

# Distribution and response of rats *Rattus rattus*, *R. exulans* to seedfall in New Zealand beech forests

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Ship Rats *Rattus rattus* were much more abundant in Silver Beech-dominated *Nothofagus menziesii* forest in the Hollyford Valley than in Red Beech-dominated *Nothofagus fusca* forest of the Eglinton Valley, northern Fiordland National Park, in 1974–78. The Hollyford also supported a small population of Kiore (Pacific Rat) *R. exulans*, but no Norway Rats *R. norvegicus*. A moderate beech seedfall in 1976 was followed by a short-lived, six to seven fold increase in a relative index of abundance of Ship Rats in both valleys. This increase, not matched by Kiore, showed up more clearly in long lines of Fenn traps set for Stoats *Mustela erminea* than in standard rodent snap-trap lines. Analysis of 122 carcasses showed a significant upward shift in age structure of Ship Rats after the seedfall, consistent with overwinter breeding. Conservation management programmes already aiming to protect threatened species in beech forests from post-seedfall irruptions of Stoats might need to be extended to include Ship Rats. Elsewhere in New Zealand, Ship Rats were much more abundant in mixed podocarp-hardwood forests than in pure beech or pine forests.

Key words: *Rattus rattus*, *R. norvegicus*, *R. exulans*, Population Structure, Habitat Preferences, Reproduction, *Nothofagus* Forest, Seedfall, Conservation, Predator Control, *Mustela erminea*.

## INTRODUCTION

THERE are three species of rats in New Zealand. The Kiore *Rattus exulans* is generally assumed to have arrived with Polynesian settlers between the ninth and 11th centuries AD (Atkinson and Moller 1990); the Norway Rat *R. norvegicus* with the first European explorers, whalers and sealers during the late 18th century (Moors 1990); and the Ship Rat *R. rattus* with European settlers from the mid-19th century onwards (Innes 1990). The Ship Rat is now the most widespread of the three, but only since about 1900. Kiore and Norway Rats have been, each in their turn, abundant on the mainland, but have declined since last century, and the locations of surviving populations are not well known.

Throughout the 1970s, the former DSIR Ecology Division conducted an extensive survey of the biology of the Stoat *Mustela erminea* in New Zealand national parks (King and Moody 1982). Fenn traps (humane steel spring type, described by King and Edgar 1977) set to collect Stoats also caught other animals, most often rats and Hedgehogs *Erinaceus europaeus*. The carcasses of Stoats and rats were returned frozen to the laboratory for analysis. Two of the best-documented survey areas, both in Fiordland National Park (southwestern South Island), provided samples that are, for several reasons, especially interesting.

1. There have been no extensive and systematic surveys of the distribution and biology of any species of rat in New Zealand. Nearly all of

the published information on Ship Rat population biology comes from the lower-latitude, low-altitude broadleaf/podocarp forests where rats are most abundant (e.g., Daniel 1978; Innes 1990), whereas the two samples described here came from areas dominated by Beech *Nothofagus* species where rats are generally scarce. In both study areas we had both Fenn and rodent traplines, so we could make independent relative density estimates for rats. The two sets of figures cannot be directly compared with each other, since the trapping regimes were different, but if they are both valid methods of monitoring the rat population they should report the same population trends. We collected data for four years spanning a range of expected population densities.

2. Heavy beech mast years are correlated with linked population irruptions of feral House Mice *Mus musculus* and Stoats (King 1982, 1983; Murphy and Dowding 1995; Fitzgerald *et al.* 1996), and consequent periods of increased predation on native biota (O'Donnell *et al.* 1996). It is not clear whether Ship Rats also respond to a heavy beech seedfall and so add to the predation damage caused by Stoats. Programmes to reduce the danger of predation by Stoats during irruptions are already operational (O'Donnell *et al.* 1996), but if there was firm evidence that rats also respond to seedfalls, conservation authorities would need to consider whether these programmes should be extended to include rats.

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3. Samples of Kiore from Fiordland are particularly valuable, because this is apparently one of the last mainland areas where they survive. The south-west of the South Island was also the last large wilderness in New Zealand to be colonized by Ship Rats and Stoats (Pascoe 1957:174), and it is also the last stronghold of several declining bird species such as the Mohua or Yellow-head *Mohua ochrocephala* (Elliott 1996) and the Yellow-crowned Parakeet *Cyanoramphus auriceps* (Elliott, Dilks and O'Donnell 1996).

### STUDY AREAS AND METHODS

The Eglinton and Hollyford Valleys, on either side of the Main Divide of the Southern Alps, support extensive forests of Southern Beech, mainly *Nothofagus menziesii*, plus *N. fusca* at low altitudes in the Eglinton. Fenn traps were set along both valley floors, according to a fixed schedule (14 days a month from June 1974 to March 1976, then 10 days a month until April 1978); for details and descriptions of study areas, see King (1980, 1983). Trap spacing varied from 100 m to 800 m during a series of field experiments from October 1974 to March 1976 (King 1980); at all other times the trap spacing was 400 m.

Fenn trapping was combined with monthly monitoring of beech seedfall and quarterly monitoring of rodent populations using standard rodent trap lines (following Fitzgerald and Karl 1979) to allow comparison with other studies of small rodents in New Zealand. A pair of wooden break-back traps (one each of rat- and mouse-size) was placed under cover at each of 36 trap stations spaced at 50 m intervals, and set for three nights every February, May, August and November, baited with peanut butter and rolled oats (Innes 1990: fig 42). The vegetation along the rodent trap lines was described by P. N. Johnson (in King 1982).

After correction for unavailable traps, the results were expressed as a relative density index, captures per 100 corrected trapnights (C/100CTN). Ship Rats, even when abundant, are seldom held in mouse traps (e.g., in Pureora Forest over five years, King *et al.* (1996) collected only three Ship Rats in 7 191 mouse trap nights, but 360 from 7 311 rat trap nights and 1 430 from 24 272 Fenn trap nights), so when presenting data on their abundance (Fig. 1, Table 8b), only the rat traps were counted as available. Kiore were as readily caught in mouse traps as rat traps (Appendix 1), so we counted both rat and mouse traps as available to catch them (see text below).

All captured rats were stored frozen, but not all are described here. The 21 Hollyford rats collected in September, October and November 1976 were destroyed in a freezer breakdown; six could not be used for certain analyses (e.g., some had data or body parts missing, or uncertain field

records); six collected in 1979/80 (King 1983) were omitted. The remaining 122 carcasses were processed by H. Moller and Allan J. Nixon at DSIR Ecology Division's laboratory in Lower Hutt. They recorded body size (whole weight, head-body and tail length) and reproductive data for all rats by the standard procedures (Cunningham and Moors 1993; Karl *et al.* 1984). Males were classified as reproductively active if they had visibly enlarged tubules in the cauda epididymis; in females, uterine scars (marking former placental attachment sites) and embryos (classed as live or resorbing) were counted, and the vagina scored as perforate or imperforate. The three distinct colour morphs of Ship Rats (*frugivorous*, brown back and white belly; *alexandrinus*, brown back and grey belly; *rattus*, black back and grey belly: see illustration in King 1990) were recorded separately. Age determination of Ship Rats was by Karnoukhova's index (illustrated in Innes 1990: fig 41). The age categories given by this method are relative only and can not be linked to chronological age. The results described in this paper replace the preliminary figures quoted by Innes (1990).

There was a moderate beech seedfall in the autumn of 1976, which strongly affected the population biology of House Mice and Stoats in Fiordland (King 1982, 1983). King (1983:159) reported the field data showing that rats also increased in numbers in 1976/77, especially in the Hollyford, and this paper adds details of their biology.

### RESULTS

#### Species distribution and abundance

The 122 rat carcasses collected from regular trap lines in the two Fiordland valleys comprised 114 Ship Rats, eight Kiore and no Norway Rats.

The eight Kiore came from the Hollyford Valley. Seven were caught in 2 598 corrected rodent (rat plus mouse) trapnights (0.27 Kiore/100CTN: 95% binomial confidence interval 0.15–0.56/100CTN), and only one in 17 074 corrected Fenn trapnights (0.006 Kiore/100CTN). There was no obvious increase in numbers of Kiore after the seedfall (Fig. 1b), and no significant difference between the capture rates in rodent traps in the year following seedfall compared with all other years combined. Necropsy data for these eight Kiore are recorded in Appendix 1.

Because Kiore are rare on the mainland, Appendix 1 also includes details of three Kiore collected from off the regular trap lines set in 1974–78. Two came from the Hollyford Valley, and the third from the Borland Valley in southern Fiordland, which is one of only five known mainland locations where Kiore have been recorded outside the Hollyford (for distribution see Atkinson and Moller 1990).

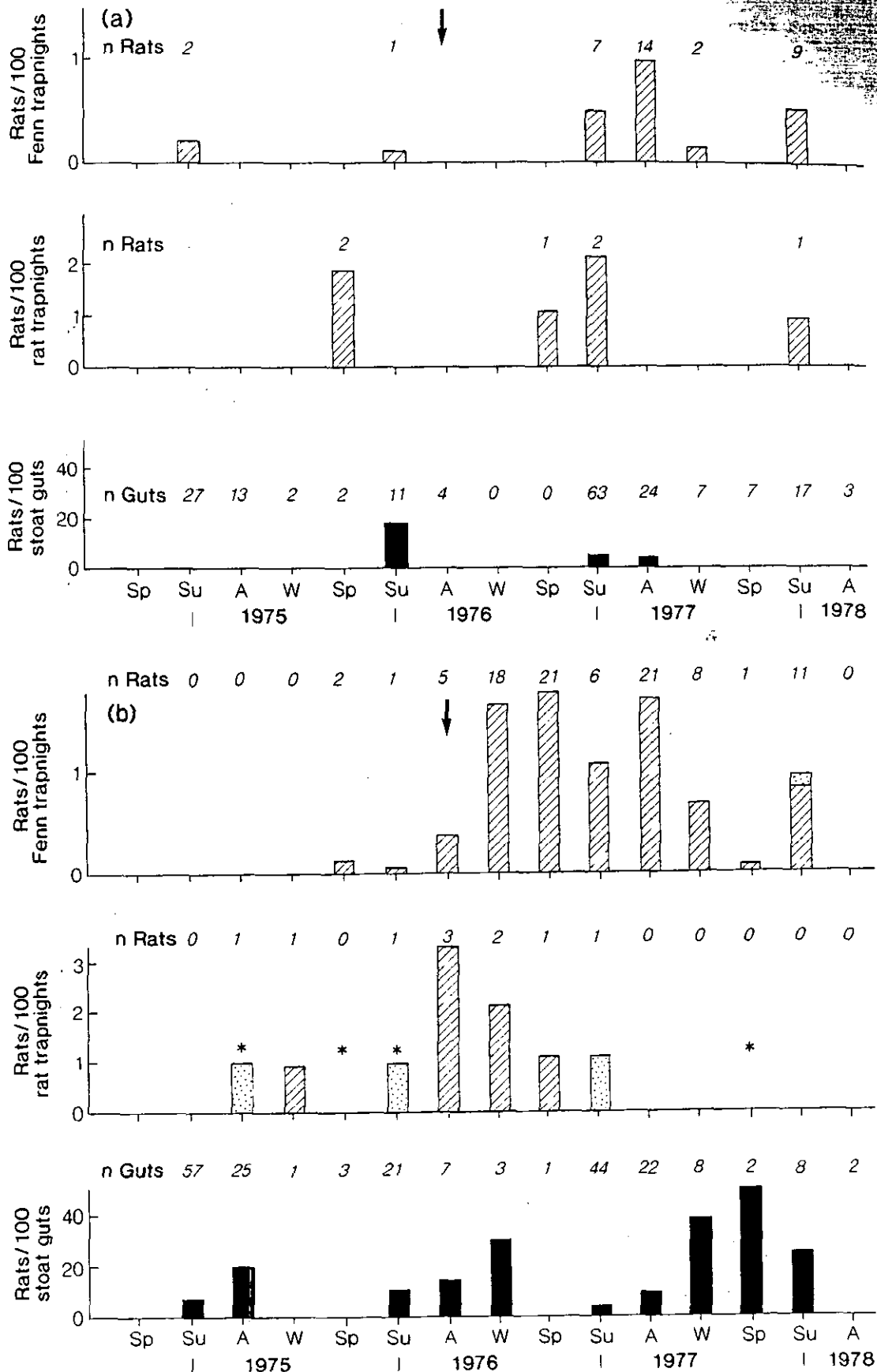


Fig. 1. Rats caught by Fenn traps (upper), rat traps (middle) and Stoats in the (a) Eglinton Valley, and (b) Hollyford Valley of Fiordland National Park. The beech seedfall of 1976 is indicated by an arrow. Asterisks represent the four Kiore *Rattus exulans* caught in mouse traps (Appendix 1). Hatched bars — *R. rattus*; spotted bars — *R. exulans*; black bars — unknown.

Table 1. Trap success for *Rattus rattus* in seed and non-seed years in the Eglinton and Hollyford valleys. The seed year was taken as August 1976 to July 1977. CTN = corrected trap nights. 95% binomial confidence intervals are given in brackets for all capture rates of  $>0.1/100$  CTN.

Trap type and area	Seed year	Non-seed years	All years combined	Fisher's Exact Test comparing seed and non-seed years P
Fenn traps, Eglinton	0.41 (0.26-0.60) CTN = 5 629	0.058 — CTN = 20 760	0.13 (0.07-0.16) CTN = 26 399	<0.0001
Fenn traps, Hollyford	1.46 (0.74-1.70) CTN = 4 671	0.23 (0.17-0.35) CTN = 12 403	0.57 (0.46-0.69) CTN = 17 074	<0.0001
Rat traps, Eglinton	0.72 (0.16-2.20) CTN = 413	0.20 (0.062-0.87) CTN = 1 486	0.32 (0.22-1.30) CTN = 1 899	0.121
Rat traps, Hollyford	0.49 (0.060-1.90) CTN = 405	0.42 (0.11-1.02) CTN = 945	0.44 (0.11-1.02) CTN = 1 350	1.000

Rats of either species were much less common in the Eglinton than in the Hollyford at any time (Fig. 1), although the difference was significant only in the Fenn traps, which were set monthly rather than quarterly (Table 1: rat traps, all years pooled,  $\chi^2 = 0.35$ , 1df,  $p = 0.7$ ; Fenn traps in seedfall year,  $\chi^2 = 31.97$ , 1df,  $p = 0.0001$ ; Fenn traps in other years,  $\chi^2 = 19.48$ , 1df,  $p = 0.0001$ ). In autumn, usually the peak of the annual cycle of numbers (Innes 1990), rats in the Hollyford Valley reached a quarterly density index of 1.70/100CTN (species and trap types pooled) in 1977, 12 months after the seedfall, compared with 0.52/100CTN in the autumn of 1976 and 1.0/100CTN in 1975: King 1983, table 2). The equivalent data for the Eglinton Valley were 0.99/100CTN, 0 and 0. The catch rates of *R. rattus* in Fenn traps were 6.3 and 7.0 times higher after the 1976 seedfall in the Hollyford and Eglinton, respectively, than in non-seed years (Fig. 1; Table 1). Hence the post-seedfall increases in numbers of Ship Rats detected by the Fenn traps were highly significant in both valleys, whereas according to the rat traps, there were no significant increases (Table 1).

There was a statistically significant decline in the number of rats caught per night as the Fenn trapping session progressed in both valleys, more so in the Hollyford than in the Eglinton (Fig. 2). There was a steady decline to about a third of the original capture rate by day 6, followed by a recovery to about half the original rate by day 10. The 14-day trapping sessions operated until March 1976 cannot add to these data as they coincided with the period when rats were rarely caught.

#### Ship Rat population structure

More males were caught than females, but not significantly so ( $\chi^2 = 1.458$ , 1df,  $p > 0.10$ ). More rats of the *alexandrinus* morph were collected than of the other two put together (Table 2).

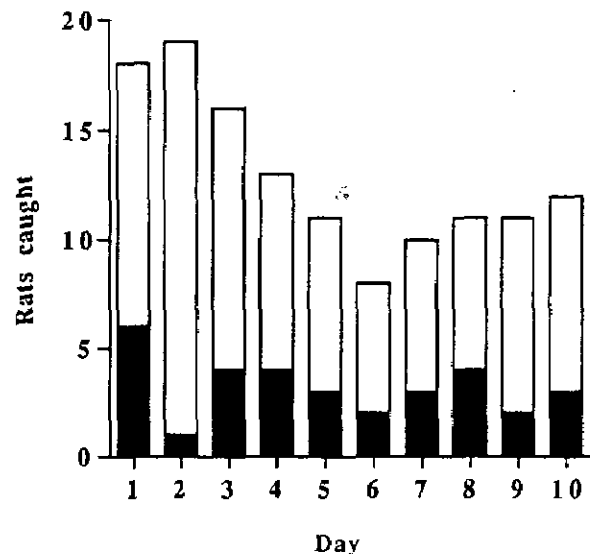


Fig. 2. Mean number of rats collected per day through each monthly Fenn trapping session in the Eglinton Valley (closed bars) and Hollyford Valley (open bars). All trapping sessions have been pooled. Spearman's rank correlation coefficient, for Hollyford and Eglinton combined,  $p = 0.0489$ .

Sex and morph proportions were not significantly different in the two valleys, so the catches are pooled in the following analyses.

Few rats were trapped before they reached age class 3; the modal age class was 4 (Fig. 3), and there was no evidence of any significant variation in sex ratio by age class ( $\chi^2 = 1.678$ , 4df,  $p = 0.795$ ; Table 3).

No age determinations are available for rats caught before December 1976, but from the summer of 1976/77 there was a seasonal shift in age classes in both sexes, reflecting the general ageing of the population (Table 3). The substantial fall in the capture rate of Ship Rats from the summer of 1976/77 to the following summer (Fig. 1) was accompanied by a significant shift to an older

Table 2. Distribution of sexes and colour morphs of Ship Rats by trap type in the two valleys. For colour photographs and national distributions of morphs, see King (1990).

Morph	Rat traps				Fenn traps			
	Eglinton		Hollyford		Eglinton		Hollyford	
	male	female	male	female	male	female	male	female
<i>frugivorous</i>	1	0	0	0	3	3	2	3
<i>alexandrinus</i>	3	1	0	0	6	8	26	18
<i>ratus</i>	0	0	0	0	10	5	14	8
total	4	1	0	0	19	16	42	29
$\chi^2$ , df					1.708, 2df (NS)		0.942, 2df (NS)	

Table 3. Distribution of Ship Rat age classes by sex and season, valleys and trap types pooled. Age classes are based on Karnoukhova's relative toothwear index as illustrated from New Zealand material by Innes (1990).

Age class	Season: Density: Sex:	Summer 76/77 High		Autumn 77 High		Winter 77 Declining		Spring 77 Low		Summer 77/78 Low	
		M	F	M	F	M	F	M	F	M	F
2		0	0	0	1	0	0	0	0	0	0
3		4	2	2	3	3	1	0	0	1	0
4		7	2	8	5	1	3	0	0	0	3
5		3	2	3	3	0	0	0	1	4	0
6		0	1	3	4	0	0	0	0	6	1
7		0	0	1	0	0	0	0	0	1	4
$\chi^2$ (M/F)		2.60		3.01		0.05		—		13.10	
df		3		5		1				4	
p		>0.05		>0.05		>0.05				>0.05	

Test comparing summer 1976/77 and summer 1977/78; 3 x 2 table;  $\chi^2 = 15.77$ ; 2df,  $p = 0.0004$ .

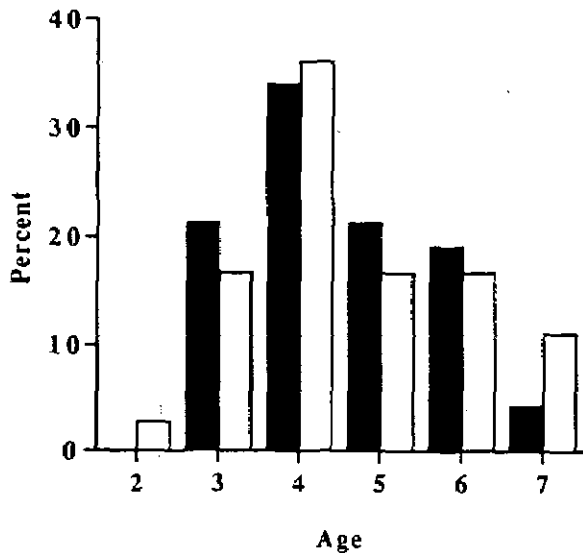


Fig. 3. Frequency distribution of tooth wear age classes assigned to Ship Rats from Fiordland National Park (Eglinton and Hollyford combined). Columns show the per cent of all male (closed bars) and female (open bars) Ship Rats caught that were classed within each of the age groups illustrated by Innes (1990).

age structure in the summer of 1977/78 compared with summer 1976/77 (Table 3).

**Growth, development and reproduction of Ship Rats**

The indeterminate growth of Ship Rats means that length and weight generally increase with age class (Fig. 4). The samples were too small to test for differences in body size between valleys or population densities while controlling for age

class and sex. Most rats were sexually mature, and some females had already bred by the time they reached age class 3 (Table 4).

If Ship Rats respond to good seedfalls by over-winter breeding, as do House Mice (King 1982), we would expect to observe the highest pregnancy rate during the winter and spring immediately following the seedfall; unfortunately the large sample of rats collected in Fenn traps during that crucial period was lost. But an unusual breeding pulse has consequences for the age structure and breeding rate of following samples, and these we can detect from our data. By the summer of 1976/77, five of the seven females caught already had visible uterine scars, i.e., evidence of having produced a litter in the winter or spring of 1976. The young born then appeared in summer 1976/77 as an influx of young rats of age classes 3 and 4 (Table 3). The pregnancy rate in that summer was 14%, but in the following summer (1977/78) it was 75% (Table 5). Comparisons must be limited, because we cannot deduce the real ages of these young and the samples are small; nevertheless, this difference was significant for all females pooled (Fisher's Exact test,  $p = 0.041$ ), though not significant ( $p = 0.21$ ) when only females with scars were considered. Females without scars were younger, so the lower overall pregnancy rate in the 1976/77 summer may simply reflect the younger age distribution and higher proportion of immature rats in that sample. No pregnant females were trapped in winter or spring 1977. Overall, 14 of 48 (29%) trapped females were pregnant. These data do not tell us anything

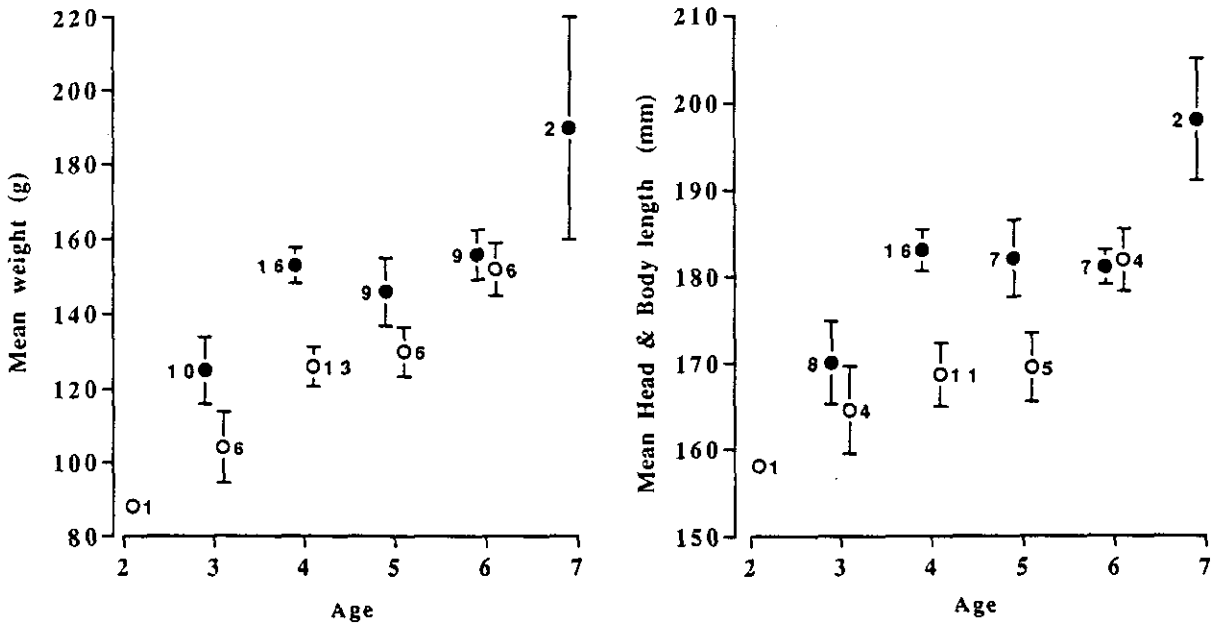


Fig. 4. Mean (a) weight and (b) head and body length of male (closed circles) and female (open circles) Ship Rats within each tooth wear age class (Eglinton and Hollyford combined). The error bar shows the standard error of the mean, and the number to the left (males) or right (females) of the circles is the sample size.

Table 4. Reproductive status in relation to age, Eglinton and Hollyford Valleys pooled. Rats without complete data omitted (including two pregnant females with age unknown).

Age class	Males			Females					
	n	Tubules visible	Tubules invisible	n	Perforate	Inperforate	Scars		Pregnant
							present	absent	
2	0			1	1	0	0	1	0
3	9	8	1	6	5	1	3	3	1
4	17	16	1	13	13	0	9	4	4
5	10	9	1	6	6	0	5	1	1
6	8	7	1	6	5	1 <sup>1</sup>	4	1	3
7	2	2	0	4	4	0	2	4	3
Totals	46			36					

<sup>1</sup>Closed secondarily.

Table 5. Numbers of females with embryos and/or scars in relation to density changes since the seedfall (see Fig. 1). Rats without complete data omitted. Eglinton and Hollyford Valleys pooled.

	Total females	Season									
		Summer 76/77		Autumn 77		Winter 77		Spring 77		Summer 77/78	
Scars		yes	no	yes	no	yes	no	yes	no	yes	no
Pregnant	12	1	0	3	2	0	0	0	0	3	3
Not pregnant	24	4	2	10	1	2	2	1	0	1	1
% pregnant		14		31		0		0		75	
n	36	7		16		4		1		8	

about the breeding of beech forest rats in a year uninfluenced by seedfall.

In the 13 pregnancies listed in Table 6, there was a total of 77 embryos, of which three (one in each of three females) were resorbing (mean 4% of embryos, 25% of pregnancies). The resorptions were recorded in December 1976, May 1977 and February 1978, i.e., they

were spread throughout the post-seedfall period. Two other pregnancies were recorded, in the Eglinton in November 1975 and in the Hollyford in April 1976, neither with any resorptions. Older rats tended to have more uterine scars (Fig. 5). One very old female (age class 7) had apparently had only one litter and was not pregnant when caught in January 1978 (Fig. 5).

Table 6. Mean number of live embryos and of uterine scars, in Ship Rats collected from the two valleys and in total.

	Hollyford			Eglington			Total		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
Live embryos	5.67	1.87	6	6.28	1.60	7	5.99	1.47	13
Scars	13.3	5.12	7	9.0	6.91	8	11.00	6.32	15

Table 7. Rats eaten by Stoats in the Hollyford Valley. Rat density data, integrating rodent and Fenn trap records, from King (1983). There was no correlation between the frequency of occurrence of rats in Stoat guts and the capture rate of rats, either in summer ( $\chi^2 = 0.245$ , 1df,  $p = 0.62$ ) or autumn ( $\chi^2 = 0.964$ , 1df,  $p = 0.33$ ).

Season	Year	Capture rate of rats (C/100TN)	Stoat guts containing:		% frequency of occurrence of rats (n)
			Rats	No rats	
Summer	1976/77	0.54	2	42	7.7 (52)
	1977/78	0.93	2	6	
Summer	1974/75	0	6	51	10.2 (78)
	1975/76	0.16	2	19	
Autumn	1977	1.70	2	20	9.1 (22)
Autumn	1975	1.0	5	20	18.8 (32)
	1976	0.52	1	6	

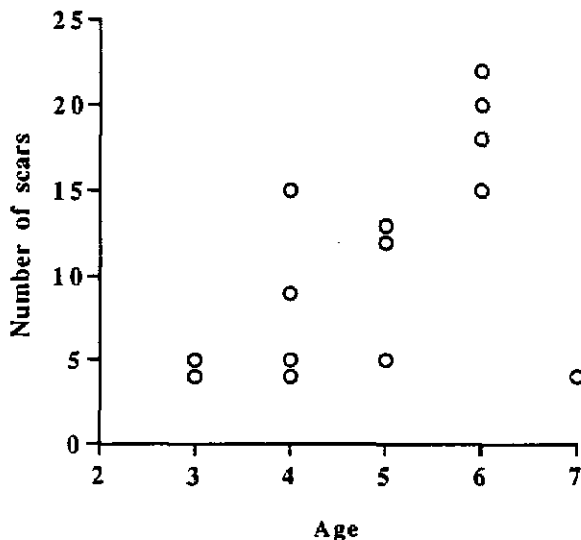


Fig. 5. Scattergram of the number of uterine scars of Ship Rats by tooth wear age class. All areas and seasons included. Spearman's rank correlation coefficient  $p = 0.066$ .

#### Predation on rats by Stoats

In the Eglington, Stoats ate rats (species unidentified) only in seasons when the traps showed that rats were present, but never frequently even then (Fig. 1a). In the summer of 1977/78, the year after the post-seedfall population crash of House Mice (King 1983), no rats were identified in Stoat guts, even though rats were still being caught in traps and House Mice had by then become scarce. Conversely, some rats were still being eaten even when House Mice were at their peak in the summer of 1976/77.

In the Hollyford, Stoats ate rats at all seasons, but only the summer and autumn samples were large enough to analyse (Fig. 1b). In the summers when rats were more common than usual, Stoats ate rats at about the same rate as in the summers when rats were scarce: likewise, Stoats did not eat rats significantly more often during the post-seedfall decline in the autumn of 1977 than during the autumns of 1975 and 1976 (Table 7).

#### DISCUSSION

##### Rat population structure, growth and reproduction

The few Kiore we collected are of particular interest because they represent the last survivors of the formerly abundant and widespread population of Kiore that disappeared after the European settlers and their animals arrived (Atkinson and Moller 1990). For the record, therefore, Appendix 1 lists the details of these individuals separately, but no analysis is possible.

For Ship Rats, the observed changes in age structure (Table 3) and in growth patterns (Fig. 4) confirm that the tooth wear index is correlated with age. The steady increase in size with age illustrates the need for caution before mean sizes can be used to infer the overall growth patterns of different populations which could have dissimilar age structures.

As in most rat populations, it is the rate of reproduction of females rather than of males that determines the productivity of the population: nearly all the males were reproductively competent (Table 4). Our data are consistent with information from more intensively studied rat populations from podocarp/broadleaf forests further north in New Zealand (reviewed by Innes 1990).

### Trappability of rats

In the Hollyford Valley, overall trap success for Kiore was 47 times higher in rodent traps than in Fenn traps. In the two Fiordland valleys, Fenn trapping yielded 6.3–7.0 times more Ship Rats per 100 corrected trap nights in the year after beech seedfall than in all other years combined (Table 1).

Although the Fenn and rodent trap lines were both set along the same roadsides, the short rodent trap lines (1 850 m) sampled much smaller areas than did the Fenn trap lines (15–20 km long). The rodent traplines also sampled some habitats more intensively than did the Fenns, e.g., the roadside verges which were well developed in the area of the trapline in the Hollyford, but virtually absent in the Eglinton (see P. N. Johnson, in King 1982). These data alone cannot distinguish whether (a) Kiore were caught less well by Fenn than by rodent traps under the field routines we used, or (b) Kiore happened to be more abundant in the areas where we chose to set rodent traps.

On the other hand, Kiore are much smaller than Ship Rats; all the Hollyford Kiore we recorded weighed <70 g (see Appendix 1), whereas all the Ship Rats except one young female of age class 2 were >100 g (see Fig. 4a). Kiore almost certainly set off the rat traps more readily than the heavier Fenn traps, as do the even smaller House Mice (15–20 g) which are much more often caught in rat traps than in Fenns. At Pureora Forest Park, Innes *et al.* (in prep.) found that the youngest Ship Rats (age class 1, averaging 41 g,  $n = 8$ ) were caught only in rat traps and not in Fenns. The Pureora Fenns also caught fewer young rats of age classes 2–3 than did rat traps, but the same proportion of older rats; hence the rats caught in Fenn traps were larger and heavier on average than rats caught in rat traps.

It is also possible that the fish baits used in Fenns were relatively more attractive to Ship Rats than the peanut butter and oat baits used in rat traps, at least in the food conditions prevailing in the seed year. Hence, the apparent correlation between seedfall and the capture rate of Ship Rats in Fenn traps, but not in rat traps, could be the result of an interaction between the availability of natural food (beech seed or insects) and the attractiveness of the trap baits. Experimental testing of this hypothesis would assist the development of accurate monitoring techniques for rats.

The net result is that, if we had been operating Fenn traps alone, we would have missed the near-continuous presence of Kiore in the Hollyford since well before the seedfall (Fig. 1). Conversely, a standard rodent line by itself would have missed the post-seedfall increase in Ship Rats in both valleys, or at most, reported it as insignificant (Table 1). These results raise questions about

whether standard rodent lines, operated without backup from Fenns, can monitor rat populations reliably.

It is important to compare capture rates and/or species ratios at different places and times only when the same trap types and layouts are used. For example, in Table 1 it is not possible to compare the capture rates of rats in different trap types, only the capture rates in seed and non-seed years in the same trap type. Likewise, we cannot conclude that rats did not respond to the seedfall in the two valleys after the following seed year of 1979/80, even though very few rats were caught then (King 1983), because no Fenn traps were set that summer. No direct comparison is possible between Table 1 and the data of O'Donnell and Phillipson (1996), who observed a heavy seedfall in the Eglinton Valley in 1990. They had 56 Fenn trap tunnels at 100 m intervals over a grid of 50 ha, in which the traps were set continuously from October to March, and recorded a capture rate of 0.03 rats/100CTN in the summer after the seedfall, but none in any other summer. They caught no rats on their two lines of 25 rodent trap stations at 25 m intervals, because all the traps were mouse traps.

The presence of one species can influence the movement patterns and trap response of smaller species: for example, in Brown *et al.*'s (1996) study in broadleaf forest in North Island, the trappability of House Mice increased sharply once *R. rattus* had been removed. Since Kiore are subordinate to Ship Rats (Atkinson and Moller 1990), their activity patterns and behaviour in our Fiordland study area may be different from that on the offshore islands where they live alone. We therefore emphasize the need for caution in deducing absolute proportions of the different rodent species from kill trapping results.

### Relative abundance of rats in different habitats

The 14 areas sampled throughout New Zealand over the four years 1972–76 (King and Moody 1982) represented most surviving native forest types, plus natural tussock grassland. A further survey covering logged and unlogged podocarp/hardwood forest plus pine plantations of various ages over five years (1983–87) at Pureora Forest Park (central North Island) used Fenn and rodent traps set out as in Fiordland (King *et al.* 1996).

Ship Rats were most numerous at three sites in dense podocarp-broadleaf or mixed forest in Egmont National Park, Westland National Park (only a fraction of the catch was sent in from either Park), and Pureora, and in Silver Beech forest with scattered podocarps in the Hollyford Valley (Table 8a). Smaller numbers were collected from pure beech forest near St Arnaud (Nelson Lakes National Park), and in the Eglinton and Borland Valleys. No rats were collected from

Table 8a. Distribution of rats caught in Fenn traps in relation to habitat. For descriptions of the Egmont, Westland and St Arnaud (Nelson Lakes National Park) study areas and locations of the 1973-76 trap lines see King and Moody (1982); for Eglington and Hollyford (northern Fiordland National Park) and Craigieburn (Canterbury) (1973-78 only), King (1983); for Borland and Grebe, southern Fiordland National Park (1979 only), King (1983 and unpubl.); and for Pureora (1982-87), King *et al.* (1986). Capture records are included even if the carcass was not analysed. NR: not recorded (general collections by National Parks rangers only, usually from 20 to 40 traps left permanently set). \*Rats from these areas were a bycatch of trapping for Stoats, and not all were sent in for examination. For distribution of their colour morphs, mean body measurements, etc., see Innes (1990, tables 38 and 39). Full details of the Pureora rats are given in Innes *et al.*, in prep., and of the Eglington and Hollyford rats herein.

Habitat	Study area	n CTN	<i>R. rattus</i>		<i>R. norvegicus</i>		<i>R. exulans</i>	
			n	C/100CTN	n	C/100CTN	n	C/100CTN
Podocarp/ broadleaf forest	*Egmont	NR	77	—	0	0	0	0
	*Westland	NR	45	—	0	0	0	0
	Pureora unlogged (line FU)	6 281	473	7.53	35	0.56	0	0
	Pureora logged (line FL)	7 746	658	8.49	8	0.1	0	0
Beech forest	Hollyford Valley <sup>1</sup>	17 074	97	0.57	0	0	1	0.006
	*St Arnaud	NR	44	—	0	0	0	0
	Eglington Valley	26 399	35	0.13	0	0	0	0
	Borland Valley	1 189	2	0.16	0	0	0	0
	Grebe Valley	1 165	0	0	0	0	0	0
	Craigieburn	27 404	0	0	0	0	0	0
Exotic forest	Pureora (planted 1978)	2 079	0	0	0	0	0	0
	Pureora (planted before 1966)	8 166	299	3.66	0	0	0	0

<sup>1</sup>with scattered podocarps.

Table 8b. Distribution of rats caught in rat (Supreme snap) traps in relation to habitat. For descriptions of the Eglington and Hollyford (northern Fiordland National Park) and Craigieburn (Canterbury) (1973-78 only) study areas, see King (1983); for Borland and Grebe, southern Fiordland National Park (1979 only), King 1983 and unpubl.; and for Pureora (1982-87), King *et al.* (1986). Capture records are included even if the carcass was not analysed. *R. norvegicus* are omitted because none was ever collected from a rat trap. Four Kiore caught in mouse traps omitted (see Methods).

Habitat	Study area	n CTN	<i>R. rattus</i>		<i>R. exulans</i>	
			n	C/100CTN	n	C/100CTN
Podocarp/ broadleaf forest	Pureora unlogged (line FU)	2 157	106	4.91	0	0
	Pureora logged (line RL1)	2 007	161	8.02	0	0
Beech forest	Hollyford Valley <sup>1</sup>	1 350	6	0.44	3	0.22
	Eglington Valley	1 899	6	0.32	0	0
	Borland Valley	310	3	0.96	0	0
	Grebe Valley	339	0	0	0	0
	Craigieburn	2 094	0	0	0	0
Exotic forest	Pureora (planted 1978)	2 156	2	0.09	0	0

<sup>1</sup>with scattered podocarps.

Craigieburn, a high-altitude (790-1 340 m) Mountain Beech forest sampled intensively over six years, or from the Grebe Valley, a low-altitude beech forest sampled in only one year; and only two from a young pine plantation at Pureora sampled over five years.

In systematic trapping along an altitudinal transect at Mount Misery (Nelson Lakes National Park), no rats were caught above the altitudinal limit for Red Beech (1 025 m asl). There was Red Beech in our Eglington (270-550 m asl) and St Arnaud (670-700 m asl) collection

areas where Ship Rats were present, but very little of it in the Hollyford Valley (90-370 m asl) where Ship Rats were abundant. These comparisons do not corroborate Innes' (1990) suggested correlation between the population density of Ship Rats and the proportion of Red Beech in a forest, nor the implied link with altitude. We caught no Ship Rats at high altitude at Craigieburn, but we suspect they are capable of reaching good numbers in the high-altitude mixed podocarp on Egmont (450-900 m), although we had no measure of trap effort from there (Table 8a).

Norway Rats were collected from only one habitat, native mixed podocarp and broadleaf forest at Pureora. Considering the massive Fenn-trapping effort invested to collect these samples, it seems reasonably safe to conclude that Norway Rats are now rare or absent in most mainland forests. Like Kiore, they are abundant in forest only on offshore islands (Moller and Tilley 1986; Moors 1990).

Even though all but one of the Kiore listed in Appendix 1 came from the Hollyford Valley, the discrepancies in trappability discussed above mean that we are unable to conclude that Kiore are absent from any of the study areas sampled by Fenn traps alone, or to estimate their relative abundance compared with Ship Rats in the Hollyford or Eglinton.

#### Responses of rat populations to beech seedfall

Kiore used to reach very high densities after seedfalls in South Island forests until about 1888 (Atkinson and Moller 1990:178), but in 1976/77 their response was scarcely noticeable. There are two possible explanations.

1. Kiore did increase in relative abundance in 1976/77, but the extent of their response was underestimated because (a) the standard transect monitoring technique is inappropriate for Kiore, or (b) they started from such low abundance that their peak density remained virtually undetectable.
2. The technique is reliable and the results can be interpreted to mean that the Kiore failed to respond to the 1976 seedfall as they used to do in the last century.

If the first is true, then we can say nothing more about Kiore from these data. If the second is true, we have to explain why Kiore have survived in the Hollyford Valley, co-existing with Ship Rats and House Mice for almost 100 years, in such small numbers, even after a seed year to which House Mice (King 1982, 1983) and Ship Rats (Fig. 1) responded notably. Perhaps competition with House Mice and/or Ship Rats is enough to curtail high densities of Kiore in contemporary forests (Taylor 1975, 1984), although predation by Stoats, feral Cats *Felis catus* and Ship Rats cannot be excluded as contributing factors. Whatever the explanation, the Hollyford Kiore population can apparently survive the increased competition and predation associated with seedfalls, since at least one Kiore was still living there in spring 1979 (Appendix 1).

We are confident that the increased density index for Ship Rats we observed from winter 1976 to autumn 1977 reflects a surge in their abundance. The steady shift in the age structure of the rats (Table 3) is consistent with a breeding pulse in winter and spring 1976 followed by a period of

reduced recruitment over the following summer, as in House Mice (King 1982). The implied correlation between the 1976 beech seed fall and the increase in Ship Rat capture rates in Fenns in both valleys (Table 1) should be confirmed from more replications of rat trapping before and after beech seedfall, but it is consistent with other studies. Rat abundance (measured by footprint tracking: King and Edgar 1977) in the Eglinton was markedly higher in the spring and summer of 1995/96 (following seedfall in autumn 1995) than in the previous year (C. F. J. O'Donnell, pers. comm.). Tracking tunnels also confirmed the presence of a large number of rats in beech forest at Maruia in February 1996 following seedfall in the preceding year (Alterio *et al.*, unpubl.). David Miller (pers. comm.) has lived on the edge of beech forest adjacent to Mt Aspiring National Park near Glenorchy for four decades. With the single exception of the 1995/96 summer, he has always trapped rats inside his house in the summer following a heavy seedfall, but never in the intervening years. C. F. J. O'Donnell (pers. comm.) reports captures of Ship Rats in Fenn traps in the Hawdon and Dart Valleys only in seedfall years, but not in other years. At Mount Misery (Nelson Lakes National Park), Ship Rat numbers increased significantly (from  $< 0.5$  to  $5.0$  C/100 trap nights) in Red Beech-dominated forests after a seedfall (R. H. Taylor, unpubl. data, quoted by Innes 1990).

Collectively these observations suggest that Ship Rat populations in beech forests respond to seedfall years in the same way that House Mice do, although the size of the post-seedfall increase may be dampened by predation if Stoats are not removed at the same time (King 1985). Daniel (1978) has also correlated Ship Rat densities with the seeding of various broad-leaved species in the Orongorongo Valley. On the other hand, Fitzgerald *et al.* (1996) have emphasized that, in beech forests at least, it may not be the seedfalls themselves but the associated pulses in abundance of litter-feeding insects that trigger rodent responses to good seed years.

Any increases in numbers of Ship Rats following good seed years will be additional to the predictable post-seedfall irruptions of Stoats, but preceding them. Stoats have a closely synchronized breeding season controlled by daylength (King and Moody 1982), and cannot produce independent young before December however much food is available. Hence early-nesting birds have a chance of producing at least one brood before the Stoat irruption reaches its highest level in January (Elliott 1996). Rats can react much more quickly to extra food supplies, and Figure 1 shows that the increase in the numbers of Ship Rats in the Hollyford was already substantial by the winter (August) quarter, before most birds had started breeding. The combined response of Ship Rats

and Stoats extends over the whole post-seedfall breeding season, compounding the risk to native biota until the numbers of both rats and Stoats have declined again. The higher mortality of Mohua and other hole-nesting birds associated with seed years has been attributed mainly to Stoats, especially since nest losses can be decreased by well-timed Fenn trapping (O'Donnell *et al.* 1996). Intensive Fenn trapping can also decrease local numbers of rats, at least temporarily (Fig. 2). Video filming at nests has challenged the reliability of the interpretation of "signatures" left at nests by Stoats and Ship Rats (Brown 1994; Brown *et al.* 1996). We agree with O'Donnell *et al.* (1996), that control of Stoats following heavy beech seedfalls, starting in October or November, might not be the only conservation management needed to protect hole-nesting birds in seedfall years. More research is needed to check whether rat control would also be advisable in the most critical areas, starting in July or August.

#### Consequences of rat control by Fenn trapping

We recorded a decline in capture rates through a Fenn trapping session until the sixth night, after which there was a slight resurgence (Fig. 2). The same pattern was observed in extensive Fenn trapping at Pureora Forest (Innes *et al.*, in prep.). Traps were not rebaited according to a regular schedule (e.g., on the sixth day) which could explain this pattern in our data. It probably means that the nearest or most trappable rats, usually considered to be the adult males (Moller and Craig 1987) were removed by continuous trapping, and were then replaced by "reinvansion", either by extension of the home ranges of surrounding residents (Innes and Skipworth 1982), or the arrival of rats from outside the area. Hickson *et al.* (1986) also detected a resurgence in poison bait take between five and eight days after poison was laid on Stewart Island. Collectively these studies demonstrate the effects of immigration in counteracting control operations.

When rats were poisoned at Mapara, a North Island forest conservation area, Stoats switched to birds (Murphy and Bradfield 1992). We have no evidence that the proportion of Stoats eating rats varied between seasons or years of relatively high rat abundance in Fiordland. In Fiordland generally, rats comprised under 10% by weight of the items identified in 383 Stoat guts (King and Moody 1982:69); even in the area with most rats, the Hollyford Valley, the frequency of occurrence of rats was seldom more than about 8-10% (Table 7). It seems that rats were not a predominant food

for Fiordland Stoats in the years we were sampling. The three most important items were birds, House Mice and insects, which together made up 54% of the diet by weight. All of these increase in abundance after seedfalls (Murphy and Dowding 1995).

King (1983:162) examined the suggestion that beech forest birds might be at increased risk from Stoats during and especially after post-seedfall summers. She concluded that the risk during a post-seedfall summer was substantial, but hypothesized that: "If sufficient effort is made to control stoats during a peak summer, then by autumn the few left, switching as usual to mice, may kill no more birds in total than after non-peak summers. If stoats are not controlled in the summer, there may be enough still present in autumn so that, even though they eat fewer birds each, the total number of birds killed may still be higher than after non-peak summers". This hypothesis was based partly on a well-documented seasonal switch in the diet of Stoats in autumn, from birds to House Mice (King and Moody 1982). There are no equivalent data for rats, but it would be interesting to know whether the incidental removal of Ship Rats during Fenn trapping for Stoats has an extra benefit for beech forest birds at special risk after a seedfall. Field experiments could test whether removing rats might confer sufficient conservation benefit to justify targeted rat control after a heavy seedfall in New Zealand lowland beech forests. Alternatively, a multi-predator poisoning technique that kills Stoats and Ship Rats in the same operation may add extra protection at little extra cost (Alterio 1996; Alterio, Brown and Moller, in press).

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## APPENDIX 1

Records of Kiore *Rattus exulans* collected in Fiordland. ED (Ecology Division) numbers assigned as described by Karl *et al.* (1984). P = preserved in alcohol, Ecology Division collection. Trap types: R = rat trap, F = Fenn trap, M = mouse trap. Three of the specimens listed (one from Murray's Dump and two from 1979) are not discussed in the present paper but are included here for the record.

Date	20 May	21 May	19 Nov.	14 Nov.	24 Feb.	25 Feb.	15 Feb.	29 Aug.	5 Jan.	14 Sep.	18 Sep.
Year	1975	1975	1975	1975	1976	1976	1977	1977	1978	1979	1979
ED number	—	—	1591	1592	1593	1594	1779	2465	1739	?	?1782
Trap type	R	M	M	F	M	R	R	M	F	M	M
Position	H9	H29	H29	Murray's Dump	H13	H30	H8	H22	H33	B11	H16
Sex	M	?	F	F	M	M	F	F	M	M	M
Body weight (g)	29.5	48.6	P	P	30.6	33.7	35.0	42.0	69.0	46.3	>50
Head-body length (mm)	215	262	P	P	P	P	226	229	270	243	264
Tail length (mm)	144	127	P	P	P	P	114	108	120	118	124

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