

## Home range and population density of black rats (*Rattus rattus*) on a seabird island: a case for a marine subsidised effect?

Grant A. Harper<sup>1,\*</sup> and Malcolm Rutherford<sup>2</sup>

<sup>1</sup>Biodiversity Restoration Specialists Ltd, PO Box 65, Murchison 7049, New Zealand

<sup>2</sup>388 Clifford St, Mangapapa, Gisborne, New Zealand

\*Author for Correspondence (Email: biodivrestoration@gmail.com)

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**Abstract:** Rodents on islands are known to exhibit differing spatial ecology than is seen in mainland habitats and in the case of invasive rats this may affect their impacts on native species. Ship rats' (*Rattus rattus*) home range size and population densities were measured on Big South Cape Island/Taukihepa, an island with a dense seabird colony, near South-west Stewart Island. Home ranges for both male and female rats were much smaller than had been recorded for virtually all sites in New Zealand. Female home ranges remained at 0.06 ha through a breeding season whereas male home ranges increased in size and also overlapped with more males later in the season. Ship rat population density ranged from 6.5 ha<sup>-1</sup> in December to 36.4 ha<sup>-1</sup> by late summer and remained high through autumn. The peaks in measured population densities are among the highest recorded in New Zealand. High population densities, small home ranges and heavy mean body weights are suggested to be due to high primary productivity attributable to the dense seabird population rather than because of the 'island syndrome'. Further comparisons with other New Zealand islands and mainland sites did not clearly support nor negate the 'island syndrome' in ship rats in New Zealand, although large increases in population densities on Big South Cape Island/Taukihepa did not influence home range sizes.

**Key words:** seabirds, invasive species, island syndrome, reproductive success, body size

### Introduction

Introductions of ship rats (*Rattus rattus*) to islands have caused declines of many plant and animal species worldwide (Atkinson 1978; Jones et al. 2008). Losses of biodiversity have been most severe on islands, where endemic species are often predator-naïve (Courchamp et al. 2003). The invasion and subsequent irruption of ship rats on Big South Cape Island/ Taukihepa in 1963 led to the extinction of two endemic birds, a bat species, a large weevil and the local extinction of an additional four bird species (Bell 1978; Ramsay 1978; Bell et al. 2016).

Research on invasive rats is increasingly being conducted on seabird islands worldwide due to their importance as biodiversity refuges and the threats posed by rats (Jones et al. 2008), as rats cause cascades of effects through these ecosystems in addition to seabird predation (Fukami et al. 2006; Wardle et al. 2007; Mulder et al. 2009; Towns et al. 2009). However, there has been relatively little research on the population biology of ship rats on seabird islands, with most research being carried out in mainland forest habitats on the very large North, South and Stewart Islands (Daniel 1972; Dowding & Murphy 1994; Innes et al. 2001; Harper et al. 2005). Although this is surprising considering the large number of seabird islands in New Zealand, the successful number of rat eradications on these islands has now limited the opportunities for conducting research on seabird-rat interactions, which can inform management responses for ship rat control on these islands.

As the population ecology of island rodents may differ from that of continental populations (Gliwicz 1980; Adler & Levins 1994; Polis et al. 1997) understanding the responses of rats to island ecosystems will assist with their management. There is evidence for increased population densities, larger

body sizes and reduced reproductive rates in rodents on islands (Key et al. 1998; Innes 2005), which have been attributed to the 'island syndrome' (Adler & Levins 1994; Russell et al. 2011b) as a response to reduced dispersal, competition and predation. Although this effect is recognised, marine subsidies from dense aggregations of seabirds are also known to lead to increased population densities and other changes in population parameters in various animals including rodents (Stapp & Polis 2003; Mulder et al. 2011; Ruffino et al. 2013), which may be a confounding factor. Certainly on Big South Cape Island/Taukihepa, ship rats exhibited elevated stable nitrogen isotope levels reflecting a high marine input in their diet, but this appeared to be largely due to bottom-up nutrient enrichment across the trophic chain via guano deposition, as little seabird predation was recorded (Harper 2007).

The purpose of this research was to measure the density and home range size of ship rats on a New Zealand island with a dense population of large burrowing seabirds, and compare them with spatial and population data on ship rats on other New Zealand islands without seabirds, competitors or mammalian predators, and from 'mainland' New Zealand. The 'island syndrome' was expected to result in, *inter alia*, increased population densities, larger body sizes and heavier body mass along with reduced reproductive output on islands compared with populations on the very large islands of the New Zealand 'mainland'. Home range size can be affected by individual energy requirements which are determined by food availability (Harestad & Bunnell 1979) or by conspecific interactions (Russell et al. 2010). Therefore minimum home range size will contract in more productive habitats due to sufficient resources being available to an individual in a smaller foraging range (McNab 1963) and/or increased territorial encounters with conspecifics. Therefore the rats on the seabird

island, Big South Cape Island/Taukihepa, were expected to have smaller home ranges, higher population densities, reduced reproductive output and heavier body mass than are found on islands without seabirds.

## Methods

### Study area

Big South Cape Island/Taukihepa (1040 ha, 47°14'S, 169°25'E), lies c. 2 km south-west of Stewart Island/Rakiura, New Zealand. It is the largest island in the southern Tītī Islands; so named because of dense populations of tītī or sooty shearwaters (*Puffinus griseus*) breeding over the austral summer and autumn (Newman et al. 2008). Soils are derived from peat and are highly modified in the upper horizons by massive mixing and addition of marine-derived nutrients from the burrowing of tītī (Hawke & Newman 2004). The climate is wet (1400 mm annual rainfall), with over 250 rain days (>0.1 mm) spread throughout the year. The mean annual temperature is 10.3°C (Sansom 1984) and strong winds are normal. Research was conducted on four 'manu' or family birding territories: Potted Head on the northwest side of the island; Parakiore on the southern coast; Parata and Manu Maaka Horomanupatu, at Murderers Cove (see Harper 2007; Rutherford et al. 2009).

The low (c. 7 m) forest canopy on Big South Cape Island/Taukihepa is dominated by the tree daisy, tūpare (*Oleria colensoi*), with occasional rātā (*Metrosideros umbellata*) and hebe (*Hebe elliptica*). There are large areas of open ground with deep leaf litter, and some smaller areas of shield fern (*Polystichum vestitum*), hound's tongue fern (*Phymatosorus diversifolius*), pūnui (*Stilbocarpa lyalii*), and various *Asplenium* species. Water fern (*Histiopteris incisa*) forms dense under canopy breaks. The density of tītī burrows in a 4 ha radio-tracking study area (see Rutherford et al. 2009) was 0.504 burrows per m<sup>2</sup> (Newman et al. 2008). This reflects the density of burrows found in tūpare forest elsewhere on the island and translates to some 20,160 burrows on the whole island.

### Rat capture and tracking

Live-trapping and radio-tracking were carried out within the tītī breeding colony at Murderers' Cove. Thirty traps, 15 each of two types of live capture traps, Elliot B (Elliott Scientific Equipment, Upwey, Australia) and 19RT (Pest Management Services Ltd, Waikanae, New Zealand), were deployed 20 m apart in an 80 x 100 m trapping area, within a 200 x 200 m sampling grid. Traps were set from 1 to 10 December 2003 and again from 18 to 21 January 2004. Each trap was baited with a peanut butter and rolled oats mix on a carrot disc. Traps were set at dusk (approximately 2120 h) and checked hourly until 0200 h. If the weather was cold and wet, traps were then closed to prevent losses due to hypothermia (Daniel 1972). If dry, traps were left open and checked at dawn. All captured rats were anaesthetised with halothane (Veterinary Companies of Australia PTY Ltd, Artarmon, Australia) and sexed and weighed. Approximate reproductive condition was also recorded using external examination of genitals: perforate vagina or descended testes to indicate sexual maturity (Cunningham & Moors 1996). Any rat exceeding 140 g had a 4.2 g SIRTRACK (Havelock North, NZ) radio transmitter attached around their neck with a nylon cable-tie, then released. Rats < 140 g were released without a transmitter, as transmitters weighing > 3% of body weight have been shown to cause

adverse effects on study animals (Kenward 2001).

Radio tagged individuals were located using a TR4 receiver (Telonics, Mesa, Arizona, United States) and a three element Yagi aerial (Sirtrack Electronics, Havelock North). Attempts to locate each rat were made by approach on foot by a single operator between two to five (normally three) times per night, approximately once an hour. Location data were recorded as coordinates corresponding to the nearest marker point on a 10 x 10 m grid square within the sampling grid. Rats were either located visually or detected within one metre with the yagi aerial detached. If rats moved outside the 200 x 200 m sampling grid their location was marked with flagging tape. Later the sampling grid was extended to include the location, or the distance to the point outside the grid was measured from a marked grid point to allow the co-ordinates of the position to be calculated. Because rat behaviour could be altered by repetitive disturbance, the order in which rats were located was varied each night to avoid repeatedly entering a rat's home range in the same place, from the same direction or at the same time of night. The previous nights' data were used each night to predetermine the tracking route. This order was maintained throughout the night irrespective of the rat's actual locations during tracking. Moving rats were recorded in the first definite location possible. Daytime sampling also occurred to survey den site selection. The same observer recorded all rat locations.

Observer accuracy was estimated by placing ten transmitters within the study site at positions unknown to the observer. After finding the approximate transmitter location using homing, the observer estimated the distance (in 5 cm increments) from each transmitter to the nearest grid point, which was compared to an independent person's exact distance to the same grid point.

### Home range analysis

Minimum Convex Polygon (MCP) and kernel density estimates (bivariate normal kernel, with smoothing parameter [h] estimated by least-squares cross validation) of home range size were calculated using a spatial analysis software 'Ranges6'™. The percentage of home range area used was plotted against the number of locations to create a curve of home range use for each rat and determine whether it reached an asymptote or continued to increase (Harris et al. 1990; Kernohan et al. 2001). Differences in home range area between two periods (December 2004 and January/February 2005) were tested using paired t-tests ( $\alpha = 0.05$  assuming unequal variance) as the population density was expected to increase due to breeding activity. Differences in average home range size between male and female used two sample t-tests ( $\alpha = 0.05$ ).

Normality of data used in all t-tests was tested with the Kolmogorov-Smirnov normality test in the computer program SPSS (Version 13.0); t-tests were conducted in MINITAB® (Version 14.1).

### Assessment of rat density and productivity

To estimate rat population density, kill-trapping grids were established on three manu; Potted Head, Parata, and Parakiore (see Harper 2007), in addition to the live-trapping grid at the radio-tracking site. Trapping grids consisted of 81 'Victor'™ snap-traps, in a grid of seven traps at 33-m intervals on 13 alternate offset rows 16 m apart. The traps were baited with a mixture of rolled oats and peanut butter and secured with wire stakes under 12 mm galvanised mesh covers. Traps were first set when they were put out and then checked daily for

the following four to five weeks. Trapping was conducted in December 2003, then in January of 2004 and 2005 and May of 2004 and 2005.

The 'Zippin removal' technique (Zippin 1958) was used to estimate the density of rats caught. Each night's catch was plotted against the cumulative total to estimate the number of rats left on the trapping-grid (see Brown et al. 1996; Harper 2006). To estimate the effective trapping area (ETA), a boundary strip was added to the edge of the trapping grids (Dice 1938). The width of the boundary strip was set by adding the radius of the circular average home range of ship rats recorded by radio-tracking in December and January/February.

Kill-trapped rats were weighed, measured and dissected to determine their age and reproductive state (see Harper 2007 for details). The mean number of embryos per female was used to measure reproductive output. The data gained from the radio-tracking study and trapping grids on Big South Cape Island/Taukihepa were then compared with data from other published research on ship rats in New Zealand.

## Results

### Home range estimation

In December 2003, seven adult females and five adult males were radio-tagged and a further two males in January 2004. No mortality was recorded so all 14 radio-tagged rats were present at the end of the study. All but three of the rats were re-trapped at the end of the study. With one exception all females were, or had been, pregnant as determined *post mortem* by the presence of placental scars.

Home range asymptotes were attained for females (~30 locations) and males (~40 locations). Kernel and MCP home ranges were estimated using 1206 night locations along with 15 initial trapping locations, 18 sightings, and 440 daytime locations including den sites. The mean actual distance (4.38 m, s.e.  $\pm$  0.33) was 6.3% longer than the mean estimated distance (4.10 m,  $\pm$  0.08), which was negligible when scaled against home range sizes.

The average 95% kernel home range estimates for male rats increased from December to January (0.12 ha, s.e.  $\pm$  0.02

vs 0.15 ha  $\pm$  0.03, see Figure 1) but the difference was not significant ( $P = 0.115$ ,  $t = -2.01$ ,  $n = 5$ ). Female home ranges decreased slightly from December to January (0.04 ha  $\pm$  0.01 vs 0.03  $\pm$  0.01) and the difference was not significant ( $P = 0.316$ ,  $t = 1.09$ ,  $n = 7$ ). The mean 95% kernel home range for males was always significantly larger than for females (December  $P = 0.007$ ,  $t = 4.4$ ,  $n = 5$ , Jan/Feb  $P = 0.013$ ,  $t = 3.48$ ,  $n = 7$ ). MCP plots were always larger for both sexes as the method includes all outliers in the calculation.

Rats were frequently recorded moving through their home range at speeds of 30 m in 3–4 minutes and also recorded moving long distances over longer periods. For example, M69 moved 107 m in 66 minutes and M97 moved 78 m in 32 minutes, which probably underestimate their speed because straight line movements between successive locations were unlikely. Assuming all rats were equally able to traverse their home range, they could reach any part of it within about 10 minutes.

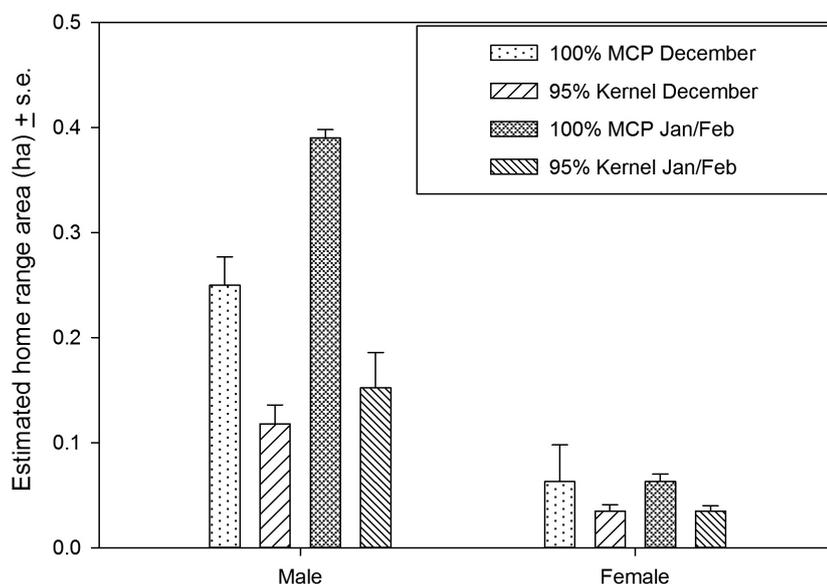
### Home range overlap

Each female was overlapped by an average of 2.3 male home ranges in December, which increased to 3.6 male home ranges in January/February. Each of the five males overlapped an average of three (s.e.  $\pm$  0.32) other male home ranges per individual (HR/I) which increased significantly to 4.5 ( $\pm$  0.37) in January/February  $t = -3.23$ ,  $P = 0.01$ ,  $n = 7$ ). Conversely, female overlap with other female ranges in December did not differ (1.57 HR/I, s.e.  $\pm$  1.27,  $n = 7$ ) from January/February (0.57  $\pm$  0.53 HR/I,  $t = 1.92$ ,  $P = 0.09$ ,  $n = 7$ ). Many home range overlap areas were very small (<5%), and the pattern of home range overlap became clearer if these minor overlaps were ignored. In these cases the number of overlaps was greater within males than females.

### Density estimates

#### Three kill-trapping grids

A combined total of 2132 ship rats were trapped over the five trapping sessions on the three trapping grids at Potted Head, Parata and Parakiore. In general rat captures were initially high, but captures declined rapidly from about the fifth day of trapping. Subsequently, most trapped rats were likely



**Figure 1.** Estimated home range sizes of male and female ship rats on Big South Cape Island/Taukihepa ( $\pm$  s.e.).

invading the trapping area from outside the grids. Therefore density estimates were only calculated for the first five days of trapping. The average radius of the radio-tracked male home range area in December gave a boundary strip 28.09 m wide outside the trapping grid (80 m x 100 m), which increased to 35.42 m in January/February. The female boundary strip remained constant at 14.15 m during both sessions. As no radio-tracking was conducted in May the ETA for these trapping sessions were estimated from the home range area recorded over January-February 2004, so it may be underestimated as the capture frequencies were high in May of both years.

The mean density estimate derived from the three grids in December 2003 was 6.52 rats/ha (s.d. 2.86). Mean density densities increased in January 2004 and January 2005 from 10.6–11.6 rats/ha (s.d. 2.71 & 3.75) to 28.1–36.4 rats/ha (s.d. 11.06 & 6.19) in May of both years (Figure 2). During December and January, 45% of the adult female rats trapped on Big South Cape Island/Taukihepa were pregnant or recently pregnant (Rutherford et al. 2009).

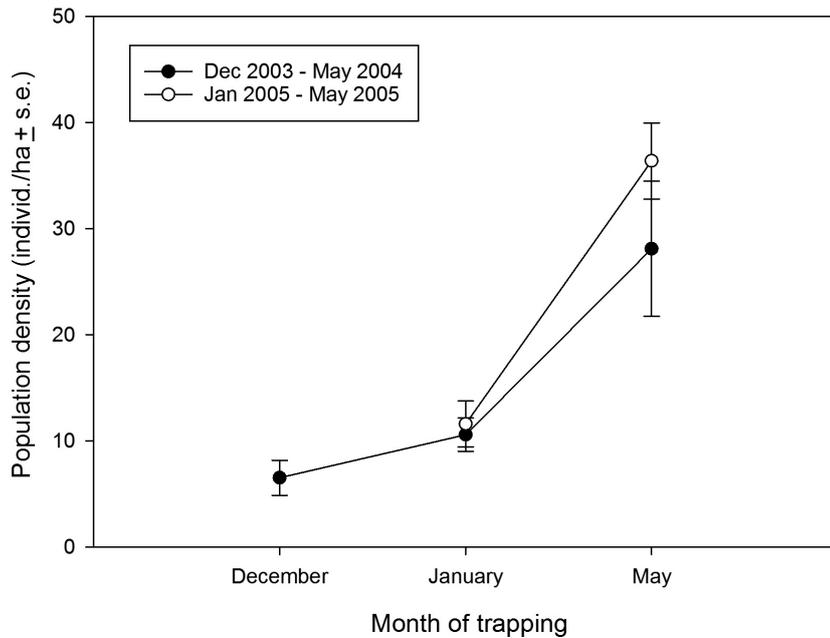
*Comparisons with other sites*

Adult ship rats on islands consistently weighed more than rats studied at New Zealand sites (Innes 2005; Latham 2006; Russell et al. 2009; Figure 3, ♂:  $t = 3.55$ , d.f. = 12,  $P = 0.004$ ; ♀: Mann-Whitney U test = 4.0, d.f. = 12,  $P = 0.01$ ). These comparisons were calculated from tests on island or site means, not raw data.

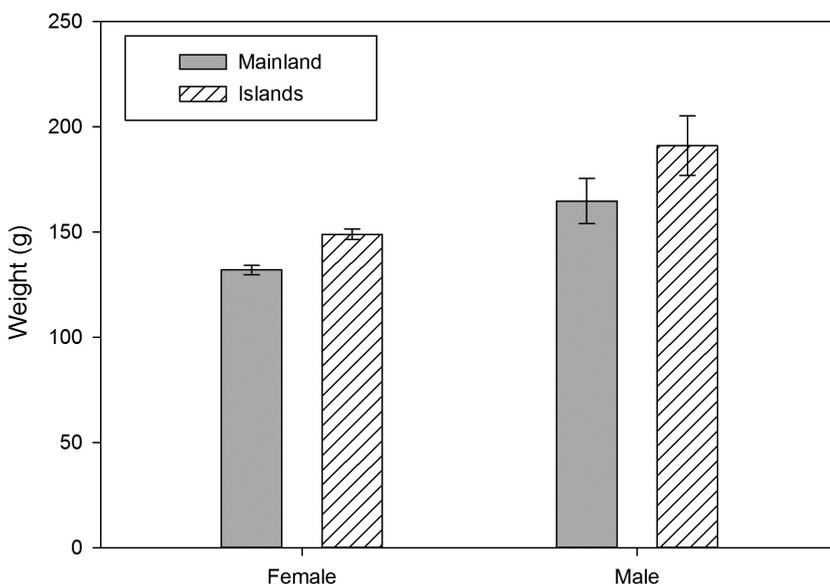
Adult female ship rats on islands had significantly more embryos than rats studied at mainland sites ( $t = -3.44$ , d.f. = 9,  $P = 0.007$ , Table 1). However, only sparse data were available from two of the three islands. These comparisons were calculated from tests on island or site means, not raw data.

There was no significant difference between the mean minimum or maximum recorded population densities on islands and mainland sites (Table 3). The data were log-transformed before analysis (minimum density:  $t = -1.22$ , d.f. = 15,  $P = 0.24$ ; maximum density:  $t = -1.5$ , d.f. = 15,  $P = 0.16$ ).

The plotted mean population density and associated home range sizes of male ship rats in New Zealand are shown in



**Figure 2.** Seasonal changes in estimated mean population densities of ship rats on three trapping grids on Big South Cape Island/Taukihepa.



**Figure 3.** Mean weights ( $\pm$  s.e.) of male and female ship rats from islands (n = 5) and mainland sites (n = 10) in New Zealand.

**Table 1.** The mean number of embryos recorded in female ship rats from New Zealand studies.

Mainland			Islands		
Author	Location	Mean no. of embryos	Author	Location	Mean no. of embryos
Innes et al. 1983	Pureora Forest, Waikato	5.2 (n = 89)	Miller & Miller 1995	Rangitoto Hauraki Gulf	7.0 (n = 2)
Innes 1979	North Tararua Range	4.95 (n = 19)	Russell et al. 2009	Goat Island Hauraki Gulf	6.33 (n = 3)
Daniel 1972	Orongorongo Valley, Wellington	6.1 (n = 26)	This study	Taukihepa Stewart Isl	6.87 (n = 209)
Best 1973	Banks Peninsula	5.9 (n = 14)			
Best 1973	Waimangaroa, West Coast	5.9 (n = 7)			
King & Moller 1997	Hollyford Valley, Fiordland	5.67 (n = 6)			
King & Moller 1997	Eglinton Valley, Fiordland	6.28 (n = 7)			
Sturmer 1988	Robertson River, Stewart Island	5.86 (n = 7)			
Mean		5.73 (s.e. 0.16)	Mean		6.73 (s.e. 0.21)

**Table 2.** Ship rat home range estimates (MCP) from New Zealand studies. Note that due to its size, Stewart Island (175,000 ha) is regarded as a mainland site.

Author	Location	Season	Average male home range (ha) ± s.e.	Average female home range (ha) ± s.e.
Daniel 1972 <sup>a,c</sup>	Orongorongo Valley podocarp forest (M)	All year	0.17±0.28	0.08±0.06
Innes & Skipworth 1983 <sup>a,c</sup>	Palmerston North forest remnant (M)	May–Jan	1.01	0.33±0.06
Hooker & Innes 1995 <sup>b,c</sup>	Rotoehu tawa forest (M)	Dec–Jan	1.52±0.28	0.49±0.07
Dowding & Murphy 1994 <sup>b,c</sup>	Northland kauri forest (M)	Sept–Oct	0.94±0.23	0.79±0.07
Hickson et al. 1986 <sup>a,c</sup>	Stewart Island coastal (M)	Dec–Feb		0.54 ± 0.07
Pryde et al. 2005 <sup>b,d</sup>	Eglinton beech forest (M)	Feb–Mar	9.43	0.27
Latham 2006 <sup>b,c</sup>	Ponui Island (I)	Dec & Oct	0.29 ± 0.19	0.21 ± 0.04
This study <sup>b,c</sup>	Taukihepa coastal tūpare (I)	Dec	0.25 ± 0.027	0.063 ± 0.008
This study <sup>b,c</sup>	Taukihepa coastal tūpare (I)	Jan–Feb	0.40 ± 0.044	0.063 ± 0.007

Notes: a – Home range estimated from trapping and tracking tunnel data – probably underestimate range size.

b – Home range estimated from radio tracking data.

c – 100% MCP estimator.

d – 95% MCP estimator used.

M – Mainland site.

I – Island site.

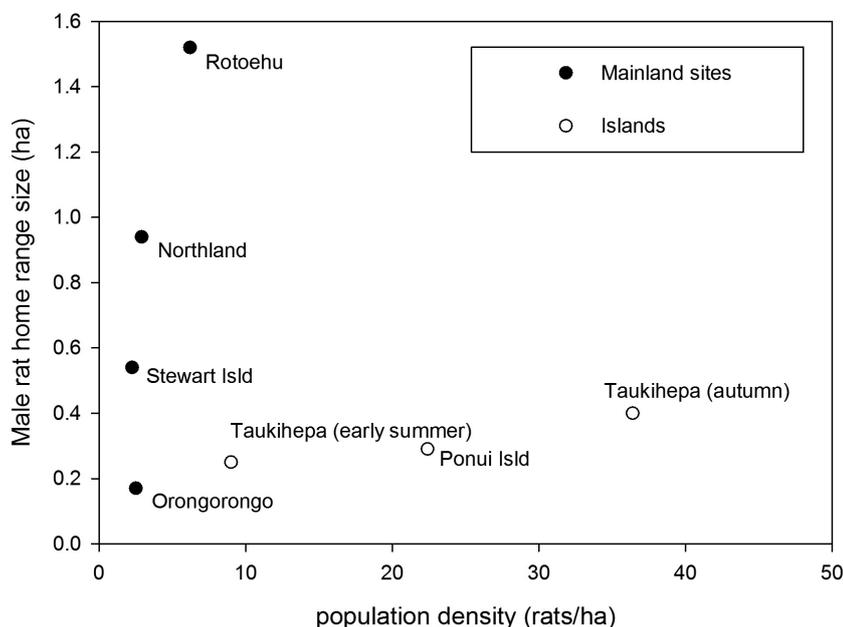
Figure 4. Only two islands, Ponui Island and Big South Cape Island/Taukihepa, had both home range and density data, and in this case the Big South Cape Island/Taukihepa data from December and February are included as the density and home range sizes had changed in the intervening period. Although the data for islands were restricted to two islands the trend in New Zealand was for density to remain consistently low with increasing home range size. On the two islands, the converse appeared to hold, with home ranges remaining consistently small with increasing density.

## Discussion

Home range sizes and population density measurements on Big South Cape Island/Taukihepa were at the extreme ends of the spectrum for ship rats in New Zealand. As expected, home range sizes on Big South Cape Island/Taukihepa were much smaller than all previous home range estimates of ship rats in New Zealand estimated from radio tracking data (Table 2). The estimates from the Orongorongo Valley were close, but were estimated from a trapping grid, a method which underestimates home range size (Ribbell et al. 2002). The key determinants

**Table 3.** Population density estimates of ship rats from New Zealand studies.

Source	Location	Season	Density estimate (indiv./ha)
<b>New Zealand mainland sites</b>			
Daniel 1972	Orongorongo Valley, Wellington	Summer	1.2-3.7
Daniel 1972	Orongorongo Valley, Wellington	Autumn	0.7-2.5
Hildreth (in Daniel 1972)	Orongorongo Valley, Wellington	Unknown (1951)	37-49 (irruption)
Hickson et al. 1986	Stewart Island	Summer	2.0-2.5
Dowding & Murphy 1994	Northland	Spring	2.9
Hooker & Innes 1995	Rotoehu, Bay of Plenty	Summer	6.2
Brown et al. 1996	Kaharoa, Bay of Plenty	Summer	6.7 (95% CI: 6.5-7.8)
Blackwell et al. 2001	Lake Waikaremoana, East Coast	Winter	8.22
Wilson et al. 2007	Orongorongo Valley, Wellington	Autumn	4.9-8.7
Christie et al. 2015	Eglinton Valley, Fiordland	Spring - Autumn	0.38
<b>New Zealand islands</b>			
Craig 1977	Goat Island, Hauraki Gulf	Autumn	12-20
Mackay & Russell 2005	Goat Island, Hauraki Gulf	Autumn-winter	3.3
Mackay 2005	Motutapere Island, Coromandel	Autumn	2.5
Mackay 2005	Tawhitinui Island, Marlborough Sounds	Autumn	2.6
Shaprio 2005	Ponui Island, Hauraki Gulf	Summer	6.04-10.2
Harper 2006	Pearl Island, Stewart Island	Autumn	2.09-2.22 (included 3 Pacific rats)
Latham 2006	Ponui Island, Hauraki Gulf	Winter-Spring	6.73-22.43
This study	Taukihepa, Stewart Island	Summer-Autumn	6.52-36.4

**Figure 4.** Male home range area and associated population densities of ship rats on islands and mainland sites in New Zealand.

of home range size are body mass, individual metabolic rate, ecosystem productivity, and conspecific interactions (McNab 1963; Harestadt & Bunnell 1979; Russell et al. 2010). As the ship rats on Big South Cape Island/Taukihepa are the largest recorded in New Zealand (Innes 2005), this would suggest they would require a larger home range than usual. The small home range sizes, particularly of females raising young, suggests high primary productivity is the principal driver for the small home range sizes observed. However, there was a repeated decline in population density to lower levels in early summer (Figure 2)

which mirrors the usual cessation in breeding over winter in New Zealand rat populations (Harper et al. 2005). This suggests an interaction of density with restricted resources through the winter, possibly related to the departure of sooty shearwaters in autumn.

The very high density population estimates from Big South Cape Island/Taukihepa support this conclusion. The measured peak densities are the highest so far recorded in New Zealand, in many cases by an order of magnitude, and have only been approached on the mainland during an apparent population irruption (Table 3). The only other site where population

densities near to those measured were recorded was at Ponui Island in the Hauraki Gulf (Latham 2006). The high densities, along with the small observed home ranges, suggests that there are fundamental differences in ecosystem function between Big South Cape Island/Taukihepa and other sites where population density has been measured. The contrast could not be greater than at nearby Pearl Island, only 20 km away, which had very similar climatic and edaphic conditions, a lack of predators and three competing rat species, but very few or no breeding seabirds. Fewer than three rats per hectare were measured there using the same technique at a similar time of year (Harper 2006). The rat population density measured on Pearl Island is very similar to densities recorded by Hickson et al. (1986) further north on Stewart Island (Table 3), where competitors and also predators are present. The relatively high rat densities seen on Ponui Island and Goat Island in the Hauraki Gulf may reflect a high background level of soil fertility (Gardner-Gee & Beggs 2009), which may be due to now absent or sparse seabird colonies or soils with generally higher fertility than exists in the peat soils of Big South Cape Island/Taukihepa. In this case the contrasting effect of seabird marine subsidies on rat densities on Big South Cape Island/Taukihepa versus Pearl Island is probably due to the large size of the subsidy relative to the base productivity of the cool, wet habitats present at Stewart Island (Marczak et al. 2007; Mulder et al. 2011; Bassett et al. 2014).

Similarly high population densities and adult body mass in ship rats have been found on dry Mediterranean Islands where seabirds are present and following heavy rainfall (Ruffino et al. 2009; Ruffino et al. 2013). Notably heavier ship rats have also been trapped within seabird colonies on tropical islands (Tetiara, French Polynesia, Russell et al. 2011a; Great Tobago Island, British Virgin islands, GH pers. obs.), and higher ship rat population densities are found in the tropics (Russell et al. 2011b; Harper et al. 2015), where primary productivity is greater (Melillo et al. 1993; Schurr 2003; Gillman et al. 2015). This suggests higher productivity is the principal driver for the small home range sizes and high rat densities observed on Big South Cape Island/Taukihepa. This mirrors the results from the Shiant Islands, Scotland, where ship rats were in higher densities (22–85 rats/ha) and heavier on the island with a large puffin colony, in contrast to rats trapped on the immediately adjacent island without seabirds (Key et al. 1998). Similarly, very heavy ship rats (mean adult weight: 246 g) were trapped in white-chinned petrel *Procellaria aequinoctialis* colonies on Ile de Possession, southern Indian Ocean (Jouventin et al. 2003).

In lieu of solar input to drive primary productivity as occurs in the tropics, marine inputs via nesting seabirds can massively increase productivity on temperate islands (Polis & Hurd 1996). Concentrations of nutrients such as nitrogen, phosphorous and potassium can be 18x greater on seabird islands (Wolfe et al. 2004) which can lead to increased plant growth (Molina-Montenegro et al. 2013). Much higher densities of arthropods (Sánchez-Piñero & Polis 2000), consumers like lizards (Barrett et al. 2005) and rodents (Stapp & Polis 2003), and predators (Rose & Polis 1998) have also been measured. Although the densities of invertebrates have not been recorded on Big South Cape Island/Taukihepa, they are also likely to be much higher than on non-seabird islands in New Zealand (Markwell & Daugherty 2002) which suggests a role for increased available food on Big South Cape Island/Taukihepa leading to the densities of rats observed. Indeed island rodent population densities will increase when experimentally supplemented with food, in contrast to control populations

(Adler 1998). Certainly the rats on Big South Cape Island/Taukihepa have a high quality, protein rich diet, comprising mainly invertebrates and birds (Harper 2006). Rodent diet does tend to have more invertebrates at higher latitude islands like Big South Cape Island/Taukihepa (St Clair 2011), but the larger proportion of bird remains in their diet contrasts with most observed prey items of New Zealand ship rats which are dominated by plant material and invertebrates (Innes 2005). A high protein diet may also result in the observed large litter sizes (Widdowson & Cowen 1972) leading to increased population densities (Adler 1998).

The contention that the diet of rats on Big South Cape Island/Taukihepa is marine subsidised relative to Pearl Island is supported by stable isotope data from rat muscle from these sites (Harper 2006, 2007). The ship rats on Big South Cape Island/Taukihepa had highly enriched stable-nitrogen isotope ( $\delta^{15}\text{N}$ ) values of 14.66 (s.e. 0.58), which were strongly suggestive of a marine subsidised component in their diet (Stapp 2002), whereas ship rats in forest on Pearl Island had  $\delta^{15}\text{N}$  values of 4.07 (s.e. 1.02). Ship rats trapped on the shoreline at Pearl Island had  $\delta^{15}\text{N}$  values of 12.97 (s.e. 0.98), which were similar to Big South Cape Island/Taukihepa values, as rats foraging in the littoral zone can have enriched  $\delta^{15}\text{N}$  values due to the preponderance of intertidal invertebrate as prey (Stapp 2002). The values on Pearl Island forest were higher still than that recorded in similar forest at the Rakeahua Valley, in central Stewart Island, where ship rats had  $\delta^{15}\text{N}$  values of only 2.0 (s.e. 0.23, Harper 2006), reflecting its distance from the sea. A similar response by ship rats to the presence of seabirds has been recorded on the Shiant Islands (Scotland) and Bagaud Island (Mediterranean) where rats resident in seabird colonies had highly enriched  $\delta^{15}\text{N}$  values of 17.1 and ~13 respectively (Stapp 2002; Ruffino et al. 2011).

In regard to the 'island syndrome' in New Zealand the data were equivocal. Ship rats on islands were heavier and larger (Yom-tov et al. 1999) than on mainland New Zealand which supports the micro-evolutionary portion of the theory, probably because a large suite of competitors and predators were absent (Adler & Levins 1994; Yom-tov et al. 1999; Ventura & Lopez Fuster 2000). Rapid morphological responses in rodents and other small mammals to changing ecological conditions are now well recorded (Pergams & Ashley 2001; Pergams & Lawyer 2009; Cucchi et al. 2014). At an ecological level however, results were less clear. For example, female rats produced more embryos on islands than on mainland New Zealand, and mean population densities were not significantly different between mainland New Zealand and the island sites, despite the highest population densities attained on Big South Cape Island/Taukihepa. On all islands except Goat Island, dispersal for the sampled islands could be regarded as nil, so the driving forces for likely responses were present. Unfortunately some of the data from islands were sparse which restricts us from coming to a firm conclusion as to the relevance of the 'island syndrome' theory in the New Zealand context but may suggest a gradient of behavioural and population responses with increasing island size. Comparisons between marine subsidised rat populations on islands and at mainland sites with seabird colonies may tease out the relative effects of seabird-driven productivity versus the island syndrome. The paucity of home range data from New Zealand islands also affected a comparison of home range with population density, but differences in the response of ship rats to the prevailing ecological conditions on the mainland and the two islands was apparent (Figure 4). On the two islands, Ponui and Big

South Cape Island/Taukihepa, home range size remained relatively constant with high population densities. This lack of response to increasing density has also been observed in Pacific rats on Kure Atoll (Wirtz 1972), where high densities are attained, and competitors and predators were absent. In contrast, at mainland New Zealand sites home range sizes were generally larger relative to the islands, and observed home ranges fluctuated about consistently low population densities. This observation may provide a useful modification of the 'island syndrome', where the relationship between home range and density (Efford et al. 2015) is one of the defining differences on islands rather than population density *per se*. Further research is required to confirm this interim result and its relevance to the 'island syndrome', and the relative effects of predators and competitors on the ecological and evolutionary response of invasive rats. What is clear is that the ship rats of Big South Cape Island/Taukihepa have specifically responded at both a micro-evolutionary and population ecology level to the prevailing conditions.

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