

Population biology of the ship rat and Norway rat in Pureora Forest Park, 1983–87

J. G. INNES

Landcare Research
Private Bag 3127
Hamilton, New Zealand

C. M. KING

Department of Biological Sciences
University of Waikato
Private Bag 3105
Hamilton, New Zealand

M. FLUX

230 Belmont Hill Road
Lower Hutt, New Zealand

M. O. KIMBERLEY

New Zealand Forest Research Institute
Private Bag 3020
Rotorua, New Zealand

Abstract Populations of ship rats (*Rattus rattus*) and Norway rats (*R. norvegicus*) were sampled over the five years 1983–87 at Pureora Forest Park, by Fenn and rat kill-traps every three months. Fenn and rat traps recorded similar capture rates in comparable habitats, although Fenns caught more heavy and fewer young rats. Ship rats ($n = 1793$ collected) were more abundant, heavier and larger in native forest, regardless of logging history, than in exotic forest of any age. Young ship rats (age classes 1–3) were most abundant in unlogged interior native forest, and in autumn and winter after summer and autumn breeding. Capture rates declined after peaking in 1985, probably due to reduced recruitment of young rats following lower pregnancy rates in adult females. The irregular annual seasonal cycle of reproduction and abundance observed at Pureora is the same as that described for non-commensal ship rat

populations elsewhere in New Zealand and the world. Thirty five of 43 Norway rats collected came from a single trap by the Waipapa Stream, apparently set near a permanent colony. Pregnant female Norway rats were trapped in every season, suggesting year-round breeding. This implies that both species can recover rapidly after control operations conducted at any time of year, but especially in spring and summer. Future research should include manipulative exploration of factors limiting ship rat abundance and Norway rat distribution.

Keywords rats; *Rattus rattus*; *Rattus norvegicus*; New Zealand; Pureora Forest Park; native podocarp forest; exotic forest; measurements; colour morphs; population structure; age; reproduction; recruitment

INTRODUCTION

Pureora Forest Park comprises a large tract of indigenous forest on the volcanic plateau of the central North Island of New Zealand. From November 1982 to November 1987 we studied the introduced small mammals resident in the Park, which at that time also contained extensive exotic forests inside its legal boundaries (King et al. 1996c). The research was intended to provide background information relevant to the control of predators of declining endemic forest fauna such as the kokako (Aves; *Callaeas cinerea wilsoni* Gmelin). We included in our survey all three mustelids present in New Zealand (*Mustela erminea*, *M. nivalis* and *M. furo*), both European rats (*Rattus rattus* and *R. norvegicus*), and the feral cat (*Felis catus*), hedgehog (*Erinaceus europaeus*) and house mouse (*Mus musculus*).

The Norway rat is the largest, and was apparently the first, of the European rats to reach New Zealand, aboard European and American sailing ships from 1769 onwards (Moors 1990). It soon became widespread and abundant on the mainland, but since about the 1860s it has been replaced throughout the North Island by the ship rat (Atkinson 1973), much

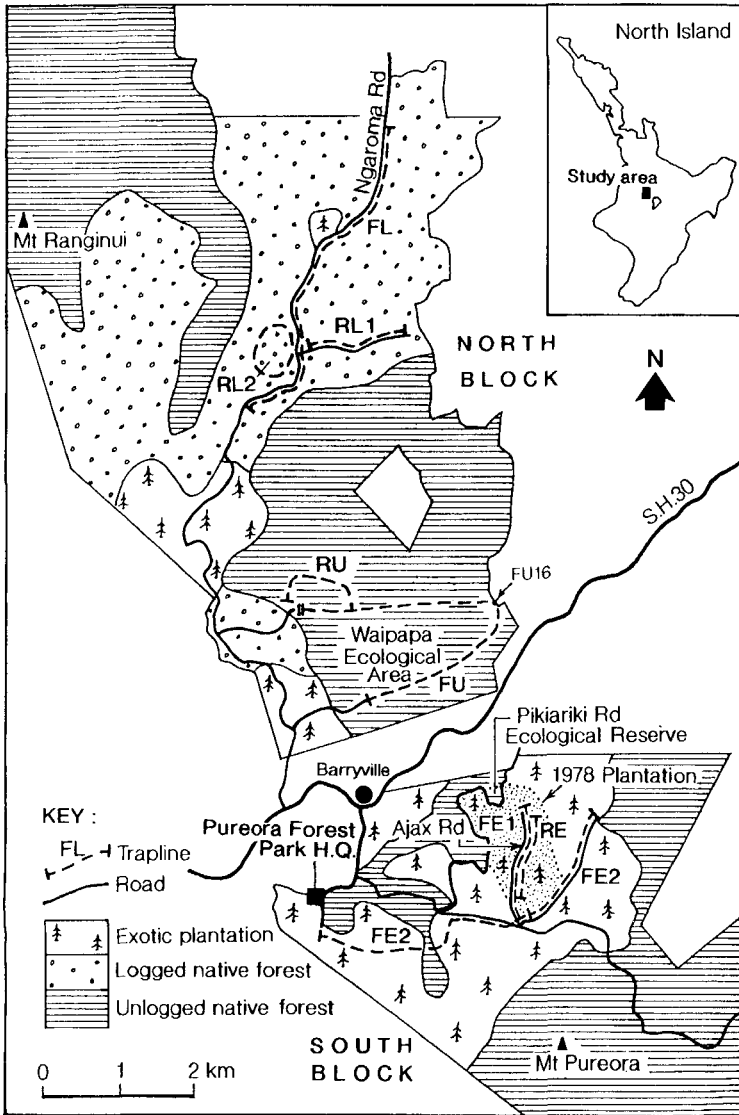


Fig. 1 Map of the study area. Pureora Forest Park boundaries are shown as they were during the field work. The Forest Park Headquarters includes the Visitor Centre and the meteorological station. The former settlement at Barryville is now deserted except for the old sawmill (closed). Traplines are identified by their codes (see text): trap FU16, on the bank of the Waipawa Stream, sampled a local population of Norway rats.

as the Norway rat had replaced the smaller kiore (*R. exulans*) that had arrived with Polynesian voyagers (Atkinson & Moller 1990), at a date still being debated (Holdaway 1999). The common rat at Pureora today is certainly the ship rat. By comparison, few Norway rats were collected during our study, but our research on them is significant because it is the first to document a mainland non-commensal population. In commensal habitats such as rubbish tips and farm buildings, Norway rats are still more common than ship rats (Moors 1990).

King et al. (1996c) described the field data on abundance, distribution and habitat preferences of

the eight species regularly monitored. Ship rats were captured both in Fenn traps set for mustelids and in rat traps set for rodents, and both techniques showed that they were common and widespread. Ship rats were more abundant in native forest, regardless of logging history, than in exotic forest of any age. In native forest they were equally abundant on forest edges and in the interior, but catch rates were highest on warmer steeper sites and lowest in early successional sites. They were virtually absent from young (4–9 years) exotic plantations, but present in older stands which had woody understories of native fruiting species. Ship rats were trapped most

frequently in autumn and winter and least so in summer. Their abundance peaked at up to 20 rats per 100 TN (trap-nights; a trap-night is 1 trap set for 1 night) in 1985 in all forest types. Figures are corrected for sprung traps after Nelson & Clark (1973). By contrast, Norway rats were rare, caught only in Fenn traps, and only in native forest.

This is the last of the three companion papers to King et al. (1996c), which describe the results of systematic necropsy of the trapped animals. The previous two dealt with mustelids and feral cats (King et al. 1996a), and feral house mice (King et al. 1996b). The aim of this paper is to record the measurements, population structure and reproduction of ship and Norway rats at Pureora in relation to habitat, season and year. The results described in this paper replace the preliminary figures quoted by Innes (1990).

Previous studies of the biology of ship and Norway rats were summarised by Innes (1990) and Moors (1990) respectively. Long term studies of ship rat demography initiated in the 1970s by the former Department of Scientific and Industrial Research in the Orongorongo Valley, Wellington and on Mt Misery, Nelson remain largely unpublished, except for the preliminary accounts given by Brockie (1992) and Wilson et al. (1998).

STUDY SITES

At the time of our study, Pureora State Forest Park occupied 75 000 ha of the ranges west of Lake Taupo. Our three study sites were all within 12 km of Pureora Village, at altitudes ranging from 550 to 700 m above sea level (Fig. 1). Two were in logged and unlogged native podocarp-broadleaved forest, and the third was in exotic forest (mostly *Pinus radiata*). For further details on the study areas and field routines, see King et al. (1996c).

In logged native forest, we set rodent traplines to sample both the narrow strip (6–12 m) of dense cover along a road edge (line RL1) and the forest interior up to 500 m from the nearest road (line RL2). A third rodent trapline (RU) sampled unlogged, unroaded native forest. In the exotic forest we set a rodent trap line in a 724 ha area of young *Pinus radiata* plantation established in 1978 (line RE), adjacent to the Pikiariki Ecological Area, but not in the older plantations east and south of it. However the latter were sampled by a Fenn trapline (FE2), and a Fenn line also sampled the young exotics (FE1); both were set along roads. A roadside Fenn line (FL)

sampled logged native forest at Ngaroma in the north of the study area, and the final Fenn line (FU) crossed the unlogged native forest of the Waipapa Ecological Area. The “roads” were single-lane gravel tracks carrying about 0–10 vehicles per day.

METHODS

Rodent traplines

Rodent traplines all had 36 trapping stations at 50 m intervals (total length 1.8 km). One each of the “Supreme Ezi-set” rat and mouse traps was set at each site, baited with peanut butter and rolled oats, according to the standard method established by B. M. Fitzgerald (Fitzgerald & Karl 1979; Innes 1990). After a pilot trapping session in November 1982, all lines were set and inspected daily for three days during four trapping sessions a year, in the last weeks of February, May, August and November of 1983–87 inclusive. One line (RL1, logged forest road edge) was closed after February 1985 (Fig. 2). The wooden bases of all traps were soaked in linseed oil before first use, and the springs were oiled periodically. We inspected all traps daily and recorded their condition, according to the routines described by Cunningham & Moors (1983).

Fenn traplines

The 122 steel Fenn traps were set singly, in wooden tunnels to protect non-target species (King & Edgar 1977), baited with fish-based catfood, and inspected daily. After 1984 we fixed two horizontal wires across the tunnel entrances in an effort to reduce interference by possums (*Trichosurus vulpecula*). Fenn traps were all spaced at 300 m intervals and set in the last weeks of January, April, July and October for 1982–87 inclusive, but the lines were of variable length depending on the extent of suitable habitat available. For further details see King et al. (1996c).

Laboratory procedures

All animals caught were returned to the laboratory frozen, and later examined for a standard list of physical attributes. The number of rats available for examination or dissection was always less than the total trapped, because some were scavenged in traps or damaged during storage, transit or processing. Norway rats were put through the same procedures as ship rats.

We collected fleas (by brushing the fur, and inspecting the plastic collecting bag) only from rats killed during the winter of 1987 (the Fenn trapping

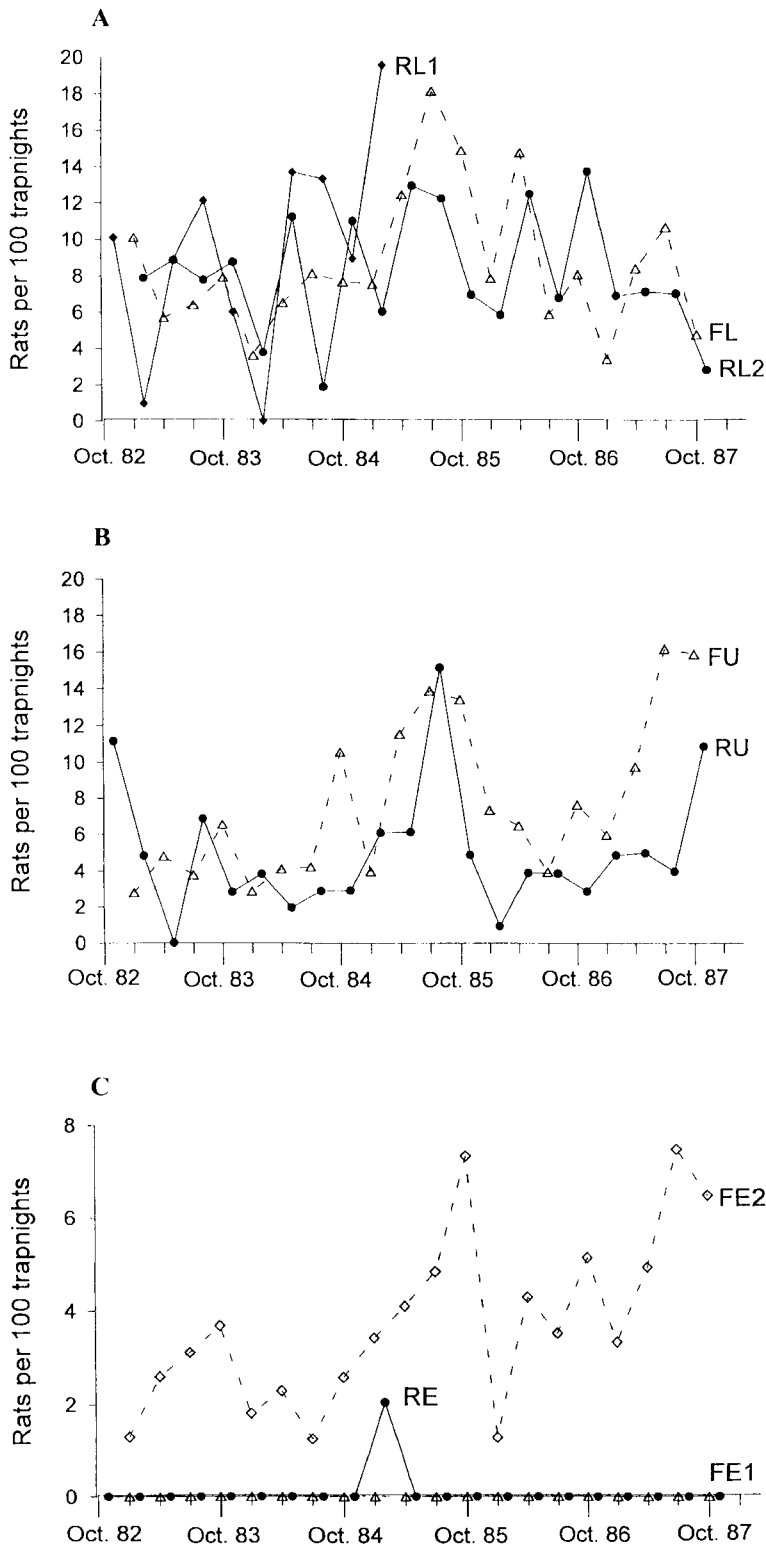


Fig. 2 Density indices (rats captured per 100 trap-nights) for ship rats through the five years, in rat traps (prefix R) and Fenn traps (prefix F). **A** Captures in logged native forest, along traplines FL (road edge), and RL2 (forest interior); **B** captures in unlogged forest interior along traplines RU and FU; **C** captures in exotic forest along traplines RE and FE1, and FE2 (in older plantations).

in July, and the rodent trapping in August). Fleas found were stored in 70% alcohol, and later passed to B. M. Fitzgerald for identification.

Measurements and morphs

We recorded whole body weight, paunched weight (after removal of stomach), total length and tail length, omitting rats that had been chewed in the trap or were missing tails or feet. In analyses of weight we excluded the pregnant females, and in analyses of length we excluded any rat with a damaged spine or tail. We classified each ship rat as representing the "rattus", "frugivorus" or "alexandrinus" morph; for colour illustrations of each, see King (1990).

Age determination

We classified all rats of both species into one of the seven age-classes described by Karnoukhova (1971) based on molar toothwear, as illustrated in Innes (1990). This method gives consistent results open to comparison with other New Zealand studies, but it has never been calibrated against known age animals in New Zealand. Moller & Tilley's (1986) recommended modifications of the method for Norway rats were published after most of our laboratory work was complete.

Criteria for assessing reproductive activity

The condition of the vagina (perforate or imperforate) is an unreliable indicator of reproductive condition, so was merely recorded without further analysis.

We took active pregnancies and lactations to define present breeding, although the number of actively breeding females is thereby underestimated. The gestation period of ship rats is 20–22 days, and of the Norway rat, 22–24 days (Brooks & Rowe 1987), but the embryos are not visible to the naked eye for about the first week in either species. Females that had bred at some time in their lives, though not necessarily during the sample period in which they were collected, were defined as those that were pregnant, lactating, or with uterine scars. Uterus condition was classified into one of three standard categories of relative thickness. Those classed as "thread" could be either immature or mature but quiescent. Enlarged uteri associated with ovarian activity were classed as "string" or "cord".

Litter size was estimated as the mean number of viable embryos (excluding resorptions) per pregnant female. The traditional criterion indicating breeding condition in males, the position of the testes (scrotal or abdominal), is unreliable, so we determined male

breeding condition mainly from whether or not the tubules in the epididymides were visible. We also tried a new method, based on the length and width of the testes in mm. By assuming that width and depth were equal, we derived a rough estimate of testis volume ($length \times width \times depth = volume$ in mm^3).

We defined recruitment as the addition of young rats (age classes 1–3) to the trapped samples. The category "young" refers to chronological age as reflected by tooth wear, not to reproductive maturity.

Statistical analysis

The statistical analysis was conducted using means calculated for each trapline \times trapping session. The statistical packages SAS and GENSTAT were used to perform a multi-factor analysis of variance (ANOVA) for each of the variables of interest (age, sex ratio, weight, length, reproductive variables etc). The factors included in the ANOVA model were trapline, year and season. The data from the pilot trapping session in November 1982 were excluded from analyses involving comparisons between years and seasons, since they represented only one season of that year. These procedures are able to accommodate unbalanced sample sizes and can test for differences in each variable whilst controlling for all the other variables appropriate to each comparison. Because the samples were large, most of the variables could be analysed adequately with PROC GLM. Percentage variables were better handled by generalised linear models with logit link function and binomial error function, and by using deviance ratios to test the significance of each factor. In all tables, significant differences were assumed if $P < 0.05$.

Because ship rats were abundant, and frequently caught both in rat and in Fenn traps, we were able to compare population parameters derived both from rodent traplines and from Fenn traplines. The two types of traps sampled the same areas, but they were set at different spacings, with different baits and in different months. The mechanism of the Fenn trap is also heavier than that of the Supreme rat traps, which might affect the weight distribution of the captures, so we analysed the results given by the two trap types separately.

Because each of the main habitats of interest was represented by a single trap line without replication, we could not make any true tests of difference between habitats. Instead, the line \times year interaction term was used as the error term for testing for differences between lines. This procedure will detect any differences between habitats that remained

consistent over the five years covered by the study. Similarly, season was tested against the season \times year interaction. Other factors were tested against the residual error. Least significant differences (LSDs) were used to detect significant (at $\alpha = 0.05$) differences between adjusted means. The raw data are available on request from MOK.

RESULTS

Ship rats

Distribution of captures

A total of 1793 ship rats was collected, mostly from indigenous forest (Table 1). Only seven of 179 traps of both types set in native forest caught no ship rats; 60 traps caught 1–3, and 14 traps caught 20 or more each. At the broad scale on which we sampled, the rats were virtually ubiquitous, although the skewed frequency distribution of trap success suggests that rat density was locally variable (King et al. 1996c).

Comparisons between catches in Fenn versus rat traps

More ship rats were caught in Fenn traps than Supreme rat traps (Table 1), since the total number of corrected trap nights recorded by Fenns was much higher. However, when the two trap types were set in comparable habitats, the capture rates they recorded were similar (Fig. 2A, C).

Rats caught in Fenn traps were significantly larger and heavier than those from rat traps (Table 2),

probably because Fenns have a stronger trigger mechanism. Fenns also caught proportionately fewer young rats (age classes 1–3), of which none was from age class 1 (Table 2). A logistic regression was used to test the relative importance of weight and age to explain these results, since the two parameters are correlated. Each parameter fitted individually affected the catch (for age as a linear function, $P = 0.0001$; for weight fitted by class, $P = 0.0001$) but in combination both were still significant (for age, $P = 0.0005$; for weight, $P = 0.005$).

Overall, 47% of the rats collected were males (Table 3). Gender ratios of the samples from the two trap types were the same, even though males are significantly heavier than females (Table 4). The minimum weight threshold required to set off a Fenn trap appears to be (usually) above the weight of the smallest rats (age class 1, averaging 41 g, Table 4).

We had previously shown (King et al. 1996c) a significant decline in numbers of captures of rats in Fenn traps through each 10 day trapping session, usually to about half the initial catch by the tenth day. Here we examined the necropsy data to see if there were any differences in dominance (as indexed by size and age) or breeding history between the rats caught at the beginning and end of the 10 day Fenn trapping sessions. The capture records for rat traps were too few, and the trapping periods too short, to do the same for them.

There were no significant correlations between the percentages of males with visible tubules, the

Table 1 Numbers of ship and Norway rats captured, and trapping effort (CTN: corrected trap nights, corrected for unavailable traps; Nelson and Clark 1973), listed by habitat and trap type (from King et al. 1996c). The capture totals include scavenged or severed remains, provided that another individual of that species with the same part missing was not later captured in the same area. A 'trap-night' is one trap set for one night.

		Habitat					Totals
		Unlogged native forest interior	Logged native forest interior	Logged native forest roadedge	plantation (planted before 1966)	Young exotic plantation (planted 1978)	
Ship rat	Mouse	1	1	1	–	0	3
	Rat	106	161	91	–	2	360
	Fenn	473	–	658	299	0	1430
Norway rat	Mouse	0	0	0	–	0	0
	Rat	0	0	0	–	0	0
	Fenn	35	–	8	0	0	43
Total CTN	Mouse	2160	1969	977	0	2085	7191
	Rat	2157	2007	991	0	2156	7311
	Fenn	6281	0	7746	8166	2079	24 272

mean number of uterine scars in females, or the distributions of age class, weight or total length with trapnight (numbered 1–10) for rats caught in Fenns. However there was a significant ($P = 0.026$) positive correlation between trap-night number and the percent of the catch comprising females which had bred or were pregnant or lactating; that is, breeding females tended to be caught later in the trapping period.

Because the two trap types sampled the populations differently, we have adjusted all the results for trap type or else present them separately in the analyses that follow.

Population structure

Rat traps set in unlogged interior native forest (line RU) consistently caught proportionally more young rats (age classes 1–3) than traps in logged interior

Table 2 Effect of trap type (Fenns compared with rat traps) on the catch of ship rats.

	Fenn traps		Rat traps		P-value
	N	mean	N	mean	
Whole body weight	1149	134 g	307	124 g	0.002
Paunched weight	1148	127 g	306	118 g	0.002
Total length	1050	366 mm	318	354 mm	<0.0001
Tail length	1074	193 mm	319	188 mm	0.0002
% young (age classes 1–3)	1256	19 %	331	34 %	<0.0001
% male	1256	46 %	331	46 %	0.38
Distribution of age classes:					
Class 1	0	0	8	2.4%	0.0001
Class 2	31	2.5%	16	4.9%	0.0351
Class 3	253	20.1%	87	26.5%	0.0151
Class 4	585	46.6%	141	43.0%	0.2716
Class 5	332	26.4%	70	21.3%	0.0694
Class 6	49	3.9%	5	1.5%	0.0522
Class 7	6	0.5%	1	0.3%	0.6743

Table 3 Age and gender of ship rats by trapline, season and year. For each factor, values in a column followed by the same letter do not differ significantly at $\alpha = 0.05$.

		% young (class 1–3)			% male		
		n	mean		n	mean	
Habitat & trap type	RU	92	41	a	92	37	a
	FU	411	28	abc	411	43	a
	RL2	157	24	bc	157	45	a
	RL1	82	35	ab	82	57	a
	FL	588	19	c	588	50	a
	FE2	257	21	c	257	45	a
Season	Spring	473	19	a	473	43	c
	Summer	298	16	a	298	51	ab
	Autumn	353	43	b	353	56	a
	Winter	463	33	b	463	45	bc
Year	1983	298	26	ab	298	54	a
	1984	259	37	a	259	51	ab
	1985	451	37	a	451	48	ab
	1986	300	16	b	300	41	b
	1987	279	21	b	279	50	ab
Total		1587	25		1587	47	

native forest (line RL2: Fig. 3, Table 3), and this difference was also apparent although not significant with the catch in Fenns (FU compared with FL: Fig. 4, Table 3).

Young rats were more abundant (from a third to almost a half of the total catch) in autumn and winter, after recruitment from summer and autumn breeding, but they still averaged about one-sixth of the catch in spring and summer (Table 3). However, the youngest rats of age classes 1–2 could appear in the traps at any season, indicating year-round breeding.

Proportionately more young rats were trapped in 1984 and 1985, when numbers were high (Fig. 2) relative to other years. During the following (post-peak) year, from October 1985 to July 1986,

significantly fewer young rats were trapped than at the same time in other years, although no fewer females were pregnant, nor males sexually active, at that time (Table 5).

Gender ratio did not vary significantly between lines, seasons or age classes, although fewer of the trapped samples were males in 1986 than in other years.

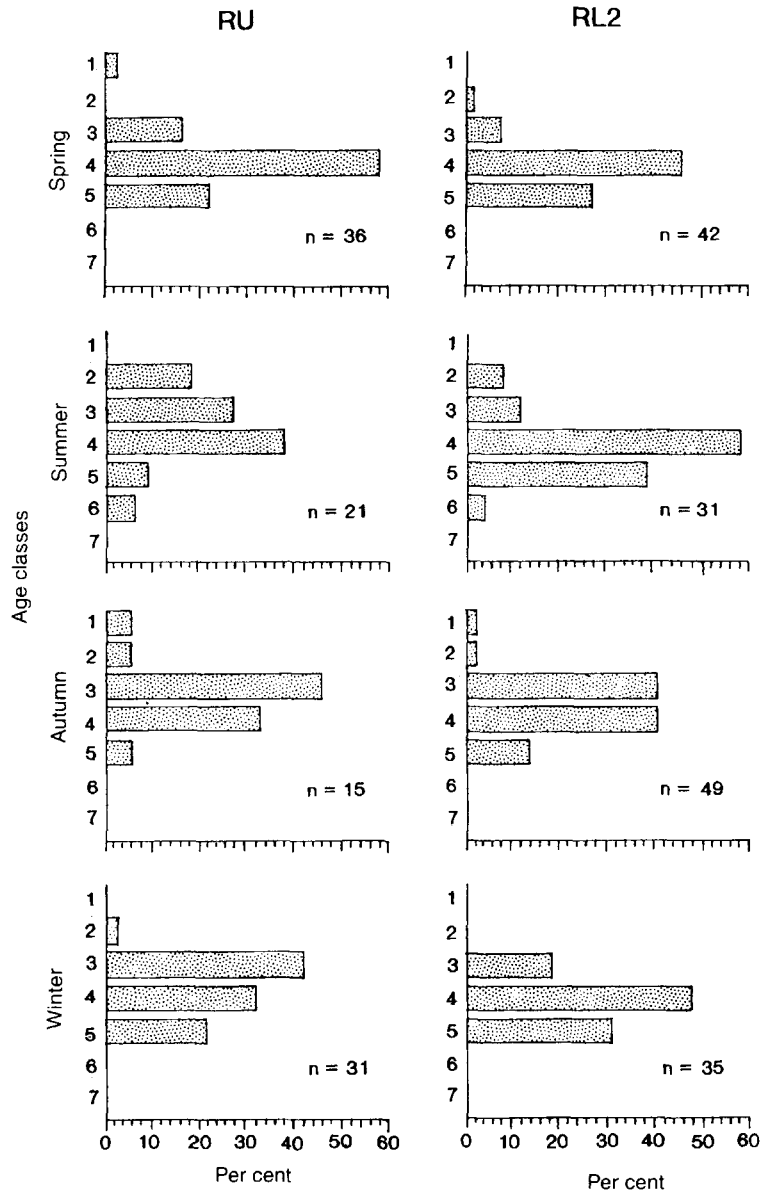
Measurements

Rats collected in the Fenn traps on line FE2, set in the older exotic plantations, were slightly shorter and lighter than those collected in Fenns set in native forest (Table 4; means adjusted for sex and age). The differences in length were significant in comparison

Table 4 Weight and length of ship rats by habitat, season, year, age class and gender. For each factor, values in any column followed by the same letter do not differ significantly at $\alpha = 0.05$.

	Whole body weight (g)		Paunched weight (g)		Total length (mm)		Tail length (mm)	
	n	mean	n	mean	n	mean	n	mean
Line								
RU	83	127 a	83	120 ab	85	361 ab	86	191 ab
FU	368	132 a	367	126 a	339	366 a	349	195 a
RL2	145	133 a	145	126 a	151	363 ab	151	192 a
RL1	76	118 ab	75	113 b	79	347 c	79	186 b
FL	527	134 a	527	127 a	488	365 a	494	193 a
FE2	238	128 b	237	121 ab	213	357 bc	215	187 b
Season								
Spring	447	128 b	446	122 a	401	362 a	405	192 a
Summer	236	133 ab	235	126 a	257	361 a	262	190 a
Autumn	303	127 a	303	121 a	304	357 a	310	190 a
Winter	451	127 ab	450	121 a	393	361 a	397	193 a
Year								
1983	253	126 b	250	119 b	263	354 c	265	188 b
1984	234	125 ab	234	119 b	228	356 bc	230	188 b
1985	426	129 a	426	123 b	391	364 ab	397	192 ab
1986	266	138 a	266	131 a	242	371 a	246	196 a
1987	258	127 ab	258	121 b	231	357 bc	236	190 b
Age								
1	8	41 a	8	39 a	8	246 a	8	130 a
2	45	79 b	45	75 b	40	318 b	40	170 b
3	318	111 c	317	106 c	295	346 c	299	184 c
4	648	134 d	646	127 d	619	366 d	630	194 d
5	362	148 e	362	140 e	344	374 e	347	197 e
6	50	152 e	50	143 e	45	378 e	45	197 ed
7	6	150 ed	6	139 ed	4	380 ed	5	189 edc
Sex								
Male	824	141 b	822	134 b	732	368 b	738	194 a
Female	613	121 a	612	114 a	623	358 a	636	192 a
Total	1437	132	1434	126	1355	364	1374	193

Fig. 3 Age distributions of ship rats caught in rat traps, by season, in unlogged native forest interior (RU) and in logged native forest interior (RL2).



with lines FU and FL, and the difference in paunched weight was nearly so for FU. Neither mean weight nor length differed between seasons, although rats trapped in 1985 and 1986 were larger than rats from other years. Males were on average longer and heavier than females.

Mice collected from Pureora during the same study showed significant seasonal variations in the inter-relationships between age, whole body weight

and head-body length (King et al. 1996b). Mice of a given age were significantly larger in summer than at any other season. There was no such seasonal variation in ship rats. Both weight and length increased significantly with age class up to class 4, after which neither parameter increased. In fact, rats in age class 7 regressed in size, so that they were not heavier or longer than rats in age class 4 (Table 4, Fig. 5).

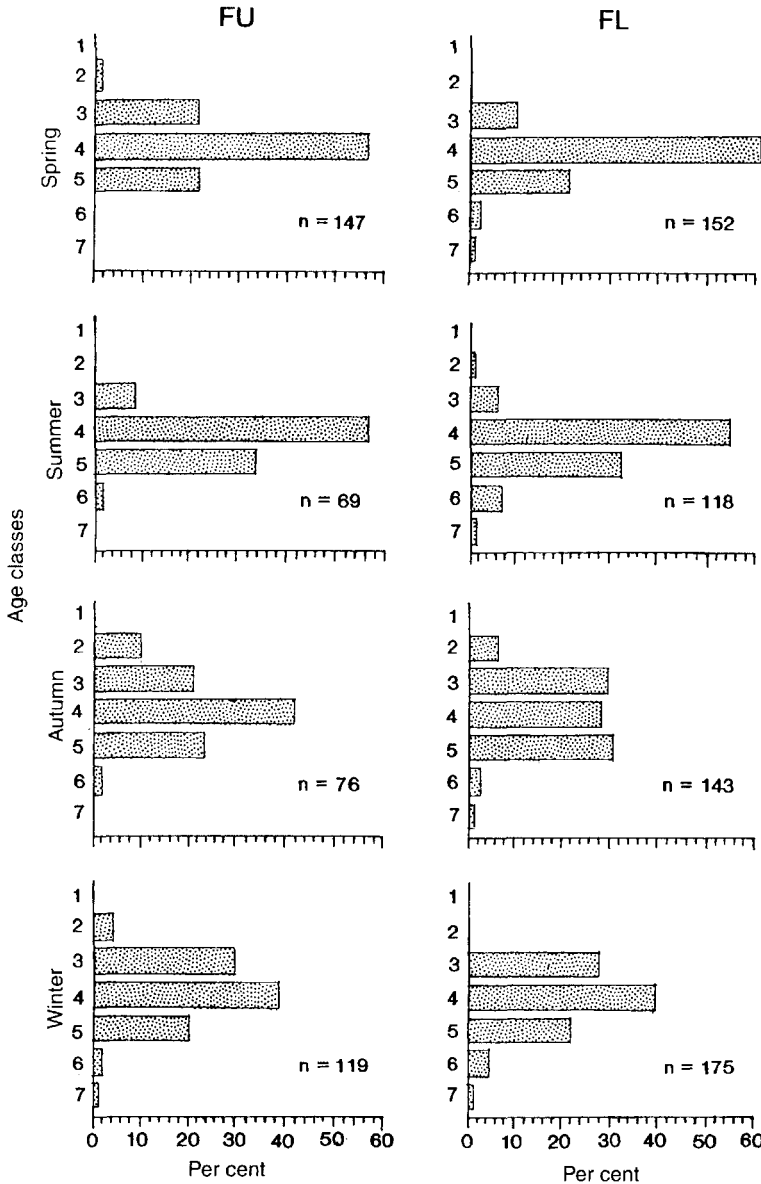


Fig. 4 Age distribution of ship rats caught in Fenn traps, by season, in unlogged native forest interior (FU) and in logged native forest roadside (FL).

Colour morphs

Of 1587 individuals classified for colour morph, 79% were the brown backed, white bellied “frugivorus” morph, 13% were the dark “rattus” morph, and 8% were the brown-backed, grey-bellied “alexandrinus” morph. In the North Island, the “alexandrinus” morph had previously been recorded only from Northland, although it is the commonest morph in South Island samples (Dowding & Murphy 1994; Innes 1990; Smith 1986), and is the typical morph in UK (Corbet & Harris 1991).

The proportion of Pureora rats classified as “rattus” morph did not vary significantly between seasons, years or genders. Fewer “rattus”, and more “frugivorus” were collected from the older exotic plantation (line FE2) compared with other habitats. The “rattus” morph rats tended to be lighter (mean weight 130 g, n = 208) than “frugivorus” rats (134 g, n = 1288), although not significantly so, and proportionately fewer “rattus” were caught in Fenn traps (12% of 1181) than in rat traps (16% of 295). Proportionately

Fig. 5 Body weight, paunched weight, total length and tail length of ship rats by age class (see Table 4).

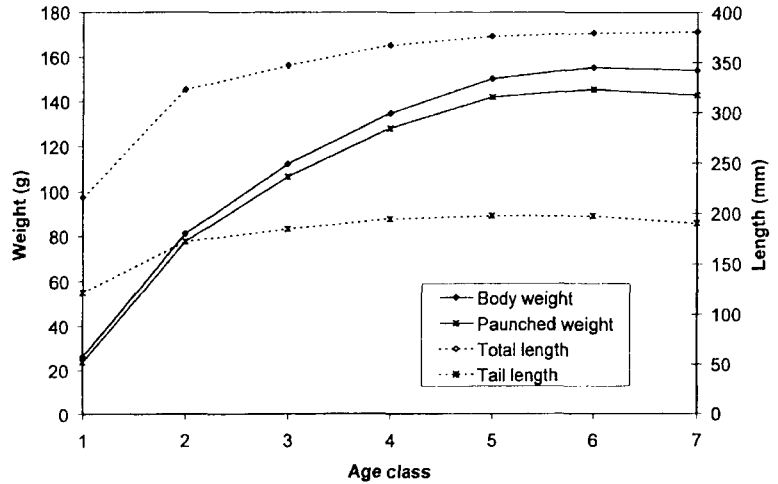


Table 5 Age, weight, length and reproductive status of ship rats trapped in the period of declining numbers (October 1985 to July 1986) compared with samples taken in the same period in other years.

	Post-peak year (Oct 85 – July 86)	Other years
% young	17.5	30.6 **
% male	50	50
Weight	137	128 **
Paunched weight	130	121 **
Length	372	358 **
Tail length	198	190 **
% perforate	98.6	97.5
% pregnant	19.9	16.2
No. embryos	5.8	5.2
No. scars	8.7	8.6
% preg or lact	36.8	29.4 +
% with scars	59.3	48.9 +
% with scrotal testes	71.7	59.6 **
% with visible tubules	80.6	72.1 *
Testes volume	2566	2381 +

+ difference significant at $\alpha = 0.1$; * significant at $\alpha = 0.05$; ** significant at $\alpha = 0.01$.

more “frugivorous” than “rattus” morph rats were trapped in exotic forests.

Reproduction

Mean measures of several parameters describing the female breeding cycle are shown in relation to habitat, season and year in Table 6.

The proportion of females with perforate vaginae increased rapidly from age classes 1–2 (60–70%) to age classes 3–7 (98–100%), so this parameter is not

informative. No indicator of female reproductive activity (% pregnant; mean number of live embryos; % with uterine scars; mean number of uterine scars; % pregnant; % lactating; % pregnant females with resorbing embryos) varied significantly with habitat. However, as expected from recruitment data, pregnant rats were trapped most often in summer and autumn. Fewer pregnancies were recorded in spring, and only six from winter during the 5 years of trapping, all from lines FU or RU in 1983 or 1984.

The mean number of embryos per female varied slightly with season, from 4.2 in spring to 5.9 in winter, although not significantly. A histogram of the number of uterine scars borne by 346 females (Fig. 6) shows peaks at 5–6, 10–11 and 18 scars, corresponding to 1, 2 and 3 litters respectively, but with considerable spread. Most pregnant females trapped in 1983 had resorbing embryos, significantly more than in other years.

No females in age class 1, and few in age class 2, were pregnant, lactating or had uterine scars when trapped, but most class 4 females were pregnant in summer and most class 5 females in autumn. There were no significant differences between age classes in the proportion of females pregnant or lactating in winter or spring. Most age class 4 females trapped in spring had not yet bred at all, whereas most females of age classes 5–7 trapped in spring and winter had bred in the previous summer or autumn. In all seasons, litter size was no greater in older females than young ones, but significantly more females of age class 5–7 had uterine scars (Table 6).

As expected, most males had scrotal testes and visible tubules in the cauda epididymus in spring,

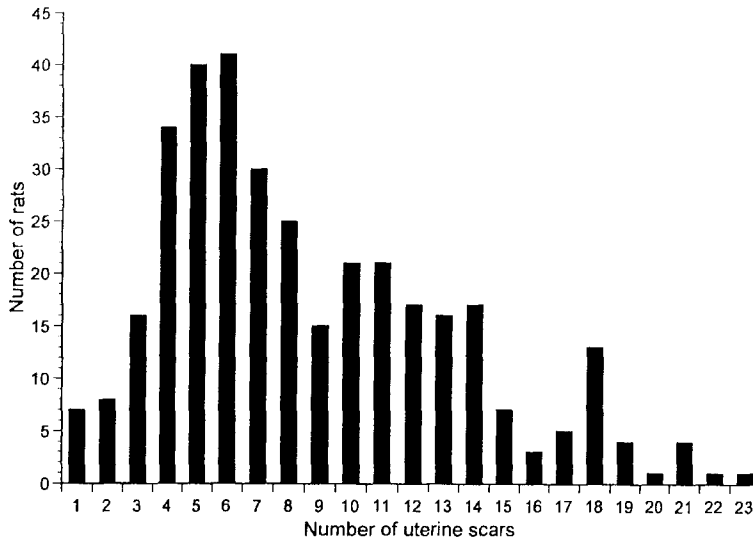


Fig. 6 Frequency distributions of uterine scars in female ship rats. The range 1–8 scars peaking at 6 represents females that have had only a single litter; the range 8–14 peaking at 10–11, those that have had two litters, and the range of 14–23 peaking at 18, those that have had three litters.

Table 6 Parameters of reproduction in female ship rats, by line, season, year and age class. For each factor, values in any column followed by the same letter do not differ significantly at $\alpha = 0.05$.

	% perforate		% pregnant		No. embryos where present		No. scars where present		% breeding		% with scars	
	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean
Line												
RU	78	100 a	77	20 a	9	3.74 c	30	8.79 a	71	29 a	66	42 a
FU	52	98 a	52	19 a	6	4.60 bc	18	8.73 a	50	33 a	45	57 a
RL2	122	98 a	122	15 a	13	5.43 abc	58	8.75 a	116	24 a	108	46 a
RL1	200	89 a	200	11 a	23	7.30 a	102	9.64 a	187	40 a	182	50 a
FL	258	100 a	258	20 a	35	5.15 abc	115	8.21 a	242	29 a	237	47 a
FE2	33	99 a	32	17 a	3	5.77 ab	17	7.90 a	29	31 a	31	57 a
Season												
Spring	200	98 a	199	9 c	14	4.27 a	72	8.87 a	190	16 b	170	40 a
Summer	147	98 a	148	36 a	39	5.59 a	67	6.87 a	131	56 a	123	53 a
Autumn	187	97 a	186	21 b	32	5.62 a	99	8.82 a	171	44 a	174	56 a
Winter	209	98 a	208	2 c	4	5.90 a	102	10.07 a	203	6 b	202	51 a
Year												
1983	155	97 a	155	25 a	16	4.25 b	75	7.01 a	155	34 a	148	49 a
1984	125	98 a	122	16 abc	17	5.92 a	61	8.90 a	107	31 a	103	57 a
1985	206	98 a	207	9 c	18	5.49 ab	94	8.98 a	189	24 a	193	48 a
1986	122	98 a	122	21 ab	24	5.70 a	50	7.81 a	117	38 a	94	50 a
1987	135	98 a	135	13 bc	14	5.37 ab	60	10.59 a	127	24 a	131	47 a
Age												
1	5	60	4	0	0	–	0	–	4	0	4	0
2	19	68 b	20	5 ab	0	–	0	–	20	5 c	20	0 d
3	161	99 a	162	11 b	13	5.23 a	33	5.79 b	155	18 c	155	21 c
4	337	100 a	335	19 a	52	5.17 a	146	7.14 b	314	27 b	302	48 b
5	187	100 a	186	19 a	21	5.33 a	137	10.25 a	172	38 a	162	85 a
6	29	100 a	29	14 ab	3	5.33 a	20	10.55 a	25	20 bc	21	95 a
7	5	100	5	0	0	–	4	16.25	5	0	5	80
Total	743	99	741	16	89	5.20	340	8.60	695	26	669	51

summer and autumn (Table 7). However, even in winter, when few females were pregnant, most males still had visible tubules. In nearly half of them the testes were still scrotal, although the volume of the testes regressed significantly in autumn and winter.

There was no significant difference in testis volume between the age classes, but most males whose testes remained scrotal in winter were age class 5 or older. By spring a majority of age class 4 males' testes were scrotal, and by summer this was true of age class 3 males.

Norway rats

Distribution of captures

A total of 43 Norway rats was collected (31 males, 11 females), but only in Fenn traps in native forest (Table 1). Thirty five of them came from a single trap on a stream bank at the edge of the unlogged forest

of the Waipapa Ecological Reserve (FU16, see Fig. 1). This trap produced a regular crop of 4–10 Norway rats of both sexes per year from an apparently permanent colony nearby (Table 8), as well as 13 ship rats and three stoats. The rest of the Norway rats came from eight sites scattered through the logged forest along the Ngaroma Road, each yielding only a single rat.

There were no significant differences in the distributions of captures by sex, season and year, probably because the samples were too small to detect any.

Age and measurements

The frequency distribution of age classes (Table 9) approximated a normal curve, peaking at class 6. We do not know what chronological age this represents.

As in all rodents, body measurements varied significantly with age class. Table 9 presents least

Table 7 Parameters of reproduction in male ship rats, by line, season, year and age class. For each factor, values in any column followed by the same letter do not differ significantly at $\alpha = 0.05$.

	% with scrotal testes		% with visible tubules		Testes volume (cc)	
	<i>n</i>	<i>mean</i>	<i>n</i>	<i>mean</i>	<i>n</i>	<i>mean</i>
Line						
RU	78	51 a	79	65 a	79	2.19 b
FU	39	62 a	40	71 a	40	2.34 b
RL2	131	69 a	133	78 a	133	2.54 b
RL1	199	59 a	207	68 a	206	2.14 b
FL	322	63 a	325	78 a	318	2.67 a
FE2	48	62 a	48	77 a	48	2.66 a
Season						
Spring	258	68 ab	270	92 a	270	2.73 a
Summer	147	75 a	147	81 a	138	2.87 a
Autumn	162	60 b	162	56 b	162	1.89 b
Winter	250	41 c	253	61 b	254	2.19 b
Year						
1983	140	55 b	140	65 a	133	2.44 a
1984	133	52 b	133	75 a	132	2.41 a
1985	241	60 b	241	76 a	241	2.23 a
1986	174	77 a	177	80 a	175	2.70 a
1987	129	63 b	141	67 a	143	2.33 a
Age						
1	3	33	3	0	3	0.13
2	26	12 d	26	8 c	26	0.37 d
3	177	38 c	179	48 b	179	1.50 c
4	376	66 b	383	86 a	378	2.66 b
5	208	80 a	214	92 a	211	3.24 a
6	25	68 ab	25	92 a	25	3.53 a
7	2	50	2	100	2	2.49
Total	817	62	832	77	824	2.50

squares estimates calculated by the weighted means model, in order to compensate for the uneven numbers of rats in each group. Such a small data set allows few conclusions, except that Norway rats appear to be still growing up to and including age class 6, and that the reduction in weight but not in linear measurements in the oldest rats of both sexes suggests a drop in condition.

Reproduction

Six of the eleven females were pregnant. Three were caught in spring, and one was also lactating; the other three represented each of the other seasons, one apiece, but none was also lactating. One fully mature

female from each habitat caught in autumn/winter was lactating but not pregnant. One from each habitat in spring had bred before, although neither was pregnant or lactating then. To find such even representation of seasonal activity in such a small sample suggests that the breeding season in Norway rats at Pureora is, like that of ship rats, not well-defined.

Three females collected from trap FU16 had 6, 8 and 8 live embryos of 2–15 mm crown-rump length, none resorbing, and one had 7 embryos in unspecified condition. One female from the logged forest had 7 embryos, 4 live plus 3 resorbing, and another had 6 embryos, all resorbing. In 8 females checked

Table 8 Seasonal and annual distribution of captures of Norway rats.

	Numbers of rats caught			
	Line FU unlogged forest		Line FL logged forest	
	Male	Female	Male	Female
Spring	10	3	1	2
Summer	7	1	1	1
Autumn	7	2	1	0
Winter	5	0	0	2
Totals	29	6	3	5
1983	4	0	1	0
1984	9	1	0	4
1985	5	3	1	1
1986	5	1	1	0
1987	6	1	0	0
Totals	29	6	3	5

Table 9 Body measurements \pm SE and sample size (n) of Norway rats by age class.

Age class	Whole body weight (g)	Total length (mm)	Tail length (mm)
Males			
3	132 \pm 27 (2)	320 \pm 30 (2)	149 \pm 20 (2)
4	213 \pm 20 (5)	368 \pm 11 (5)	163 \pm 4 (5)
5	209 \pm 16 (10)	359 \pm 9 (8)	160 \pm 4 (9)
6	248 \pm 19 (11)	370 \pm 9 (9)	164 \pm 4 (9)
7	233 \pm 15 (2)	352 \pm 18 (2)	160 \pm 11 (2)
F-ratio	2.19 ($P = 0.10$)	1.57 ($P = 0.22$)	0.61 ($P = 0.66$)
All ages (n = 30)	220 (range 104–345)	361 (290–418)	161 (130–180)
Females			
3	151 (1)	314 (1)	140 (1)
4	162 \pm 6 (2)	341 \pm 6 (2)	158 \pm 6 (2)
5	198 \pm 15 (6)	342 \pm 12 (6)	155 \pm 8 (6)
6	152 (1)	339 (9)	150 (1)
All ages (n = 10)	181 (range 150–230)	339 (312–384)	154 (121–175)

for uterine scars, five had none and the others (all in age class 5) had 14, 15 and 20 visible scars. So far as they go, these data suggest that litter size in non-commensal Norway rats is about 6–8 in both habitats.

The testes of most (27 of 30, with 2 unclassified) adult males contained visible tubules. The majority had fully descended into the scrotal position in all seasons except winter, but there were always some in the abdominal position in any season, even with visible tubules. The only males without visible tubules were a juvenile (age class 3) caught in spring, and two mature adults caught in winter. One of these two had visible tubules in abdominal testes, and the other had non-visible tubules in testes that were still scrotal. It is impossible to say from these data whether or not males remain fertile in winter, or whether scrotal position reliably indicates breeding condition in Norway rats.

Fleas

The fleas identified from rodents sampled during winter 1987 are listed in Table 10. In such a small collection, it is remarkable that the most common flea on each species was different: *Nosopsyllus fasciatus* dominated on ship rats, *Pygiopsylla hoplia* on Norway rats, and *Leptopsyllus segnis* on mice. One female ship rat carried all three species (ten *N. fasciatus*, one *P. hoplia* and one *L. segnis*), but most rat carcasses yielded only one or two fleas of a single species.

DISCUSSION

This study was originally planned to survey the species distribution in, and monitor the population variations of, the small mammal fauna of podocarp and exotic forest of Pureora Forest Park, with especial reference to providing information to

managers about potential predators of kokako. We used the same techniques developed previously in beech forest (King 1983) in order to be able to compare the faunas of small mammals living in these different habitats. The beech forest traplines collected mainly stoats and mice, plus a few ship rats mostly in Fenn traps (to 1.7 C/100 CTN) in certain years only (King & Moller 1997). In sharp contrast, at Pureora the same methods collected eight species of small mammals, including huge numbers of ship rats (to 20 C/100 TN (Fig. 2A)). Furthermore, the large samples of ship rats from the mixed broad-leaved podocarp forests of Pureora were distributed relatively evenly between seasons, years and sites. Smaller samples were collected from closed-canopy exotic forest, but practically none from a young plantation.

Both Daniel (1978) and Brockie (1992:158) tabulated the abundance of ship rats in different parts of New Zealand as determined by trap catch. Unfortunately, most such comparisons are weak, because not all studies used the same trap spacings, layouts, seasonal schedule and bait. Nevertheless it is clear that few ship rats inhabit dairy farmland or pure beech forest. Numbers were highest (82 captures per 100TN) on Rosa I., off Stewart Is. (Hickson et al. 1986). Feral cats and stoats, which may limit ship rat numbers on the New Zealand mainland (Daniel 1972, 1978; data from the Orongorongo Valley, North Island; B. M. Fitzgerald & B. J. Karl, unpubl.) are absent from Rosa I.

Ship rats

Demography

The demography of ship rats in podocarp forest at Pureora is consistent with that reported from similar non-commensal habitat elsewhere on mainland New Zealand, as summarised by Daniel (1978) and Innes (1990).

Table 10 Fleas carried by rodents at Pureora in winter 1987.

Host	No. of hosts examined	Flea species	No. and sex of fleas
<i>Rattus rattus</i>	15	<i>Nosopsyllus fasciatus</i>	13 M + 20 F
		<i>Pygiopsylla hoplia</i>	2 M + 2 F
		<i>Leptopsyllus segnis</i>	3 F
<i>R. norvegicus</i>	2	<i>Nosopsyllus fasciatus</i>	1 F
		<i>Pygiopsylla hoplia</i>	4 M + 2 F + 1?
<i>Mus musculus</i>	8	<i>Nosopsyllus fasciatus</i>	1F + 1 M
		<i>Leptopsyllus segnis</i>	3 M + 5 F + 1?

In New Zealand, although male ship rats are capable of producing sperm all year round, pregnant or lactating females have been trapped mainly between September and April. Winter breeding is recorded occasionally, apparently following heavy fruit fall. Otherwise, breeding normally stops in winter, even in Northland, where temperature and food quality do not seem to be limiting (Smith 1986). At Pureora, pregnant rats were, as expected, trapped most often in summer and autumn. Most males had scrotal testes and visible tubules in the cauda epididymes in spring, summer and autumn, and young rats were significantly more abundant (from a third to almost a half of the total catch; Table 3) in autumn and winter after spring and summer breeding. We collected significantly fewer ship rats in Fenn traps in summer (King et al. 1996c), which is consistent with sparse winter breeding.

Innes (1990) suggested that this seasonal breeding, plus an annual pulse in recruitment of young, would result in a corresponding seasonal fluctuation in abundance, from a low in spring and early summer to a high in autumn and winter. Fenn trap success at Pureora increased between January and July in 13 of 15 line \times year comparisons, and in eight comparisons it had increased again by October (Fig. 2). Long-term studies of ship rat abundance (Daniel 1978; King et al. 1996a) do indeed show a weak annual cycle of abundance, more so in the Orongorongo Valley (fig. 1 of Daniel 1978) than at Pureora, perhaps because there was more winter breeding at Pureora.

However, seasonal changes were small compared with annual changes. At Pureora, Fenn traps detected significant differences between years; abundance was highest on all Fenn lines during July to October 1985. Lines in unlogged native forest and older exotics also caught many rats in July 1987, although this second peak was not detected by line FL in logged native forest. A similar clear peak in abundance was recorded in the Orongorongo Valley in late 1971, following the heaviest fruit fall of an 8-year live-trapping study (Daniel 1978). Daniel suggested (p. 146) that "...both the length of the breeding season and the over-winter survival of ship rats are directly controlled by the size of the autumn seed and fruit crops".

Comparable increases at Pureora were observed simultaneously in both the native and older exotic forests. This suggests either that the plant species responsible were the common shrub hardwoods (e.g. mahoe *Melicytus ramiflorus*, five-finger *Pseudopanax arboreus*, wineberry *Aristotelia serrata*, pate

Schefflera digitata, *Coprosma robusta*) abundant under both canopies, or that some other mechanism is involved. We did not measure fruit abundance or rat mortality in this study, and so cannot advance Daniel's (1972) hypothesis that "...the combined effects of continual predation by feral cats and possibly mustelids and moreporks, and the occasionally abundant food supply in winter, are the two most important factors affecting the density of ship rats.". Neither did we find any evidence at Pureora to support Daniel's (1978) suggestion, that many Orongorongo ship rats starve to death in winters following light seed years. At Pureora the rats were not lighter in winter than other seasons (Table 4).

The increase in density indices for rats in all habitats in 1985 followed a substantial reduction in density indices for stoats and cats over the first two years of the study (King et al. 1996c). In the Orongorongo Valley, an increase in density of ship rats following the removal of cats was interpreted by Fitzgerald & Karl (1979) as evidence that predation by cats controls the numbers of ship rats there. However, Blackwell et al. (1998) experimentally removed mustelids and feral cats from the Puketukutuku Peninsula at Lake Waikaremoana, and rodents (ship rats and mice) did not increase there relative to a non-treatment block. They suggested that rodent populations were more likely to be limited by food supply than by predation.

We cannot explain why the proportions of female ship rats pregnant, and the mean testis volume of males, were lower in 1985 and 1987 than in other years, as in mice collected from the same habitats (King et al. 1996b). The declining pregnancy of females in 1985 can be linked to a reduction in recruitment of young rats and the consequent population decline of October 1985–July 1996 (Table 5).

Indices of unmanaged ship rat populations sometimes decrease steadily as a breeding season progresses. We observed this effect from October 1985 to July 1986 on the Fenn line FU (native unlogged) at Pureora (Fig. 2B), and in other studies elsewhere (Innes et al. 1995, 1999). Such changes in abundance remain inexplicable from these data.

Recruitment of young ship rats seemed to be more effective in the forest interior than along the road edges; in mice the difference ran in the opposite direction and was much more pronounced (King et al. 1996b). Nevertheless, ship rats were indifferent to the nett effects of the removal of large podocarps and the increase in ground cover after logging, both

in their numbers (King et al. 1996c) and in their breeding biology.

Smith (1986), Dowding & Murphy (1994) and Alterio et al. (1999) caution that variation in kill-trap success may be caused by factors other than abundance, such as trappability, food supply and home range size. For these reasons, kill trap studies are easiest to interpret when they are compared with non-treatment blocks, for examining a treatment perturbation such as a control operation (Innes et al. 1995).

Female age and productivity

Laboratory studies show that ship rats wean at 21–28 days (Cowan 1981), and may reach sexual maturity at 2–4 months (Watts & Aslin 1981; Brooks & Rowe 1987). The actual chronological ages of wild-caught ship rats in relation to their tooth-wear indices are unknown, but it would be valuable and interesting to know. Without this information, it is impossible to check how far the lab data can be applied to field conditions. Most age class 5–7 females trapped in spring had bred in the previous season, suggesting they were at least eight months old, having matured (minimum age two months) by at latest the previous April. By contrast, most age class 4 females trapped between September and November had not yet bred, suggesting that they did not mature in the previous breeding season and were therefore only 6–8 months old by the following spring. These ages are similar to those derived by Karnoukhova (1971) from caged rats, and repeated by Miller & Miller (1995) in their Rangitoto Island research.

Overall mean litter size was 5.33 (\pm S.D. 1.2), and the distribution of uterine scars (Fig. 6) indicated that no female had had more than three litters when trapped. These data would be consistent with a peak lifetime productivity of 16 young per female. This is less than the calculated 29 young per year of Daniel (1972), who recorded a maximum longevity of 17 months for a female ship rat. Daniel's mortality data suggest that females in the Orongorongo Valley may breed in one or two, but not three, seasons.

Ship rats in exotic forests

Exotic forests are apparently poor habitat for ship rats, especially the younger plantations with open canopy. Only two ship rats were collected from line RE (set in thick grass under young pines planted in 1978), where mice were common. Ship rats were always present but not abundant in older exotic plantations established in or before 1966 (line FE2).

The rats that did live at low density in the older exotic forests were also smaller and lighter than rats from other habitats. In a 15-year old second-crop stand at Tokoroa, a brief study recorded a somewhat higher density index for ship rats (13.5/100CTN) although with a different trapping regime (Clout 1980).

Comparisons with overseas studies

In Australia, northern Africa, southern Europe, North America and South America, the ship rat is primarily coastal, rarely found more than a few hundred kilometres inland, and is an important pest damaging citrus fruits, macadamia nuts, cocoa, coconut, sugarcane, date palms, carob and avocado fruits (Brooks & Rowe 1987). It greatly extended its range in the Pacific during the Second World War, and non-commensal ship rats have had their greatest impacts on endemic fauna on these and other islands (Atkinson 1985). Ship rats are remarkably adaptable, occupying for example tussock grassland on sub-antarctic (54°S) Macquarie Island (Pye et al. 1999), sugarcane fields and rainforest from sea level to 2500m in Hawaii (Tomich 1986; Lindsey et al. 1999) and five different non-agricultural habitats in the Galapagos Islands (Clark 1980). Clark attributed its extraordinary world-wide success as an invasive species to its "dispersibility, competitive superiority over similar species in disturbed or secondary habitats, and the ability to reproduce successfully in a wide variety of environments".

The few accounts of non-commensal ship rat populations overseas (Tamarin & Malecha 1971; Clark 1980; Watts & Aslin 1981; Stroud 1982; Tobin et al. 1994; Downes et al. 1997; McDonald et al. 1997; Lindsey et al. 1999; Pye et al. 1999) confirm that, as in New Zealand, ship rats are omnivorous, nocturnal and frequently or occasionally arboreal. They usually breed for 10–12 months per year in the tropics (Tamarin & Malecha 1972; Taylor et al. 1990; Tobin et al. 1994), but for 7–9 months in temperate zones such as New Zealand. However, even in Hawaii, with year-round breeding, there was still a seasonal breeding peak in summer and autumn (June to November; Lindsey et al. 1999) and higher populations from late autumn to winter (Tomich & Bridges 1981).

The somewhat irregular seasonal cycle of reproduction and abundance which we have documented at Pureora has been described before for non-commensal *R. rattus* by Tamarin & Malecha (1971, 1972) in Hawaii, and by Clark (1980) in the Galapagos Islands. In Hawaii, fortnightly survival rates of marked rats decreased with increasing

density, and, as in New Zealand, the relative importance of environmental and social factors in controlling the timing of the cycle was unclear. In the Galapagos, rat density was positively correlated with vegetation density, suggesting an important role for food supply, but Clark (1980) could not explain the seasonality of breeding there (Galapagos ship rats do not breed for five months or more of each year).

Mortality estimates calculated by Daniel (1972) of 93% per annum for non-commensal Orongorongo Valley females and 99% for males were similar to another estimate for ship rats in Puerto Rico (97%: Weinbren et al. 1970). If this short longevity is general for individuals in non-commensal populations, then the seasonal cycle of overall abundance is due primarily to seasonal breeding and recruitment followed by the rapid disappearance of each annual cohort as its members die without replacement until the following breeding season. The cycle will be blurred by fluctuations both in extended breeding and in increased longevity. Our five year study of kill-trapped ship rat populations at Pureora, and the eight-year live-trapping study of Daniel (1978), provide data series longer by far than any other published accounts in the world. Clearly the even longer unpublished studies undertaken by the former Department of Scientific and Industrial Research in the Orongorongo Valley, Wellington and on Mt Misery, Nelson, are uniquely long term projects whose results should be analysed and published.

Effect of trap type on captures

Fenn and rat traps showed the same trends of abundance for ship rats (Figs 2A,C), but rat traps caught significantly more young ship rats in age classes 1–2 (Table 2). In Fiordland, trapping success for kiore (*Rattus exulans*, range of body weights from 29 to 69 g, $n = 9$) was 47 times higher in rat traps than in Fenns (King & Moller 1997). Perhaps the older and heavier ship rats learned to avoid rat traps, or were less likely to be detained by them, or preferred the meat bait in Fenns. More importantly, the heavier trigger mechanism on Fenns probably selected against the lighter, younger animals.

Where rats are not abundant, large samples are needed in order to detect population changes. The total number of catches recorded, both at Pureora and in Fiordland, was much higher in Fenn traps than in the standard Supreme rat traps, since Fenns were set for longer. In Fiordland, highly significant post-seedfall increases in numbers of ship rats were detected by Fenn traps in both the Eglinton and Hollyford Valleys, which the rat traps, set in the

same areas on standard lines, missed altogether. Conversely, Fenn traps failed to detect the near-continuous presence of kiore in the Hollyford Valley since well before the seedfall (King & Moller 1997). Therefore, these authors concluded, it is important to allow for these differences when presenting detailed comparisons of population samples of rats collected by different methods.

At Pureora, Fenn traps again detected significant differences in ship rat abundance between seasons and years which were missed by rat traps, and only the Fenn traps detected the presence of Norway rats. However, we cannot say whether the heavier Norway rats escaped from rat traps, or were confined to streamside trapsites that were sampled by Fenns but not by rat traps.

Norway rats

Remarkably little is known or published about *Rattus norvegicus* in New Zealand, other than on islands. We are aware of no mainland study which has targeted them since that of Wodzicki (1950), and trapping at that time yielded only three Norway rats! Wodzicki's statements that "cornricks, cornfields, haystacks, barns and sheds, orchard stores, and homesteads" contain both *R. norvegicus* and *R. rattus*, while "River and stream banks and shores of ponds and lakes seem to be occupied almost entirely by *R. norvegicus*" are based on a questionnaire sent to "some 50" observers around the country. Our research at Pureora has therefore provided the only demographic account of a mainland *R. norvegicus* population, whether commensal or non-commensal.

The trapping of most Norway rats in streamside traps at Pureora is consistent with the general conclusions of Wodzicki (1950) and Watson (1961), that mainland non-commensal populations are relictual near water. By contrast, Norway rats range widely on islands such as Stewart (Hickson et al. 1986), Kapiti (Bramley 1999), and others in the eastern Bay of Islands (Moller & Tilley 1986) which are free of mustelids, especially stoats. In the 1840s–1870s, huge populations of Norway rats caused extensive damage on the mainland (Gillies 1878; Reischek 1930:251; King 1984:68–70). Taylor (1978, 1984) contended that, since then, Norway rats have been confined to their present limited distribution by the introduction of stoats in the 1880s. But the correlation between the historical decline of Norway rats and spread of stoats is confounded by the contemporaneous spread of ship rats, especially in the South Island (King 1984). Stoats do not seem to limit the broad-scale distribution of Norway rats in

UK (Corbet & Harris 1991; Tapper 1992) or of ship rats in New Zealand. On the local scale, Norway rats in commensal habitats such as waste landfills, or small streamside colonies with well-established deep burrows, might be able to avoid or defend themselves against stoats. Whether effective stoat control near these habitats would result in the expansion of Norway rats depends on whether Norway rats are also limited by competition with ship rats. Evidence from distribution patterns on islands and from size-based dominance relations suggests that Norway rats may limit ship rats, but not the reverse (Yom-Tov et al. 1999). These questions could be practicably tested by field experiments.

Interactions between ship rats and Norway rats are of interest because in historical time, ship rats have largely replaced Norway rats in non-commensal habitats in New Zealand (Atkinson 1973), whereas Norway rats have replaced ship rats in all habitats in U.K. (Watson, 1961; Yalden 1999). In U.K., ship rats now survive in any numbers only on a few offshore islands (McDonald et al. 1997), while in New Zealand non-commensal Norway rats seem to survive in patches on the mainland, but not in great abundance as on islands. Clearly, more long-term and detailed study of the Norway rat in New Zealand ecosystems is required, as noted by Moller & Tilley (1986).

Implications for conservation

At Pureora (altitude 550–700 m above sea level), the winter climate is severe; the average annual temperature for 1947–70 was 10.3 °C, with ground frosts on an average of 87 days a year. If ship rats living in podocarp forests can breed year-round in such conditions, they are probably capable of rapid recovery after control operations conducted at any season. However there is a clear seasonal peak in recruitment in summer and autumn, so it is likely that post-control recovery will be faster then. Most control operations against ship rats in New Zealand forests are conducted in spring, but even when rat densities were reduced by 90%, they recovered within 2–5 months (Innes et al. 1995).

If winter rat mortality is high and there has been no winter breeding, ship rat numbers may be low when North Island kokako start nesting in November (Innes & Hay 1995). However, results from projects comparing areas in which ship rats were reduced to varying degrees suggest that both the percentage of kokako pairs fledging young, and the percentage of nesting attempts which succeeded, declined rapidly and substantially when ship rat tracking rates

(indexed using particular techniques) exceeded 5% (Innes et al. 1999). In the absence of control, rat tracking rates in North Island broadleaved-podocarp forest are typically 40–80%, rarely as low as 15% (Innes et al. 1995, 1999). Our data have confirmed that ship rats are abundant and widespread at Pureora, and that, although rat abundance can vary greatly between years, even in 'low' years there are still too many ship rats for most kokako to nest successfully.

Our research has verified a pattern of demography of ship rats at Pureora which is also typical of non-commensal ship rats in other countries. There is a seasonal peak in breeding, high annual mortality (Daniel 1972), and year-to-year variation in total numbers controlled by some combination of food, predation and social limitation of breeding. Understanding these patterns better should assist in the development of rational and efficient strategies for ship rat control.

The conservation impact of Norway rats on mainland fauna is unknown, but at Pureora it can hardly be regarded as serious when they are apparently confined to small local colonies.

Future research

We suggest that the highest priority should be given to further (Blackwell et al. 1998) manipulative explorations of the key hypotheses already suggested by Daniel (1972, 1978) regarding the relative importance of predation and food supply as factors limiting ship rat abundance. More research which examines the actual impact of ship rats on New Zealand's native biodiversity, and the effectiveness of population control to reduce that impact, is also badly needed to improve the targeting and sustainability of pest control on the New Zealand mainland. Finally, much remains to be learned about the distribution, demography, ecology and conservation importance of Norway rats on the New Zealand mainland. Taylor's (1978, 1984) hypothesis that stoat predation limits Norway rat distribution and abundance could be tested directly by reversible removal experiments like those of Tapper et al. (1996), and documenting the consequences for the numbers and productivity of Norway rats.

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