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Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand.

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Abstract: The relative abundance of ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), and Pacific rats (*R. exulans*), was measured in four vegetation types on Stewart Island/Rakiura, over six consecutive seasons. Ship rats were found in all four vegetation types and dominated in podocarp-broadleaf forest and riparian shrubland. Norway rats were most common in subalpine shrubland and Pacific rats dominated in manuka (*Leptospermum scoparium*) shrubland. Analysis of micro-habitat affinities for the three species showed that ship rats were habitat generalists. Norway rats were associated with plants of damp sites. Pacific rats showed a significant positive relationship with increasing amounts of the ground cover wire rush, (*Empodisma minus*). Reasons for the observed habitat use on Stewart Island could include physiological adaptation to cold and wet conditions in Norway rats; the avoidance of predation or inter-specific competition by Pacific rats; and possibly preference for more structurally complex vegetation types by ship rats.

Keywords: habitat use; *Rattus* spp.; Stewart Island; Rakiura; ship rat; Norway rat; Pacific rat

Introduction

Numerous studies worldwide have shown that small rodent species sharing a habitat generally exhibit either inverse numerical or inverse spatial relationships (Grant, 1972). These relationships occur because habitat sharing requires interspecific partitioning of resources such as food and/or space (Grant, 1972). Mechanisms for resource partitioning are varied: examples include rodents using resources at different times (Kotler *et al.*, 1993); foraging of different food sizes or densities (Ziv *et al.*, 1995); or, most commonly, dividing a habitat into smaller portions or microhabitats (Higgs and Fox, 1993; Seamon and Adler, 1996). Resource partitioning is often dependent on a species' ability to use and defend a resource or their vulnerability to predators within a habitat, in relation to another species' abilities (Morris *et al.*, 2000). This ability relative to another species within a habitat can be regarded as a species' competitive ability (Schoener, 1989). Competitive ability is often positively related to body size; larger species generally dominate smaller species (Fox and Kirkland, 1992; Brannon 2000). Competition between species in a habitat is often not apparent as species will have partitioned the habitat in the past to minimise conflict for resources. This has been coined the "ghost of competition past" (Rosenzweig, 1981; Morris *et al.*, 2000). Interspecific competition is best shown when

one species increases in abundance or expands its use of resources after a competitor is experimentally excluded (Brown, 1987).

Very few studies have investigated habitat use by two or more rat species in New Zealand (Dick 1985; Sturmer, 1988; Bramley, 1999). In general, Norway rats (*Rattus norvegicus*) are regarded as wetland or riparian specialists (Moors, 1990), but on Stewart Island they are found some distance from water (Hickson *et al.*, 1986). Ship rats (*R. rattus*) are regarded as generalists (Innes, 2001), and the superior competitor of the three species in New Zealand (Russell and Clout, 2004). Pacific rats (*R. exulans*) are generally found in areas with well-vegetated ground cover and well-drained soil (Williams, 1973; Taylor, 1975b). The main aim of this research was to determine which rat species were present within associated vegetation types on Stewart Island. The relative competitive abilities of these rat species in different habitats elsewhere and their differences in size suggest that where all three species occur, habitat partitioning will be apparent (Yom-Tov *et al.*, 1999, Russell and Clout, 2004).

Ship rats are widespread on Stewart Island, which they share with the Pacific rat and the Norway rat, which have restricted distributions on the island (Taylor, 1975b; Sturmer, 1988). Pacific rats, the smallest species, were possibly introduced to Stewart Island about

1600AD (Holdaway, 1999), and were established and common long before the other rat species arrived (Taylor, 1975a). The largest rat, *R. norvegicus*, probably arrived on the island with the first Europeans about 1790–1800 (Atkinson, 1973) and became very common (Thompson, 1922). Ship rats became established about 1890 (Atkinson, 1973). The historic distribution and current distribution of these rats, along with the timing of their introductions, suggests that as each new species invaded, they often excluded other rat species from habitat previously suitable for the resident. For example, ship rats are now the most common rat in podocarp-broadleaf forest, with only small numbers of Norway rats present (Hickson *et al.*, 1986; Harper, 2005). Mice are not present on Stewart Island and are probably not able to establish with three rat species occupying the available niches (Taylor, 1975a).

This study documents the distribution of three rat species in different vegetation types and relates their distributions to aspects of the vegetation where the rat species were trapped.

Methods

Study site

The study area was in the Rakeahua Valley (47°S, 167°50'E), Stewart Island (Fig. 1). The valley is low lying, and consists of undulating low ridges separated by marshes and streams with low scrub or wetland vegetation. It is bounded on the south side by a steep forested escarpment rising to 400 m a.s.l. and on its north and west sides by low hills and isolated massifs, the highest being Mount Rakeahua (681 m a.s.l.). The soils of the valley are generally of low fertility (Wilson, 1987).

The climate is cool and windy (Wilson, 1987) with rainfall of approximately 2265 mm per year (K. Tredrea, National Institute of Water and Atmospheric Research, pers. comm.). Snow may lie to above 500 m in winter and occasionally is recorded in the valley floor. As temperature may affect the use of habitats by rats (Studholme, 2000), air temperature was measured at a shaded site on the valley floor with a maximum–minimum thermometer fixed 1.7 m above ground.

Four main vegetation types were identified following Wilson (1987) and were confirmed by survey (Harper, 2002):

A. Podocarp-broadleaf forest

This forest type was the dominant vegetation cover and was found on well-drained slopes of the valley sides from sea level to about 350 m a.s.l. The forest canopy height was about 25 m near sea level and consisted of emergent rimu (*Dacrydium cupressinum*¹) over a canopy of kamahi (*Weinmannia racemosa*), southern rata (*Metrosideros umbellata*), miro (*Prumnopitys ferruginea*), and some Hall's totara (*Podocarpus hallii*). The midstory was a mix of young canopy trees, shrubs and tree-ferns. Crown fern (*Blechnum discolor*) dominated the ground cover.

B. Subalpine shrubland

Subalpine shrubland existed from 400–500 m a.s.l. in the Rakeahua catchments on a continuum of wet to well-drained sites. In exposed sites subalpine shrubland may extend down to 300 m a.s.l. This shrubland was generally tangled and dense. The average canopy height was 2–3 m. It was dominated by manuka (*Leptospermum scoparium*) and leatherwood (*Olearia*

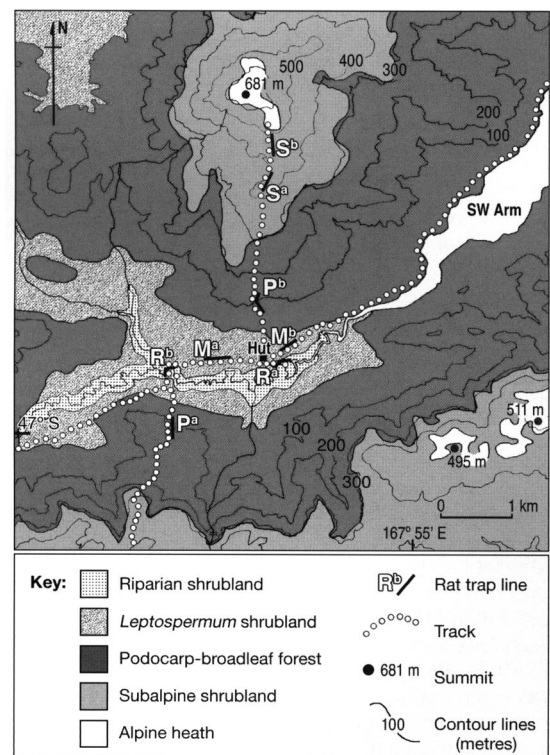


Figure 1. Map of the Rakeahua Valley, central Stewart Island, showing the location of the rat trap-lines (R = river traplines, M = manuka (*Leptospermum*), P = podocarp-broadleaf, S = subalpine).

¹ Nomenclature follows Connor and Edgar (1987) and references therein for gymnosperms and dicotyledons; Moore and Edgar (1976) for monocotyledons; and Brownsey and Smith-Dodsworth (1989) for ferns.

colensoi), along with inaka (*Dracophyllum longifolium*), southern rata, kamahi, and pink pine (*Halocarpus biformis*). The tussock sedge (*Gahnia procera*), was the obvious ground cover along with mosses, liverworts and small herbs.

C. Manuka shrubland

These shrublands almost covered the valley floor, and were only absent in permanent wetlands. The canopy and sub-canopy was invariably manuka, with a mean canopy height of 5–6 m. Some mingimingi (*Cyathodes juniperina*) was present in the subcanopy also. The ground cover consisted mainly of mosses, liverworts, wire rush (*Empodisma minus*), and patches of the tangle fern (*Gleichenia dicarpa*).

D. Riparian shrubland

This vegetation type covered the well-drained soils skirting the main river and some of its larger lower tributaries. It extended back from the river edge for 20–30 m before merging with the less fertile manuka shrublands (Wilson, 1987). This vegetation zone has flooded several times a year (G. Harper, pers. obs.). The dominant canopy tree was manuka. The understory comprised several divaricating species (filiraculate *sensu* Wardle 1991), *Coprosma ciliata* predominating, along with *Pseudowintera colorata*. Ground cover was complete, mainly comprising bush rice grass (*Microlaena avenacea*).

Rat trapping

Snap-trap index lines were run in the four main vegetation types. A standard trapping method was used to obtain indices of abundance and record the distribution of the three species (Cunningham and Moors, 1996). Because rats cannot be assumed to be found in similar relative abundance in similar vegetation types (Dowding and Murphy, 1994), two rat-trapping lines of seven paired traps were laid out in each of three vegetation types and set for a minimum of nine consecutive days in the four seasons from March 2000 to June 2001: winter (June), spring (September), summer (December), and autumn (March). An additional pair of trap lines was established in a fourth vegetation type, riparian shrubland, from June 2000 until June 2001, as few Norway rats had been trapped until then. This gave 126 uncorrected trap-nights for each line for each season and a measure of variability of rat distribution within habitats. The large number of days that traps were set was to increase the chance of subordinate individuals being trapped once a dominant individual or species had been removed by trapping.

Within vegetation types, transects were a minimum of 350 m apart, to preclude sampling the same population of rats. This distance was beyond the maximum recorded range length of the rat species at

the start of the study (Hickson *et al.*, 1986; Moors, 1990). All transects were set out adjacent to walking tracks. Traps were set at 50-m intervals next to logs or at the base of trees.

Rats were trapped using “Ezeset” snap-traps under 12-mm square mesh covers to exclude non-target species (Weihong *et al.*, 1999). The trapping procedure followed Harper (2005). The traps were baited with a mixture of peanut butter and rolled oats. Rats were processed on the day of capture. Processing of rats followed the methods of Cunningham and Moors (1996) and included details of species, approximate age (adult or juvenile; judged by perforate or imperforate vagina for females and presence or absence of visible tubules within the cauda epididymis for males), reproductive condition, and sex. Any scavenged rats were identified to species, sex or age as best as possible, depending on the state of the remains. The rate of rat capture was defined as the number of rats (R) caught (C) per 100 trap nights (TN) corrected for all sprung traps (Nelson and Clarke, 1973) and notated as R/100CTN (Cunningham and Moors, 1996).

Data analysis

Seasonal rat abundance

Temporal variations in resources influence seasonal abundance of rats in different habitats and the three rat species exhibit seasonal cycles in relative abundance on mainland New Zealand (Innes, 2001; Atkinson and Towns, 2001). An ANOVA was used to test whether relative abundance differed between the six seasons. Replicates were the trap success on each trap line in each season. A post-hoc Tukey test was used to identify any significant differences between seasons.

Overall rat abundance within habitats

Small rodents respond to small-scale differences within a habitat (e.g. the amount of low cover), which will affect abundance within apparently similar habitats (Morris, 1984; Dowding and Murphy, 1994, Cox *et al.* 2000). An ANOVA was used to test whether overall relative abundance differed between trap lines within vegetation types. The trap success on each trap line was the replicate.

Habitat use by rats

Differences in abundance between habitats would suggest that resources may be distributed unevenly. This could affect habitat selection, as other rat species immigrate to use a rich resource (Wolff, 1996; Banks and Dickman, 2000). An ANOVA was used to test whether overall relative abundance of the three species differed between vegetation types. The relative abundance of each species in each vegetation types was tested, with the overall trap success on each trap line in each vegetation type being the replicates.

Micro-habitat use by rats

Habitat variables

Surveys of habitat variables on each rat-trapping transect were undertaken in January 2001 to confirm the four described vegetation types and to establish microhabitat site selection by rat species. This gave eight samples in each of the vegetation types. The survey was carried out using the Reconnaissance (RECCE) description (Allen, 1992). 'Reconnaissance plots' of 20-m diameter were centred on rat-traps at alternate (i.e. four out of seven) trap sites at 100-m intervals (Allen, 1992). The plots were linked to the trap sites to test for effects of microhabitat variables on species capture. Vascular plant species were recorded in seven height tiers following Dickinson and Mark (1999): tier 1, emergent trees >12 m; tier 2, canopy trees >12 m; tier 3, small trees 5–12 m; tier 4, tall shrubs 2–5 m; tier 5, small shrubs 0.3–2 m; tier 6, herbs ≥ 0.3 m; tier 7, ground layer, including bryophytes ≤ 0.3 m. Epiphytes were listed. Overall percentage cover in each tier was visually estimated. Species with percentage cover over 10% in each tier were also recorded, along with their estimated contribution to the cover in that tier. Height of emergent trees and the canopy height were measured using an Abney level.

A rank correlation between the rat captures and site variables was carried out to clarify the combination of site variables that best explained any microhabitat partitioning by the three rat species, using the software package BIO-ENV. This system measured the degree of similarity between a matrix of the rat species caught at the sites (assuming equal catch effort at each site) and subsets of variables from the matrix of vegetation parameters of the same sites (Clarke and Warwick, 1994). The matching elements in the two matrices are correlated using a weighted Spearman rank correlation coefficient, r . The vegetation parameters were: vascular species (presence/absence), litter (percentage of cover, 1 = 0–24%, 2 = 25–49%, 3 = 50–74%, 4 = 75–100%), low cover (tier 6; herbs: >0.3 m, percentage of cover as per 'litter'), ground cover (0–0.3 m, percentage of cover as per 'litter'), canopy cover (percentage of cover as per 'litter'), height (mean height of canopy), layers (the number of tiers at a site), diversity (the total number of plant species present), ground diversity (the number of plant species in the ground layer, 0–0.3 m), tier 4 diversity (the number of plant species in tier 4, 2–5 m), tier 5 diversity (the number of plant species in tier 5), and tier 6 diversity (the numbers of species in tier 6). All analyses were carried out using PRIMER version 5 (K. R. Clarke and R. N. Gorley, Plymouth Marine Laboratory, UK).

Results

Rat captures

Total captures were 173 rats (3.26 rats/100CTN) over 5307.5 corrected trap nights. Ninety-four (54.3%) were ship rats, 44 (25.5%) were Pacific rats and 35 (20.2%) were Norway rats. Ship rats were significantly more likely to be trapped than the other species ($F_{2,66} = 7.69$, $P < 0.001$).

Seasonal rat abundance

The relative abundance of rats fluctuated through the year and the overall relative abundance was statistically significantly lower in summer than winter ($F_{5,40} = 10.38$, $P < 0.001$, Tukey's test: winter 2000: $P = 0.003$, winter 2001: $P = 0.036$, Fig. 2). The peak in relative abundance was generally more pronounced in subalpine and riparian habitats than in other habitats, but the trough in relative abundance was of a similar magnitude over all the habitats (Fig. 2). The peak in relative abundance was explained by an increase in the proportion of juvenile rats over early winter in all vegetation types. Only eight (21%) of the 37 adult female ship rats trapped were pregnant, whereas 53% (8) of the 15 adult female Pacific rats were pregnant. Pregnant female ship rats and Pacific rats were mostly trapped in early autumn, although some were present in winter and early spring. Seventeen adult female Norway rats caught. Eight (47%) pregnant individuals were trapped in total, with captures spread through the year.

Habitat use by rats

The overall relative abundance did not differ between trap lines within vegetation types ($F_{6,38} = 0.68$, $P = 0.67$) or between vegetation types ($F_{3,42} = 0.86$, $P = 0.47$). Pacific rats and Norway rats exhibited strong habitat associations ($F_{6,21} = 5.67$, $P = 0.001$, Fig. 3), but there was no statistically significant difference of relative abundance of ship rats between any of the vegetation types ($F_{3,42} = 2.33$, $P = 0.09$, Fig. 3). Twenty-eight ship rats and only one Norway rat were caught in podocarp-broadleaf forest. Ship rats were also the most common species in riparian shrubland ($n = 34$). Eleven Pacific rats and one Norway rat were caught in the riparian shrubland.

Norway rats were the most common species of rat in subalpine shrubland ($n = 29$) with a smaller number of ship rats ($n = 21$) and five Pacific rats. Norway rats were trapped significantly more often in subalpine shrubland than any of the other vegetation types ($F_{3,42} = 7.56$, $P = 0.001$, Fig. 3). The Pacific rats were caught in two adjacent traps 50 m from each other, within six months.

In manuka shrubland, 28 Pacific rats, 11 ship rats

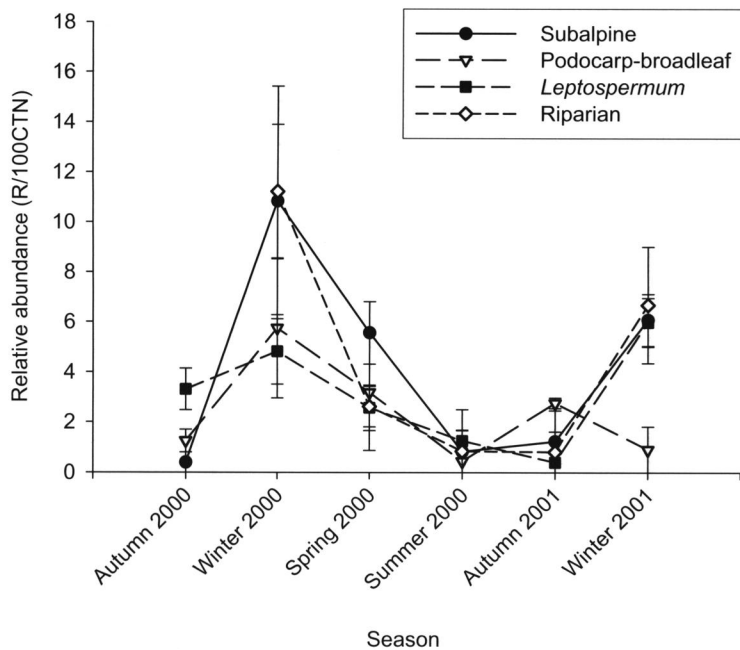


Figure 2. Seasonal changes (\pm s.e.) in the relative abundance of rats in four vegetation types, Autumn 2000–Winter 2001. Rakeahua Valley, Stewart Island.

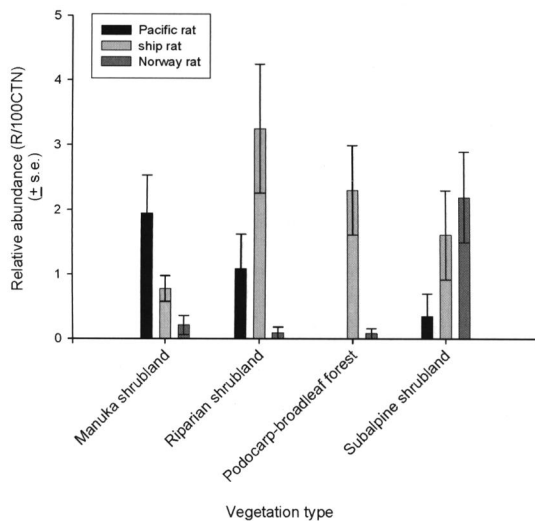


Figure 3. Mean (\pm s.e.) relative abundance of three rat species in four vegetation types over 5307.5 corrected trap nights. March 2000–June 2001, Rakeahua Valley.

and four Norway rats were caught, the latter at two adjacent traps. Pacific rats were trapped significantly more often in manuka shrubland and riparian shrubland than in the other vegetation types ($F_{3,42} = 4.59$, $P = 0.007$, Fig. 2).

Micro-habitat use

The BIO-ENV rank correlation between rat captures and site parameters showed that the combination of the presence of *Empodisma minus* and *Lepidosperma australe*; for Pacific rats; and *Drosera stenopetala* and *Schoenus pauciflorus*; for Norway rats; coupled with low canopy height, best explained the variation in habitat use of both these rat species (Spearman rank correlation: $r = 0.68$). These pairs of plant species are found in damp to wet grassland, and shrubland in lowland and subalpine sites, respectively. Canopy height in these sites is generally less than 5 m.

Of the four plant species, only *Empodisma minus* contributed a significant percentage of ground cover in the manuka and riparian shrubland sites, and the remaining three plant species were only recorded as present or absent at these sites. It was suspected that an increase in ground cover would result in an increasing abundance of Pacific rats, as they are restricted by other rat species to habitats with substantial ground

cover (Atkinson and Moller, 1990; Bramley, 1999). A regression of the numbers of trapped Pacific rats against the percentage of ground cover of *Empodisma minus* (arcsine transformed to normalise the data) at trap sites in the manuka and riparian shrubland revealed a significant positive relationship between Pacific rats and the amount of ground cover provided by *Empodisma minus* ($R^2 = 0.73$, $P < 0.001$).

Ship rat trapping data had only statistically weak relationships with a few vegetation parameters. This is probably due to ship rats being trapped at most of the sample sites.

Discussion

Three rat species were present, and distributed unevenly, in four vegetation types in the Rakeahua Valley. Ship rats were the most abundant and most pervasive species, found in all vegetation types and were virtually the sole rat species present in podocarp-broadleaf forest. Norway rats were numerically dominant in subalpine shrubland and were found in small numbers in other vegetation types. Pacific rats were the most common rat in manuka shrubland, but were also found in riparian shrubland, and a few were trapped in subalpine shrubland. As expected, Norway rats had strong affinities with plants associated with damp sites, whilst Pacific rats were more abundant in areas with large amounts of ground cover below 0.3 m. Compared with their congeners, ship rats exhibited markedly generalist habitat use.

There was no overall difference in mean relative abundance of all rats between the vegetation types, suggesting that resources such as food were either not limiting rat numbers, or were equally limiting, in any forest type (Banks and Dickman, 2000). The relative abundance of all rat species fluctuated seasonally and concurrently in all vegetation types, which suggested the three species were responding to the same seasonal availabilities of food in each vegetation type (Banks and Dickman, 2000). Maximum relative abundance was in early winter, which Sturmer (1988) also recorded. Winter maxima in relative abundance coincided with a substantial increase in the percentage of juvenile rats within the populations of all the rat species. Minimum relative abundance was in early summer through to early autumn. This timing of breeding is similar to breeding seasons for rats on mainland New Zealand (Innes, 2001).

In the relatively low stature manuka shrubland, Pacific rats were the most common species, followed by ship rats. If this habitat were suitable for the other two species, they would be expected to occupy it, as Pacific rats are subordinate to them (McCartney and Marks, 1973; Twibell, 1973; Russell and Clout, 2004).

Although Pacific rats are known to be arboreal (McCartney, 1970), the results of this present study suggest that ground cover, in this case *Empodisma minus*, is the most important habitat feature for them in the manuka shrubland, as well as in the riparian forest. The importance of low ground cover in these two habitats suggests that Pacific rats may be using it as an escape site from either predation (Atkinson and Moller, 1990) or competitive interactions with larger rat species (Falkenberg and Clarke, 1998). Pacific rats and ship rats will exist together in a confined space when ground cover is available (Strecker and Jackson, 1962).

The lack of Pacific rats on the New Zealand mainland, in apparently suitable habitat, is intriguing. Competition with mice has been suggested, along with the presence of one or both of the larger rat species, and is likely a major factor (Taylor 1975), as mice prefer similar sites with thick ground cover (King *et al.* 1996). A lack of long-term trapping in sites preferred by Pacific rats, and confusion of identification (with young ship rats), may also contribute to the conclusion that Pacific rats are not more widely distributed on the mainland (Ruscoe 2004). Small enclaves of Pacific rats can persist in podocarp-dominated forest (Ruscoe 2004), indeed, five were trapped in four adjacent traps in ship rat-dominated podocarp-broadleaf forest in the Freshwater Valley, Stewart Island, in spring 1999 (G. Harper, *unpubl. data*). However, unlike the appearance of Pacific rats in the Waitutu forest after a rimu mast-seed event in 2002 (Ruscoe 2004), Pacific rats were not trapped in podocarp-broadleaf forest during simultaneous heavy rimu mast-seeding in the Rakeahua Valley (Harper 2005).

The reasons for the low numbers of ship rats in the manuka shrublands may reflect a simpler forest structure and lower plant diversity compared with the other vegetation types. Overseas, ship rats prefer forest types with more structural complexity (Braithwaite and Gullan, 1978; Cox *et al.*, 2000). In New Zealand ship rats tend to prefer forests with more complex structure in indigenous and old exotic forest (King *et al.* 1996). In the present study, ship rat abundance did not vary with the amount of forest litter, as found by Cox *et al.* (2000), or canopy height (Braithwaite and Gullan, 1978).

Norway rats were occasionally caught in manuka shrubland, and they may have been dispersing from wetland areas between the slightly more elevated manuka shrubland sites. Indeed, Norway rats are the most commonly caught species in manuka shrubland in the nearby Freshwater Valley, probably because of the presence there of large wetland areas. Although Norway rats are usually associated with water on the New Zealand mainland (Moors, 1990; Innes, 2001), almost no Norway rats were trapped in the riparian habitat in this study, which augments the results of

Hickson *et al.* (1986). Similarly, many of the Norway rats in the subalpine shrubland were trapped over 200 m from the small streams that cut across the rat trap-lines. Norway rats have also been trapped several hundred metres away from areas of water on Raoul Island in northern New Zealand (G. Harper, pers. obs.), Campbell Island in the New Zealand subantarctic (Taylor, 1986) and on Kapiti Island off the coast of the North Island (Bramley, 1999). On Raoul and Kapiti Islands, the only competitor was the subordinate Pacific rat. Norway rats appear to use a wider range of habitat when they have a comparative advantage (e.g. size or physiology) over other rats present. This situation would suggest that in the riparian shrubland ship rats had some competitive advantage in excluding Norway rats from an apparently suitable habitat.

Although Pacific rats were present in the riparian shrubland, ship rats were more abundant. The riparian shrubland was more structurally complex than the manuka shrubland that, as discussed above, may have favoured its use by ship rats.

In the subalpine shrubland, Norway rats were the most abundant species, followed by ship rats. This pattern was also recorded in subalpine shrubland on Table Hill, to the south of Mt Rakeahua (G. Harper, *unpubl. data*). There has been very little systematic trapping of rats in this forest type (Moors, 1990; Innes, 2001), and the only recorded trapping in subalpine forest has been in high altitude *Nothofagus* forest and alpine tussock at Mt Misery, Nelson Lakes National Park (Innes, 1990). In this case, no ship rats were trapped above 1025 m a.s.l., and apparently no other rats were trapped in this zone either (Innes 1990). Norway rats were recorded in substantial numbers in the subalpine shrubland of Fiordland in 1884 (Reischek, 1887), but have since disappeared (Riney *et al.*, 1959).

Norway rats may dominate subalpine shrubland on Stewart Island because of a physiological advantage over ship rats (Wolff, 1996), which may be at the limit of their cold tolerance (Macdonald and Barrett, 1993). Although ship rats were trapped in subalpine shrubland when snow had lain for a few days, it has been suggested that prolonged cold (2.0°C minimum mean monthly temperature) affects the ability of ship rats to forage for food (Studholme, 2000). The wet conditions at this altitude, where rainfall probably exceeds 3200 mm/year (Sansom, 1984), may also limit the foraging ability of ship rats. Norway rats, on the other hand, are excellent swimmers (Moors, 1990) and appear adapted to wet, cold conditions in New Zealand and Europe (Macdonald and Barrett, 1993).

The virtual absence of Norway rats and Pacific rats from podocarp-broadleaf forest is intriguing and casts some doubt on the theory that Norway rats are excluded from lowland forest areas through predation by mustelids in New Zealand (Taylor, 1984; Russell

and Clout, 2004), as mustelids are absent from Stewart Island. The ubiquity of ship rats in the Rakeahua Valley does suggest they have a broader 'niche breadth' than either Norway rats or Pacific rats.

Niche breadth in the three rat species

Species can be regarded as having a "fundamental" and a "realised" niche breadth (Hutchinson, 1957). The fundamental niche is the niche occupied when competitors are absent, and the realised niche the niche occupied when competitors are present. The three rat species in New Zealand have large fundamental niches. Pacific rats were found throughout the New Zealand mainland before Norway rats were introduced (Atkinson, 1973; Holdaway, 1999). On islands without other rodents, they will occupy all available habitats (Williams, 1973; Roberts and Craig, 1990; Little Barrier Island and Whenua Hou/Codfish Island, G. Harper, pers. obs.). Norway rats were ubiquitous in New Zealand (Moors, 1990) before ship rats arrived (Atkinson, 1973). They will expand their use of habitat in unoccupied habitats (Pye and Bonner, 1980; Taylor, 1986; Thorsen *et al.*, 2000). Ship rats have a similar ability (Patton *et al.*, 1975) and are now found in various habitats in the tropics to the subantarctic (Twibell, 1973; Patton *et al.*, 1975; Pye *et al.*, 1999).

In the presence of competitors in New Zealand, rat species exhibit narrower realised niches, and historical records suggest that the habitat partitioning occurred before predators became widespread (Atkinson, 1973). Although predation has been suggested as a way of allowing habitat partitioning to occur by reducing the density of dominant species (Stapp, 1997), historical records, and recent modelling (Russell and Clout, 2004), imply that partitioning through competition has occurred between the three species. The continued sympatry of dominant and subordinate species in habitats may be due to extensive gene flow within the subordinate population, from habitat where the dominant is absent. This mechanism could impede local selection for reduced competition (Maitz and Dickman, 2001).

This paper has presented results that require testing experimentally to ensure their validity. To experimentally show competition, selective removal of one or more species, within a habitat or across a habitat boundary, often produces the most compelling results (Higgs and Fox, 1993). For example, removal of ship rats within a grid of traps at a podocarp-broadleaf forest/manuka shrubland boundary would allow Norway rats or Pacific rats to occupy the vacant space in the podocarp-broadleaf forest, where they are essentially absent. Experiments of this nature have not been done in New Zealand, but could be used to test the hypotheses suggested.

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