

Habitat use by kiore (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, New Zealand

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Abstract: The continued coexistence of ecologically similar species relies on niche separation in space or time. Four similar species of introduced rodent occur in New Zealand, but the mechanism(s) allowing them to coexist in varying species combinations throughout the country is poorly understood. In order to investigate the coexistence of kiore or Pacific rats (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, rats were kill-trapped in exotic grassland and four forest types between 1992 and 1996. At each trap site, vegetation and microhabitat variables were measured and related to rat capture at that site with the aim of identifying and describing the preferred habitat of each species in the presence of the other. The demography and productivity of each species in each habitat was measured to determine the distribution and success of rats over the island. From 12 202 corrected trap nights, 923 rats were caught (391 Norway, 518 kiore, 14 unknown). Kiore were associated with low-growing vegetation in well-drained, flat areas whereas Norway rats were associated with taller vegetation, growing in steeper areas that were poorly drained. There was no significant inverse relationship between species capture rates. The number of kiore captured varied with year, season, and habitat. Kiore were most common in grassland and kānuka (*Kunzea ericoides*) forest. However, kiore were larger and produced more offspring per female in kohekohe (*Dysoxylum spectabile*) forest. Norway rat capture also varied with year and habitat, but was unaffected by season. Norway rats reached similar sizes, and produced similar numbers of offspring per female, in all habitats. The coexistence of rats on Kapiti Island appears to be due to the variety of habitats present combined with spatial partitioning of those habitats and the presence of some habitats in which kiore are, at least seasonally, very successful.

Keywords: coexistence; kill trapping; Pacific rat

Introduction

Four species of introduced rodents (house mice *Mus musculus*, black or ship rat *Rattus rattus*, Norway rat *R. norvegicus*; and kiore or Pacific rat *R. exulans*) have arrived in New Zealand as human commensals and are now found in a wide range of habitats. Kiore arrived with Māori voyagers at least 1000 years ago and were common throughout the main islands and many offshore islands prior to the arrival of the other three species with European migrants 200–250 years ago (Atkinson & Towns 2005; Wilmshurst et al. 2008). Kiore were largely displaced by Norway rats initially and then by later arriving ship rats (Atkinson & Moller 1990; Moors 1990).

Currently ship rats and mice are common in most habitats on both the North and South Island. Norway rats are most common near human habitations on both islands and kiore are confined to areas of Fiordland, Southland and south Westland (Atkinson & Towns 2005; Innes 2005a, b; Golding & Harper 2008). On offshore islands kiore and/or Norway rats occur more frequently than ship rats or mice, but varying combinations of two, or occasionally three, species of rodent are known (Atkinson & Moller 1990). All four species of rodent are not known to coexist anywhere in New Zealand although they do in Hawai'i (Tomich 1986; Atkinson & Moller 1990).

The primary mechanism that facilitates coexistence of ecologically similar species involves interspecific segregation of resources such as food and space, possibly with a temporal component (Schoener 1974; Castro-Arellano & Lacher 2009).

Although rats and mice are generalists, with broad habitat and food preferences, their wide ecological niche can apparently be restricted in the presence of competitors (Harper et al. 2005). Using species removal experiments Ruscoe et al. (2011) suggested that food availability and competition were more important regulators of ship rat and mice populations in North Island forests than predation. On that basis, when two species of morphologically similar rodent coexist, it is likely that the presence of one will influence the ranging behaviour and habitat use of the other (Taylor 1975; Dueser & Porter 1986; Dickman 1991; Ziv et al. 1993; Tomblin & Adler 1998). Sympatric rodent species generally partition resources by adopting inverse numerical, spatial or temporal relationships (Grant 1972; Coppeto et al. 2006) although the scale and applicability of many studies investigating sympatry in small mammals have been questioned (Jorgensen 2004).

Rodents as a group have been extremely successful worldwide and they exhibit a degree of behavioural, ecological and physiological plasticity that may predispose them to successful adoption of new niches. Thus the interactions between rodent species in New Zealand are likely to be multifaceted and complex and may include inter- and intra-specific interactions mediated by behaviour (including predation), morphology and diet. Knowledge of the demography, habitat use and behaviour of rodents in different habitats is necessary to understand population dynamics and inter- and intra-specific interactions of rodents in different areas and, ultimately, to manage mixed rodent assemblages

efficiently for the purposes of conservation of endemic species, crop protection or human health.

Prior to 1996, Kapiti Island was home to Norway rats and kiore. At that time Kapiti Island was seen as a candidate for rodent eradication because it had already been the subject of other successful mammal eradications including cats (*Felis catus*), sheep (*Ovis aries*), pigs (*Sus scrofa*), goats (*Capra hircus*), cattle (*Bos taurus*), deer (*Axis axis* and *Dama dama*), and brushtail possums (*Trichosurus vulpecula*), leaving rodents as the only alien mammals on the island (Esler 1967; Cowan 1992). Rats were hindering the re-establishment of the threatened endemic wattlebird, the New Zealand saddleback (*Philesturnus carunculatus*) (Lovegrove 1996), and preventing the island from realising its full potential as a sanctuary. Kapiti Island represented a more difficult eradication problem than other islands previously cleared of rodents, not only because of its size and steep topography, but also because it had two species of rats and it was unknown how their interactions might affect bait uptake (Bellingham et al. 2010). This study is the first to investigate how habitat type affects kiore and Norway rat captures replicated across seasons and consecutive years. The objectives were to characterise the habitat used by each rat species on Kapiti Island, and to quantify variation

in productivity and abundance according to habitat, season, and year to determine whether spatial, numerical or temporal habitat partitioning occurred and whether differential success in some habitats could explain the coexistence of Norway rats and kiore.

Methods

Study area

Kapiti Island (40°51' S, 174°56' E) is a large (1965 ha) island sanctuary approximately 5.2 km from the south-western coast of the North Island, New Zealand (Fig. 1). Kapiti Island is approximately 9 km long by 2.3 km wide and reaches 521 m above sea level at its highest point. The western face of the island is steep, with exposed cliffs, but there are small areas of flat land along the eastern side of the island. Kapiti Island was designated a nature reserve in 1897. The island has been extensively modified by burning and human occupation (for farming and as a whaling base) in the past, but is now covered by a variety of regenerating forest types (Esler 1967; Fuller 1985; Atkinson 1992). The prevailing winds come from the west and north-west.

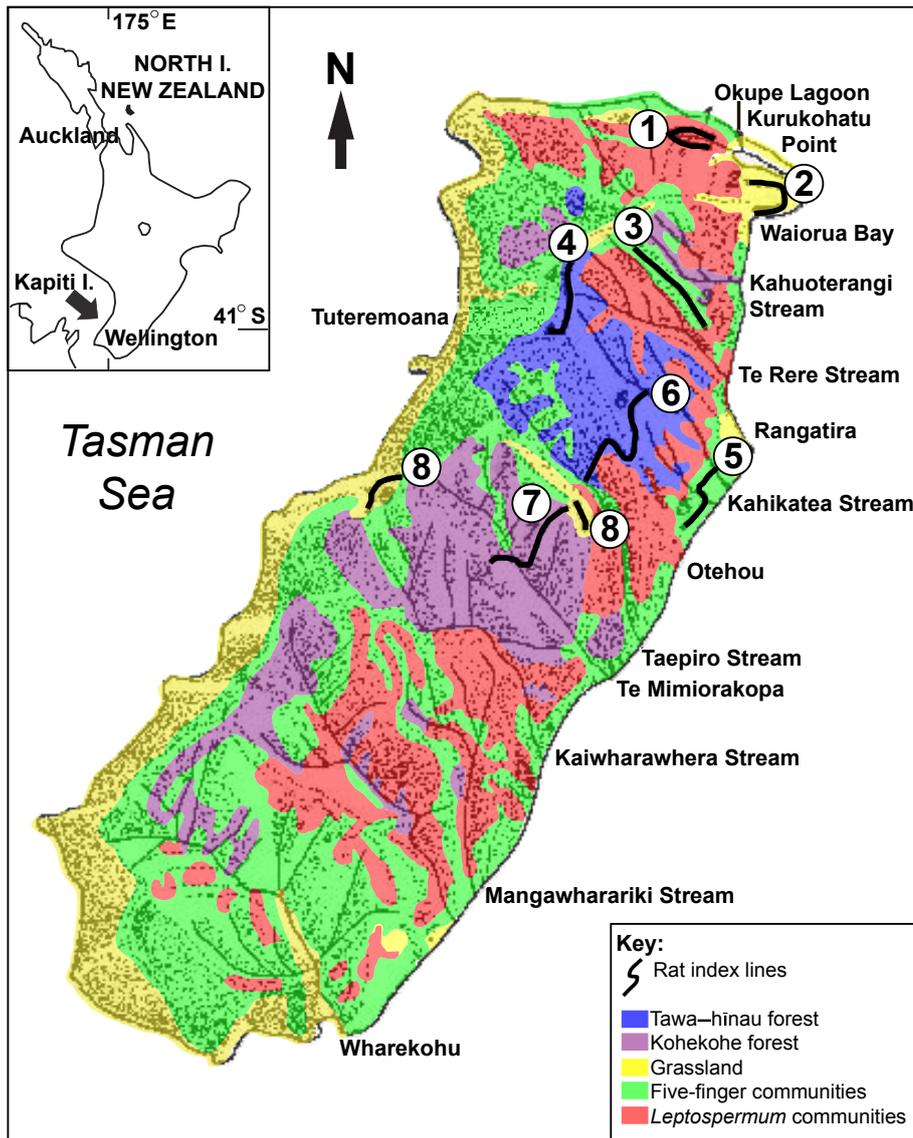


Figure 1. Oblique view of Kapiti Island, New Zealand, showing location and indicative vegetation cover, with the eight rat index lines marked. Modified from Esler (1967) and Fuller (1987). Not drawn to scale.

Norway rats and kiore were simultaneously eradicated from Kapiti Island in 1996 following two aerial drops of cereal baits containing brodifacoum (Empson & Miskelly 1999). Prior to 1995 there was localised rat control carried out at both Waiorua Bay and Rangatira Point as required to reduce adverse effects of rats in the gardens and houses there, but no island-wide control efforts were attempted. Apart from the trapping described here, efforts to control rats anywhere on the island ceased at least one year before the eradication operation so as to ensure all rats were poison-naïve when the aerial drops occurred (R. Empson, Zealandia Sanctuary, Wellington, pers. comm.).

Rat distribution and abundance

Eight lines of 35 'Ezeset' rat traps were established in July and September 1992 in a range of habitat types from sea level to the summit of the island to provide an index of rat distribution, abundance, population structure, breeding, and habitat use. The five major habitat types identified by Fuller (1985, 1987) were sampled. The location of each trap line is shown in Fig. 1 and the habitat types for each line described in Table 1. Vegetation types described by Fuller (1985, 1987) are indicatively mapped in Fig. 1, but this should not be regarded as definitive because

Fig. 1 is an oblique view not drawn to scale. Traps were spaced at 25-m intervals on seven of the lines and 50-m intervals on line 6. Line 8 (in higher elevation grassland habitat) was divided into two shorter lines near each other because there was not enough grassland at either location to have 35 traps spaced 25 m apart. Initially traps were covered with wire mesh, but there was a high level of interference with the traps by non-target animals, mostly weka (*Gallirallus australis*) and New Zealand robins (*Petroica australis*). In July 1993 (on lines 4 and 6) and October 1993 (on the other lines), the mesh covers were replaced with aluminium trap covers with wire mesh ends to reduce this interference. Rats were trapped for three consecutive nights in January (summer), April (autumn), July (winter) and October (spring) between October 1992 and July 1996. Traps were baited with peanut butter and rolled oats, replaced as necessary to maintain bait freshness. Traps were checked daily and all captures or sprung traps recorded. One trapping session consisted of approximately 100 trap nights (after adjustment for captures and sprung traps) on each line, in each season, of each year. Captured rats were assigned to an age and sex class, weighed, and their head and body length measured using the protocol outlined by Cunningham and Moors (1983). Imperforate females with plugged vaginas and

Table 1. Vegetation on the rat-trapping lines, Kapiti Island, New Zealand (see Fuller 1985).

Line	Vegetation type	Characteristics
1	Kānuka (<i>Kunzea ericoides</i>) forest with a dense canopy and sparse understorey of <i>Coprosma</i> spp., five-finger (<i>Pseudopanax arboreus</i>) and akiraho (<i>Olearia paniculata</i>).	Line 1 has sparse ground cover of <i>Carex</i> , <i>Uncinia</i> and ferns (Fig. 1). Kānuka and mānuka (<i>Leptospermum scoparium</i>) forest covered 22% of Kapiti Island in 1985 (Fuller 1985).
2	Coastal shrub/grassland. Rank grass dominated the vegetation with sparse <i>Coprosma propinqua</i> , <i>Ozothamnus leptophyllus</i> and <i>Muehlenbeckia</i> spp.	The plants are growing in very shallow soils over shingle and boulders between Okupe Lagoon and Waiorua Bay (Fig. 1). About 15.5% of Kapiti Island was covered by grassland or shrub/grassland in 1985, although mostly on the Western Cliffs (Fuller 1985).
3	Diverse young forest with dominant five-finger and common kānuka, hīnau (<i>Elaeocarpus dentatus</i>), rewarewa (<i>Knightia excelsa</i>), tawa (<i>Beilschmiedia tawa</i>) and kohekohe (<i>Dysoxylum spectabile</i>).	Line 3 was located on a ridge between Te Rere and Te Kahuoterangi catchments (Fig. 1). Five-finger forest covered 25% of Kapiti Island in 1985 (Fuller 1985).
4	Tawa-hīnau forest with other common canopy species being māhoe (<i>Melicytus ramiflorus</i>), rewarewa, five-finger and kāmahī (<i>Weinmannia racemosa</i>).	Line 4 was on the summit ridge, north of the trig (Fig. 1).
5	Diverse forest with dominant five-finger. Kohekohe, akiraho, and lancewood (<i>Pseudopanax crassifolius</i>) were also common.	Line 5 was near the coast from Rangatira to Otehou (Fig. 1).
6	Mid-altitude tawa-hīnau forest with rewarewa, toro (<i>Myrsine salicina</i>), mataī (<i>Prumnopitys taxifolia</i>) and miro (<i>P. ferruginea</i>).	The long transect (traps 50 m apart) between Kahikatea and Te Rere catchments (Fig. 1).
7	An almost pure canopy of kohekohe with pukatea (<i>Laurelia novae-zelandiae</i>) near streams.	Kohekohe forest covered about 15% of Kapiti Island in 1985 (Fuller 1985). Line 7 was in the Te Mimiorakopa catchment (Fig. 1).
8	Grassland at Te Mimi is being succeeded by <i>Hebe</i> , <i>Urtica</i> and bracken (<i>Pteridium esculentum</i>). The grass around the hut was more open, with scattered <i>Hebe</i> and five-finger.	Followed the cliff edge grassland at Te Mimi (25 traps) and the grassland around Seismometer Hut (10 traps) (Fig. 1). The two grasslands were at similar altitude and had similar species, but neither was long enough to have all 35 traps at 25-m spacing.

small males without scrotal testes or visible epidymal tubules were also classed as juveniles. Rats were autopsied as soon as possible after collection and then discarded.

For the purposes of some analyses, trap lines were grouped into habitat types as described by Fuller (1985; Table 1, Fig. 1). Each habitat type was assigned a number as follows: 1 = kānuka (*Kunzea ericoides*, formerly *Leptospermum ericoides*) forest (line 1); 2 = grassland (lines 2 and 8); 3 = five-finger (*Pseudopanax arboreus*) forest (lines 3 and 5); 4 = tawa (*Beilschmiedia tawa*)/hīnau (*Elaeocarpus dentatus*) forest (lines 4 and 6); 5 = kohekohe (*Dysoxylum spectabile*) forest (line 7).

Description of habitats

In November 1996 each trap site was visited to quantify the vegetation and local environment using a 'Recce' plot (Allen 1992) that was roughly 10 m in diameter and centred on the trap location. Six height tiers were used: >15 m (emergent); 12–15 m; 5–12 m; 2–5 m; 0.3–2 m; and <0.3 m. The cover abundance for each species in each height tier was visually estimated in one of five classes (using the Braun-Blanquet scale; Kent & Coker 1992). Epiphytic species were recorded as present but were not assigned a cover value unless cover exceeded 5%. The mean height of the canopy was estimated by eye and the aspect, slope, physiography, drainage, and relative contribution to the ground cover of live vascular vegetation, bryophytes, forest litter, bare earth, and exposed rock were also recorded. Physiography and drainage were assigned to one of the units described by Conacher and Dalrymple's (1977) nine-unit classification and Taylor and Pohlen's (1970) six-unit classification, respectively.

Data were coded using PC-RECCE (Hall 1992) for analysis by CANOCO (ter Braak 1987). Trap-site vegetation data were ordinated using the detrended canonical correspondence (DCCA) function of CANOCO thus condensing them onto one or a few meaningful axes (Ludwig & Reynolds 1988; Kent & Coker 1992).

Because the habitat classifications are arbitrary and were decided a priori, I also analysed rat capture by line to indicate differences between lines within a habitat type. This comparison should be interpreted cautiously since there was no replication of lines and only partial replication of habitats. Thus, it may be inappropriate to generalise these results to other, similar, forests. Furthermore, it is possible that I may have underestimated the number of Norway rats caught since large rats may be able to escape from Ezeset traps (King & Moller 1997; C.M. King, University of Waikato, Hamilton, pers. comm.).

The weighted mean species scores for each plot from the DCCA analysis were plotted against the different environmental variables measured using CANODRAW (Smilauer 1992) to interpret each of the two main axes derived from the DCCA output, and to explain vegetation patterns in terms of the variables measured.

Relating rat capture success to temporal and site factors

Rat capture rate was defined as the number of rats caught (R) per 100 trap nights (TN) after correcting (C) for sprung traps and captures (R/100CTN; Cunningham & Moors 1983). In order to determine whether trap line, year, habitat, or season affected rat capture rate, only years when trapping was completed in all seasons were used to create the models (i.e. 1992 and 1996 were removed). The effect of year (1993–1995), season, trap

line (1–8) and habitat type (1–5) on $\log_t(R+1/100CTN)$ for kiore, Norway rat and total captures was investigated using the General Linear Model procedure of MINITAB (version 12.1). The models incorporated year, season and either line or habitat and two-way interactions between these variables. Those interaction terms and factors that did not significantly affect the models were progressively removed. Hence the final models included only significant predictors. Post hoc Tukey's tests were used to compare pairwise combinations of samples.

To consider the effect of abiotic site factors on rat capture, the total number of rats caught at each trap was compared with the ordination scores obtained from the first two axes of the DCCA ordinations and with each of the environmental variables. Since the data were not normally distributed, ranked data were used and a Pearson correlation of ranked data was performed using MINITAB. A sequential Bonferroni test was used to correct the *P*-value to account for the large number of correlations (Rice 1989). Analysis using backwards stepwise elimination regression was then completed using the number of rats caught as the response and the habitat variables as predictors ($n = 12$, including the first two ordination axes). Analysis using backwards elimination regression considers all the variables, whereas correlations consider one variable at a time, and the two tests were used to confirm each other.

Population parameters in different habitat types

The R/100CTN of pregnant females of each species from each habitat type was compared using a Friedman two-way ANOVA by rank in MINITAB to investigate the hypothesis that females in some habitats were more likely to be pregnant. I assumed that the distribution of rat ages was the same in all habitats and that traps in any area were not age-biased in their capture rates. I investigated the effect of habitat, season, and year on female productivity by comparing the number of uterine scars and embryos (summed together) per female with each of these variables, using a generalised linear model. In creating the model I used habitat, season, and year as predictors and specified body weight and length as covariates to account for the fact that larger females could have been older and had more opportunities to reproduce. I used Tukey's tests to detect significant pairwise differences.

Results

Rat abundance

Trapping achieved a total of 12 202 corrected trap nights. A total of 923 rats were caught, of which 518 (56.1%) were kiore and 391 (42.4%) were Norway rats. Fourteen rats (1.5%) had been scavenged to the point where the species could not be determined.

Temporal and spatial variability in rat capture

A peak capture rate for kiore of 55.1 per 100CTN was recorded in grassland (on line 2) during the winter (July) 1994 trapping session. Both Norway rat and kiore numbers fluctuated across years (Fig. 2a), but kiore showed more seasonal variation in capture rate than Norway rats (Fig. 2b). Rats were distributed across all lines and habitats, with most rats of both species being caught on lines 1 (kānuka) and 2 (grassland) at the northern end of the island (Fig. 2c, d). Captures of Norway rats varied according to year, trap line, habitat, and the interaction between season and year. The capture rate for kiore was affected by

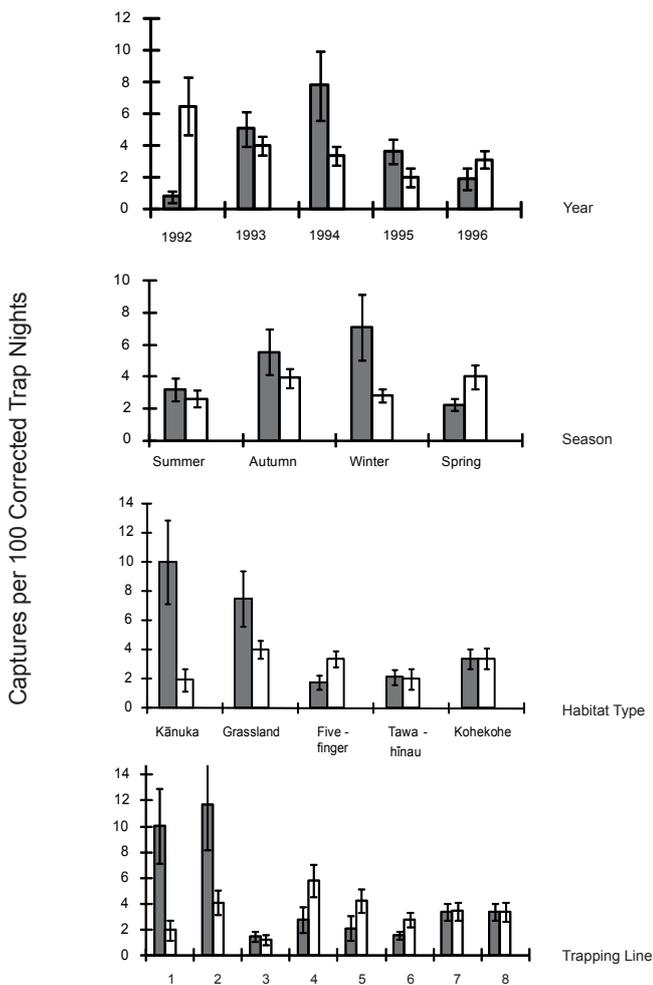


Figure 2. Rat (*Rattus* spp.) captures per 100 corrected trap nights on Kapiti Island, New Zealand, by (a) year, (b) season, (c) habitat, and (d) trapping line. Note that Line 6 had traps spaced at 50-m intervals. Dark bars represent the number of kiore (*R. exulans*) and white bars, the number of Norway rats (*R. norvegicus*). Errors are shown as ± 1 SEM.

season, trap line, habitat, and the interaction between year and line (Table 2). Large numbers of kiore were caught in the grassland and kānuka habitats. Norway rats were never caught in such abundance in any habitat type, but were also most common in grassland (Fig. 2c). On line 1, where capture rates of kiore were high, Norway rat capture rates were low, but this relationship was not consistent across all trap lines (Fig. 2d). There was no significant correlation between species' capture rates over all lines ($r = 0.148$, $P = 0.096$).

Microhabitat use as defined by vegetation and abiotic features

Across all habitats, axis 1 of the ordination was associated with a decreasing mean canopy height, physiography score, and drainage score (Table 3). In grassland habitats declining slope and litter cover and increasing moss cover were also associated with axis 1, while in kohekohe forest declining slope was negatively correlated with axis 1 (Table 3). When all canopy vegetation was considered and ordinated, it became clear that on a broad scale the habitats used by kiore and Norway rats were quantifiably different (Fig. 3). A Mann–Whitney U test revealed a significant difference between ordination scores on axis 1 for traps that were successful at catching kiore and those that were successful at catching Norway rats ($U = 590.0$, $P = 0.0001$) but not on axis 2 ($U = 825.5$, $P = 0.153$). Also, traps that were successful at catching kiore were different on axis 1 from those that did not catch kiore ($U = 11146.5$, $P < 0.001$). Successful kiore traps may have also differed from unsuccessful ones on axis 2 ($U = 8741.5$, $P = 0.06$). These differences suggest that kiore were more often associated with low-growing vegetation on flat, well-drained foot slopes and alluvial toeslopes. Norway rats were generally associated with steeper, more open and poorly drained sites with taller vegetation.

Sequential Bonferroni tests indicated that a P -value of 0.00028 was required to indicate significant correlations between rat capture and trap site attributes at the 0.05 level. None of the environmental variables was significantly correlated with Norway rat capture across all habitats (Table 4).

The preference by Norway rats for tall vegetation and damp ridge-top habitat (i.e. an increase in axis 1) was evident

Table 2. F -statistics for linear models designed to investigate the effect of temporal and spatial variables on rat (*Rattus* spp.) capture on Kapiti Island, New Zealand.*

Model	Degrees of freedom	Norway rats (<i>R. norvegicus</i>)	Kiore (<i>R. exulans</i>)	Total rat capture
Year	2, 742	5.77**	1.18	9.96**
Season	3, 742	1.60	4.79*	3.83*
Line	7, 742	4.00*	5.18**	6.26**
Habitat	4, 742	3.13*	11.14**	6.32**
Year \times Season	6, 742	2.04*	2.11	3.03*
Year \times Line	21, 742	0.86	1.99*	1.42
Year \times Habitat	14, 742	0.69	1.09	1.35
Season \times Line	21, 742	1.16	1.49	1.74*
Season \times Habitat	12, 742	1.55	0.7	1.66

* F -statistics marked with an asterisk were significant at $P = 0.05$. Two asterisks indicates significance at $P = 0.01$. Separate models were created to look at interactions between line and habitat with the other variables, and non-significant factors were removed to calculate final models.

Table 3. Correlations between the axes derived from detrended canonical correspondence analysis (DCCA) and 10 environmental variables for habitats on Kapiti Island, New Zealand (see Table 1 for plant names).*

Habitat	Grassland		Kānuka		Five-finger		Tawa-hīnau		Kohekohe	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Aspect	-0.22	-0.13	-0.16	0.06	0.20	0.17	-0.24	-0.20	-0.06	-0.35
Slope	-0.46*	-0.09	0.35	0.12	0.35	0.11	-0.12	0.04	-0.48*	0.18
Vegetation cover	0.02	0.09	-0.2	-0.19	-0.10	0.16	-0.21	-0.09	0.09	-0.19
Moss cover	0.60*	-0.09	0.10	-0.11	0.22	0.02	-0.21	0.08	-0.05	0.03
Litter cover	-0.66*	0.16	-0.00	0.23	-0.13	-0.37	0.19	0.07	-0.13	0.03
Exposed soil	-0.21	-0.12	0.31	-0.09	0.35	0.10	0.08	-0.01	-0.25	0.10
Exposed rock	0.09	-0.20	0.17	0.20	0.08	0.38	-0.33	-0.15	-0.42	-0.41
Mean canopy height	-0.41*	-0.14	-0.21	0.24	-0.01	0.26	-0.67*	-0.22	-0.14	0.12
Physiography	0.76*	-0.22	-0.19	-0.43	0.23	0.13	-0.44*	-0.04	-0.57*	-0.09
Drainage	0.79*	-0.23	-0.00	0.02	0.05	-0.06	-0.44*	-0.11	-0.53*	-0.01

*An asterisk indicates significance at $P = 0.05$ after correction using sequential Bonferroni tests (Rice 1989).

Table 4. Significant predictors of rat capture on Kapiti Island, New Zealand, determined by backwards elimination regression on environmental variables.*

Rattus species caught	Grassland ($n = 70$ traps)	Kānuka forest ($n = 35$ traps)	Five-finger forest ($n = 70$ traps)	Tawa-hīnau forest ($n = 70$ traps)	Kohekohe forest ($n = 35$ traps)
Norway (<i>R. norvegicus</i>)	Exposed soil ($T = -0.68$) Physiography ($T = -2.67$) Drainage ($T = 4.91$) Axis 1 ($T = -2.85$) Axis 2 ($T = -2.09$) SD = 1.38, $R^2 = 32.84$	Aspect ($T = 2.59$) Axis 2 ($T = -2.04$) SD = 0.679, $R^2 = 33.65$	Slope ($T = -2.87$) Vegetation ($T = -2.44$) Litter ($T = -6.05$) Exposed soil ($T = -3.09$) Physiography ($T = 2.66$) SD = 1.01, $R^2 = 45.66$	Axis 1 ($T = 2.14$) S = 1.49, $R^2 = 16.40$	Vegetation ($T = 3.4$) Moss ($T = 3.35$) Litter ($T = 3.45$) Exposed soil ($T = 3.75$) Exposed rock ($T = 2.65$) Drainage ($T = 3.07$) SD = 0.86, $R^2 = 74.25$
Kiore (<i>R. exulans</i>)	Axis 1 ($T = 5.09$) SD = 2.13, $R^2 = 27.63$	Axis 1 ($T = 3.26$) SD = 2.38, $R^2 = 31.42$	Vegetation ($T = -4.07$) Moss ($T = -2.78$) Litter ($T = -3.75$) Axis 1 ($T = 2.75$) SD = 1.02, $R^2 = 24.21$	S = 0.987, $R^2 = 0.0$	Axis 1 ($T = 2.97$) SD = 1.34, $R^2 = 22.72$
Percentage kiore	Axis 1 ($T = 2.77$) SD = 33.6, $R^2 = 10.57$	Aspect ($T = -3.09$) Exposed soil ($T = 2.32$) Mean top ht ($T = 2.18$) Axis 2 ($T = 3.49$) SD = 16.1, $R^2 = 51.47$	Exposed soil ($T = 2.70$) Axis 1 ($T = 2.78$) SD = 36.2, $R^2 = 23.65$	Aspect ($T = 2.25$) Exposed rock ($T = -2.03$) SD = 34.0, $R^2 = 9.63$	Vegetation ($T = 3.12$) SD = 30.6, $R^2 = 32.18$

*Captures are divided by habitat and rat species. Note that R^2 is presented as a percentage, T is the t -statistic and SD is the standard deviation about the regression line. See Table 1 for plant species names.

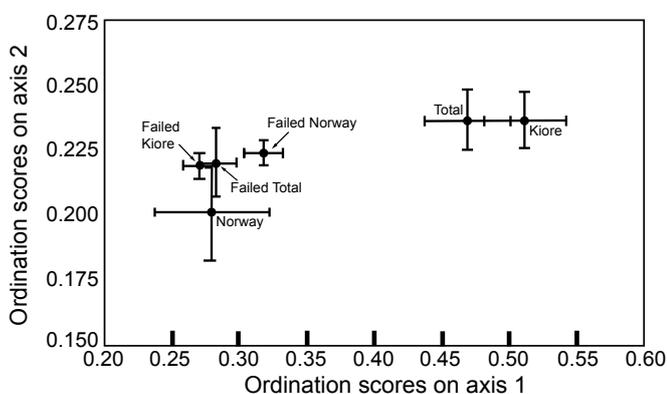


Figure 3. Ordination plot for successful and unsuccessful traps on Kapiti Island, New Zealand. The mean value ± 1 SEM are shown. A successful trap was defined as one that caught ≥ 4 rats of a given species or ≥ 6 rats in total between October 1992 and July 1996. Unsuccessful traps were those that did not catch this many rats and are labelled 'failed' traps with the species they failed to capture.

in tawa-hīnau forest, kānuka forest, and grassland, but was not consistent across all the habitats sampled. In five-finger forest, Norway rat capture was associated with stream edges and alluvial toeslopes (i.e. a high score for physiography). In grassland, Norway rats were also related to axis 2, which did not correlate with any of the measured variables. In kohekohe forest, Norway rats were associated with areas with sparse ground cover (and abundant bare soil) and areas that were well drained (Table 4).

More Norway rats were caught on line 8 than line 1 (Fig. 2d). Line 8 was steeper and located at higher altitude, and succession was more advanced there than at line 1. Line 8 was likely to be fog-covered more often because of its altitude (Fuller 1985) and also to be less fertile, with nutrients leaching to lower slopes. Parts of line 8 were also more exposed to the westerly weather and salt spray.

Microhabitats associated with kiore were different in different habitats. In grassland, kiore capture correlated with an increasing amount of moss cover ($r = 0.42$, $P = 0.0001$) and

Table 5. Summary of rat (*Rattus* spp.) capture data from Kapiti Island, New Zealand.*

Species	Norway rat (<i>R. norvegicus</i>)		Kiore (<i>R. exulans</i>)	
	Male	Female	Male	Female
% of species capture	46.05	53.95	45.12	54.88
Average weight (g)	223.9 ± 5.6 (168)	200.9 ± 4.8 (197)	80.4 ± 1.4 (247)	74.3 ± 1.1 (235)
Head–body length (mm)	181.9 ± 2.0 (198)	174.7 ± 1.9 (198)	133.6 ± 0.9 (252)	129.0 ± 0.9 (236)
Percentage reproductive		28 (164)		16 (180)
Average litter size		8.9 ± 1.1 (28)		5.6 ± 0.3 (21)

*The numbers of animals from which the statistics are calculated (*n*) are shown in brackets. Data are shown ±1 standard error of the mean.

Table 6. Weight and productivity variables in each year, habitat and season for rats (kiore *Rattus exulans*; Norway rat *R. norvegicus*) caught on Kapiti Island, New Zealand.

Predictor	Weight of female rats (g)		Uterine scars and embryos		Weight of male rats (g)	
	Kiore	Norway	Kiore	Norway	Kiore	Norway
Year						
1992	79.7 ± 12 (3) ^a	222.7 ± 7.8 (26) ^a	5.0 ± 2.9 (3) ^{ab}	9.6 ± 1.3 (29) ^a	90.0 ± 4.9 (3) ^{ab}	217.2 ± 10.1 (16) ^b
1993	73.8 ± 1.6 (63) ^a	192.1 ± 8.7 (60) ^b	3.4 ± 0.6 (66) ^{ab}	7.5 ± 1.3 (62) ^a	87.8 ± 2.4 (74) ^a	229.0 ± 9.9 (50) ^b
1994	72.9 ± 1.0 (88) ^a	201.3 ± 10.8 (50) ^b	4.6 ± 0.6 (89) ^{ab}	10.7 ± 1.7 (50) ^a	74.1 ± 2.4 (103) ^b	213.8 ± 11.4 (49) ^a
1995	77.0 ± 2.1 (53) ^b	198.9 ± 13.7 (33) ^a	2.9 ± 0.5 (53) ^a	6.9 ± 1.2 (34) ^a	78.5 ± 2.5 (50) ^b	229.7 ± 19.2 (70) ^b
1996	74.1 ± 2.5 (28) ^a	201.4 ± 10.2 (28) ^b	6.5 ± 1.3 (28) ^b	8.4 ± 1.4 (28) ^a	90.2 ± 4.7 (17) ^a	230.9 ± 12.3 (33) ^{ab}
Habitat						
Grassland	71.6 ± 1.5 (91) ^a	180.5 ± 9.7 (39) ^a	3.0 ± 0.5 (91) ^a	6.1 ± 1.0 (40) ^a	78.0 ± 1.8 (99) ^b	217.4 ± 13.5 (34) ^a
Kānuka	75.1 ± 1.8 (75) ^a	190.8 ± 14.5 (31) ^a	5.9 ± 0.7 (76) ^b	4.5 ± 1.0 (33) ^a	75.4 ± 3.4 (66) ^b	196.2 ± 16.4 (22) ^a
Five-finger	70.5 ± 4.8 (21) ^a	230.1 ± 10.5 (37) ^a	1.8 ± 0.6 (21) ^{ac}	11.1 ± 1.7 (38) ^a	83.0 ± 4.1 (32) ^b	254.7 ± 6.9 (34) ^a
Tawa–hīnau	75.6 ± 3.6 (24) ^a	193.2 ± 8.9 (62) ^a	3.9 ± 0.9 (25) ^{abc}	10.1 ± 1.4 (64) ^a	85.7 ± 3.5 (27) ^{ab}	211.3 ± 10.8 (56) ^a
Kohekohe	84.2 ± 3.5 (24) ^b	219.8 ± 7.8 (28) ^a	4.9 ± 0.9 (26) ^{abc}	10.0 ± 1.6 (28) ^a	95.3 ± 4.6 (23) ^a	246.0 ± 12.0 (22) ^a
Season						
Summer	84.3 ± 2.3 (45) ^a	181.5 ± 13.5 (44) ^a	5.4 ± 0.7 (47) ^a	8.0 ± 1.2 (44) ^{ab}	92.2 ± 1.8 (47) ^a	200.9 ± 14.5 (32) ^a
Autumn	76.3 ± 2.2 (67) ^b	198.6 ± 9.0 (52) ^b	5.8 ± 0.7 (68) ^a	9.3 ± 1.4 (53) ^{ab}	78.6 ± 2.2 (82) ^a	215.9 ± 9.7 (54) ^a
Winter	68.0 ± 1.6 (86) ^b	200.7 ± 9.3 (39) ^b	2.7 ± 0.5 (88) ^a	4.5 ± 1.1 (39) ^a	74.8 ± 2.8 (89) ^a	253.7 ± 9.9 (40) ^a
Spring	73.2 ± 1.8 (37) ^b	216.8 ± 6.7 (62) ^b	2.7 ± 0.7 (36) ^a	10.8 ± 1.3 (67) ^b	83.7 ± 4.3 (29) ^a	223.2 ± 10.5 (42) ^a

*Mean values ± 1 SEM are shown. Values in brackets are the number of individuals contributing to the dataset and vary because some rats were partially scavenged and were unable to be weighed. Note that rows in the same column marked with different letters are significantly different from each other at $P = 0.05$. See Table 1 for plant names.

a decreasing amount of litter cover ($r = -0.39$, $P = 0.0001$). Kiore capture also increased with physiography and improved drainage ($r = 0.47$, $P = 0.0001$ and $r = 0.51$, $P = 0.0001$ respectively). In grassland, captures of kiore also varied according to axis 1. Thus in grassland most kiore were caught in flat, well-drained areas with abundant low vegetation. Backwards elimination regression (Table 4) confirmed that result. In kānuka and kohekohe forest, kiore were associated with axis 1. Backwards elimination regression showed that Axis 1 did not correlate with any of the variables measured (Table 4), but in kohekohe forest Axis 1 was negatively correlated with slope, physiography, and drainage (Table 3). In tawa–hīnau forest kiore capture was unrelated to the variables measured, but in five-finger forest kiore captures were associated with sparse ground cover (Table 4).

Population parameters in different habitats

Sex and age classes were determined for 859 rats (373 Norway and 486 kiore). Trappers could assign species, but not sex or age, to 18 Norway rats and 32 kiore. Trappers were able to measure the head and body length of some of these scavenged animals, but did not weigh any of them. These data are summarised in Table 5.

Twenty-one pregnant kiore had between three and nine embryos, whereas 28 pregnant Norway rats had between two and 32 embryos. Two of the pregnant Norway rats appeared to be in the early stages of pregnancy and had large numbers of embryos (32 and 18). It is unlikely that they could have successfully reared this many offspring, and when these two rats are removed from the dataset, Norway rats averaged 7.6 embryos per pregnant female (SE = 0.5, range 2–12). There was a summer peak in the number of pregnant females of both species and very few pregnant females of either species were collected in winter (Fig. 4). Reproductive (pregnant or lactating) female rats were caught year round and there may have been a significant difference in capture rate according to season (Friedman test: for kiore $S = 7.13$, $P = 0.068$; for Norway rats $S = 6.72$, $P = 0.08$). Only a few reproductive female kiore were caught in spring (October). Reproductive female Norway rats were trapped in all habitats, but no reproductive female kiore were caught in five-finger forest (lines 3 or 5). The proportion of reproductive females caught in each line blocked by season did not vary according to line (kiore $S = 6.82$, $P = 0.45$; Norway $S = 4.5$, $P = 0.72$).

The number of uterine scars and embryos found in female kiore adjusted for weight and length varied with year

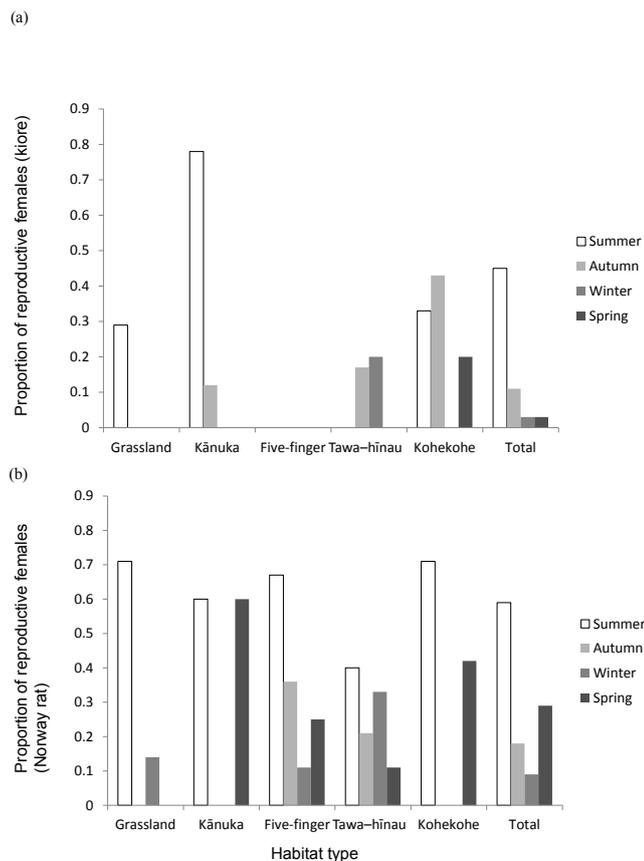


Figure 4. Proportion of pregnant or lactating (i.e. ‘reproductive’) female (a) kiore (*Rattus exulans*) and (b) Norway rats (*R. norvegicus*) caught on Kapiti Island, New Zealand, between October 1992 and July 1996 grouped by habitat and season.

($F_{4,230} = 2.92$, $P = 0.022$). Females were most productive in 1996 (mean = 6.54 scars per female caught, $SD = 6.72$, $n = 28$). The number of scars also varied with season and most scars and embryos were observed in October and January ($F_{3,230} = 3.18$, $P = 0.025$). The habitat was also a significant predictor of scar and embryo number for kiore ($F_{4,230} = 3.83$, $P = 0.005$). More scars and embryos were recorded per female in kānuka and kohekohe forest (mean = 5.9 and 4.8, respectively) than in the other three habitat types (range 1.8 in five-finger forest to 3.9 in tawa-hīnau forest; Table 6). The number of uterine scars and embryos found in female Norway rats did not vary with year ($F_{4,194} = 0.23$, $P = 0.919$) nor with the habitat ($F_{3,194} = 0.84$, $P = 0.504$). However, it did vary seasonally ($F_{3,194} = 4.38$, $P = 0.005$), with animals caught in July having fewer scars and embryos than those caught in other months.

The weight of female kiore, when adjusted for body length, varied according to the year ($F_{4,232} = 28.44$, $P = 0.0001$), season ($F_{3,232} = 13.86$, $P = 0.0001$), and habitat ($F_{4,232} = 4.25$, $P = 0.002$; Table 6). Female kiore were: (1) heavier in summer and autumn than in winter and spring; (2) lightest in 1995; and (3) heaviest in kohekohe forest (Table 6).

The weight of male kiore, when adjusted for length, also varied with year ($F_{4,245} = 14.72$, $P = 0.0001$; Table 6). Male kiore were heavier in 1992, 1993 and 1996 and those captured in kohekohe forest were heavier than kiore from other habitats except tawa-hīnau forest ($F_{4,245} = 3.44$, $P = 0.009$). Season was not a significant predictor of male kiore weight ($F_{3,245} = 2.15$, $P = 0.09$; Table 6).

Length-adjusted female Norway rat weights varied according to year ($F_{4,191} = 6.16$, $P = 0.0001$) with rats being heaviest in 1992, and season ($F_{3,191} = 6.34$, $P = 0.0001$) with lightest rats captured in summer. The weight of female Norway rats may also have varied according to the habitat in which they were trapped ($F_{4,191} = 2.12$, $P = 0.08$; Table 6). Male Norway rat weights varied with year ($F_{4,165} = 9.82$, $P = 0.0001$) but were unaffected by season ($F_{3,165} = 1.48$, $P = 0.223$), or the habitat ($F_{2,165} = 0.84$, $P = 0.502$).

Discussion

In general, similar species are sympatric if they differ in either (1) their partitioning of available resources, (2) their temporal or spatial partitioning of a shared resource, or (3) the level of density- or frequency-dependent predation (see Chase & Leibold (2003) for a review of niche theory). All three mechanisms may play a part on Kapiti Island where kiore and Norway rats occupy different microhabitats, kiore are seasonal breeders and Norway rats probably prey on kiore.

Competition appears to be biologically important in assembling and structuring small-mammal communities and habitat partitioning is thought to contribute directly to community assemblage (Kelt et al. 1995; Ruscoe et al. 2011; Dammhahn et al. 2013). If habitats exist where a particular species of rat is a better competitor, then they are likely to be those where that species achieves larger sizes and reproduces either more often or more successfully and/or those with the highest density of individuals. On the basis of body size and reproductive success, it appears that habitat quality in each of the five vegetation types on Kapiti Island is similar for Norway rats, since they lived everywhere on the island and bred at all times of the year with a similar degree of success regardless of habitat type. On the basis of density, grassland and kānuka forest caught more Norway rats than the other habitats, suggesting those habitats might be better. For kiore, however, the results are less clear cut. On the basis of body weight and female reproductive success kohekohe and perhaps tawa-hīnau forest provide better habitat for kiore. However, on the basis of density, it appears grassland and kānuka forest are the best kiore habitats. Although the capture rates of Norway rats and kiore caught in kill traps varied in different microhabitats, because the capture rates were only weakly related to each other, and the home ranges of radio-transmitter-carrying kiore and Norway rats overlapped (Bramley 1999), it seems probable that habitat structure was more important than behavioural interactions in determining local abundance of rats on Kapiti Island, although competition and predation cannot be ruled out.

Although more kiore were caught in grassland, food has been shown to be seasonally limiting for kiore in grassland areas, suggesting that grassland habitats alone are not ideal (Taylor 1984; Bunn & Craig 1989; Craig & Bunn 1989; Atkinson & Moller 1990). Furthermore, kiore breeding in grassland habitat consists of a short spring and summer pulse, while on forested islands breeding is generally more prolonged (Atkinson & Moller 1990). On Kapiti Island, pregnant kiore were caught in grassland only in January; and most pregnant kiore (from all habitats) were caught in summer and autumn. Thus, on the same island, some habitats appear to have allowed longer breeding than others, which suggests that there are differences in habitat quality for kiore and, that whilst kiore can live in grassland, they might be more successful in

kohekohe, tawa-hīnau and kānuka forest. There are at least two hypotheses that could explain why kiore might be more commonly captured in grassland; first, grassland may provide more opportunities to escape predators than forest habitats. This might allow greater survival of kiore in grassland relative to other habitats. Second, grassland habitats may act as a sink with dispersal of juvenile or adult kiore from forest habitats. These explanations are not mutually exclusive. Roberts and Craig (1990) considered that kiore were more abundant in grassland because it provided better refuges. King et al. (1996) similarly suggested that mice were most abundant in grass and disturbed habitat at Pureora because it was there that they could escape predation by ship rats and this was supported in laboratory and field trials (Hancock 2008; Bridgman 2012). It is possible that most kiore are produced in forest habitats and then disperse into the adjacent grasslands, perhaps in response to summer seed production. Slade et al. (1996) suggested that dispersal or habitat selection by rodents should occur at small sizes (i.e. early in life) so that females might maximise their growth rate and thereby achieve larger sizes and higher lifetime fitness. Nothing is known about size- or age-specific dispersal in rodents in New Zealand and this could be a suitable area for future research.

If better habitats for kiore exist, and they are not the ones with the most kiore, then it is possible that some kiore are being excluded from better habitats, either directly or indirectly, by the larger Norway rat. The trapping results reported here indicate that spatial partitioning of habitat contributes to coexistence of kiore and Norway rats on Kapiti Island, although seasonal breeding by kiore and variations in local abundance and productivity may also have played a part. Care is necessary in interpreting trapping studies because different species probably differ in their trappability (King et al. 1996; King & Moller 1997) and dominant animals or species may exclude others from traps directly or indirectly (Drickamer 1997; Harper & Veitch 2006). Both Dick (1985) and Harper and Veitch (2006) showed that Norway rat captures correlated negatively with kiore captures. That was not the case in this study. It is possible that Norway rats occupy all available habitats and kiore distribute themselves according to the abundance of Norway rats. The role of predation by Norway rats on kiore remains unknown.

Atkinson and Moller (1990) suggested that the density of kiore fluctuated less on predominantly forested islands such as Kapiti Island than it does on grass-covered islands. This is not supported by the data collected during this study; kiore numbers in forested areas experienced fluctuations in just the same way as in grassland habitats, with numbers varying strongly with season, habitat, and year. Dick (1985) concluded that seasonal weight changes were greater for kiore than Norway rats, which is supported by this study.

In New Zealand, there has been prolonged speculation about behavioural and other interactions between introduced rodents that might explain the observed lack of sympatry for all four species (Watson 1961; Taylor 1975, 1978, 1984) and several studies have investigated habitat use by two or more rodent species (Dick 1985; Sturmer 1988; King et al. 1996; Bramley 1999; Blackwell 2000; Innes et al. 2001; Russell & Clout 2004; Harper et al. 2005; Harper 2006; Harper & Veitch 2006; Hancock 2008; Foster et al. 2011; Ruscoe et al. 2011; Bridgman 2012). These New Zealand studies have tended to focus on resource partitioning, but have more recently considered interspecific interactions, including predation. Most field studies have used kill trapping of sympatric species

to infer habitat use (Dick 1985; Sturmer 1988; King et al. 1996; Innes et al. 2001; Harper et al. 2005; Harper & Veitch 2006) and some authors have investigated diet in an attempt to identify niche overlap (Dick 1985; Sturmer 1988; Harper 2006; Bridgman 2012). Live-trapping studies can be of use in understanding what factors allow the coexistence of two or more species, how those species interact and for understanding spatial behaviour. As already alluded to, however, trapping results could be affected in unknown ways by the social status or species of the previous trap occupant (Innes & Skipworth 1983; Dickman 1991; Drickamer 1995; Harper & Veitch 2006). Furthermore, when animals are trapped, they are immobilised at the point of capture and their normal ranging behaviour is disrupted while they remain in the trap. Managed encounters under laboratory conditions might provide useful data about behaviours when species come into contact, but their applicability in the field generally remains untested (Bramley 1999; Hancock 2008; Foster et al. 2011; Bridgman 2012). Harper and Cabrera (2010) recommended radio-telemetry studies be undertaken to investigate habitat and home range use of sympatric rodents. Radio-telemetry of free-living animals has the advantage that, after initial capture, animals are free to range normally, and potentially unbiased information can be gathered about their resource selection and habitat use within their natural home range (Aebischer et al. 1993). Radio tracking of both species of rat on Kapiti Island provided only weak evidence of avoidance since home ranges of Norway rats and kiore overlapped in time and space (Bramley 1999).

Sturmer (1988) explained the coexistence of Norway rats and kiore on Stewart Island by concluding that while both were generalist species, Norway rats had a wider niche, and thus were better competitors in more marginal habitats, whilst kiore were extremely successful in the habitats they preferred. This was supported by analysis of stable isotopic ratios of rat muscle from Pearl Island, which suggested that Norway rats exploited more marine food sources than ship rats and this allowed coexistence of these two species near the coast, but not in forests where ship rats were superior competitors (Harper 2006). Stable isotope analysis has also proven useful in investigating the structure of small-mammal communities in Madagascar where a combination of microhabitat and trophic separation (identified using stable isotopes) partly explained the coexistence of 21 endemic small mammals (Dammhahn et al. 2013). In addition to trophic segregation, Harper (2006) thought it possible that kiore were able to coexist with ship rats in forest because of an inverse temporal relationship whereby a delay in breeding by kiore, relative to ship rats, provided habitat separation.

Using a Monte Carlo approach Kelt et al. (1995) demonstrated that small-mammal community assemblages in 31 communities at the interface between rainforest and steppe grassland in southern Chile were structured by competition, although they could not distinguish between resource competition and interference competition. Furthermore, the geographic origin of the species was relatively more important than habitat affinities in structuring the communities they studied. Larger sample sizes than I achieved may be necessary to detect any small competitive effects on Kapiti Island (Gliwicz 1980; Dueser & Porter 1986).

Differences in litter size in different habitat types have been recorded for rodents (e.g. hispid cotton rats, *Sigmodon hispidus*; Slade et al. 1996), but this is the first record in New Zealand. Litter size in hispid cotton rats is correlated with maternal size. By specifying both length and weight as

covariates to adjust for body size, I was able to exclude the possibility that this result is due to the different size of female kiore in different habitats.

The coexistence of kiore and Norway rats on Kapiti Island appears to have been possible because Norway rats have a wider niche than kiore (or kiore niche is restricted in the presence of Norway rats), there are varied habitats available, and there are some habitats in which kiore are very successful. The wider fluctuations in abundance and productivity of kiore according to year, season and habitat observed here may be brought about by the narrower niche of kiore restricting the population except in particularly productive habitats or when conditions are very favourable, such as during summer seeding. The seasonality of kiore–Norway rat interactions is unknown and should be examined.

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