

# UC Agriculture & Natural Resources

## Proceedings of the Vertebrate Pest Conference

### Title

Trappability of Low Density Invasive Rats

### Permalink

<https://escholarship.org/uc/item/402476qd>

### Journal

Proceedings of the Vertebrate Pest Conference, 29(29)

### ISSN

0507-6773

### Authors

Gronwald, Markus

Russell, James C.

### Publication Date

2020

# Trappability of Low Density Invasive Rats

Markus Gronwald and James C. Russell

School of Biological Sciences, University of Auckland, Auckland, New Zealand

**ABSTRACT:** 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 abundance. 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.

**KEY WORDS:** black rat, camera, interspecific competition, invasive species, Pacific rat, *Rattus exulans*, *Rattus rattus*, rodents, ship rat

Proceedings, 29<sup>th</sup> Vertebrate Pest Conference (D. M. Woods, Ed.)  
Paper No. 36. Published November 13, 2020. 8 pp.

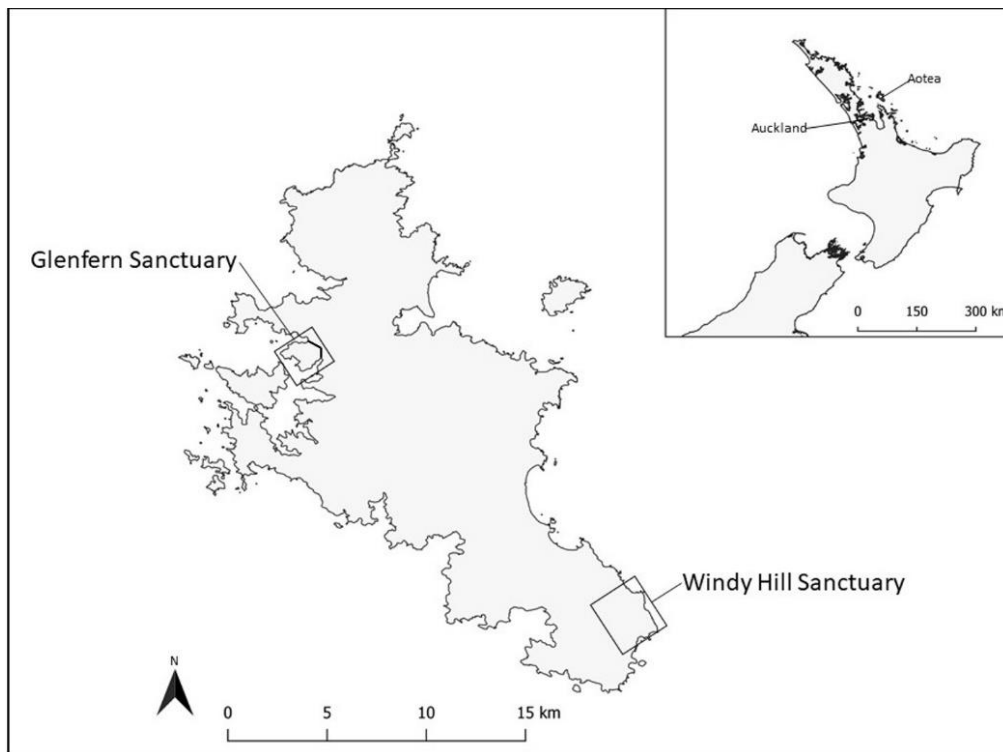
## INTRODUCTION

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; this 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 associated threats to its unique ecosystems and high number of endemic species.

The damage done by invasive rats has been recognized early and New Zealand has performed rat eradication on offshore islands for more than 50 years (Russell and Broome 2016). Rats are omnivorous and opportunistic, having an impact on both plants and animals either by direct predation or competition (Crook 1973, Lovegrove 1996, Penloup et al. 1997, Campbell and Atkinson 1999, Meyer and Butaud 2009). 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). 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 play now a key role in conservation and reintroduction of wildlife (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 in 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



**Figure 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.**

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 and 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 sensed trail cameras to analyse rat behaviour around devices. This

study aimed to understand the behaviour of invasive rats in low population densities. It set out to determine 1) how *R. exulans* population density and detection probability is affected by interspecific competition with *R. rattus* or by season, and 2) if the behaviour of *R. exulans* around detection devices is affected by population density.

## METHODS

### Study Site

Aotea/Great Barrier Island lies in the Hauraki Gulf 100 km north-east of Auckland (Figure 1). Pacific rats and ship rats are present on the island, but Norway rats 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 (*Knightsia excelsa*). Some forest patches are dominated by tree-ferns (*Cyathea dealbata*). The sanctuary is protected by a 2.1-km predator-proof fence, isolating Kotuku peninsula. 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. 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).

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 abundant in low numbers. Vegetation for Windy Hill Sanctuary and Glenfern Sanctuary was described in detail by Perry et al. (2010).

### Population Density

Live trapping was conducted using live cage traps (Model 201, Tomahawk, Hazelhurst, WI) 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 and 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 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 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

### 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 × 5 camera grid (Figure 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.

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 by 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.

- *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.

	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 2. Trapping grid and camera set-up. Distance between devices is 25 m. “x” – cage trap, “o” – cage trap with trail camera.**

### Statistical Analysis

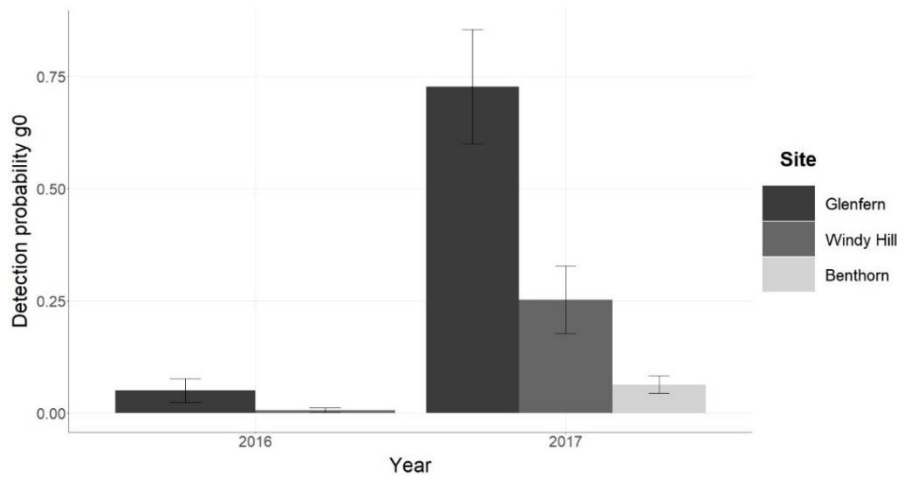
Two data sets were used for the analysis containing 1) only Pacific rat captures and 2) both Pacific rat and ship rat captures. All analyses were conducted in R Version 3.4.0 (R Core Team 2019).

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 winter 2016 and autumn in 2017. The detection function in SECR models is shaped by the two parameters  $g_0$  (detection probability at home range centre) and  $\sigma$  (distance of detector to home range centre). Site and time were the covariates for density  $D$  and  $g_0$ , while  $\sigma$  was assumed to be constant across sites to avoid over-parameterization 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  $g_0$ . As expected for a capture-mark-recapture study of rats in 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

**Table 2. Live trapping results from Aotea from August 2016 to October 2017 for the two invasive species *R. 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.**

		<i>R.ex.</i>			<i>R.rat.</i>			Night of 1 <sup>st</sup> Capture		
Site	Year	I	C	R	I	C	R	Session	<i>R.ex.</i>	<i>R.rat.</i>
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



**Figure 3. Detection probability estimates at home range centre  $g_0$  and standard errors for *R. exulans* from three sites on Aotea in 2016 and 2017.**

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:

$$\text{Count} \sim \text{Behaviour} * \text{Population density} + (1 | \text{Trap})$$

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*).

## 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 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.

The number of trap nights until the first Pacific rat was captured differed between sites (Table 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 10<sup>th</sup> night in both years and at Benthorn in the 11<sup>th</sup> 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  $g_0$  of Pacific rats. In autumn 2016 the population density estimate for Pacific rats was  $2.9 \pm 1.7$  rats/ha at Glenfern and  $4.1 \pm 3.4$  rats/ha at Windy Hill. In winter 2017 it was  $1.1 \pm 0.5$  rats/ha at Glenfern and  $1.6 \pm 0.6$  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 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.

### 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). Significant interactions between population density and behaviour (essentially non-linear density-dependent behavioural effects) could be observed (Table 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 killed.

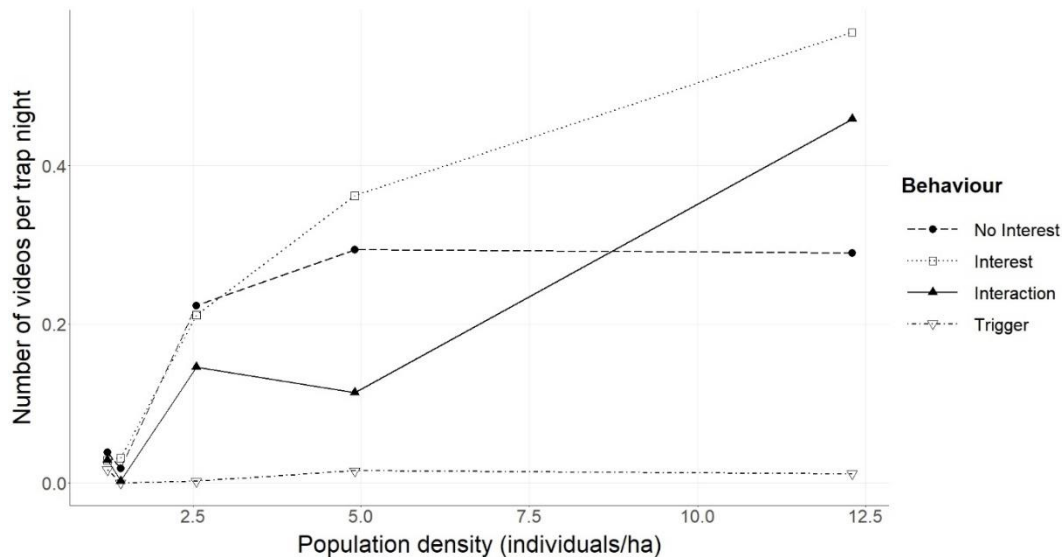


Figure 4. Number of videos per trap night plotted against population density across four categories of behaviour of invasive rats around live traps (combined *R. exulans* and *R. rattus*) monitored on Aotea in 2016 and 2017.

Table 3. Results of the generalised mixed model analysing the effect of population density on the behaviour of invasive rats (combined *R. 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) × Density	0.05	0.02	2.99	0.003
B (Interaction) × Density	0.05	0.01	3.62	<0.001
B (Trigger) × Density	-0.10	0.06	-1.62	0.105

## 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 and 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 2016 were conducted in winter when abundance of natural food was lower compared to autumn 2017. 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.

## ACKNOWLEDGMENTS

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.

## LITERATURE CITED

- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.
- Bridgman, L., J. Innes, C. Gillies, N. Fitzgerald, S. Miller, and C. M. King. 2013. Do ship rats display predatory behaviour towards house mice? *Animal Behaviour* 86(2):257-268.
- Brown J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80(2):385-399.
- Campbell, D. J., and I. A. E. Atkinson. 1999. Effects of kiore (*Rattus exulans* Peale) on recruitment of indigenous coastal trees on northern offshore islands of New Zealand. *Journal of the Royal Society of New Zealand* 29(4):265-290.
- Crook, I. G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (PEALE). *Proceedings of the New Zealand Ecological Society* 20:115-120.
- Davis, S. A., L. K. Akison, L. N. Farroway, G. R. Singleton, and K. E. Leslie. 2003. Abundance estimators and truth: accounting for individual heterogeneity in wild house mice. *Journal of Wildlife Management* 67(3):634-645.
- Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman. 2016. Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences* 113(40):11261-11265.
- Duron, Q., A. B. Shiels, and E. Vidal. 2017. Control of invasive rats on islands and priorities for future action. *Conservation Biology* 31(4):761-771.
- Efford, M. 2019. secr: spatially explicit capture-recapture models. R package version 3.2.0. <https://CRAN.R-project.org/package=secr>.
- Efford, M., D. K. Dawson, Y. Jhala, and Q. Qureshi. 2016. Density-dependent home-range size revealed by spatially explicit capture-recapture. *Ecography* 39(7):676-688.
- Fea, N., W. Linklater, and S. Hartley. 2020. Responses of New Zealand forest birds to management of introduced mammals. *Conservation Biology*. <https://doi.org/10.1111/cobi.13456>
- Harper, G. A., K. J. Dickinson, and P. J. Seddon. 2005. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. *New Zealand Journal of Ecology* 29(2):251-260.
- Harris, D. B., and D. W. Macdonald. 2007. Interference competition between introduced black rats and endemic Galapagos rice rats. *Ecology* 88(9):2330-2344.
- Heithaus, M. R., A. J. Wirsing, J. A. Thomson, and D. A. Burkholder. 2008. A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology* 356(1-2):43-51.
- Innes, J., B. Burns, A. Sanders, and M. W. Hayward. 2015. The impact of private sanctuary networks on reintroduction programs. Pages 185-200 in D. P. Armstrong, M. W. Hayward, D. Moro, and P. J. Seddon, editors. *Advances in reintroduction biology of Australian and New Zealand Fauna*. CISRO Publishing, Clayton South, Australia.
- Innes, J., R. Hay, I. Flux, P. Bradfield, H. Speed, and P. Jansen. 1999. Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. *Biological Conservation* 87(2):201-214.
- Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1-7.
- Lovegrove, T. G. 1996. A comparison of the effects of predation by Norway (*Rattus norvegicus*) and Polynesian rats (*R. exulans*) on the saddleback (*Philesturnus carunculatus*). *Notornis* 43:91-112.
- Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, New Zealand.
- Meyer, J.-Y., and J.-F. Butaud. 2009. The impacts of rats on the endangered native flora of French Polynesia (Pacific Islands): drivers of plant extinction or coup de grâce species? *Biological Invasions* 11:1569-1585.
- Nathan, H. W. 2016. Detection probability of invasive ship rats: biological causation and management implications. Ph.D. dissertation, School of Biological Sciences, University of Auckland, New Zealand.
- Parsons, D., H. Michael, P. B. Banks, M. A. Deutsch, and J. Munshi-South. 2018. Temporal and space-use changes by rats in response to predation by feral cats in an urban ecosystem. *Frontiers in Ecology and Evolution* 6:146.
- Penloup, A., J.-L. Martin, G. Gory, D. Brunstein, and V. Bretagnolle. 1997. Distribution and breeding success of pallid swifts, *Apus pallidus*, on Mediterranean islands: nest predation by the roof rat, *Rattus rattus*, and nest site quality. *Oikos* 80(1):78-88.
- Perry, G. L., J. Ogden, N. J. Enright, and L. V. Davy. 2010. Vegetation patterns and trajectories in disturbed landscapes, Great Barrier Island, northern New Zealand. *New Zealand Journal of Ecology* 34(3):311.
- Prout, D., and C. King. 2006. The effect of handling under anaesthetic on the recapture rate of wild ship rats (*Rattus rattus*). *Animal Welfare* 15:63.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Russell, J. C., and K. G. Broome. 2016. Fifty years of rodent eradications in New Zealand: another decade of advances. *New Zealand Journal of Ecology* 40(2):197.
- Russell, J. C., J. G. Innes, P. H. Brown, and A. E. Byrom. 2015. Predator-free New Zealand: conservation country. *BioScience* 65(5):520-525.
- Russell, J. C., N. S. Sataruddin, and A. D. Heard. 2014. Over-invasion by functionally equivalent invasive species. *Ecology* 95(8):2268-2276.
- Shapira, I., E. Walker, D. H. Brunton, and D. Raubenheimer. 2013. Responses to direct versus indirect cues of predation and competition in naïve invasive mice: implications for management. *New Zealand Journal of Ecology* 37(1):33.
- Simberloff, D., J.-L. Martin, P. Genovesi, V. Maris, D. A. Wardle, J. Aronson, F. Courchamp, B. Galil, E. García-Berthou, and M. Pascal. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution* 28(1):58-66.
- Starling-Windhof, A., M. Massaro, and J. V. Briskie. 2011. Differential effects of exotic predator-control on nest success of native and introduced birds in New Zealand. *Biological Invasions* 13:1021-1028.
- Stokes, V. L., P. B. Banks, R. P. Pech, and D. M. Spratt. 2009. Competition in an invaded rodent community reveals black rats as a threat to native bush rats in littoral rainforest of south-eastern Australia. *Journal of Applied Ecology* 46(6):1239-1247.



- Weerakoon, M. K., and P. B. Banks. 2011. Not just a matter of taste: palatability of bait markers is influenced by the need to search for alternative food. *Wildlife Research* 38(7):596-602.
- Wilson, D. J., M. G. Efford, S. J. Brown, J. F. Williamson, and G. J. McElrea. 2007. Estimating density of ship rats in New Zealand forests by capture-mark-recapture trapping. *New Zealand Journal of Ecology* 31(1):47-59.
- Wirsing, A. J., M. R. Heithaus, and L. M. Dill. 2007. Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? *Oecologia* 153: 1031-1040.
- Yom-Tov, Y., S. Yom-Tov, and H. Moller. 1999. Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *Journal of Biogeography* 26(5):947-958.