

## Denning behaviour of ship rats (*Rattus rattus*) on Taukihepa, a seabird breeding island

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**Abstract** Den sites of 14 ship rats (*Rattus rattus*) were located daily during the rat breeding season on Taukihepa (Big South Cape), a seabird island south-west of Rakiura (Stewart Island). In contrast to other New Zealand studies, no arboreal dens were found. Den sites on Taukihepa were in ferns, under logs, in woodpiles, or underground in sooty shearwater (*Puffinus griseus*) breeding burrows. The number of times known den sites used was positively related to the amount of leaf litter and woodpiles near the den sites. Overall, 24% of radio-tagged rats were sharing den sites on any given day. While there was considerable individual variation in the number of

times den sites were used, female rats tended to re-use den sites more than males. Many rats were found in dens alone, but frequently males and females shared. Occasionally two females and one male denned together, as did two females, whereas males never denned with another male.

**Keywords** *Rattus rattus*; den sites; habitat use; social behaviour; sooty shearwater; Stewart Island

### INTRODUCTION

Introductions of ship rats (*Rattus rattus*) to islands have caused declines of many plant and animal species worldwide (Atkinson 1978; Robertson et al. 1994; Shaw et al. 2005). Losses of biodiversity have been most severe on islands, where endemic species are often predator-naïve (Burger & Gochfeld 1994; Stone et al. 1994; Courchamp et al. 2003). The invasion and subsequent irruption of ship rats on Taukihepa (Big South Cape) in 1964 is one of the best-documented island invasions by rats and 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).

Although social behaviour is well documented from laboratory and urban groups of rats (Ewer 1971; Barnett 1975), little is known about den site sharing in forest populations and none on islands, where rats arguably have the most severe impact on native fauna. In kauri (*Agathis australis*) forest Dowding & Murphy (1994) recorded inter- and intra-sexual den site sharing before breeding began. Male-male sharing apparently stopped after the breeding season started, which suggested that male/female nest sharing may be linked to sexual activity. In contrast, during a ship rat breeding season in lowland forest, Hooker & Innes (1995) did not find any rats sharing den sites. While it is relatively easy to make conclusions about the mating system from home range data alone, investigating patterns of den site sharing provides more information on social interaction than has been previously recorded.

The aim of this study was to determine which microhabitat characteristics were common to ship rats' den site areas on a seabird island, and to investigate the social organisation within these dens. This study supported research on the impact of rats on tītī/sooty shearwater (muttonbird) (*Puffinus griseus*) being carried out by *Kia Mau Te Tītī Mo Ake Tōnu Atu* ("Keep the Tītī Forever") research group, in collaboration with Rakiura Māori, into the impact of predators, climate change and large scale cultural harvest on the sustainability of tītī populations on tītī islands (Moller et al. 2003, 2009a,b this issue; Fletcher et al. in press).

## METHODS

### Study area

Taukihepa, or Big South Cape Island (797 ha, 47°14'S, 169°25'E), lies c. 2 km south-west of Stewart Island (Rakiura), New Zealand (Fig. 1). It is the largest island in the southern Tītī Islands, so named because of dense populations of tītī or sooty shearwaters (*Puffinus griseus*) that breed there 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 2005). The climate is wet (1400 mm), 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 Manu Maaka Horomanupatu, a family birding territory or "manu", near Murderers Cove, on Taukihepa. The low (c. 7 m) canopy was dominated by the tree daisy, tūpare (*Oleria colensoi*), with occasional rātā (*Metrosideros umbellata*) and hebe (*Hebe elliptica*). There were 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*) formed dense under canopy breaks. A small portion of the southern corner of the study site was dominated by water fern and *H. elliptica* shrubland. The density of tītī burrows in the study area is 0.504 burrows per m<sup>2</sup> (Newman et al. 2008) which translates to some 20 160 burrows within the study site. A small number of blue penguin (*Eudyptula minor*) burrows were also present.

Fallen branches and logs on the site have been collected into woodpiles for many years by the muttonbirders to clear their manu to promote tītī abundance (Kitson & Moller 2008). These piles range from less than 1 m high to substantial piles 2 m high and 4 m across the base. There was no still or flowing fresh water available.

The site was situated on a small peninsula and had a central flat area off which come three small valleys. The site ranged from 13–37 m above sea level (Fig. 1). During December and January, 45% of the adult female rats trapped on Taukihepa were pregnant or recently pregnant (G. Harper unpubl. data). Tītī were sitting on eggs in December, which began hatching about 12 January (G. Harper pers. obs.).

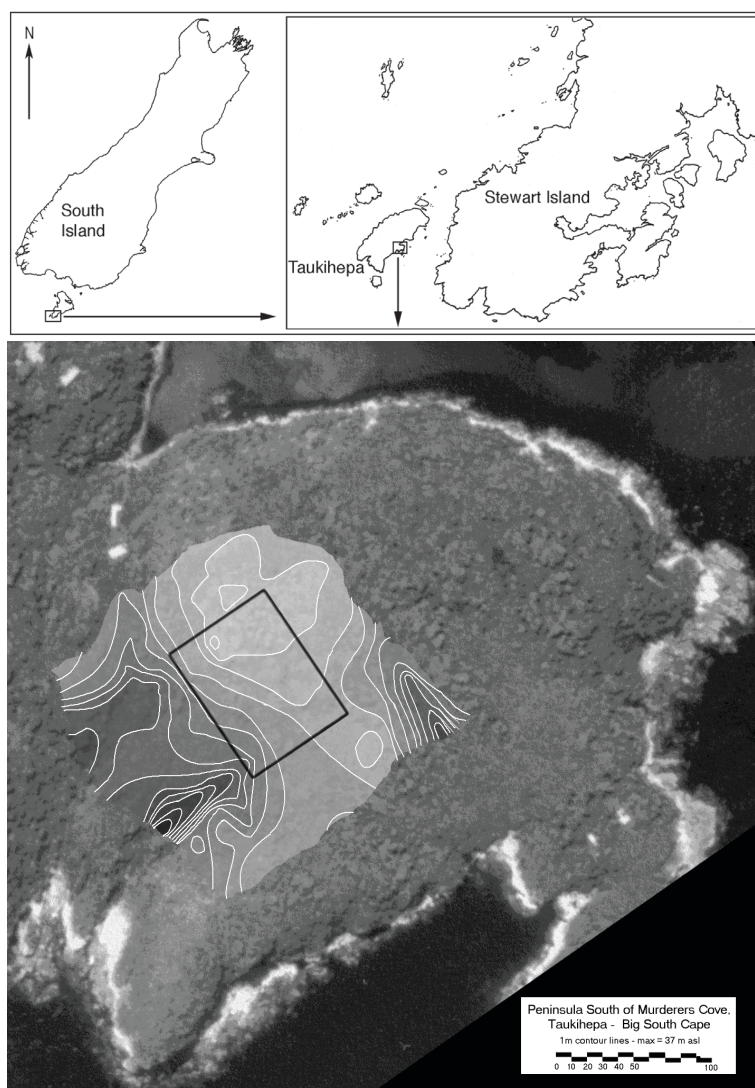
### Rat capture and tracking

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 in a 200 × 200 m trapping 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, and was periodically renewed. 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 were 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). A 4.2 g SIRTRACK (Havelock North, New Zealand) radio transmitter was attached to any rat weighing more than 140 g, as transmitters weighing more than 3% of body weight have been shown to cause adverse effects on study animals (Kenward 2001). Transmitters were secured around the neck with a nylon pull tie. Any individual weighing less than 140 g was released without a transmitter.

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 two to five (normally three) times per night, approximately once an hour. Each location was assigned to within a 5 × 5 m grid square

**Fig. 1** Map of the South Island and Stewart Island, New Zealand, showing the location of Taukihepa and the location of the study site and trapping grid at Murderers Cove.



within the sampling grid. If rats moved outside the  $200 \times 200$  m grid their location was marked with flagging tape. Later the sampling grid was extended to include the location or the distance to the point 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 was 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.

Habitat use associated with diurnal den site use was determined by tracking radio-tagged rats. Each rat was located once each day between 1000 h and 1800 h. It was important to be sure that rats were stationary in dens when located, and only the stationary locations are included in the dataset. Confirmation that rats were not moving was achieved by making two or more quick fixes from varying angles on the

radio-tagged animal within less than 10 m. Stationary rats in dens could be located very accurately; therefore error was not measured and was assumed to be insignificant.

### Habitat characteristics

Habitat was characterised in each  $5 \times 5$  m square in which a rat had been previously observed. Fourteen habitat characteristics based on vegetation type and cover adapted from Cox et al. (2000) were recorded for each square. The percentage cover of leaf litter, water fern, tūpare canopy, rātā canopy and shield fern, was estimated by eye and recorded in one of four "percentage cover" classes (0, 1–33, 34–66, and 67–100%). When percentage cover was not immediately obvious, a more precise estimate of cover was obtained by pacing out regions of cover or by using a tape measure. Because the most common canopy trees, tūpare, often split into multiple trunks near the ground, the standard measurement of diameter at breast height was not used. Rather, the trunk diameter 50 cm above the ground was used to split trees into two broad categories ( $\leq 10$  cm, or  $>10$  cm diameter), and the number of trees in each category was counted for each grid square. These categories were later split into four classes (0, 1–3, 4–6, and 7+ trunks). As they were generally present in very small numbers we recorded presence or absence for some ground cover species, *Asplenium* spp., hounds tongue fern, pūnui, and *Hebe elliptica*. In addition to vegetation, we quantified other habitat structure including number of logs, number of woodpiles, and number of sooty shearwater burrows for each grid square. Logs were defined as  $>1$  m long and  $>10$  cm diameter. Woodpiles were counted as being present in a square even if only a small part of it was in a square. The number of burrow entrances in each square was split into four categories *post hoc* (1–6, 7–9, 10–13, and 14+ burrows).

### Statistical analysis

The den occupation data were analysed to find the differences between sexes in the mean number of nights spent in a den site. To determine whether sex affects the combinations in which rats den together, den-sharing data were analysed using a chi-squared test. Because there is no way of knowing how many dens could potentially be used by tagged rats, and because not all rats in the population were radio tagged, there is no way of creating an absolute probability distribution for the number of times rats will be found denning together. Some dens apparently occupied by one radio-tagged rat may in fact have been

sharing with one or more other rats without radio-transmitters. A probability of den sharing function could be calculated if all overlaps and potential den sites were considered, but this is very complex and probably required a larger sample size than this study provides. Instead, we assigned the number of male and female rats randomly amongst the observed instances of two rats together; and separately amongst instances of three rats sharing as follows:

- (1) Let  $D_2$  be the number total number of occasions where two rats were together, and  $D_3$  be the number total number of occasions where three rats were together.
- (2) Let  $M_2$  be the number of instances of days where radio-tracked males were found sharing a den with one other rat and  $F_2$  be the number of instances of days where radio-tracked females were found sharing a den with one other rat. Then the total number of sharing events in pairs,  $N_2 = M_2 + F_2$ . The overall probability of a male being present in each observed pairing is therefore  $Pm_2 = M_2/N_2$ , and the overall probability of a female being present in an observation of a shared den is  $Pf_2 = F_2/N_2$ .
- (3) The expected frequency of finding each sex denning in pairs is then given by
  - (a) Expected number of occasions of two males together =  $Pm_2^2 \cdot D_2$
  - (b) Expected number of occasions of two females together =  $Pf_2^2 \cdot D_2$
  - (c) Expected number of one male and one females together =  $2 \cdot Pm_2 \cdot Pf_2 \cdot D_2$
- (4) By the same logic, if  $M_3$  is the number of males sharing with two other rats, and  $F_3$  the number of females,  $N_3 = M_3 + F_3$ , and the probability of encountering a male in triples is  $Pm_3 = M_3/N_3$  and for females is  $Pf_3 = F_3/N_3$ . The expected frequencies of each sex in those cases of three rats sharing a den was then calculated as:
  - (a) Expected number of occasions of three males together =  $Pm_3^3 \cdot D_3$
  - (b) Expected number of occasions of three females together =  $Pf_3^3 \cdot D_3$
  - (c) Expected number of one male and two females together =  $3 \cdot Pm_3 \cdot Pf_3^2 \cdot D_3$
  - (d) Expected number of two males and one female together =  $3 \cdot Pm_3^2 \cdot Pf_3 \cdot D_3$

We tested the fit of observed versus expected frequencies of each sex within pairs and triples separately using  $\chi^2$  tests.

To investigate which habitat characters were common to areas ship rats repeatedly used for den sites



a General Linear Model (GLM) was fitted using the computer software Minitab (Release 14.1).

The response variable (the number of times an individual rat was found denning in a grid square) was log transformed to balance residuals, and all the habitat characteristics (listed in previous section) were tried as predictor variables.

## RESULTS

Fourteen rats (7♀ and 7♂) were fitted with transmitters; 12 in December and a further two in January. Of these, five males and six females were re-caught over 5–8 February to remove the transmitters. One of the females had never been pregnant (F77), but the remaining five had either been pregnant (F81, F90), or were pregnant when trapped (F71, F85, F87).

### Den site use

During the sampling periods, the rats were located a total of 434 times across 155 different den locations spread amongst 149 (5 × 5 m) grid squares. These dens were spread over a total area of 1.51 ha.

Fifty-eight percent of male den sites and 42% of female den sites were only used for one night. Individual male and female rats re-used various den sites for up to 15 days over the period of the study.

When the 12 rats located in both sampling sessions were considered, males tended to use more den sites than females (12.43 den sites per female and 15.80 per male;  $t = 2.23$ , d.f. = 10,  $P = 0.095$ ). Correspondingly, males used den sites for fewer nights over the two sampling sessions (males 2.15 nights; females 2.78 nights;  $t = 1.85$ , d.f. = 8,  $P = 0.1$ ).

There was substantial variation in the length of time spent in different sites and the number of different den sites used by individuals. For example, over the two 18-day study periods, Male 91 used 20 different den sites. He spent a maximum of 5 nights in two of these. In contrast, Female 90 used only nine sites, two of which were used for 10 nights each.

In some cases, the position of den sites shifted as the rat shifted its home range. For example, in early

December 2003, Male 75 was located during the day and at night in one area of approximately 25 m radius, after which he took nightly trips to a new location approximately 50 m away. After 6 days, he began denning in the new location. He later moved back to the original den site. In January/February 2004, he moved his nocturnal activity area again and subsequently chose den sites in the new area.

Rats were found to be active during the day on only five of 440 daytime locations (1.1%). In each case, the rat was close to a previously used den site and its position was located periodically until it had become stationary.

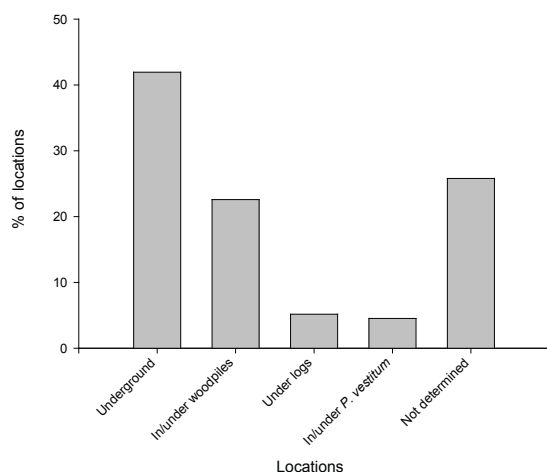
Over the entire study period on any given day, an average of 29 (SE ± 2.7) percent of rats were sharing den sites (Table 1). The two females and one male that denned together also denned with other individuals in various dens. Of interest was Female 77, which shared a den site with Male 79 nine times, but when re-trapped in February had no placental scars or embryos. In one session she was found denning with Male 79 on 6 days within an 8-day period. She also shared a den with Male 75 on one occasion.

Combinations of den sharing were significantly different from what was expected by random assortment of sexes amongst pairs ( $P < 0.001$ ), and nearly so amongst cases of three rats sharing the same den ( $P = 0.07$ ; Table 2). This arose mainly because no males shared den sites with each other, and correspondingly males denned with females more often than expected by chance. There are too few data to determine whether female-only threesomes were significantly less frequent than expected by chance. Overall the data suggest strong avoidance amongst males and attraction of males to share dens with one or two females.

Rat den sites were always found in woodpiles, under logs, in the shield fern *P. vestitum*, or underground (Fig. 2). For 25% of observations the exact position of the den site could not be determined, as there was a combination of possible locations for the den site, for example a log within thick shield fern.

**Table 1** The sex of adult radio-tagged ship rats and the number of den site nights for each combination of sex that shared dens on Taukihepa. Five males (M) and seven females (F) were tracked in December 2003, and seven of each sex in January/February 2004.

	Single M	Single F	M + M	M + F	F + F	2F + 2M
Dec	50	66	0	20	2	9
Jan/Feb	109	106	0	15	1	0



**Fig. 2** Percentage of times radio-tagged ship rats were located in different den site locations on Taukihepa during December 2003 and January–February 2004.

The GLM found no evidence of significant association ( $P > 0.10$ ) of the logarithm of the number of denning events and any of the habitat variables we measured for each grid square where one or more dens were found ( $R^2$  value of 19.0%).

## DISCUSSION

### Den site locations

This is the first study to record forest-dwelling ship rats in New Zealand preferentially using den sites on or underground. Ship rats commonly use arboreal den sites in New Zealand forests (Best 1968; Hooker & Innes 1995; Innes 2005; Pryde et al. 2005). In New Zealand, ship rats are known to prefer dens in clumps of epiphytes and tree hollows but can also make nest-like structures, built from woven twigs and

leaves, in both shrubs and canopy trees (Best 1968; Hooker & Innes 1995; Innes 2005). Rats have also been observed in den sites in flax bushes (*Phormium* spp.) and in pre-existing cavities at ground level (Best 1968; Pryde et al. 2005). In Hawaii ship rats dig burrow systems underground (Flannelly et al. 1986) or nest in porous lava (Tobin et al. 1996) or up trees. In Californian riparian forest ship rats preferentially nest in trees, but occasionally on the ground (Whisson et al. 2007). Where trees are not available, on Macquarie Island, ship rats burrow in the base of tussocks (Pye et al. 1999). On Barrow Island, West Australia, ship rats shared burrows with burrowing bettongs (*Bettongia lesueur*) (Morris 2002).

The lack of arboreal dens probably relates to the forest structure. New Zealand studies have been in forest habitats more complex than Taukihepa, where there is an almost monospecific canopy of tūpare over sparse ground cover. Tūpare trees lack cavities and epiphytes that usually provide forest-dwelling rats with potential den sites on the mainland (Best 1968; Hooker & Innes 1995; Pryde et al. 2005). In contrast, there were a large number of possible den sites on the ground within burrows, logs, woodpiles, and ferns. In addition, a rat nest built in tūpare would be subject to disturbance or damage by tītī landing in the canopy almost nightly during their breeding season, and strong and persistent winds for many nights of the year.

Siting dens on the ground on Taukihepa may also be related to the lack of non-climbing predators like feral house cats (*Felis catus*), Norway rats (*Rattus norvegicus*), hedgehogs (*Erinaceus europaeus*) and feral ferrets (*Mustela furo*) that inhabit New Zealand mainland sites. Weka (*Gallirallus australis*) are present on Taukihepa but apparently few eat rats (Harper 2007). Choice of below-ground and woodpile denning may reduce risk of weka predation. Elsewhere rodents are known to change their habitat use in response to the presence of predators (Dickman 1992; Arthur et al. 2005). Arboreal nest-

**Table 2** Observed, expected, and  $\chi^2$  values for den site sharing combinations by 14 radio-tagged male (M) and female (F) ship rats on Taukihepa during December 2003 and January–February 2004.

Combination	Singles ( $n = 331$ )		Pairs ( $n = 38$ )			Threesomes ( $n = 9$ )			
	M	F	2M	M + F	2F	3M	2M + F	2F + M	3F
Expected	—	—	8.1	18.9	11.1	0.3	3.1	4.0	2.7
Observed	159	172	0	35	3	0	0	9	0
$\chi^2$ tests	NA		$\chi^2 = 28$ , d.f. = 2, $P < 0.001$			$\chi^2 = 3.15$ , d.f. = 1, $P < 0.07^\dagger$			

<sup>†</sup>Cases of 3 males and 2 males + 1 female were aggregated, as were cases of 3 females and 2 females and 1 male, in order to avoid low expected frequencies.

ing and frequent den site changes possibly decreases predation risk (Shibata et al. 2004) and may be such a predator avoidance strategy as it is for golden mice (*Ochrotomys nuttalli*; Wagner et al. 2000) although the evidence for this is equivocal as ship rats will nest in porous lava in Hawaii with mongoose and cats present (Tobin et al. 1996) and ricefield rat *Rattus argentiventer* nests are subterranean despite their main predators probably being cobras (*Naja* spp.; Tristiani et al. 2003).

Use of terrestrial den sites may reflect a more general pattern for feeding activity to be on the forest floor or within breeding burrows. Ship rats were only located moving in trees on 3% of observations (Rutherford 2005). We radiotracked only rats that were heavier than 140 g, and there is a possibility that smaller rats could be more arboreal (Maitz & Dickman 2001). However, other studies also suggest preponderance of terrestrial foraging activity in ship rats. For example, 94% of records of moving ship rats in Northland kauri forest were terrestrial but all den sites were arboreal (Dowding & Murphy 1994). Similarly almost all ship rat dens in Californian riparian forest were arboreal (Whisson et al. 2007) even though most nocturnal activity records (86%) were on or near the ground in dense thickets. Cox et al. (2000) also found ship rats were most active on the ground. In contrast, all den sites located by Hooker & Innes (1995) were arboreal and also found ship rats were most active up trees (73% of nocturnal observations were recorded at least 2 m above ground).

Virtual restriction of movement to ground level on Taukihepa may be explained by the location of food sources. In tūpare forest there is a conspicuous lack of the abundant fleshy fruits that form an important part of ship rat diet on mainland New Zealand (Daniel 1973; Innes 1990). Large amounts of leaf litter is drawn into breeding burrows by the shearwaters (McKechnie 2006) and the tītī research team often saw large insects within the burrows when using a burrowscope to monitor sooty shearwater populations. Invertebrates formed the largest portion of rat diet on Taukihepa (Harper 2007) and along with scavenged remains of dead or dying “kiaka” (starving chicks, Hunter et al. 2000) could provide considerable amounts of food gathered from within breeding burrows. A large number of invertebrates used leaf litter for shelter and food, particularly amphipods, and invertebrates comprise about 50% of ship rat diet by occurrence on Taukihepa (Harper 2007). Extensive use of burrows adds another element to the ship rats’ broad spectrum of habitats,

further confirming their wide fundamental niche in the absence of other rodents (Harper et al. 2005).

### Habitat characteristics preferred for denning

We found no significant associations between the number of times a grid square was used for denning and several habitat characteristics. Tītī breeding burrow density is lower where leaf litter and ground debris is thicker (Moller et al. 2009a; Charleton et al. in press), yet dens were not apparently associated with more or less litter, ground cover or higher density of shearwater burrows. This suggests that den site selection has little to do with proximity to food on Taukihepa. Elsewhere, sites with leaf litter are preferred by ship rats, even in the presence of mammalian predators (Cox et al. 2000).

### Patterns of den site use

Male and female ship rats on Taukihepa changed den sites frequently with no apparent pattern in the re-use of dens. However, the mean number of den sites used by ship rats on the island during the observation period, at 12 and 16 dens used by females and males respectively, is at least twice the number reported elsewhere (2–7 den sites over 8 weeks by Whisson et al. 2007; 2–9 over 5 weeks by Dowding & Murphy 1994; and 3–5 over 3 weeks by Hooker & Innes 1995). Use of so many den sites on Taukihepa may simply relate to their abundance as approximately 20 000 seabird burrows were within the study area. We do not know whether rats were using only tītī burrows or excavated dens within the tītī burrow walls, nor whether they denned within woodpiles themselves or in burrows under woodpiles.

Contrary to other studies, no males were found sharing den sites with other males, even when one or two females were also present. Male rats expand their home range size during breeding both on the mainland and on Taukihepa (Dowding & Murphy 1994; Rutherford 2005) and presumably chase away subordinate males to maximise mating access to females (Hooker & Innes 1995). Males are known to share dens when not breeding (Dowding & Murphy 1994; Whisson et al. 2007), but have not been recorded sharing dens during a breeding season.

It has been suggested that intra-sexual den site sharing is linked to sexual activity (Dowding & Murphy 1994), but our observations suggest a degree of sharing for other reasons. Of particular interest was Female 77, which never became pregnant despite sharing her den site on nine observed occasions with one male and once with another male. Only 45% of adult females trapped on Taukihepa were

pregnant or had post-partum scars at the time of this study (G. Harper unpubl. data). However, as ship rat oestrus has a 4- to 6-day periodicity she would have been able to become pregnant during at least one den-sharing session. This suggests that not all interaction between males and females during the breeding season is of a sexual nature, and raises the possibility that the rats were closely related. Another possibility is that this female did not come into oestrus because of the transmitter, which was unlikely. Although there was some rubbing around the neck from the transmitter when she was re-trapped, she had gained weight. Another female with transmitter rubbing was pregnant and had also gained weight. These observations suggest further research investigating den site sharing and kinship could yield insights into ship rat population structure and social interactions.

Some sharing of den sites between non-radiotagged rats and tagged rats was highly likely. Consequently, the number of nights rats appear to have denned alone is almost certainly an over-estimation. Females 71 and 83 were the only females with a large proportion of their home ranges overlapping (Rutherford 2005) and they shared a den.

### Management and research implications

Despite the importance of island refuges and the threats to biodiversity posed by ship rats, little research has been conducted on the ship rat population or the impact on the island's ecological communities (Harper 2007). Very little is known about ship rat ecology on seabird islands, as most research in New Zealand has been carried out in mainland forest habitats (Daniel 1972; Dowding & Murphy 1994; Innes et al. 2001; Harper et al. 2005). Population ecology of island rodents differs from that of mainland populations (Gliwicz 1980; Polis et al. 1997), so it is surprising that more research has not been conducted on islands. Generalist feeding habits and adaptability have allowed ship rats to colonise a wide range of habitats (Clark 1981) and a flexible social structure will facilitate exploitation and rapid population growth when ecological conditions permit. Similarly, our results show very different denning patterns of ship rats on a seabird breeding island compared to mainland New Zealand.

This study and the small amount of research on den site selection in non-commensal ship rats has revealed a variable fine-scale spatial ecology, influenced by habitat structure, food quantity and dispersion, sexual activity and possibly relatedness (Dowding & Murphy 1994; Hooker & Innes 1995;

Cox et al. 2000), with larger-scale effects including predation risk and inter-specific competition (Innes et al. 2001; Harper et al. 2005; Harper 2006; Harper & Veitch 2006). Our results emphasise the importance of underground activity of ship rats on Taukihepa, and showed that radio-tracked rats moved and denned freely underground despite a dense population of sooty shearwater adults sitting on eggs and newly hatched chicks. Our results strongly suggest that many of the effects of ship rat activities on biodiversity and ecosystem function on an island with burrowing seabirds will result from underground encounters. Research on fine-scale habitat use in future should investigate kinship between associating animals and how this influences their breeding success, use of space and dispersal. Control measures, especially bio-control, are likely to benefit from this research direction.

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