

Home ranges and interactions of kiore (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, New Zealand

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Abstract: Two species of rat (kiore or Pacific rat *Rattus exulans* and Norway rat *R. norvegicus*) coexisted on Kapiti Island (1965 ha) until 1996, when they were simultaneously eradicated. I radio-tracked rats of both species from June 1996 to September 1996, when the first of two aerial poison drops occurred. The aim of the study was to describe the home-range parameters of both species of rat in an area of grassland where they coexisted. Radio-tagged kiore occupied overlapping home ranges that varied from 26 to 89 m in diameter. Norway rats occupied larger home ranges (218–916 m in diameter), which overlapped the home ranges of both other Norway rats and kiore. Jacobs' indices of cohesiveness indicated that kiore and Norway rats might avoid each other, despite the fact that their home ranges overlapped. Patterns of habitat use suggest that kiore prefer denser habitats than Norway rats. Differing habitat preferences, possibly driven by higher predation risk for kiore in open habitats, might be sufficient to explain coexistence of rodents on Kapiti Island. Further research is needed to elucidate the relative importance of diet, home range use, and predation risk in permitting multi-species assemblages in New Zealand.

Keywords: coexistence; habitat structure; kiore; radio tracking; telemetry

Introduction

Rodents have a comparatively recent history in New Zealand, with Pacific rats or kiore (*Rattus exulans*) arriving with Polynesian invasions several centuries ago and the other two species of rats (Norway rats *R. norvegicus* and ship or black rats *R. rattus*) and mice (*Mus musculus*) arriving more recently with Europeans (Innes 2005). Although this pattern of arrival is similar to other Pacific islands, rodent species are not uniformly distributed on Pacific islands today, although there is a significant relationship between island size and the number of rodent species present (Yom-Tov et al. 1999). All four rodent species found in New Zealand coexist at some locations (e.g. the large Hawaiian islands), but they are not known to coexist anywhere on the main islands of New Zealand (Atkinson & Towns 2005). On most of the smaller New Zealand islands, there are only one or two species of rodent present and there is a significantly higher probability of Norway rats and kiore occurring together on these islands than other possible species combinations (Atkinson & Towns 2005; Yom-Tov et al. 1999). Current rodent distribution in New Zealand and elsewhere probably reflects the historical accidents inherent in chance introductions as well as perhaps the colonisation order of the islands and predatory or competitive exclusion by some species at some locations (Taylor 1975, 1984).

The primary mechanism that facilitates species' coexistence involves interspecific segregation of resources such as food and space, possibly with a temporal component (Schoener 1974; Castro-Arellano & Lacher 2009). On that basis, when two morphologically similar species of rodent coexist, it is likely that the presence of one would influence the ranging behaviour and habitat use of the other (Taylor 1975; Dueser & Porter 1986; Dickman 1991; Tomblin & Adler 1998). The mechanisms that allow coexistence and drive community assembly for rodent communities elsewhere in the

world have been thoroughly investigated (e.g. Swartz et al. 2010; Stevens & Tello 2012), but the nature of interspecific interactions between free-living rodents in New Zealand has received comparatively little attention.

Previous studies of habitat use by rodents in New Zealand have generally relied on kill-trapping studies (e.g. King et al. 1996; Harper et al. 2005; Harper 2006; Bramley 2014). Managed encounters between species under laboratory conditions might provide useful data about behaviours when species come into contact, but their applicability in the field remains unknown (Bramley 1999; Bramley & Waas 2001; Hancock 2008; Foster 2010). For these reasons, 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 (Wilson et al. 1992; Aebischer et al. 1993).

Body size is often an important determinant of the outcome of behavioural interactions between rodents, with larger species and individuals dominating smaller ones (Storer 1962; McCartney & Marks 1973). Norway rats are much larger than kiore and on that basis could be expected to dominate most encounters: wild adult Norway rats typically weigh 150–300 g (Innes 2005), whilst wild adult kiore typically weigh 60–80 g (Atkinson & Towns 2005). Harper and Veitch (2006) trapped more Norway rats than kiore on Raoul Island, with the number of captured kiore increasing only after Norway rats were removed. An increase in detectability after removal of a larger species has also been observed for mice in the presence of ship rats (Brown et al. 1996). Increased detectability could be due to an increase in abundance and/or activity of the smaller species. Since the response is usually rapid (occurring

within days), it is most likely that the response is behavioural (i.e. functional) rather than numerical, although elements of both are likely in the longer term (Bridgman 2012). On that basis, it is assumed that the larger ship and Norway rats are behaviourally dominant in some way and exclude mice (or kiore) from traps and tracking tunnels where they co-exist (Harper & Cabrera 2010). The outcome of such interspecific behavioural interactions has implications for management and control of rodent pests.

Kapiti Island presented an opportunity to study kiore and Norway rats in the absence of rodent predators. Kapiti Island is a nature reserve where, prior to their successful eradication in 1996, both species coexisted in a variety of forest and grassland habitats (Dick 1985; Bramley 2014). Kiore are known to use habitats with a high proportion of ground cover (Storer 1962). For example, kiore on Stewart Island used areas with a higher proportion of wire rush (*Empodisma minus*) than did either Norway or ship rats (Harper et al. 2005). In order to determine whether this habitat preference was exhibited on Kapiti Island, I used the proportion of incident light reaching the ground as a proxy for ground cover density at each rat location. The aim of this study was to compare spatial and temporal habitat use by radio-tagged Norway rats and kiore living in grassland at the north end of Kapiti Island during one season and describe home range use in an area where both species occurred at relatively high density. By calculating Jacobs' index of cohesiveness (Jacobs 1974) at two different temporal scales (within the same hour or within the same night), I expected to determine whether rats living together avoided either conspecific or heterospecific individuals occupying the same area. This is the first published study to radio-track Norway or kiore where they co-exist, in order to investigate how they use habitat in the presence of the other species.

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). The island is described by Fuller (1985, 1987) and Cowan (1992). Kapiti Island is approximately 9 km long, 2.3 km wide, reaches 521 m above sea level at its highest point and was designated a nature reserve in 1897, after which nine exotic mammals were progressively eradicated culminating in the simultaneous eradication of Norway rats and kiore in 1996 (Cowan 1992; Empson & Miskelly 1999; Bellingham et al. 2010). The island vegetation includes a variety of regenerating forest types. In 1996, when this study commenced, the vegetation in some areas continued to be dominated by exotic grassland. Previous trapping had indicated that both rat species were reliably captured in grassland habitat throughout the year (Bramley 2014). The study area was located in an area of grassland vegetation at the north end of the island where the habitat was dominated by rank exotic grasses, with emergent *Cyperus ustulatus*, cottonwood/tauhinu (*Ozothamnus leptophyllus*), mingimingi (*Coprosma propinqua*) and *Muehlenbeckia* spp. The vegetation in the study area was growing in very shallow soils over shingle and boulders.

Capturing rats for radio tagging

Within the study area, a 150-m-square grid was laid out

consisting of numbered 1-m-long poles marked with reflective tape and positioned at 15-m intervals. Four lines of poles with reflective markers every 10 m extended the grid 100 m in each direction (Fig. 2). These numbered poles were used as reference points to help define rat locations during the study. When rats ventured off the grid, their position was estimated from 1:2000

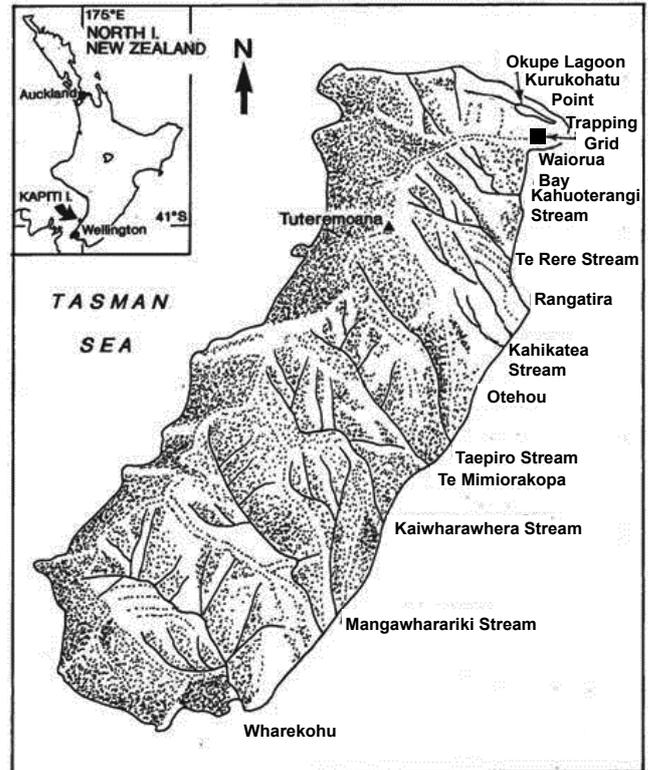


Figure 1. Map showing location and topography of Kapiti Island, New Zealand, as viewed from the air. Modified from Esler (1967). Not drawn to scale.

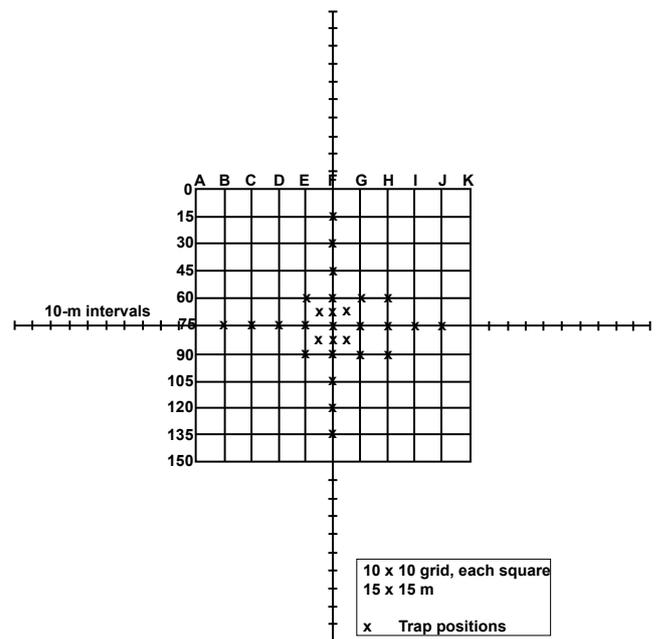


Figure 2. Grid layout of the radio-tracking study area on Kapiti Island, New Zealand, 1996.

aerial photographs on which the grid was overlaid. Within the study grid was an asymmetric trapping grid. Live-capture cage traps were set at the grid-markers in the centre of the study area at the positions shown in Fig. 2. By locating the traps in the centre of the grid, I attempted to capture as many of the animals that lived there as possible, given that the trap layout was constrained by the limited number of traps. Rats of both species were captured in these traps. After each capture, the traps were immersed in hot water and scrubbed with a small brush then allowed to air dry before being returned to their original location. Traps were baited with a segment of apple coated with peanut butter and were opened at dusk and closed near dawn to minimise capture of weka (native flightless rail, *Gallirallus australis*). Traps were checked at least three times each night they were set, in order to minimise the amount of time any animal spent in a trap. Trapping was carried out in 1996 on 18–28 June, 27 July to 4 August, 25 August to 1 September, and 18–26 September, by which time the first of two aerial brodifacoum drops to eradicate rats from Kapiti had commenced. Radio-tagged rats were also located during these times, which coincided with my visits to the island.

Captured rats were released into a large clear plastic bag, then weighed using a spring balance and visually sexed. The rats were then anaesthetised by placing a pad of cotton wool soaked in laboratory-grade di-ethyl ether into the bag. While each rat was sedated, it was fitted with a single-stage radio transmitter. The radios were attached using replaceable non-release cable-tie collars around the rat's neck. Twenty-six rats (8 Norway and 18 kiore) carried radios for varying lengths of time during the study. Fourteen radio transmitters were used. Seven of the radios (weighing 5.1 g each) emitted pulses at a rate of 40 pulses per minute and were fitted with 1-mm stainless steel whip-type aerials. The remaining seven (weighing 5.7 g each) pulsed at 36 pulses per minute and had a lighter gauge whip-type aerial. Transmission frequencies were set between 160 and 162 MHz (Sirtrack Telemetry Electronics, Havelock North, New Zealand). Rats were released at the site of capture when they had recovered from the anaesthesia.

Radio tracking

A Telonics TR-4 receiver, combined with a hand-held three-element Yagi antenna, was used to locate radio-carrying rats. The transmitter signals were generally detectable over a distance of more than 100 m, but the range decreased in strong winds. I determined the position of each rat in rotation during either the first or the second half of the night. This meant that at least 30 min separated each individual rat location and most locations were more than 1 h apart. Each rat was also located at least once each day during daylight, to locate daytime nests. Each time a rat was located I estimated its position by triangulation from a distance of less than 10 m and marked the location with a numbered marker pole. Positions relative to the nearest two grid markers were measured the following day, using a 30-m tape measure. I found no evidence that rats were disturbed by this procedure. Rats were commonly seen moving about their home range at night, but were more often out of sight below the vegetation canopy.

Measuring incident light

During the day after fixes were collected, I returned to each marker pole and used a portable hand-held incident light meter to measure the light intensity above and below any vegetation. The proportion of light that penetrated the vegetation was used as an estimate of the density of the cover provided to the

rats by the habitat they were using. I measured incident light in $W m^{-2}$, using a LiCor Li200SB Pyranometer (University of Waikato Electronics, Hamilton, New Zealand and LiCor Electronics, USA), or in lux, using a Gossen Lunasix 3 incident light meter (Gossen Electronics, Berlin, Germany). All measurements were converted to $W m^{-2}$ for analysis. Light measurements were made only on sunny days, between 1200 and 1700 hours. I assumed by doing this, and converting the measurements to the proportion of light reaching the ground, that there would be less variability due to weather conditions on any one day or relative angle of the sun during the day. For each radio-carrying rat (including those with few fixes), I calculated an average value for the proportion of light penetrating the vegetation in the sites they frequented. These averages were grouped according to species and compared using a Mann–Whitney U test.

Home-range analysis

I recorded all fixes on aerial photographs at a scale of 1:2000. Radio-location data were analysed using the RANGES computer package (version 5.02; Institute of Terrestrial Ecology, Wareham, UK). One hundred percent minimum convex polygons (MCPs) were used to calculate home ranges, along with a cluster analysis to calculate 95% isopleths. Cluster analysis is useful for eliminating outlying fixes and separating range cores (Kenward & Hodder 1996). For cluster analysis, I used the 'nearest neighbour distance' joining method, which determines that the distance between fix clusters must be larger than the distance within a fix cluster. Convex polygons are then constructed around each cluster of fixes and the total area summed (Kenward & Hodder 1996). From the aerial photographs, I calculated range diameter and the distance moved between locations by each rat. The distance moved between fixes was averaged for each animal and then averaged across animals to yield the estimates presented here.

The autocorrelation function of RANGES was used to determine, for each animal, the length of time necessary between fixes to make them statistically independent. I set the fix interval at 30 min and tracking session interval 30 h apart to determine the time to independence between fixes (i.e. the optimal time between fixes to collect data). Independence was reached in a period of 1 h by five of the 10 rats that met the autocorrelation criteria (mean = 234 min, SD = 218 min, $n = 10$). Two of these were Norway rats (one male and one female) and three were kiore (one female and two males). This indicates that, at least for those rats, a period of 1 h between fixes was adequate to ensure independence.

The potential overlap of home ranges estimated using the harmonic mean method and Jacobs' indices of cohesiveness were calculated using RANGES. Jacobs' index measures social cohesion by using x and y coordinates from individuals in an effort to identify the degree to which individuals are found close together. To examine interactions in real time, it is necessary to look at locations taken within the same general period to see if individuals were attracted to each other or whether they tended to avoid each other. To get these statistics, the observed and possible distances between animals are compared. The possible distances were calculated in RANGES using random generation of possible locations within the known home range. The index varies from -1 (strong avoidance) to $+1$ (strong cohesiveness), and values close to zero indicate that the animals are distributed at random with respect to each other. In calculating Jacobs' indices, I considered two situations: one where I treated fixes up to 1 h apart as simultaneous, and the

second where I treated fixes collected on the same night as simultaneous. Jacobs' indices for Norway–Norway, Norway–kiore and kiore–kiore pairs were compared using two-tailed Wilcoxon signed rank tests. Jacobs' indices for male–female kiore, male–male kiore and female–female kiore were also compared using Wilcoxon signed rank tests.

Results

Radio tracking and home-range analysis

Home-range data from 11 kiore and 8 Norway rats are presented here. Graphs of incremental range area against the number of fixes reach an asymptote for mean range area after approximately 25 fixes, although the confidence limits at 25 fixes were approximately 40% (unpubl. data). Therefore, only animals from which more than 30 fixes were obtained are presented here.

Home range size, length and overlap

The 100% MCPs showed that Norway rats used much larger home ranges (> 5 ha) than kiore (c. 0.15 ha) (Table 1). Female rats did not move significantly further between fixes than male rats.

There were 342 potential pairwise overlaps of home ranges from the 19 home ranges I estimated using the harmonic mean method (Table 2, Figs 3 and 4); each rat could potentially have overlapped the home range of 18 others ($19 \times 18 = 342$). Of those, 124 did not overlap. For the 218 overlapping ranges, the average overlap was ~34%. The percentage of overlap appears to be largely a function of the fact that Norway rat ranges were large and overlapping (Fig. 3). Therefore, they may have overlapped the entire small ranges of several kiore as well as smaller parts of other Norway rat ranges. Kiore ranges overlapped both the ranges of other kiore (Fig. 4) and the ranges of Norway rats. Because they were much smaller, kiore home ranges made up a very small percentage of Norway rat ranges.

Wilcoxon signed rank tests on Jacobs' indices of habitat use (when fixes up to 1 h apart were treated as simultaneous) indicated that kiore and Norway rats may avoid each other, but this avoidance was marginally non-significant (Wilcoxon statistic = 229.0, $P = 0.07$, $n = 25$). Norway rats showed no avoidance or cohesion with other Norway rats (Wilcoxon statistic = 33, $P = 0.24$). Likewise kiore distribution appeared to be random with respect to other kiore (Wilcoxon statistic

= 42, $P = 0.83$). For kiore, male–male pairs, male–female pairs and female–female pairs were also randomly distributed with respect to each other (Wilcoxon statistic = 1, $P = 1.0$, Wilcoxon statistic = 13, $P = 0.53$ and Wilcoxon statistic = 5, $P = 0.42$, respectively). When fixes from the same night were considered simultaneously, none of the six pairwise interactions was significant.

During this study, I observed what I believe to be an incidence of predation by a Norway rat upon a kiore. The kiore

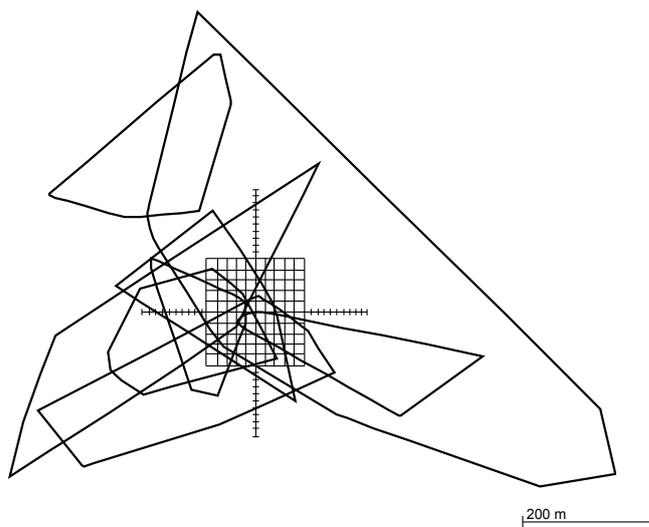


Figure 3. Home ranges (95% Isopleth) of Norway rats (*Rattus norvegicus*) on Kapiti Island, New Zealand.

Table 2. Home-range overlap¹ of rats (*Rattus* spp.) on Kapiti Island, New Zealand.

	Kiore	Norway rat
Kiore	43/110 (26<20%)	66/88 (66<20%)
Norway rat	64/88 (34>90%)	42/56 (21<30%)

¹From the 19 home ranges recorded, a maximum of 19×18 (or 342) overlaps could have been recorded if all ranges overlapped with all others. This table presents overlapping species in rows, and overlapped species in columns. For example 66/88 (top right) indicates that 88 cases could have occurred where kiore overlapped Norway rat home ranges but 66 instances of overlap were recorded; all these overlaps were <20%.

Table 1. Home-range descriptors (mean \pm SE) for kiore (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, New Zealand.

	Kiore Male	Female	Norway rats Male	Female
Sample size (n)	6	5	7	1
Size (ha, MCP method ¹) (range)	0.14 ± 0.04 (0.03–0.3)	0.18 ± 0.05 (0.05–0.31)	5.78 ± 3.25 (1.59–21.01)	5.13
Size (ha, harmonic mean method)	0.04 ± 0.008	0.08 ± 0.03	1.75 ± 0.79	3.52
Number of nuclei	3.2	0.84	2.6	1
Home range length (m) (range)	51.8 ± 3.8 (26–77)	67.2 ± 8.2 (40–89)	438.7 ± 95.3 (218–916)	459
Distance moved between fixes (m)	15.5 ± 7.7	17.5 ± 4.3	80.3 ± 34.59	115.7
Mean no. fixes (range)	40.5 ± 7.80 (21–76)	35.2 ± 3.85 (28–48)	37.9 ± 9.11 (25–82)	19

¹MCP = minimum convex polygon.

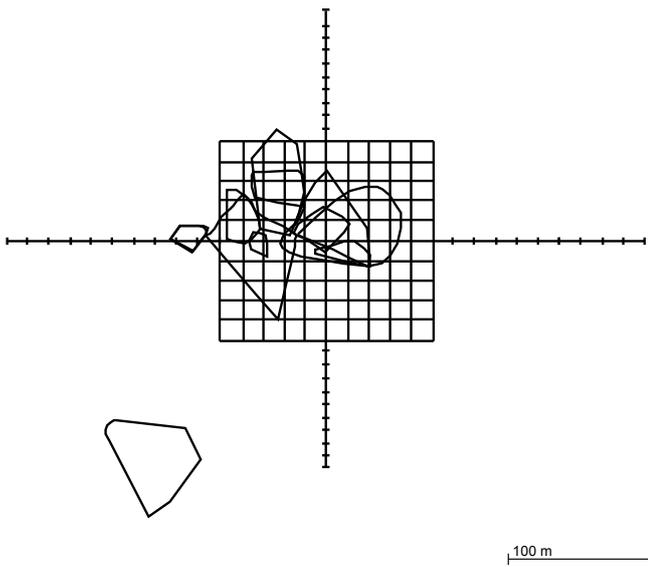


Figure 4. Home ranges (95% Isopleth) of kiore (*Rattus exulans*) on Kapiti Island, New Zealand.

was moving about its range normally in the early evening, and was then recorded from the same position as a male Norway rat on two occasions about an hour apart. The following day the kiore was collected dead and mostly eaten, with fresh Norway rat faeces near the body.

Cover provided by habitat used by each species

Kiore used habitats that provided more cover than the habitats used by Norway rats. Norway rats used vegetation that allowed an average of 8.3% of incident light to penetrate it (SE = 1.6%, range 2.4–13.9%, $n = 7$). Kiore used denser vegetation that allowed only 2.6% of incident light to penetrate it (SE = 0.5%, range 0.2–7.5%, $n = 15$; $U = 119.0$, $P = 0.007$).

On 30 July 1996, I excavated an underground tunnel to find a radio-tagged male kiore that had not appeared to have moved during the preceding 48 h. The radio-tagged kiore and another kiore (of unknown sex) were found alive together within the tunnel, which had at least two entrances and two leaf-filled nests. The tunnel was up to 25 cm deep, more than 1.5 m long and had a diameter of 2.5–3 cm. The tunnel was too small to have been excavated or inhabited by large Norway rats.

Discussion

Radio tracking revealed that kiore used much smaller home ranges than Norway rats, and within those home ranges they used denser habitats. There was only weak evidence that the two species avoided direct contact with each other, and there was no evidence of prolonged avoidance of jointly used areas by either species.

I recorded home range lengths up to 89 m for kiore, which is outside the range of 37–60 m estimated by live-trapping studies and previously reported (Atkinson & Towns 2005). The only published study of Norway rat home ranges in New Zealand also used live trapping and reported a maximum length of 330 m, which is likely to be an underestimate (Moors 1985). Norway rats on Kapiti used much longer ranges than this (up to 900 m), and were more similar to radio-tracked Norway

rats in Britain, which travelled several hundred metres to feed (Taylor & Quay 1978).

McCartney and Marks (1973) observed mixed colonies of kiore and ship rats from the Marshall Islands, in enclosures. Under these conditions, the kiore became subordinate to ship rats and McCartney and Marks hypothesised that, in areas of sympatry, reproduction by kiore would be adversely affected, perhaps leading to exclusion. Exclusion was not apparent on Kapiti Island. The home ranges of kiore and Norway rats overlapped and kill trapping over the wider island showed capture rates of the two species were only weakly related (Bramley 2014). Both kiore and Norway rats carrying radio transmitters were occasionally found with conspecifics. In the absence of rodent predators (except other rats) on Kapiti Island it appears that habitat structure, including microhabitat factors such as drainage and the proportion and density of ground cover, may be more important than competitive interactions in determining the local abundance of rats (Harper 2006; Bramley 2014; this study). However, I cannot rule out that Norway rats distribute themselves according to habitat preferences and kiore distribute themselves according to the abundance of Norway rats, since I obtained weak evidence that the two species may have avoided each other (the difference in Jacobs' index for Norway and kiore pairs was significant at the 0.1 level). The risk of predation affects habitat use in small mammals and may explain why kiore prefer denser habitats (Atkinson & Towns 2005; Harper 2006). Norway rats are larger and more likely to win direct physical encounters with kiore, although whether kiore form a significant component of Norway rat prey remains unknown. Stomachs of both Norway rats and kiore collected on Kapiti during 1994 included fur (S. Fuller, pers. comm. 2012). This was probably consumed while grooming, but may also indicate predation.

Habitat structure, including the amount of cover, can influence factors such as predation risk (Schooley et al. 1996) and food availability (Guerra & Vickery 1998). The use of dense vegetation and underground tunnels as reported here is consistent with kiore attempting to avoid detection by Norway rats in areas where their home ranges overlap, but radio tracking only weakly supports this conclusion. The coexistence of two species of rat on Kapiti appears to depend in part on the heterogeneity of habitats available, in particular the presence of some habitats in which kiore are very successful (Bramley 2014). The presence of excavated or natural nests that are small enough to exclude Norway rats may also contribute to reduced predation and increased breeding success and kiore survival where they occur. The length of the seasonal food pulse, which is thought to be important in maintaining kiore populations on other islands (Moller & Craig 1987; Bunn & Craig 1989) and mice in the presence of ship rats (Blackwell et al. 2003), might allow kiore to increase in number in some habitats or in some years. It is unlikely, however, to be able to contribute significantly to the long-term persistence of these short-lived rats over the whole island.

Interference competition has been suggested as the principal mechanism for partitioning habitat by the three rat species in New Zealand (Yom-Tov et al. 1999; Harper & Veitch 2006) with predation also playing a role (Harper 2006). There was only weak evidence to suggest that kiore modify their behaviour in the presence of Norway rats as would be expected if either predation of kiore by Norway rats or interference competition was a significant driver of kiore habitat use. The results reported here confirm the preference of kiore for dense habitats reported by Harper et al. (2005), but indicate

that Norway rats may not always exclude kiore from traps as occurred on Raoul Island (Harper & Veitch 2006) and, at some locations, interspecific interactions between Norway rats and kiore may be less important in determining relative abundance than differences in habitat use. Nonetheless it appears likely that the two factors are linked. Additional studies of habitat use at sites where Norway rats and kiore coexist are required to confirm the relative importance of habitat structure, predation risk, and food availability in allowing their coexistence in New Zealand.

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