.04636499	-149.544863
B5	-17.04635904	-149.544942
B6	-17.04663497	-149.544972
B7	-17.04658602	-149.545013
B8	-17.04671703	-149.545054
B9	-17.046783	-149.545073
B10	-17.04689004	-149.545161
C1	-17.04604103	-149.544925
C2	-17.04613701	-149.544953
C3	-17.04621102	-149.544988
C4	-17.04631101	-149.545023
C5	-17.04642501	-149.545026
C6	-17.046496	-149.54507
C7	-17.04660798	-149.545105
C8	-17.04671703	-149.545125
C9	-17.04680999	-149.545139
C10	-17.04690102	-149.545261
D1	-17.04604296	-149.544987
D2	-17.04618101	-149.545035
D3	-17.04627003	-149.545024
D4	-17.04637698	-149.545078
D5	-17.04642601	-149.545056
D6	-17.04648997	-149.54509
D7	-17.04657798	-149.545141
D8	-17.04671804	-149.545178
D9	-17.04682499	-149.545203
D10	-17.04687403	-149.545239

E1	-17.04605503	-149.545088
E2	-17.04613399	-149.54516
E3	-17.04623097	-149.545196
E4	-17.04626299	-149.545175
E5	-17.04635602	-149.545243
E6	-17.04645803	-149.545223
E7	-17.04658804	-149.545271
E8	-17.046711	-149.545287
E9	-17.04675701	-149.545236
E10	-17.04687503	-149.545316

Appendix B.

Calculation of the width of an animal's path when approaching the camera detection zone

Camera traps in Rowcliffe et al. (2008) were installed with a horizontal view. The detection zone is a circle segment and the apparent width of the detection zone, averaged over all approach bearings is $\frac{2+\theta}{\pi}$. In this thesis cameras were installed with a vertical view resulting in a rectangular detection zone. Therefore, the calculation of the width of the path has to be adjusted.

Figure 1 shows width of the detection zone $d(u)$ when approaching the detection zone at bearing u. A bearing of 0 is the direction due north (approaching from the south), and bearings are measured in radians. We wish to find the expected bearing for an animal approaching from a random bearing. We consider a rectangular detection zone with height a and width b. At first, we consider an animal approaching the detection zone at a random bearing u that is uniformly distributed between due south (from the north, Figure 1a) and west (from the east, Figure 1b), $\pi \leq u \leq \frac{3\pi}{2}$.

In Figure 1c, we partition $d(u)$ into two components, $d_1(u)$ and $d_2(u)$, so that $d(u) = d_1(u) + d_2(u)$.Using the notation defined in this figure, we have:

$$cos(\theta_1) = \frac{d_1(u)}{b}$$

$$d_1(u) = b * cos(\theta_1)$$

and

$$cos(\theta_2) = \frac{d_2(u)}{a}$$

$$d_2(u) = a * cos(\theta_2)$$

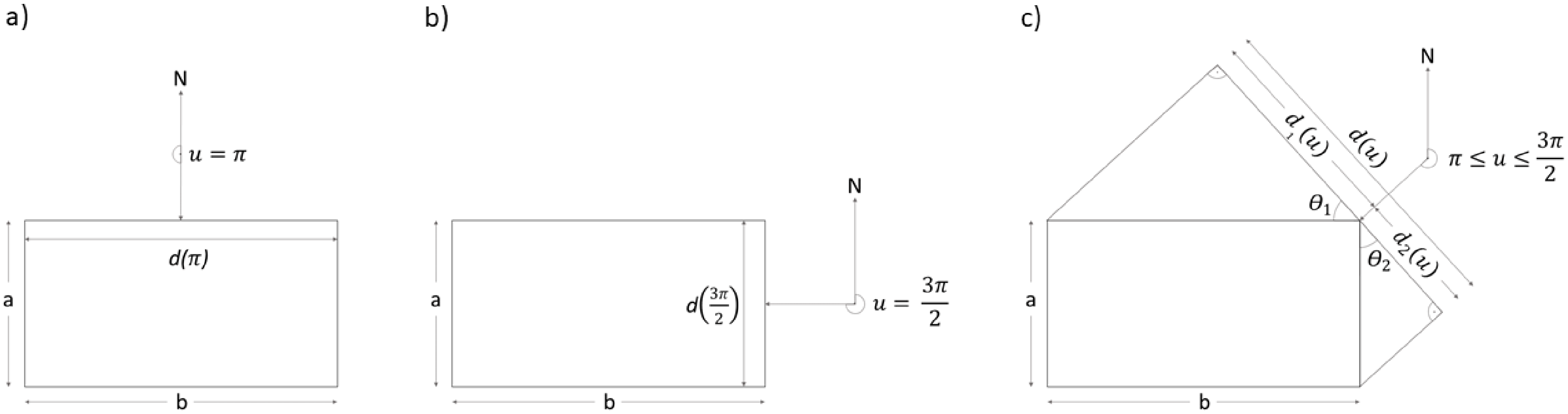
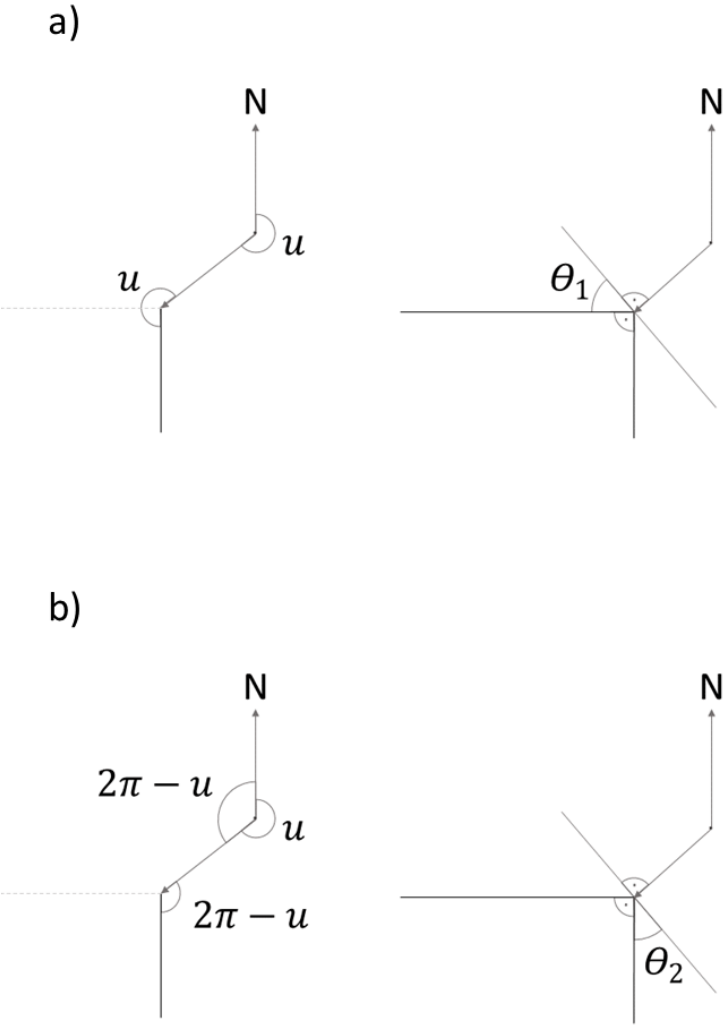


Diagram showing different animal approach angles. The detection zone is the rectangle with height *a* and width *b*. Right angles are indicated using a dot within the circle sector associated with the angle. Two limiting cases are shown for approaches directly from North and East, a general case is shown for all remaining angles of approach (*u*). **a)** Limiting case 1: $u = \pi,\ d(\pi) = \mathrm{b}$; **b)** Limiting case 2: $u = \frac{3\pi}{2}, \mathrm{d}\left(\frac{3\pi}{2}\right) = \mathrm{a}$; **c)** General case for π ≤ u ≤ $\frac{3\pi}{2}, d(u) = d_1(u) + d_2(u)$.

The above specifications of $\mathrm{d}_1(u)$ and $\mathrm{d}_2(u)$ are in terms of θ_1 and θ_2 instead of u. We can specify θ_1 and θ_2 in terms of u with the following simplifications of figure 1c:



Two simplified depictions of the upper right vertex of the rectangular detection zone, showing **a)** $u = \theta_1 + \pi$ and **b)** $2\pi - u = \theta_2 + \frac{\pi}{2}$

We have

$$u = \theta_1 + \pi$$
$$\theta_1 = u - \pi$$

and

$$2\pi - u = \theta_2 + \frac{\pi}{2}$$

$$\theta_2 = \frac{3\pi}{2} - u$$

We can now provide $d_1(u)$ and $d_2(u)$ in terms of u as follows:

$$\begin{aligned} d_1(u) &= b * \cos(\theta_1) \\ &= b * \cos(u - \pi) \end{aligned}$$

and

$$\begin{aligned} d_2(u) &= a * \cos(\theta_2) \\ &= a * \cos\left(\frac{3\pi}{2} - u\right) \end{aligned}$$

The full specification of the width of an animal's covered path, given bearing u (with $\pi \le u \le \frac{3\pi}{2}$) is:

$$\begin{aligned} d(u) &= d_1(u) + d_2(u) \\ &= b * \cos(u - \pi) + a * \mathrm{cs}\left(\frac{3\pi}{2} - u\right) \end{aligned}$$

We wish to find the expected value of d(u) given *u~uniform* (π, $\frac{3\pi}{2}$). A well known result in statistical theory is that the expected value of a transformation of a continuous random variable is given by

$$\mathbb{E}\,[g(x)] = \int_{-\infty}^{\infty} g(x) f(x) dx$$

where *g(x)* is the transformation of the random variable *x* and *f(x)* is the probability density function of *x*.

We have:

$$\mathbb{E}\,[d(u)] = \int_{\pi}^{\frac{3\pi}{2}} d(u)f(u)du$$

$$= \int_{\pi}^{\frac{3\pi}{2}} \left[b * \cos(u-\pi) + a * \cos\left(\frac{3\pi}{2} - u\right)\right] \frac{2}{\pi}\,du, \text{ because } f(u) = \frac{2}{\pi} \text{ for } \pi < u \le \frac{3\pi}{2}$$

$$= \frac{2}{\pi}\int_{\pi}^{\frac{3\pi}{2}} b * \cos(u-\pi) + a * \cos\left(\frac{3\pi}{2} - u\right) du \quad \text{, because } f(u) = \frac{2}{\pi} \text{ for } \pi < u \le \frac{3\pi}{2}$$

$$= \frac{2b}{\pi}\int_{\pi}^{\frac{3\pi}{2}} \cos(u-\pi)\,du + \frac{2a}{\pi}\int_{\pi}^{\frac{3\pi}{2}} \cos\left(\frac{3\pi}{2} - u\right) du$$

$$= \frac{2b}{\pi}\left[-\sin\left(\frac{3\pi}{2}\right) - \sin\,(\pi)\right] + \frac{2a}{\pi}\left[\cos\left(\frac{3\pi}{2}\right) - \cos\,(\pi)\right]$$

$$= \frac{2b}{\pi}[1+0] + \frac{2a}{\pi}[0+1]$$

$$= \frac{2b+2a}{\pi}$$

$$= \frac{2(a+b)}{\pi}$$

The expected width of the detection zone is $\frac{2(a+b)}{\pi}$ if the animal approaches from a bearing u, where $\pi \le u \le \frac{3\pi}{2}$. By symmetry, this result also applies for the other three intervals $\left(0, \frac{\pi}{2}\right]$, $\left(\frac{\pi}{2}, \pi\right]$ and $\left(\frac{3\pi}{2}, 2\pi\right]$. Therefore, the result holds for an animal approaching from any bearing $0 \le u \le 2\pi$.

Rowcliffe, J. M., 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.

Appendix C. Results of model comparison with session, age and sex as covariates on *g0* (detection probability at home range centre) and *σ* (distance of detector to home range centre). D.1 is rat population density in rats/ha for the December trapping session, D.2 for the trapping session in June 2018. (Samaniego et al., 2019)

g0	**σ**	**npar**	**AICc**	**dAICc**	**AICcwt**	**D.1**	**D.2**
age	age+sex+session	6	1111.5	0	0.084	96.881	99.688
1	age+sex+session	5	1112.3	0.79	0.0566	100.12	110.7
age	age+age:sex+session	6	1112.7	1.178	0.0466	96.27	97.268
1	age+age:sex+session	5	1112.9	1.423	0.0412	98.281	105.17
age+age:sex	age+sex+session	7	1113.4	1.876	0.0329	100.03	98.592
age+sex	age+sex+session	7	1113.6	2.079	0.0297	99.17	99.503
age+session	age+sex+session	7	1113.7	2.184	0.0282	98.175	99.914
age	age*sex+session	7	1113.8	2.25	0.0273	96.971	99.995
age+age:sex	age+session	6	1114.1	2.557	0.0234	97.381	86.947
age+sex	age+session	6	1114.2	2.718	0.0216	96.865	87.401
1+session	age+sex+session	6	1114.2	2.721	0.0215	102.8	110.38
sex	age+sex+session	6	1114.3	2.779	0.0209	102.82	110.47
age+session	age+sex	6	1114.3	2.823	0.0205	80.513	111.53
age+sex	age+age:sex+session	7	1114.5	2.947	0.0192	99.51	96.35
age+age:sex	age+age:sex+session	7	1114.5	2.965	0.0191	99.784	96.258
1+session	age+sex	5	1114.5	2.975	0.019	85.454	120.18
1	age*sex+session	6	1114.5	3	0.0187	100.58	111.91
sex	age+age:sex+session	6	1114.8	3.242	0.0166	101.41	104.41
sex	age+session	5	1114.8	3.255	0.0165	100.31	96.349
1	sex+session	4	1114.8	3.282	0.0163	92.145	92.724
age+session	age+age:sex+session	7	1114.9	3.37	0.0156	97.487	97.466
1+session	age+age:sex+session	6	1114.9	3.386	0.0154	100.68	104.82
1+session	age+age:sex	5	1115.2	3.712	0.0131	83.555	113.83
age	age+sex	5	1115.3	3.775	0.0127	64.98	124.16
age*sex	age+sex+session	8	1115.5	3.99	0.0114	99.625	98.135
age+session	age+age:sex	6	1115.6	4.065	0.011	80.103	108.61
age+age:sex	age*sex+session	8	1115.6	4.087	0.0109	100.5	99.001
age+age:sex+session	age+sex+session	8	1115.6	4.104	0.0108	101.5	98.812
age	age+session	5	1115.8	4.274	0.0099	91.431	83.827
age+sex+session	age+sex+session	8	1115.8	4.311	0.0097	100.52	99.742
age+sex	age*sex+session	8	1115.9	4.362	0.0095	99.32	99.942
age+session	age*sex+session	8	1116	4.48	0.0089	98.212	100.16
sex+session	age+sex+session	7	1116.3	4.765	0.0078	105.69	110.23
age*sex	age+session	7	1116.3	4.796	0.0076	97.312	86.907
1	age+sex	4	1116.3	4.802	0.0076	66.779	137.02
age+age:sex+session	age+session	7	1116.3	4.817	0.0076	97.673	86.948
1	age+session	4	1116.4	4.864	0.0074	94.756	92.413
age+age:sex+session	age+sex	7	1116.5	4.953	0.0071	81.6	111.57

1+session	age*sex+session	7	1116.5	4.978	0.007	103.11	111.21
age+sex+session	age+session	7	1116.5	4.979	0.007	97.108	87.406
sex	age*sex+session	7	1116.5	5.025	0.0068	103.47	112.12
age+sex+session	age+sex	7	1116.6	5.069	0.0067	80.936	111.82
age+session	age*sex	7	1116.6	5.079	0.0066	80.546	111.2
age	age+age:sex	5	1116.6	5.102	0.0065	64.558	121.31
sex+session	age+sex	6	1116.7	5.165	0.0063	86.078	120.6
age+sex+session	age+age:sex+session	8	1116.7	5.19	0.0063	100.82	96.556
1+session	age*sex	6	1116.7	5.195	0.0063	85.35	119.64
age+age:sex+session	age+age:sex+session	8	1116.7	5.209	0.0062	101.09	96.47
sex	sex+session	5	1116.7	5.235	0.0061	94.424	92.3
age*sex	age+age:sex+session	8	1116.8	5.243	0.0061	99.706	96.226
sex+session	age+age:sex+session	7	1116.8	5.256	0.0061	104.09	104.1
1+session	sex	4	1116.8	5.282	0.006	80.993	102.85
1+session	sex+session	5	1116.8	5.306	0.0059	93.967	92.868
age	sex+session	5	1116.8	5.328	0.0058	92.248	92.953
sex+session	age+session	6	1116.9	5.389	0.0057	101.78	95.97
1	age+age:sex	4	1117	5.512	0.0053	65.633	129.66
sex+session	age+age:sex	6	1117.3	5.814	0.0046	84.58	114.1
age*sex	age*sex+session	9	1117.3	5.836	0.0045	99.788	96.743
age+age:sex	age+sex	6	1117.4	5.921	0.0043	65.361	124.56
sex	1+session	4	1117.5	5.947	0.0043	91.47	80.12
age	age*sex	6	1117.5	5.994	0.0042	64.985	123.95
age+sex	age+sex	6	1117.5	5.994	0.0042	65.074	124.37
age+sex+session	age+age:sex	7	1117.7	6.161	0.0039	81.179	108.98
age+age:sex+session	age+age:sex	7	1117.7	6.201	0.0038	81.163	109.03
age*sex+session	age+sex+session	9	1117.8	6.247	0.0037	101.17	98.315
1	sex	3	1117.8	6.25	0.0037	65.895	116.4
age+age:sex+session	age*sex+session	9	1117.9	6.371	0.0035	101.84	99.184
age+session	age+session	6	1118	6.493	0.0033	91.197	83.819
age+sex+session	age*sex+session	9	1118.2	6.643	0.003	100.6	100.11
age*sex+session	age+sex	8	1118.4	6.895	0.0027	81.43	109.73
sex	age+sex	5	1118.5	6.977	0.0026	66.923	137.38
1	age*sex	5	1118.5	6.984	0.0026	66.733	136.65
1+session	age+session	5	1118.5	7.019	0.0025	95.396	92.204
sex+session	age*sex+session	8	1118.6	7.06	0.0025	106.16	111.43
age*sex+session	age+session	8	1118.6	7.098	0.0024	97.607	86.909
age+sex	age+age:sex	6	1118.7	7.208	0.0023	64.989	122
age+age:sex	age+age:sex	6	1118.8	7.252	0.0022	64.936	121.98
age+age:sex+session	age*sex	8	1118.8	7.259	0.0022	81.602	111.61
age+age:sex	sex+session	6	1118.8	7.266	0.0022	94.838	92.345
age+session	sex	5	1118.8	7.271	0.0022	81.305	103.3
sex+session	sex+session	6	1118.8	7.312	0.0022	96.309	92.482
age+sex	sex+session	6	1118.8	7.328	0.0022	94.465	92.507
age+session	sex+session	6	1118.8	7.341	0.0021	94.393	93.214
age+sex+session	age*sex	8	1118.9	7.368	0.0021	80.953	111.49

sex+session	sex	5	1118.9	7.424	0.0021	81.628	103.18
sex+session	age*sex	7	1118.9	7.427	0.002	85.977	120.1
age*sex+session	age+age:sex+session	9	1119	7.53	0.0019	101.01	96.438
sex	age+age:sex	5	1119.1	7.632	0.0018	65.937	130.16
age*sex	age+sex	7	1119.4	7.855	0.0017	65.196	122.66
age+age:sex+session	age	6	1119.4	7.907	0.0016	72.036	99.671
age+sex	1+session	5	1119.5	7.951	0.0016	91.541	80.303
1	1+session	3	1119.5	7.953	0.0016	85.826	76.627
age+age:sex	1+session	5	1119.5	7.979	0.0016	92.01	80.111
age+sex+session	age	6	1119.5	8.03	0.0015	71.608	100.07
sex+session	age	5	1119.6	8.045	0.0015	75.674	106.81
sex+session	1+session	5	1119.6	8.11	0.0015	92.092	80.105
age*sex+session	age*sex+session	10	1119.7	8.161	0.0014	101.11	96.931
age+age:sex	age*sex	7	1119.7	8.185	0.0014	65.364	124.62
age+sex	age*sex	7	1119.8	8.255	0.0014	65.074	124.16
sex	sex	4	1119.9	8.379	0.0013	66.085	116.76
age	sex	4	1119.9	8.384	0.0013	65.794	116.63
age*sex+session	age+age:sex	8	1120	8.463	0.0012	81.097	108.97
age*sex+session	age*sex	9	1120.5	9.038	0.0009	81.1	109.43
sex	age*sex	6	1120.7	9.199	0.0008	66.88	137.04
age+age:sex	age	5	1120.8	9.289	0.0008	57.55	111.66
age+age:sex+session	sex+session	7	1120.8	9.329	0.0008	97.165	92.624
age+sex	age	5	1120.9	9.349	0.0008	57.384	111.83
age+sex+session	sex+session	7	1120.9	9.399	0.0008	96.675	92.806
age+age:sex+session	sex	6	1120.9	9.409	0.0008	82.285	103.59
age*sex	age+age:sex	7	1121	9.453	0.0007	64.922	121.89
age+sex+session	sex	6	1121	9.459	0.0007	81.891	103.6
age*sex	sex+session	7	1121	9.523	0.0007	94.808	92.354
age	1+session	4	1121.3	9.805	0.0006	86.069	76.867
age*sex	age*sex	8	1121.5	9.973	0.0006	65.018	122.44
age+session	age	5	1121.5	9.986	0.0006	66.427	96.755
1+session	age	4	1121.6	10.071	0	70.101	103.33
1+session	1+session	4	1121.6	10.098	0	85.859	76.627
age*sex	1+session	6	1121.6	10.108	0	91.902	80.204
age*sex+session	age	7	1121.6	10.127	0	71.977	99.612
age+sex+session	1+session	6	1121.6	10.131	0	92.464	80.311
age+age:sex+session	1+session	6	1121.7	10.153	0	93.017	80.115
sex	age	4	1121.7	10.23	0	58.884	122.13
sex+session	1	4	1121.8	10.259	0	72.3	92.191
age+age:sex	sex	5	1122	10.526	0	66.138	117.13
age+sex	sex	5	1122.1	10.553	0	65.982	116.98
age	age	4	1122.6	11.132	0	54.353	107.51
age*sex	age	6	1123	11.449	0	57.536	111.57
sex	1	3	1123.1	11.554	0	58.477	104.84
age*sex+session	sex	7	1123.1	11.615	0	82.35	103.29
age*sex+session	sex+session	8	1123.1	11.622	0	97.152	92.631

age+session	1+session	5	1123.5	11.981	0	86.378	76.883
1	age	3	1123.5	12.009	0	55.895	117.44
age+sex+session	1	5	1123.7	12.238	0	72.483	92.516
age+age:sex+session	1	5	1123.8	12.281	0	72.859	92.325
age*sex+session	1+session	7	1123.8	12.325	0	92.891	80.204
1+session	1	3	1124.1	12.611	0	66.795	88.928
age*sex	sex	6	1124.2	12.706	0	66.157	116.85
1	1	2	1125.2	13.658	0	55.3	100.27
age+sex	1	4	1125.2	13.688	0	58.376	105.03
age+age:sex	1	4	1125.3	13.809	0	58.444	104.96
age*sex+session	1	6	1125.9	14.393	0	72.792	92.391
age+session	1	4	1126	14.449	0	67.077	89.354
age	1	3	1127.2	15.718	0	55.146	100.68
age*sex	1	5	1127.3	15.838	0	58.472	105.01

Appendix D. Coordinates of sightings of Pacific rats with radio collars on Reiono in August 2018

Rat ID	Sex	Date	Time	Latitude	Longitude
1	F	13.08.18	18:01	-17.0462	-149.544883
		13.08.18	19:01	-17.0461	-149.544917
		13.08.18	20:00	-17.046283	-149.544833
		13.08.18	21:20	-17.046167	-149.54485
		13.08.18	22:06	-17.046167	-149.54485
2	F	12.08.18	20:25	-17.0461	-149.544967
		12.08.18	21:25	-17.04615	-149.544867
		12.08.18	22:59	-17.0461	-149.544717
		12.08.18	23:14	-17.046167	-149.544867
		13.08.18	17:57	-17.04605	-149.5448
		13.08.18	18:56	-17.046183	-149.5447
		13.08.18	20:03	-17.046217	-149.54485
		13.08.18	21:02	-17.046183	-149.5448
		17.08.18	19:58	-17.046217	-149.54465
		17.08.18	21:00	-17.046233	-149.544983
4	M	18.08.18	20:41	-17.04365	-149.545817
		18.08.18	22:12	-17.04375	-149.546067
		18.08.18	23:22	-17.043867	-149.5459
5	F	18.08.18	09:48	-17.043283	-149.54555
		18.08.18	10:54	-17.043917	-149.54555
		18.08.18	12:05	-17.0433	-149.545467
		18.08.18	13:15	-17.04425	-149.545717
9	F	13.08.18	17:53	-17.046067	-149.5448
		13.08.18	19:37	-17.046067	-149.545017

Appendix E. Predation on green sea turtle, *Chelonia mydas*, hatchlings by invasive rats

CSIRO PUBLISHING

Pacific Conservation Biology, 2019, **25**, 423–424
https://doi.org/10.1071/PC18087

Field Note

Predation on green sea turtle, *Chelonia mydas*, hatchlings by invasive rats

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Fig. 1. Predation on a green sea turtle hatchling by a ship rat.

Sea turtle populations worldwide are in decline. Important reasons are habitat loss, commercial fishing by-catch, unsustainable harvesting of eggs and adults, pollution and predation by invasive species. Natural predation rates on adults of the endangered green sea turtles are low and so are the number of potential predator species. Green sea turtle hatchlings, however, are exposed to predation, both in the water and on land. Potential predators include mammals, birds, fish and invertebrates. Hatching at night is a strategy to avoid high temperatures and reduce the risk of predation by sea birds but exposes the hatchlings to nocturnal enemies, e.g. ghost crabs, *Ocypode* spp. (Hendrickson 1958). However, Caut *et al.* (2008) have suggested that sea turtle hatchlings may also be a familiar food source for *Rattus rattus* on Surprise Island, New Caledonia. Various studies provided indirect evidence of predation on sea turtle eggs and hatchlings by invasive rats on tropical islands (Harper and Bunbury 2015).

Tetiaroa is an atoll 50 km north of Tahiti, French Polynesia. On Tiaraunu, the largest motu, invasive rats, *R. rattus* and *R. exulans*, are established. It is the main nesting site for *C. mydas* in Tetiaroa, with 354 nests documented during the breeding season between July 2017 and April 2018. Activity of *R. rattus* around monitored turtle nests is high.

We monitored a nest of *C. mydas* with a motion-triggered camera for four days (see Video S1 available as Supplementary Material). The footage shows rats, adults as well as juveniles, visiting the nest several times. They indicate strong interest by sniffing and digging where hatchlings emerge an hour later. First rat activity at the nest was recorded two days before the hatchlings emerge from the ground, by which time hatching

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Received 12 November 2018
Accepted 20 January 2019

from the egg had been completed for at least 2–3 days (Hendrickson 1958). It is not known whether the rats had visited the nest before the observation period. When the hatchlings appear close to the surface the rat bites into the head and pulls the hatchling out of the nest (Fig. 1). The footage strongly supports that invasive rats deliberately exploit sea turtle nests as a food source.

Our video footage adds further direct evidence to the existing reports. This underlines the importance of the control of invasive rats in the management of turtle nesting sites.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

This work was part of the green sea turtle monitoring by the NGO *Te mana o te moana*, with the support of the Direction de l'Environnement de la Polynésie française. Support was provided by the Tetiaroa Society.

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