

Population ecology of Norway rats (*Rattus norvegicus*) and interference competition with Pacific rats (*R. exulans*) on Raoul Island, New Zealand

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Abstract. Norway rats (*Rattus norvegicus*) are sympatric with, and more often trapped, than the smaller Pacific rat (*R. exulans*) on Raoul Island, New Zealand. Rats were removed from a four-hectare grid by trapping and poisoning in the winters of 1994, 1995 and 1996. Pacific rats were trapped in increasing numbers only after Norway rats were removed. Norway rats also ate significantly more bait than Pacific rats. Competitive interference of Pacific rats by Norway rats was apparent, which casts doubt on the ability to accurately monitor individual species abundance within assemblages of rat species and to effectively manage them in control grids. Snap-trapping lines provided baseline data on the abundance of the two species before, during and after the removal grids were operated. Maximum abundances of rats were recorded in late summer and autumn following spring and summer breeding.

Introduction

Although competitive exclusion of Pacific rats (*Rattus exulans*) by Norway rats (*R. norvegicus*) has been predicted where they occur together, it has not been tested directly (Atkinson and Moller 1990). Larger rodent species tend to dominate in a competitive situation (Lidicker 1966; Grant 1972; Henttonen *et al.* 1977) and even between individual Norway rats social dominance is generally related to size, the larger animals dominating the smaller individuals (Berdoy *et al.* 1995). Norway rats are also known to kill Pacific rats in the wild and in enclosures (Twibell 1973; Meeson 1884). In addition, the two species partitioned habitat on Kapiti Island (Dick 1985), which suggested that the smaller Pacific rats would be excluded from habitat favoured by Norway rats where they co-existed elsewhere.

Grant (1972) suggested that competition between two rodent species is likely to trigger partitioning in diet and spatial and temporal use of space. Many Northern Hemisphere field studies have since shown resource partitioning between rodent species but these studies have largely concentrated on native guilds of rodents that have presumably been present together for several millennia (Brown 1971; Henttonen *et al.* 1977; Dueser and Hallett 1980; Montgomery 1980; Heske *et al.* 1994).

The Pacific rat reached New Zealand ~1300 AD, when Polynesian migrants settled in New Zealand (Brook 2000; Wilmshurst and Higham 2004). Humans probably introduced the Pacific rat to Raoul Island, New Zealand, at about this time (Holdaway 1999). Circumstantial evidence indicates that this small rodent, alone, caused the local extinction

of some bird and lizard species, serious depletion of many insect species and significant modification of floral assemblages (Holdaway 1989). Norway rats (*R. norvegicus*), ship rats (*R. rattus*) and mice (*Mus musculus*) were introduced to New Zealand in the past 200 years. Norway rats probably invaded Raoul Island in September 1921 when the schooner 'Columbia River' was wrecked (Venables 1937; Ingram 1972). Seabirds on Raoul Island have undergone serious decline, local extinction or extinction attributable to the presence of rats and cats (*Felis catus*) or to habitat modification caused by goats (*Capra hircus*) (Veitch *et al.* 2004). Cats probably reached Raoul Island in the 1830s (Morton 1957).

Pacific rats and Norway rats have therefore been sympatric on Raoul Island for the past 80 years and Norway rats have been the most commonly trapped species since 1950 (Watson 1961). We predicted that if the two species compete on Raoul Island (a) there would be spatial separation and (b) if Norway rats were removed then a habitat shift and/or numerical response by Pacific rats would occur (Scott and Dueser 1992). We set out to test these predictions because social dominance by one species has practical implications for monitoring and control of assemblages of rat species. On control grids for mixed rat species in Hawaii, for example, Pacific rats used poison-bait stations less than did the larger ship rats, and Pacific rats were still being trapped on control grids after ship rats were removed (Nelson *et al.* 2002). More knowledge of rat ecology and how best to control and monitor them would greatly aid management of mixed rat assemblages for conservation of other endemic species on islands.

Methods

Study area

Raoul Island is ~1000 km north-east of the North Island, New Zealand (Fig. 1). It is the northernmost and largest (2978 ha) island of the Kermadec Group, an archipelago of small active volcanic islands. The island is roughly triangular in shape, ~10 km long and 7 km wide, and rises to an altitude of 516 m.

The island's topography consists of a steep-sided caldera with major ridges to the west and south, from which run sharply dissected ridges and ravines. A boulder and rock coastline flanked by cliffs up to 250 m high surrounds most of the island though sand and gravel beaches occur at Denham Bay and, to a lesser extent, on the north coast. Three lakes on the floor of the caldera are periodically affected by volcanic activity. Little other free water is present as the soils are derived from basalt, andesitic ash and pumice and are very free draining.

Rainfall averages 1538 mm annually, distributed evenly throughout the year. The mean annual temperature is 19°C with small seasonal and daily variation. Frosts have not been recorded. South-easterly and easterly winds predominate in the summer and north-westerlies in other seasons.

Raoul Island forest is dominated by Kermadec pohutukawa (*Metrosideros kermadecensis*) with *Myrsine kermadecensis* and *Ascarina lucida* var. *lanceolata* as the predominant understorey. Other

common species include kawakawa (*Macropiper excelsum* var. *majus*), tutu (*Coriaria arborea* var. *kermadecensis*), wharangi (*Melicope ternata*), karaka (*Cornynocarpus laevigata*), the tree ferns *Cyathea kermadecensis* and *C. milnei*, and nikau palm (*Rhopalostylis baueri* var. *cheesmanii*) (Sykes 1977).

The Kermadec Islands have no indigenous land mammals or herpetofauna.

Seasonal breeding and population fluctuations

A monthly rat trap-line was run at Low Flat from 1993 to 1994, and along the Boat Cove Road (Fig. 1) from 1995 to 1997 to assess seasonal abundance, species composition and breeding status. Trapping grids were operated at Low Flat (Fig. 1) in the winters of 1994, 1995 and 1996, first as part of a study on the effectiveness of a grid to protect nesting birds, then to test differential poison take by the two rat species.

Low Flat trap line

From October 1993 to October 1994 a rat trapping line was run at Low Flat (Fig. 1). This consisted of 25 pairs of 'Ezeset' snap-traps placed at 50-m intervals in the forest beside the gravel road. The traps were laid out for the entire period. The traps were set for three consecutive nights in the middle of each month, baited with a mixture of rolled oats and peanut butter and sprayed with insect spray to deter ants from stealing the bait. No trap covers were used. All rats caught were identified to species, sex and approximate age: adult or juvenile (perforate or imperforate vagina for females and presence or absence of visible tubules within the cauda epididymis for males). The same operator (GH) operated the trap line for the period. The data were recorded as both the actual number of rats trapped, and the catch of both species, per 100 corrected trap-nights (100 CTN). This correction factor accounts for the non-availability of sprung traps whether they have captured a rat or not (Nelson and Clark 1973).

Boat Cove trap line

From December 1995 to October 1997 a trapping line was run along the Boat Cove Road (Fig. 1). This consisted of 50 pairs of 'Ezeset' snap-traps placed at 50-m intervals in the forest beside the gravel road. The traps were laid out for the entire period and were set under a cover made from the curved section of a 200-L fuel drum cut into six parts. The traps were set for five consecutive nights each month. They were baited with a mixture of rolled oats and peanut butter and this was replaced as necessary. No action was taken to deter insects from eating the bait. All rats caught were identified to species and sex. Females were autopsied to determine pregnancy. Several different operators carried out this work.

Removal grid

A rat-trapping grid, measuring 200 m by 200 m (4 ha) (Fig. 2) running north-south and east-west, was set up on Low Flat in July 1994. The same grid was used in July and August 1995 and 1996. The same operators tended the traps for the duration of each winter but differed from year to year. When traps were set the grid was checked every morning and all rats removed from traps. All rats caught were identified to species, sex and approximate age: adult or juvenile (perforate or imperforate vagina for females and presence or absence of visible tubules within the cauda epididymis for males), and in adult females, pregnancy, as evidenced by obvious embryos, was recorded. In 1994 and 1995 all trapped rats were checked for ingestion of poison baits. Each year the traps were set for one continuous 20-day period.

The 1994 trial sought to test the effectiveness of a rat-removal grid for nest protection of endangered ground-nesting birds. Thirty-six single 'Ezeset' snap-traps were set under open-ended tin covers, and 49 bait stations made from 300-mm sections of 100-mm-diameter 'Novacoil' drainage pipe fixed in place with a loop of wire at each end were set out as shown in Fig. 2. The traps were baited with a rolled oats and peanut

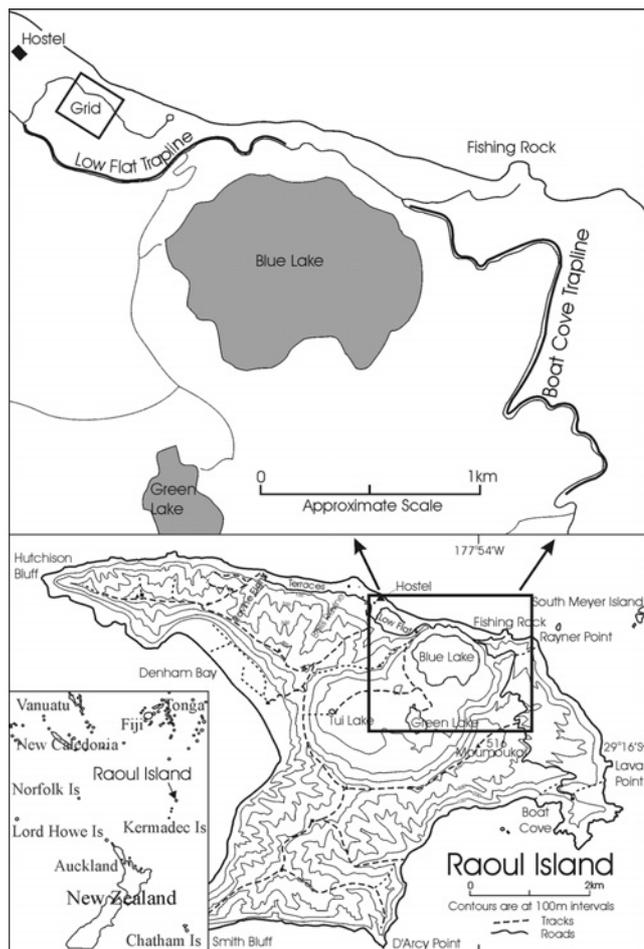


Fig. 1. Raoul Island showing the location of the Low Flat and Boat Cove trap-lines used for monthly rat trapping and the removal grid used in the winters of 1994–96.

butter mix and the bait stations were baited with Rentokil Rid Rat blocks (a wax and grain block containing bromadiolone at 50 ppm) fixed in place with a horizontal wire through the centre of the pipe.

The 1995 trial sought to test whether greater visibility improves the bait take and whether a change of trap setting methods would detect Pacific rats earlier in a multi-species situation. The placement of trap and bait stations on the grid lines was the same as in 1994 (Fig. 2). Novacoil bait stations (as used in 1994) were paired with clear plastic tubes of similar dimensions. Mouse traps were also used to test whether they would capture Pacific rats. Single 'Ezeset' wooden mouse traps under 20-mm wire mesh covers were placed ~30 cm from single 'Ezeset' rat traps under open-ended tin covers. All traps were baited with a rolled oats and peanut butter mix.

The 1996 trial was used to test whether Norway rats suppress access by Pacific rats to broadcast rat bait, as might be aerially spread in an eradication operation. To reduce the probability that neophobia was a contributor to the difference in capture rates of the two species, the traps were laid out 20 days before being set. On 5 July, 81 pairs of 'Ezeset' rat snap-traps under open-ended tin covers were laid, unset, on all lines of the 200-m grid at 25-m intervals (Fig. 2). No poison bait stations were used. Twenty days after the traps were laid out non-toxic 2-g pollard baits dyed with Rhodamine were hand-spread at a rate of ~8 kg ha⁻¹ over the grid area and 25 m beyond the grid boundary. Three days after the bait was spread the traps were baited using a rolled oats and peanut butter mix and set.

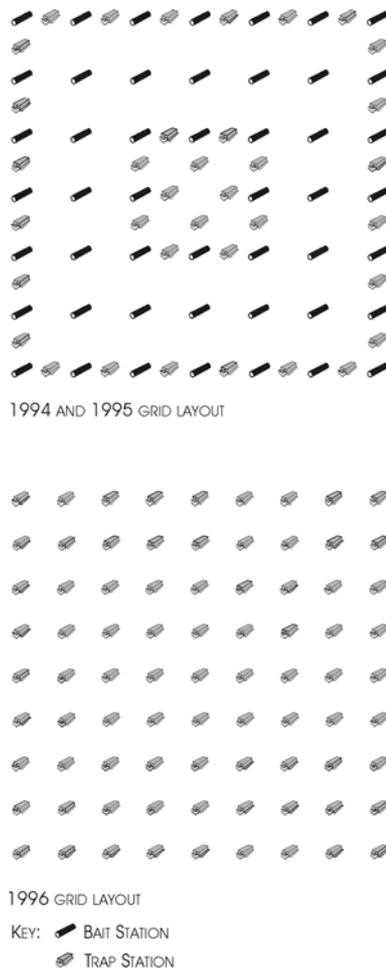


Fig. 2. The layout of traps and bait stations within the trapping grids.

Trapping success is given as total number of rats per grid, and converted to total numbers of rats caught per 100 trap-nights (100 TN) to enable comparisons between species and between years. Capture rates of the separate species per 100 TN are corrected for capture of the other species but we were unable to make a correction for sprung traps. Addition of the separate capture rates may therefore give a slightly higher capture rate than the total capture rate per 100 TN.

Bait take

A G-test was used to test for homogeneity in bait take by both rat species on the rat-grid in 1996.

Competitive interference

An ANOVA for repeated-measurements of the 3-year rat-grid dataset was used to test whether there was variation in the numbers of the two species caught on each grid and the timing of rat species capture over the 20 days of the grid operation. Numbers of rat captures per 100 TN was the dependent variable. The ANOVA was done on SYSTAT 10.

Density estimate for Norway rats

We used the 'Zippen removal' technique (Zippen 1958) to estimate the density of Norway rats caught on the trapping grids. Each night's catch is plotted against the cumulative total to estimate the number of rats left on the trapping-grid. Before we could do this we had to estimate the number of animals present on the grid at the start of trapping. In this case we expected immigration from outside the trapping grid to result in an increase of animals some days into the trapping session, which would result in an inflexion in the plotted line of nightly caught animals. The inflexion point was used as the last day of trapping before immigration began. A two-dimensional Loess smoothing technique, with a bandwidth setting of 0.3, was applied to each of the three plots of the nightly catch rate of rats on the grids. Where the negative angle of the smoothed plot (i.e. rat catch rate declining over time) became positive or level was regarded as the point (the trap-night) where immigration into the trapping grid had begun. The cumulative number of rats caught

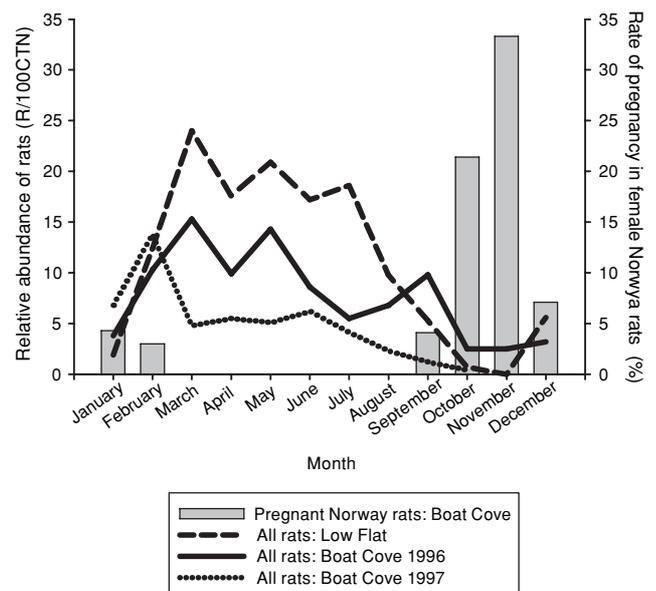


Fig. 3. Monthly changes in relative abundance of rats caught on the Low Flat trap-line (1994) and Boat Cove trap-line (1996-97), and the percentage of female Norway rats caught each season that were pregnant.

up until the inflexion point/trap-night was used for the Zippen removal density estimation.

To estimate the effective trapping area, a boundary strip was added to edge of the trapping grid (Dice 1938). The boundary strip was determined by adding the radius (159.5 m) of a circular average home range (5.45 ha) of male and female Norway rats (5.8 ha and 5.1 ha respectively). This home range was based on the radio-telemetry of Bramley (1999) on a similar-sized island (Kapiti Island) with Pacific rats present. The boundary strip was restricted to 40 m where the trapping grid was bounded by a beach (Fig. 1). The resulting effective trapping area was estimated at 15.2 ha.

Results

Historic trapping results

Occasional rat trapping on Raoul Island has consistently caught substantially more Norway rats than Pacific rats (Table 1).

Breeding and population fluctuations

Low Flat trap line

On the trap line 125 rats were caught over 13 months from November 1993 to November 1994 (1950 trap-nights). Only four Pacific rats were trapped, one in July, two in August and one in December. Rat catch peaked in early autumn, and began a steep decline in winter to a trough in late spring (Fig. 3). Juvenile Norway rats began to be trapped in November on Low Flat, their numbers peaking in February and declined to zero by July (Fig. 4).

Table 1. Rat trapping results from Raoul Island from 1966 to 1997

Date	Norway rats	Pacific rats
December 1966 – February 1967	10	9
August–October 1972	38	2
October–November 1974	14	1
November 1980	7	1
March 1984	20	6
March 1984	5	2
September 1990	2	2
September 1990	1	0
March 1991	15	4
March 1991	53	2
May 1991	20	7
May 1991	33	2
October 1993 – October 1994	121	4
June 1994	40	2
June 1994	22	0
June 1994	1	2
September 1996	22	2
September 1996	17	0
September 1996	24	0
September 1996	6	9
October 1996	39	0
October 1996	1	0
October 1996	16	0
October 1996	3	12
December 1995 – November 1997	544	51
Totals	1074	120

Boat Cove trap line

In the 23 five-day trapping sessions from December 1995 to October 1997 (11 500 trap-nights), 544 Norway and 51 Pacific rats were caught. Of these, 57 Norway rats and 4 Pacific rats had been eaten by a scavenger to the point where sex or breeding condition could not be determined. Of the 221 female rats caught, 15 were pregnant. In both years the trap catch followed a similar pattern to the Low Flat trap-line, with a peak in the late summer and autumn then a decline to a trough in catch rate by spring (Fig. 3). Overall rat catch was lower in 1997 than 1996, and the maximum catch rate for both years was lower than on the Low Flat trap-line in 1994. More Norway rats and Pacific rats were caught in almost all months in 1996 than in 1997 (Fig. 5). Significantly fewer Pacific rats than Norway rats were trapped on the Boat Cove line (Kolmogorov–Smirnov test, $P < 0.001$). Most Pacific rats were caught in summer and autumn.

Pregnant female Norway rats were caught from spring to mid-summer. The data are shown in Fig. 3 as a percentage of the females caught each month. Breeding of Norway rats began in spring (September), peaked in November, and was finished by March. Only one pregnant female Pacific rat was caught, in October 1996.

Removal grid

In 1994, 87 rats were caught on the removal grid during 720 trap-nights. This was equivalent to 12.1 rats per 100 TN. In total, 71 Norway rats (10.1 per 100 TN) and 16 Pacific rats (2.5 per 100 TN) were caught. In 1995, total rat captures were substantially lower than in either 1994 or 1996 (Table 2). Sixteen rats were caught during 720 trap-nights (2.2 per 100 TN). Fifteen Norway rats (2.1 per 100 TN) and one Pacific rat (0.1 per 100 TN) were caught. No Pacific rats were caught in

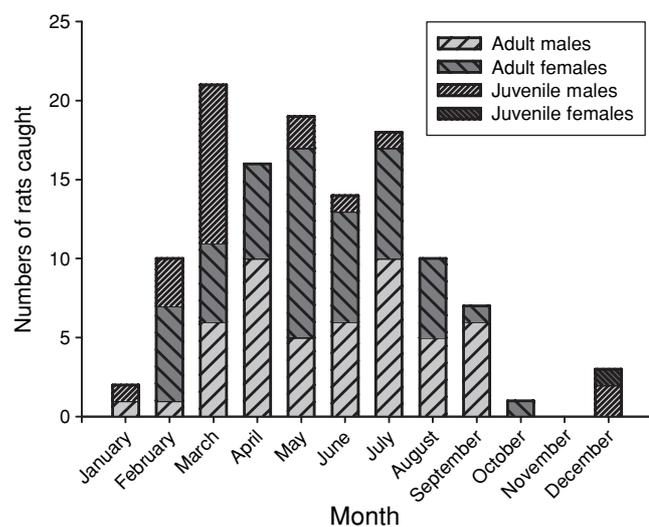


Fig. 4. Differences in the monthly capture of adult, juvenile, male, and female Norway rats on the Low Flat line 1993–94.

mouse traps. In 1996, 291 rats were caught during 3240 trap-nights (9.4 per 100 TN). In all, 174 Norway rats (5.7 per 100 TN) and 117 Pacific rats (4.1 per 100 TN) were caught. The capture rates from each trapping grid are shown in Fig. 6.

Laying traps 20 days earlier, without setting, did not appear to affect capture rates. Capture rates of Norway rats in

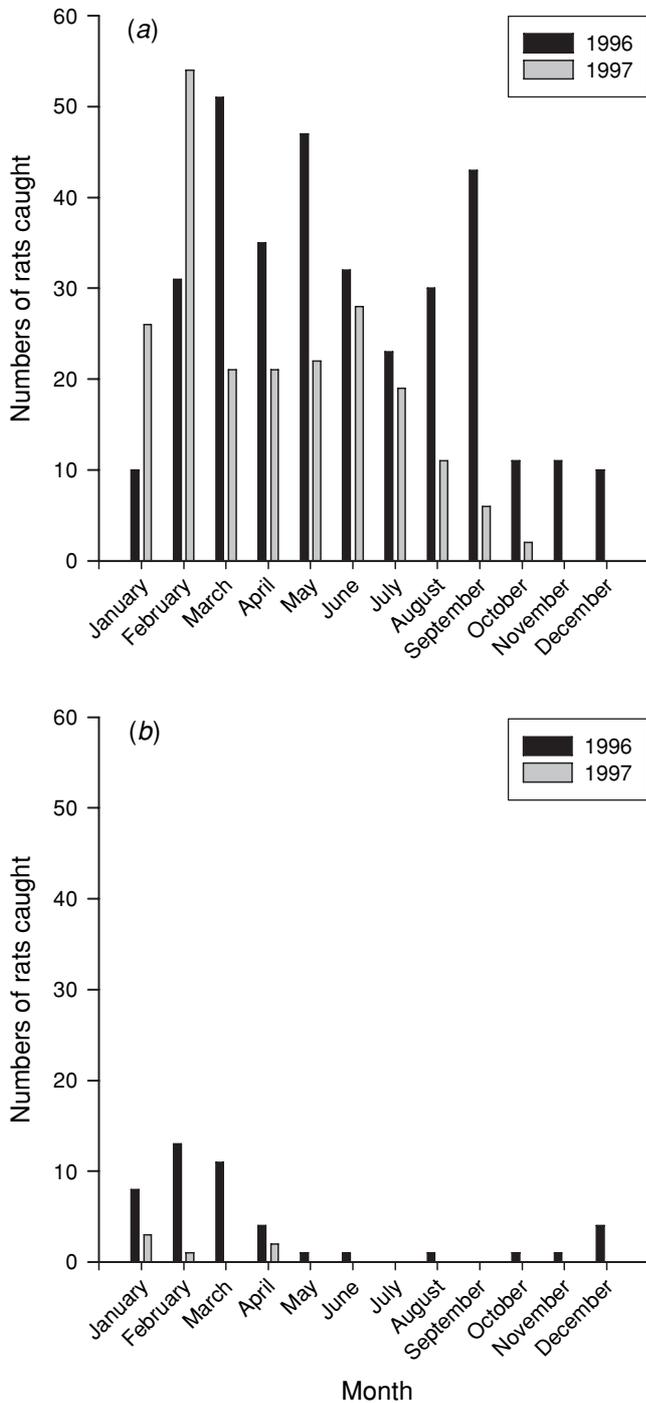


Fig. 5. Number of (a) Norway rats and (b) Pacific rats trapped each month on the Boat Cove trap-line, 1996–97.

1996 (5.5 rats per 100 CTN) were lower than in 1994 (9.9 rats per 100 CTN) when traps were not laid out earlier and for Pacific rats the reverse was true, with 3.8 rats caught per 100 CTN in 1996 and 2.2 per 100 CTN in 1994.

Bait take

In 1994 and 1996 rat interactions with baits and traps continued in all areas of the grid throughout the 20 days of the operation. In 1996, bait had been ingested by 146 (82%) of the Norway rats caught but only 73 (59%) of the Pacific rats. This difference was highly significant ($G = 17.00$, d.f. = 1, $P < 0.001$). On the inner traplines (Table 2) 90% of Norway rats and 65% of the Pacific rats had consumed baits. Rats that had not consumed bait were trapped throughout the grid, but in decreasing numbers, throughout the 20-day operation. One Pacific rat that had not ingested bait was caught near the centre of the grid on Day 20.

In 1995 there was no discernible difference in bait take between the black and clear plastic bait stations.

Competitive interference

Norway rats were the predominant species caught in the first 10 days of all the removal grids, with Pacific rats becoming more abundant in the second half of the 20-day period (Fig. 6). The timing of capture of each rat species was significantly different over the 20-day removal period for all three years (Table 3). There was also a significant difference in the number of the two species caught overall, with more Norway rats being removed in total.

In 1994, the number of Norway rats caught peaked in the first few days then declined. No Pacific rats were caught in the first 10 days, during which time 62% of the Norway rats had been trapped, but they began to appear in increasing numbers after this. In 1995 only slightly fewer Norway rats were caught in the second half of the trapping session, due to the low numbers of rat captures overall. The trend in the rate of capture of Norway rats in 1996 was an initial peak then a decline. Very few Pacific rats were caught initially but then

Table 2. Norway and Pacific rats trapped and consuming baits on the inner portion of the removal grid

Year	Species	Days of operation			
		1–5	6–10	11–15	16–20
1994	Norway rat, trapped	5	4	0	0
	Pacific rat, trapped	0	0	3	4
	Baits eaten	9	12	12	20
1995	Norway rat, trapped	5	4	4	2
	Pacific rat, trapped	0	0	1	0
	Norway rat, eaten bait	18	15	2	1
1996	Norway rat, trapped	20	17	2	2
	Pacific rat, trapped	1	12	17	13
	Norway rat, eaten bait	1	2	0	1
	Pacific rat, eaten bait	1	9	13	5
	Pacific rat, no bait	0	3	4	8

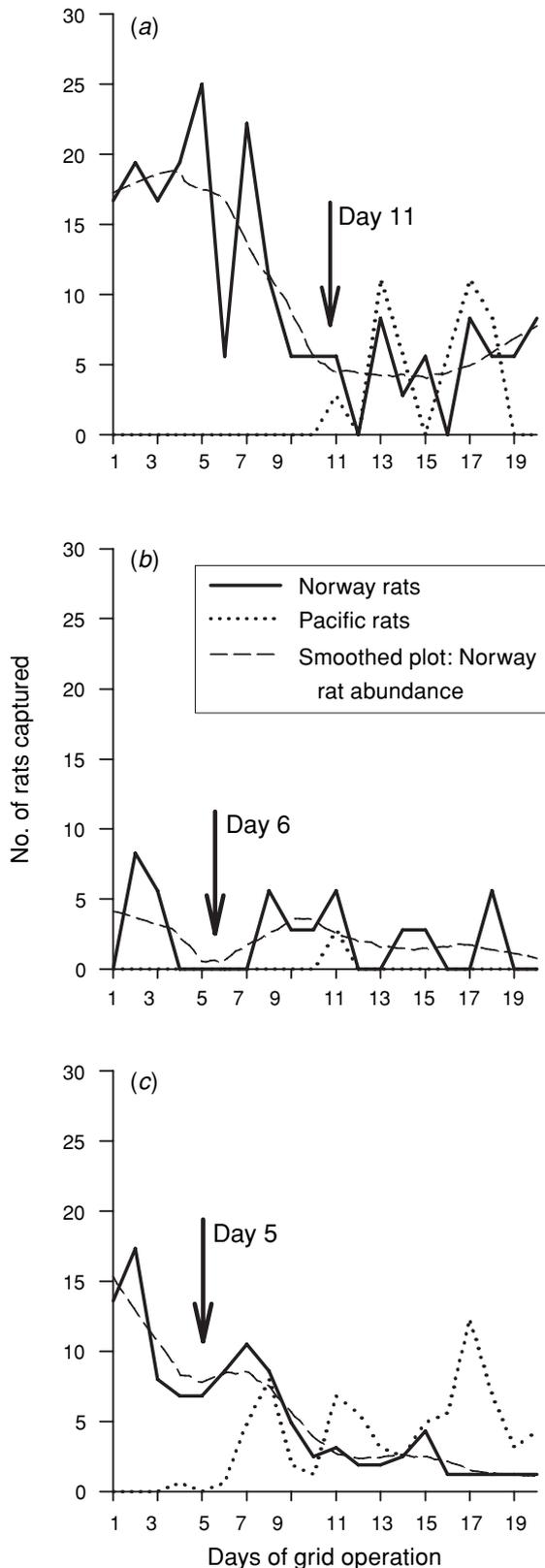


Fig. 6. The mean daily capture rate of Norway rats and Pacific rats on the removal grid in (a) 1994, (b) 1995 and (c) 1996. Arrows show estimated point of inflexion on smoothed plot.

increased after ~10 days, by which stage 49% of the Norway rats had been removed.

Density estimate

The smoothing of the rat captures in each trapping-grid produced suitable inflexion points (Fig. 6). In 1994, the inflexion point occurred at Day 11, when a total of 55 Norway rats had been caught. A simple regression of daily captures against cumulative captures gave an estimated 92 rats (95% CI: 55–136) in the trapped grid (Fig. 6a), a density of 6.05 rats ha⁻¹ (95% CI: 3.62–8.94). Maximum estimated density was 8.94 ha⁻¹. There were very few captures in 1995, and only five rats were trapped by Day 5, with Zippen estimate of 5.4 present (Fig. 6b). The minimum density was 0.33 rats ha⁻¹ and estimated density was 0.35 rats ha⁻¹. In 1997, 85 Norway rats were caught by the inflexion point at Day 5, with a Zippen estimate of 132 (95% CI: 85–167) rats present at that time (Fig. 6c), and a density estimate of 8.68 rats ha⁻¹ (95% CI: 5.59–10.99).

Discussion

Breeding and population fluctuations

Results from both trap lines showed a peak in numbers of rats caught in late summer and autumn, with the lowest catch rate in late spring. This seasonal trend in capture rates is similar to the findings of studies carried out on Pacific rats in northern New Zealand. On forested islands the peaks in relative abundance were lower but declines less steep than on grassed islands, probably owing to a longer breeding season because of more diverse food sources (Moller and Craig 1987). Speed (1986) trapped the minimum number of Pacific rats on forested Little Barrier Island/Hauturu in October, and maximum numbers in autumn and early winter. On the nearby Hen and Chicken islands, two years of trapping Pacific rats caught most rats in autumn and winter and the fewest over late spring and summer (Newman and McFadden 1990), and pregnant females were trapped only over four months from February to May. In grassland on Tiritiri Matangi island, population density had a pronounced peak in autumn and declined over winter and spring (Moller and Craig 1987; Roberts and Craig 1990), with pregnant rats being caught for five months from November to March. Only one pregnant Pacific rat was caught on Raoul Island, in October, and the small pulse in Pacific rat numbers suggests a truncated breeding season for Pacific rats over the late spring–early summer period. In addition, the increase in captures of Pacific rats follows the seasonal decline in Norway rat numbers in late spring–early summer, suggesting possible relief from competitive pressure. Norway rats probably have a longer breeding season than Pacific rats on Raoul Island but a shorter season than on mainland New Zealand. Pregnant Norway rats on Raoul Island were trapped only between September and February, whereas on the New

Table 3. Repeated-measures ANOVA of the timing of capture and relative abundance of Norway rats and Pacific rats trapped on three 20-day trapping grids in the winters of 1994–96, Raoul Island
*, $P < 0.05$; **, $P < 0.01$

Source	s.s.	d.f.	m.s.	F	Pr(F)
Between species: relative abundance	214.89	1	214.89	21.34	0.001**
Between species: timing of capture	405.46	19	21.34	2.12	0.011*
Between residuals	805.54	80	10.07		

Zealand mainland breeding can occur all year round (Bramley 1999; Innes *et al.* 2001; Harper *et al.* 2005). On Raoul Island juveniles began to appear in early summer, with their peak in numbers in early autumn, about three months after the peak in the number of pregnancies. Juveniles eventually disappeared from the trapped population by July, probably as they entered the adult population.

As the main factor affecting rat population numbers is probably the length of the seasonal food pulse (Moller and Craig 1987; Blackwell *et al.* 2003; Harper 2005a), the availability of food to Pacific rats appears to have been very restricted, possibly because of interference by Norway rats, which in turn also appear to have been constrained by food limitations. If food availability is the main driver of rat abundance then 1995 was a poor food year for rats on Raoul Island. On the trapping grids, the densities of Norway rats were higher, by an order of magnitude, in 1994 and 1996, than in 1995, when very few rats were caught. Captures of Pacific rats in these years mirror these trends. Between-year differences in overall abundances of rats was apparent from both the trap-lines and the trapping grids. Fewer rats were trapped on the trap-lines in 1997 than in either 1994 or 1996. Alternatively, cat numbers may have increased during years with higher rat numbers, and subsequently depressed rat population growth in the following year. This appears less likely as cat populations are often controlled by rat numbers on islands with limited prey (Harper 2005b).

Grid-trapping and bait take

Grid layouts of traps and/or poison have been used to substantially reduce numbers of rats around the nests of rare birds to prevent egg stealing or predation of chicks. Generally, they have been used where a single species of rat is present (Taylor and Thomas 1993; Innes *et al.* 1999). On nest-protection grids established in autumn, when rodents are most abundant, reinvasion 5–7 days after the initial knockdown is a problem (GH, personal observation). Results from the Raoul Island grid operations in 1994 and 1996 show that invasion of the grid by Pacific rats occurs repeatedly once captures of Norway rats have declined to below about eight rats per night. In addition it is obvious that rats can remain within the grid for at least 20 days and that there is invasion from beyond the grid area, even in winter when rodent abundance is relatively low. The 1995 comparison of

bait stations and trap-setting methods showed no conclusive result because total rat abundance was too low.

The use of rhodamine-dyed bait in 1996 and the subsequent capture of rats showed that in this two-species situation the presumed subordinate species, Pacific rats, could be within a poisoned area and not gain access to bait up to 23 days after the bait was first available. Many of the rats that had not consumed bait may have moved into the grid as trapping reduced rat abundance. In an eradication situation the death of the early bait consumers should leave bait available to such subordinate animals. This type of situation was observed on Browns Island where mice (*Mus musculus*) were alive 18 days after the aerial spread of poison intended to kill all Norway rats and mice; all the mice have since died (Veitch 2002).

Interference competition

In short-term snap trapping on trap lines on Raoul Island the average catch ratio was one Pacific rat to 10 Norway rats (Table 1). When traps were set in a grid pattern that might remove most of the Norway rats the average catch ratio was 1:2 (Table 2). When cat stomachs were examined (Fitzgerald *et al.* 1991) they were found to contain 12 Pacific rats to one Norway rat. These observations lead to the conclusion that we have no idea of the relative abundance of the two rodent species on Raoul Island.

We expect that the cats were selectively preying on the smaller rats, in this case the Pacific rats and young Norway rats, as they have been observed doing in other locations (Leyhausen 1979; Childs 1986). We have no evidence to suggest that they were taking so many Pacific rats that few were left to be caught in our traps. Cat predation on Pacific rats may have depressed overall numbers of Pacific rats relative to Norway rats, resulting in fewer of the smaller species being trapped on the grids. However, the frequency of capture of Pacific rats by the cats suggests that more Pacific rats should have been caught on the trap-lines if those traps were equally available to the two rodents. The results of the grid-trapping strongly suggest that short-term trap lines have a low probability of determining the abundance of Pacific rats when Norway rats are also present.

In the only other studies we know of where only Norway and Pacific rats were present, on Kapiti Island, the observers suggested that Pacific rats were avoiding the habitat occupied by Norway rats (Dick 1985; Bramley 1999). Both

studies involved kill-trapping in different vegetation types and the latter included a radio-tracking study. These studies suggested that Norway rats occupy favourable habitats and Pacific rats tend to avoid areas with high abundances of Norway rats. This is supported by trapping on Raoul Island where Pacific rats were in higher abundances than Norway rats only in apparently suboptimal beach fore-dune habitat (F. Kemp, personal communication).

Areas of dense ground cover are preferred by Pacific rats when larger rat species are present (Daniel 1969; Taylor 1975; Harper *et al.* 2005), possibly to escape interference from congeners. In the Raoul Island grid-trapping studies, Pacific rats may have invaded from an area of grassland to the east. On Kapiti Island, however, more Pacific rats than Norway rats were caught in habitats where ground cover was less than 30% on the surveyed area, and more Norway rats were caught on a trap-line and trapping grid in grassland (Dick 1985). Bramley (1999) had similar results in forest with sparse groundcover, but trapped more Pacific rats in coastal grassland. These apparent paradoxes may be influenced by the availability of higher-quality food (Craig and Bunn 1989), with Norway rats excluding Pacific rats from sites with better food (Bramley 1999), regardless of the cover. Dominant Norway rats will exclude subdominant conspecifics from food (Barnett and Spencer 1951) and this food exclusion probably applies to smaller congeners also.

The arboreality of Pacific rats suggests that climbing trees may be an escape mechanism for them also (Strecker 1962; McCartney 1970). Pacific rats will preferentially nest in trees when larger predatory animals are present (Wodzicki 1969), but the preponderance of Pacific rat remains in cat scats on Raoul Island implies that Pacific rats are also spending large amounts of time on the ground (Fitzgerald *et al.* 1991). Concurrent trapping on the ground and in trees may clarify temporal and population differences in the use of arboreal and terrestrial habitats by Pacific rats sympatric with larger congeners.

Total removal of Norway rats was not required for Pacific rats to be trapped more often. This may be due to the removal of established territorial Norway rats, with a subsequent collapse of the hierarchy within the Norway rat community (Berdoy *et al.* 1995). The remaining subdominant Norway rats may be more interested in establishing dominance relationships with neighbouring Norway rats rather than controlling a subordinate species. Alternatively, a lower abundance threshold of the dominant species may allow Pacific rats to operate relatively unhindered, as remaining dominant Norway rats enlarge their home-ranges to encompass vacant territories.

A very similar response in the numbers of mice (*Mus musculus*) to the removal of ship rats on a trapping grid has also been recorded by Brown *et al.* (1996).

Management and control

Competitive interference of a subdominant rat species by another species affects the control or monitoring of multi-rodent assemblages, because the subordinate rat species' access to bait, traps, or tracking tunnels is compromised. Eradication of mixed populations of Norway and Pacific rats is unlikely to be affected, as shown recently by several successful eradications on Kapiti Island and Tuhua (island), New Zealand (Towns and Broome 2003). However, studies of the population ecology of sympatric rat species are likely to be skewed by the capture of proportionally more of the dominant species. This strongly suggests that more intensive trapping (e.g. grids), and/or longer periods of trapping are required when studying an assemblage of two or more rodent species.

Snap-trap lines are used to give indications of rat abundance and species composition (Hickson *et al.* 1986; Brown *et al.* 1996; Cunningham and Moors 1996; Weihong *et al.* 1999). Competitive exclusion will affect the results of index trapping in areas of mixed species of rats. On a trap-line there appears to be a need to trap for longer than the recommended three days per session (Cunningham and Moors 1996) or to intensively grid trap for many days to clarify the species composition and abundance.

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