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DISTRIBUTION AND ABUNDANCE OF SMALL MAMMALS IN RELATION TO HABITAT IN PUREORA FOREST PARK

Summary: Populations of ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), feral house mice (*Mus musculus*), stoats (*Mustela erminea*), weasels (*M. nivalis*), and ferrets (*M. furo*) were sampled with killtraps every three months from November 1982 to November 1987 in logged and unlogged native forest and in exotic plantations of various ages at Pureora Forest Park, central North Island. Mice (n=522 collected) were fewest in unlogged native forest, more abundant in road edge cutover forest, and most abundant in a young (5-10 year old) plantation. Traps catching most mice were set in dense ground cover under a low, sparse canopy. Ship rats (n=1793) were absent from the young plantation, present but not abundant in older exotic forest, and abundant in all native forest regardless of logging history. Traps set on warmer, steeper sites caught most ship rats, and those set in early successional habitats caught fewest. There was a marked reciprocal relationship between the distributions of ship rats and of mice: the proportion of mice in the total catch of rodents decreased significantly at the least disturbed forest sites ($P < 0.001$). Most (81%) Norway rats (n=43) were caught in a single trap in unlogged native forest on the bank of a stream. Stoats (n=57) were most abundant in the older exotic plantations; weasels (n=16) in the young plantation and along road edges in native forest; and ferrets (n=11) in unlogged native forest. Hedgehogs (n=290) were common in unlogged native forest far from any roads and also in older exotic forest. Our data suggest that selective logging and conversion to exotics have different effects on each of the six species we monitored. We hypothesise that (1) selective logging is likely to stimulate temporary increases in the numbers of mice and weasels, but not rats or stoats, and (2) after conversion to exotic forest, mice and occasionally weasels will be abundant at first but will gradually be replaced by ship rats and stoats as the forest matures.

Keywords: Rodents; mustelids; cats; hedgehogs; distribution; abundance; habitat preferences; Pureora Forest Park; logging; exotic conversion; kokako; conservation.

Introduction

Pureora Forest Park, on the volcanic plateau of the central North Island of New Zealand west of Lake Taupo, supports a rich fauna of introduced small mammals. Three of the four rodent species known in New Zealand are present (*Rattus norvegicus*, *R. rattus*, *Mus musculus*), and all three mustelids (*Mustela erminea*, *M. nivalis*, *M. furo*), plus feral cats (*Felis catus*), hedgehogs (*Erinaceus europaeus*), hares (*Lepus europaeus*), rabbits (*Oryctolagus cuniculus*) and possums (*Trichosurus vulpecula*).

Leigh and Clegg (1989) reviewed the likely times of arrival at Pureora of the small mammals now living there. Norway rats probably arrived first, spreading inland from coastal settlements in huge numbers from the early 1800s. Ship rats followed, from the 1860s onwards. Less is known of the spread of mice; they were present in the Bay of Islands by about 1830, but were not widespread elsewhere until the turn of the century (Murphy and Pickard, 1990). These three have now replaced the

first rodent species to enter the forests, the Polynesian rat or kiore (*Rattus exulans*). Kiore arrived with the Polynesian settlers and had become very widespread by AD 1000, but disappeared from most of the North Island by about 1850-1860 (Atkinson and Moller, 1990). The dates of arrival of feral cats and the three mustelids are all undocumented, but any or all of them could have been present throughout the forest since the early twentieth century.

Rabbits and hares have been abundant in the adjacent farmland since at least the mid 1880s, but probably did not reach the park until forest clearing this century advanced close enough to provide them with suitable habitat nearby. Hedgehogs were uncommon in the district until the 1950s, and were, until this study, believed to avoid the forest interior.

The only reasonably precise data are for possums, which have been well observed not only because they arrived very recently but also because, until the fur industry declined in the mid 1980s, they provided a useful source of income for local

trappers. Possums were relatively slow to reach the central North Island; according to a 1968 survey, they were then still colonising most of the park except the Waipapa Ecological Area, which was one of the last patches of forest in the whole district still more or less free of possums at that date. Significant modification of the forest by possums has been observed only since 1978 (Leathwick, Hay and Fitzgerald, 1983).

Pureora Forest Park is an important conservation area because, among other things, it supports several remnant populations of threatened native fauna such as the North Island kokako (*Callaeas cinerea wilsoni*), whose populations are still declining (Meenken, Fechny and Innes, 1994). Competition with and predation by introduced mammals are probably the main causes of kokako decline (Innes and Hay, 1991).

This study aimed to document the local, seasonal and annual variation in distribution and abundance of all six species of rodents and mustelids, plus contingent observations on hedgehogs and feral cats. A secondary objective was to investigate more closely the habitat preferences of small mammals in relation to human disturbance of the forest, especially logging and road-building. This paper describes the field data concerning the abundance, distribution and habitat preferences of the small mammals sampled, so far as these parameters could be determined from the trapping records. In a series of companion papers we will describe the physical characteristics (measurements, population structure and reproduction) of the animals collected.

Methods

Study sites

Pureora State Forest Park is located in the ranges west of Lake Taupo, and covered 80,500 ha at the time of our study in 1982-7 (Fig.1). We chose three different habitats for study, an unlogged and unroaded native forest, a logged and roaded native forest, and an exotic plantation separated by roads into compartments of various ages. The "roads" were single-lane gravel tracks carrying perhaps 0-10 vehicles per day. Site characteristics are given in Appendix 1.

The study site in unlogged forest, located in the 4,000 ha Waipapa Ecological Area, was a stand of podocarp-hardwood forest dominated by tawa (*Beilschmiedia tawa*) with scattered to locally dense emergent conifers, mainly rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*) and

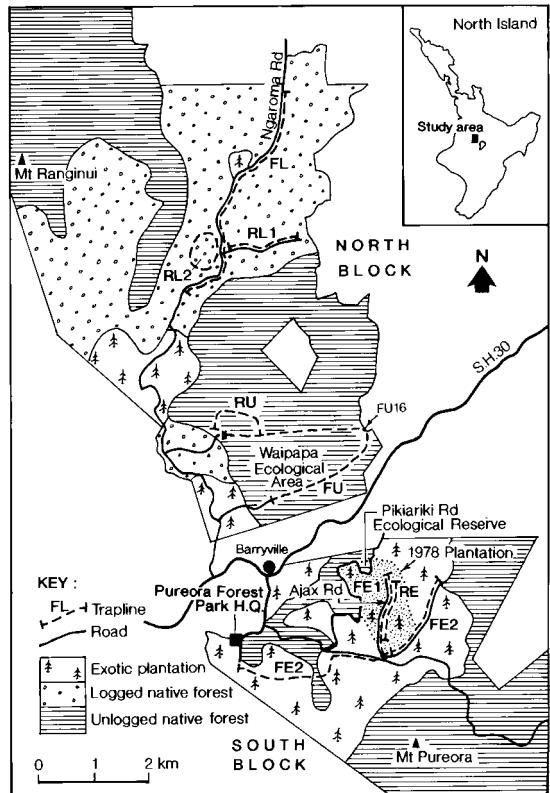


Figure 1: Map of the study area. Pureora Forest Park boundaries are shown as they were during the field work. The Forest Park Headquarters includes the Visitor Centre and the meteorological station. The former settlement at Barryville is now deserted except for the old sawmill (closed). Traplines are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

miro (*Prumnopitys ferruginea*). Common understorey plants were kamahi (*Weinmannia racemosa*), wheki (*Dicksonia squarrosa*), soft treefern (*Cyathea smithii*) and mahoe (*Meliccytus ramiflorus*). Treeferns and five-finger (*Pseudopanax arboreus*) were dominant in the lower-stature forest in the gullies.

The logged native forest study site was located adjacent to the Ngaroma Road to the north of the Waipapa Ecological Area, in more dissected country that originally had a lower density of podocarps than the flatter unlogged land to the south. The area was logged between 1939 and 1963, when almost all merchantable timber, mostly podocarps, was removed (McKelvey, 1963). The present forest has a semi-continuous canopy of tawa, hinau

(*Elaeocarpus dentatus*), kamahi and rewarewa (*Knightia excelsa*), with occasional relict conifers, especially miro. The most obvious signs of past logging in the forest today are the scarcity of large podocarps and the compacted, overgrown hauling and access tracks lined with tree ferns, lawyer (*Rubus cissoides*), putaputaweta (*Carpodetus serratus*), ferns (especially *Blechnum* species), small-leaved coprosma (*Coprosma rotundifolia*), bush rice grass (*Microlaena avenacea*) and hook sedges (*Uncinia* spp.) (Smale *et al.*, 1987). Roadsides and old landings are characterised by browntop (*Agrostis capillaris*), bracken (*Pteridium esculentum*) and toetoe (*Cortaderia fulvida*) which also provide a narrow band of dense cover along some road margins.

The exotic plantation study site located south of State Highway 30 once carried dense podocarp-hardwood forest, but was logged between 1950 and 1978 and then clear-felled, burnt or windrowed and

planted with exotic trees. The study site was in a large (724 ha) compartment of *Pinus radiata* planted in 1978, plus parts of older blocks of *Eucalyptus delegatensis* and Douglas fir (*Pseudotsuga menziesii*) east and south of it, which were planted in or before 1966. The young trees (Fig. 2) were thinned in March 1985 and November 1986 (to 245 stems ha⁻¹), and pruned in October 1986 to 4 m above ground level.

All study sites were within 20 km of the meteorological station at Pureora Forest Park Headquarters (NZMS station C85551, altitude 549 m). They were at altitudes ranging from 550 to 700 m asl, on podsolised yellow-brown pumice soils of the Tihoi series (Rijkse and Wilde, 1977). During the six years 1982 to 1987 inclusive, mean annual rainfall ranged from 1513 mm in 1982 to 1759 mm in 1986. The lowest mean annual temperature was 10.1 °C in 1983 and the highest was 10.9 °C in both 1984 and 1985. The normals for 1947-70 were 1829 mm of rainfall, and 10.3 °C annual temperature. Ground frosts were recorded on an average of 87 days per year, at any season, and snow on two days a year.

Trapping and estimates of animal abundance

Two types of trap line were established at each study site in November 1982 (Fig. 1, Table 1). All traps were set in wooden tunnels within 2 m of a permanent site marker and inspected daily. These trapline layouts are standard designs (Fitzgerald and Karl, 1979; King, 1983; illustrated in Innes, 1990), and, with some assumptions, give indices of abundance which are comparable between areas.

Two sizes of wooden break-back rodent traps (Supreme "Ezeset") were set in tunnels at each station on the rodent trap lines to catch rats and mice. Each was baited with peanut butter and rolled oats. They were inspected daily during four trapping sessions a year, in the last weeks of February, May, August and November. The rodent traps were always set for three nights per session. The wooden bases of new traps were soaked in linseed oil before first use, and the springs were oiled periodically. The ends of the rodent trap tunnels were covered with wire netting (5 cm mesh at the rat trap end and 3cm mesh at the mouse trap end) to exclude possums.

Fenn traps, a humane type of steel spring trap (King and Edgar, 1977), were set in tunnels and baited with fish-based catfood to catch mustelids. Fenns also catch rats, hedgehogs, feral cats, and possums, but from July 1984 we attempted to exclude hedgehogs, cats and possums by nailing two horizontal wires across the Fenn trap tunnel entrances.

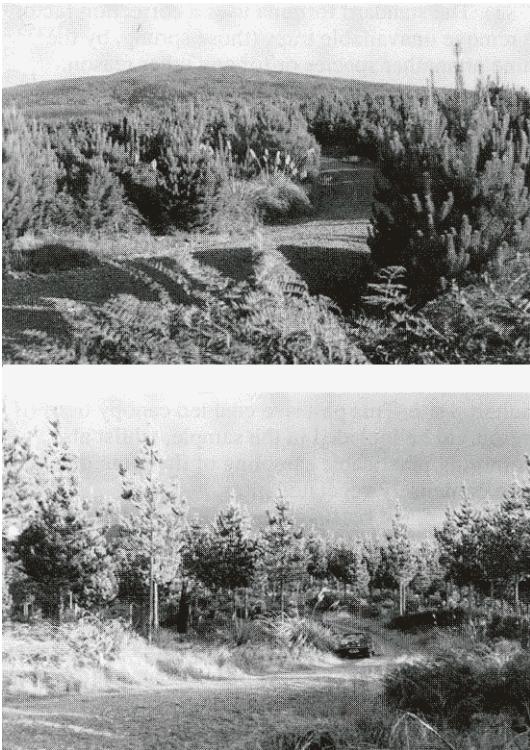


Figure 2: Photographs showing the growth of the pine trees, planted in 1978, along the RE line in the South Block. Pureora Mountain (1165 m) was visible in the background in February 1984 (above) but not in September 1987 (below).

Table 1: Configurations of trap lines. All rodent traplines were 1.85 km long with 36 sites at 50 m spacing and were set in the last weeks of February, May, August and November, but RL2 began later than the others and RL1 finished earlier. Fenn traplines all used 300m spacing and were set in the last weeks of January, April, July and October 1982-87 inclusive, but were of variable length depending on the extent of suitable habitat available.

HABITAT	UNLOGGED NATIVE FOREST		LOGGED NATIVE FOREST		EXOTIC FOREST	
	interior		interior	road edge	planted 1978	planted >1966
Rodent traplines	RU		RL2	RL1	RE	-
Dates set (inclusive)	Nov82-Nov87		Feb83-Nov87	Nov82-Feb85	Nov82-Nov87	-
Fenn traplines	FU	-	-	FL	FE1	FE2
Length (km)	9.9	-	-	11.4	3.0	12.6
N sites	32	-	-	39	10	41

Because ship rats were very abundant, and frequently caught both in rat and in Fenn traps, we are able to include here a comparison of capture indices derived both from rodent traplines and from Fenn traplines. The two types of traps sampled the same areas, and should indicate the same population trends even though they were set at different spacings, with different baits and in different months.

Traps which held only a clearly identifiable severed tail or foot were counted as having made a capture, provided another individual of that species with the same part missing was not later captured in the same area; traps holding tufts of fur were not so counted, but recorded as "sprung, empty". Also, a few captured animals were eaten by scavengers, or lost during storage, transit or processing.

Rats often set off mouse traps, and three rats were held by them (Table 2), but most escaped. The mouse trap-nights were therefore not counted as available for catching rats. Mice were regularly caught both in mousetraps and in rat traps (Table 2), so in calculating local and seasonal capture data for mice, the records for both trap types were pooled. Hence, there were twice as many trap-nights available to catch mice as there were to catch rats.

The total number of trap-nights set was higher for Fenn traps (25 864) than for rodent traps (15 552). After making allowances for sprung traps, the total numbers of trapnights available to the animals were 24 272 and 14 502 respectively (Table 2). Fenn traps also sampled a much larger area, because mustelids are much scarcer and range much further than rodents. Each rodent trapline had more traps in total than each Fenn line, but rodent traps were set for fewer days per quarter.

Abbreviated labels for each trapline indicate the trap type (R for rodent traps, F for Fenn traps) and habitat (U for unlogged, unroaded; L for logged, roaded; E for exotic). Logged forest was sampled both along roadsides (L1) and in the interior (L2),

and exotic forest was sampled both in the young compartment planted in 1978 (E1) and in older ones planted in 1966 or before (E2).

Field records were expressed as indices of abundance, i.e., numbers of captures per hundred trapnights ($C/100TN$: Cunningham and Moors, 1983). The standard formula uses a correction factor to remove unavailable traps (those sprung, by the same or another species or for any other reason, from the total number of trapnights), which means that the capture data for each species are independent of those for any other species. Worked examples are given by Cunningham and Moors (1983) and King, O'Donnell and Phillipson (1994).

Description of vegetation and other trap site attributes

We used a modified reconnaissance plot (Allen and McLennan, 1983), of roughly 15 m diameter centred on the trap location, to describe the vegetation at each trap site. This plot size enabled canopy trees (if present) to be included in the sample, whilst also permitting practicable sampling of the ground cover even on densely vegetated plots.

We defined six height tiers (20m+ emergent, 12-20 m, 5 - 12 m, 2 - 5 m, 0.3 - 2 m, < 0.3 m). We visually estimated cover abundance for each species in each height tier, using 6 of the 7 classes of Bailey and Poulton (1968), i.e. 2, 1-5%; 3, 6-25%; 4, 26-50%; 5, 51-75%; 6, 76-95%; 7, 96-100% (excluding species with a percent cover of less than 1 in any tier). We consider that the omission of the latter category is unlikely to have affected the outcome of the analyses because rodents in New Zealand typically eat a wide range of foods. For traps less than 15 m from a road, we truncated the plots at the road edge. We estimated the mean height of the tallest plants, and canopy cover (proportion of sky blocked by vegetation over 1.35 m high), by eye.

Table 2: Total number of captures recorded (including identifiable escapes) in each area by trap type and species. Trap types: M, mouse trap; R, rat trap; F, Fenn trap.

HABITAT	UNLOGGED NATIVE FOREST interior	LOGGED NATIVE FOREST interior	road edge	planted 1978 RE, FE1	EXOTIC FOREST older plantings FE2	TOTAL
Trap line	RU, FU	RL2	FL, RL1			
Mouse						
M	20	59	58	222	-	
R	14	9	11	125	-	
F	0	0	3	1	0	522
Ship rat						
M	1	1	1	0	-	
R	106	161	91	2	-	
F	473	-	658	0	299	1793
Norway rat						
R	0	0	0	0	0	
F	35	-	8	0	0	43
Stoat						
R	0	1	0	0	0	
F	10	-	15	1	30	57
Weasel						
F	0	-	7	3	6	16
Ferret						
F	5	-	4	0	2	11
Cat						
F	4	-	1	2	1	8
Hedgehog						
F	95	-	8	22	165	290
Grand total captures						
M	21	60	59	222	-	
R	120	171	102	127	-	
F	622	-	704	29	503	
All traps						2740
Total trapnights available (corrected for sprung traps, see Methods)						
M	2160	1969	977	2085	-	7191
R	2157	2007	991	2156	-	7311
F	6281	-	7746	2079	8166	24 272

For each trap site, we calculated an importance value for each species by summing the cover values in each tier but weighting upper height tiers to be more important - i.e., using the log (base 10) of the tier height as tier weights, scaled to bring the minimum weight (for tiers 6 and 7) to 1. The final weightings were: tier 1 (20 m+ emergents), 4.95; tier 2, 4.39; tier 3, 3.70; tier 4, 2.50; tier 5, 1.58; tiers 6 and 7, 1.00. We then performed separate ordinations for indigenous and exotic forest sites, using the technique of detrended correspondence analysis (DCA) as implemented in the program CANOCO (ter Braak, 1987a,b). This technique produces simultaneous ordinations of plots and species summarising the principal gradients in floristic

variation. These were then used to examine overall patterns of trap success in relation to floristic composition, independent of trapline, using multiple regression to relate catches to scores for each site from their respective ordination axes. The resulting regressions were then used to calculate contours of predicted trap success across each ordination space.

Environmental factors we examined were: altitude, aspect, slope, physiography (a 9-unit classification after Dalrymple, Blong and Conacher, 1968), drainage (a 6-unit classification of Taylor and Pohlen, 1970) and the relative contribution to ground cover of live vascular vegetation, non-vascular vegetation, forest litter, exposed soil and exposed rock.

We recorded the distance from each trap to the nearest road, and to small mammal escape cover (any cover which would shelter a small mammal from a predator hunting by sight, e.g., a hollow log or dense vegetation) in three classes, < 1 m, 1 to 3 m, > 3 m.

We surveyed all vegetation between May and September 1985. Because the young pine trees were growing so rapidly (Fig. 2), the 1978 plantation was surveyed again in December 1987 - January 1988. Data from the 1987-88 survey are presented here for line RE.

Relationships between trap success and site attributes

We tabulated mean values of trap success (captures per 100 trapnights, $C/100TN$) by species, line, year and season, testing the effects of year, season and the interaction between year and line by analysis of variance (ANOVA). Because the distribution of $C/100TN$ was clearly positively skewed, we transformed the data to $\log(C/100TN+1)$ first. We tested for differences between lines, although inferences regarding the habitat in which each line was placed should be made with caution. There was no true replication of traplines within habitats, for two reasons. First, in a complex environment such as Pureora, all potential replicate areas are slightly different; and second, replicate traplines for wide-ranging species such as mustelids demand more space and effort to operate than we had in the habitat and time available.

We examined the relationships between the recorded trap success for each species (as measured by mean $C/100TN$) and the attributes of the trap sites, treating indigenous and exotic sites separately. We considered categorical site attributes such as vegetation floristics (as summarized by the first two axes of the ordination analysis), vegetation structure (canopy height and density, vegetation cover abundance by tier), environmental variables (drainage, aspect, altitude, slope, physiography, ground cover densities), and other factors (distance to escape cover and to nearest road), and tested their distributions with ANOVA (for definitions of these terms, see Appendix 1). For attributes measured by continuous or ordinal variables, we calculated Spearman rank correlation coefficients between site attributes and trap success. Finally, we obtained multiple regression equations incorporating all significant site attribute variables.

We used the General Linear Model Procedure (PROC GLM) of SAS and the generalised linear model procedures in GENSTAT. We used a split-plot analysis of covariance to analyse each of the

variables of interest (trap line, season, year etc). 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 each of the main habitats of interest were represented by single trap lines 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 line interaction. Other factors were tested against the residual error. Least significant differences (LSDs) were used to detect significant (at $P=0.05$) differences between adjusted means. The raw data are available on request from MOK.

Most of the variables could be analysed adequately with PROC GLM, but 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.

Nomenclature for plants follows Allan (1961), Moore and Edgar (1970), Healy and Edgar (1980), Webb, Sykes and Garnock-Jones (1988), Connor and Edgar (1987), Brownsey and Smith-Dodsworth (1989); for birds, OSNZ (1990); and for mammals, King (1990).

Results

The total catch of small mammals

A total of 2740 captures was recorded, distributed between species, main habitat types and trap types as shown in Table 2.

Vegetation of trap sites

Tall podocarps were recorded near the trapsites only in unlogged forest (lines RU and FU). These sites were overshadowed by high emergents (mean 32 m), and dense vegetation in the 20m+, 12-20 m and 5-12 m height tiers. Trapsites in logged forests of lines RL2, RL1 and FL were under lower canopies (15-19 m) and had less vegetation in the 20m+, 12-20 m and 5-12 m tiers, but more in the 2-5 m tier (Appendix 1).

At trapsites in the young *P. radiata* plantation (RE and FE1), mean canopy height and cover increased rapidly throughout the study. Canopy height was 6 m at the time the vegetation survey was

done in December 1987, and 14 m under the older exotics along line FE2. Canopy cover was sparse in the young plantation, especially in the earlier years (Fig. 2).

Ground cover type was similar in all forests, with growing vegetation and leaf litter together making up on average 99% of cover (Appendix 1).

These variations in floristic composition across the trap sites are summarised in Figs. 3 and 4. The close intermingling of plots on the ordination of trap sites in indigenous forests (Fig. 3) indicates strong similarities in floristic composition between all the lines set in indigenous forest. However there is a degree of separation between the road edge sites in

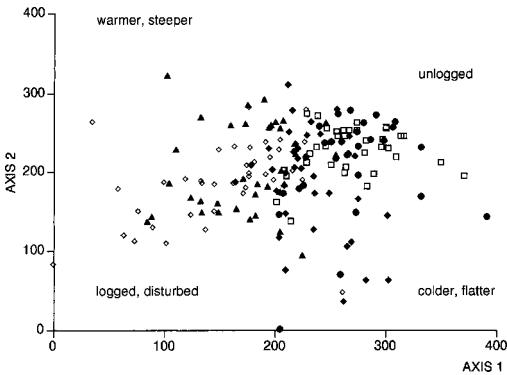


Figure 3: Ordination plot for trap sites in indigenous forests. Key: hollow diamonds, trapline FL; solid triangles, RL1; solid diamonds, RL2; hollow squares, RU; solid circles, FU.

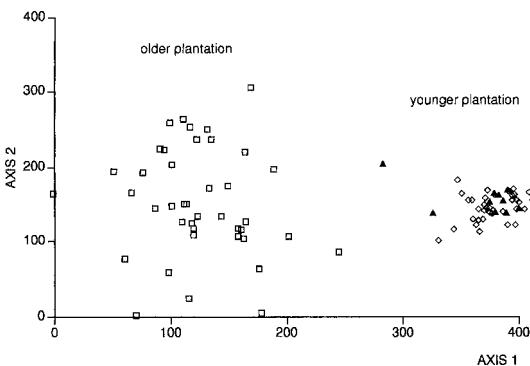


Figure 4: Ordination plot for trap sites in exotic forests. Key: hollow squares, FE2; solid triangles, FE1; hollow diamonds, RE.

logged forest (lines RL1, FL) on the left of the ordination, through the non-road edge sites in logged forest (line RL2) in the centre, to interior sites in unlogged forest (lines RU, FU) in the centre and right of the ordination. By contrast, the ordination of exotic sites gives a clear floristic separation between the 1978 *P. radiata* block (lines RE and FE1 on the right of Fig. 4) and the older Douglas fir and eucalypt compartments (line FE2, on the left of Fig. 4). The relationships between floristic composition and trap success are described in more detail below.

Distance to escape cover and road

There was cover suitable to hide a small mammal from a visually searching predator within one metre of most traps on all lines except FU (21% within one metre) and RL2 (36%: Appendix 1). Along the road edge lines (RL1, FL, RE, FE1 and FE2) traps were 6–12 m into the forest, well clear of the dust and immediate road edge disturbance but within or close to the zone of distinct road edge vegetation. The three forest interior lines (RU and FU through the Waipapa Ecological Area, and RL2 off the Ngaroma Road: Appendix 1) each started and finished near a road, but the average distance to the road of sites on these lines was >400 m. The importance of these two factors for each species is examined below.

Local, annual and seasonal variations in density indices for small mammals

Mice

Analysis of trapline catches showed that there were fewest mice in unlogged forest, more in logged native forest (especially along the road edge), and by far the most in the 1978 *Pinus radiata* plantation (Fig. 5; Table 3). The proportion of mice in the total catch of rodents decreased significantly on the least disturbed lines, i.e., those furthest from roads or without a history of logging ($P < 0.001$).

The habitat preferences of mice examined in relation to trap site attributes confirm the broader patterns suggested by the simple between-line comparisons. The correlation coefficients in Table 4 show that on the indigenous forest lines, more mice were caught near roads, at sites with low canopy height, and in valley floors or on footslopes. In the logged forest interior (line RL2), most mice were caught where escape cover was close, canopy cover was sparse, and vascular ground cover (mostly weeds) was dense.

There were also significant negative correlations with both ordination axes, showing highest captures on the most disturbed sites (Fig. 6). We interpret this ordination space as follows. Trapsites falling to the

lower left of Fig. 3 support vegetation including species falling mostly in the lower left of Fig. 6a. These are typical of disturbed sites, particularly old landings and hauling-tracks such as the one along which line RL1 was set, e.g. *Peridium esculentum*, *Holcus lanatus*, *Agrostis capillaris*, *Erica lusitanica*, *Leptospermum scoparium* and *Aristotelia serrata*. Mouse capture rates at these sites were the highest of any in indigenous forests (Fig 6b).

By contrast, plant species such as *Weinmannia racemosa*, *Cyathea smithii*, *Melicytus ramiflorus*, *Elaeocarpus dentatus*, and *Dicksonia squarrosa*, which are widespread both in logged and unlogged forests, fall in the centre of Fig. 6a. Those which are typical of warmer sites, such as ridges with good cold-air drainage, e.g. *Cyathea dealbata*, *Hedycarya arborea*, *Knightia excelsa* (Leathwick, 1987) are

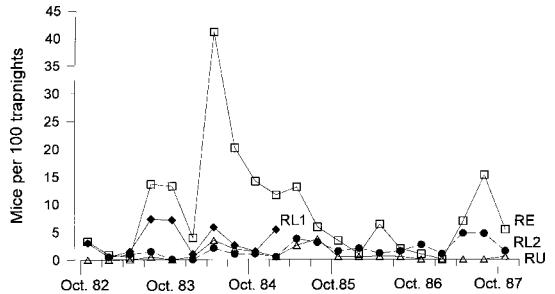


Figure 5: Density indices (C/100TN) for mice through the five years, along traplines RL1 (logged forest road edge), RL2 (logged forest interior), RU (unlogged forest interior), and RE (exotic forest, as illustrated in Fig. 2).

Table 3: Local variation in five-year means of capture rates (captures per 100 trapnights) of all species by area. Values in any row followed by the same letter do not differ significantly at P=0.05; rows without letters were not tested because of small sample size. All means are controlled for all other variables using the General Linear Model (GLM).

Line	UNLOGGED	LOGGED		EXOTIC	
	RU, FU	interior RL2	road edge FL, RL1	1978 RE, FE1	older FE2
Mouse	0.79 a	1.71 b	3.51 c	8.18 d	-
Ship rat					
Rat traps	4.91 a	8.02 b	9.18 ab	0.09 c	-
Fenn traps	7.53 a	-	8.49 a	0 c	3.66 b
Norway rat					
Rat traps	0	0	0	0	-
Fenn traps	0.56 a	-	0.10b	0 c	0 c
Stoat	0.16 a	-	0.19 ab	0.05 a	0.37 b
Weasel	0	-	0.09	0.14	0.07
Ferret	0.08	-	0.05	0	0.02
Feral cat	0.06	-	0.01	0.10	0.01
Hedgehog	1.51 ab	-	0.10 c	1.06 b	2.02 a

Table 4: Relationship between abundance of mice (C/100TN) and trapsite attributes on four trap lines in three habitats. Spearman rank correlation coefficients range from -1 to +1. * P<0.05; ** P<0.01.

SITE ATTRIBUTE	RU	RL2	RL1	ALL INDIG.	RE
Physiography	0.08	0.30	0.25	0.31**	0.13
Drainage	0.08	-0.10	-0.22	-0.01	0.00
Altitude	0.07	-0.27	-0.19	0.05	-0.07
Slope	-0.07	-0.30	-0.04	-0.01	0.25
Distance to escape cover	0.14	-0.43**	-0.02	-0.11	-0.29
Distance to road	-0.20	-0.23	-0.30	-0.39**	0.18
Canopy cover	-0.20	-0.49**	0.17	-0.13	0.09
Vascular ground cover	0.05	0.64**	0.20	0.20*	0.24
Canopy height	0.23	-0.35*	0.42*	-0.36**	0.09
Cover abundance, 2-5m tier	0.01	0.17	0.30	0.20*	0.13
Cover abundance, 0.3-2m tier	0.03	0.18	0.15	0.15	0.43**
Cover abundance, 0-0.3m tier	0.04	0.50**	-0.11	0.02	-0.02
Axis 1	-0.13	0.03	-0.49**	-0.34**	-0.39*
Axis 2	0.05	-0.57**	-0.42*	-0.37**	-0.30

found in the upper left of Fig 6a. These species grow both within enclaves of untouched forest in logged areas, and in more extensive stands of unlogged forest in the more dissected hills free of cold-air pondage to the west and northwest of the Waipapa Ecological Area. Conversely, species such as

Podocarpus totara, *Eleocharis hookerianus*, *Pruinosopitys ferruginea*, *Quintinia serrata*, and *Griselinia littoralis*, which are most common on the colder, frosty sites in the extensive flat areas of unlogged forest in the centre and east of the Waipapa Ecological Area, fall to the right. Mouse

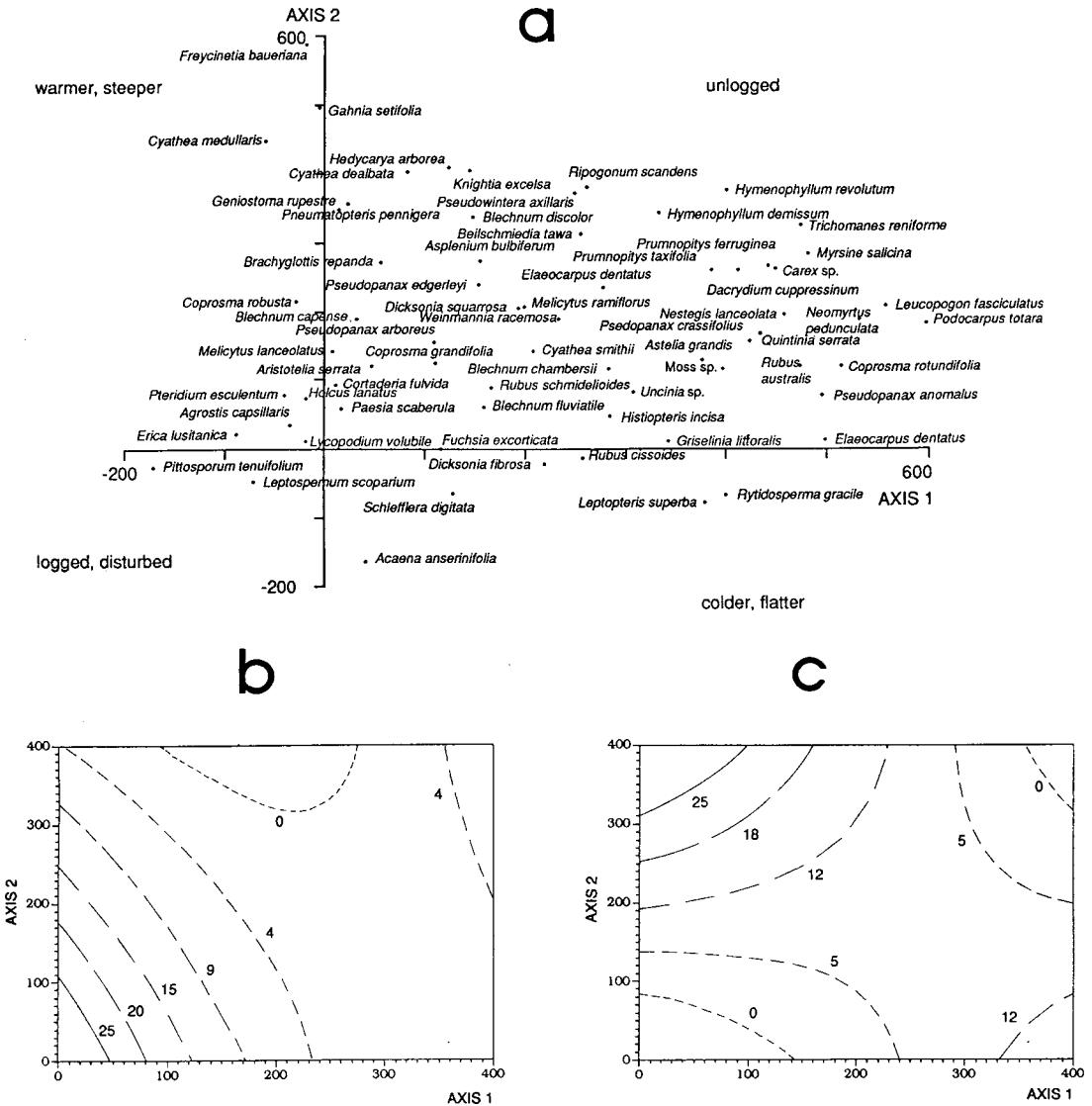


Figure 6: (a) Ordination plot for plant species growing within 15 m of traps set in indigenous forests. (b) The relationship between the vegetation ordination and the density indices of mice (0-25 C/100TN). (c) The relationship between the vegetation ordination and the density indices of ship rats (0-25 C/100TN). Plant and animal species which are closely associated in ordination space will also be closely associated on the ground. The environmental interpretations (e.g., logged, disturbed) of Axis 1 are derived from the positions along the axis of species with known site preferences.

capture rates in association with all these species were intermediate to low (Fig 6b).

In the young pine plantation (line RE), most mice were caught under thick cover of 0.3-2m tier vegetation. No mouse traps were set in the older exotic forest, but if mice had been as abundant there as in the young plantation, some would certainly have turned up in the Fenn traps. Table 2 shows that one mouse was caught in 2079 Fenn trap-nights in the young plantation; in the older exotics, four times as many Fenn trap-nights (8166) produced no mice. Together with the above analysis of habitat preference, these data suggest that mice do not favour exotic forest after the canopy has closed and the ground cover has declined.

The abundance indices for mice varied substantially from year to year (Table 5). The peak capture rate, 41.1 C/100TN in the young plantation

in May 1984 (Fig. 5), was by far the highest recorded in any habitat in this study, although it has been exceeded elsewhere both in pine plantations and in beech forests (Murphy and Pickard, 1990). The abundance of mice in the other areas varied much less from year to year, but the variance between areas was still significant even when controlled for year (Table 5). Mice were significantly more abundant in autumn and winter than in summer (Table 6).

Ship rats

Both Fenn and rodent traplines showed that rats were more abundant in native forest, logged or not, than in exotic forests of any age (Table 3). Within native forest (Figs. 7a and 7b), there was no significant difference between capture rates on the road edge (line RL1) and in the interior of the forest

Table 5: Annual variation in five-year means of capture rates (captures per 100 trapnights) of all species (excluding November 1982, and also line RL1 which was not run the full five years). Values in any row followed by the same letter do not differ significantly at $P=0.05$; rows without letters were not tested because of small sample size. All means are controlled for all other variables using the General Linear Model (GLM).

	1983	1984	1985	1986	1987
Mouse	2.53 a	6.86 b	4.13 b	1.55 a	3.27 ab
Ship rat					
Rat traps	3.93 a	3.31 a	5.91 a	4.02 a	3.98 a
Fenn traps	4.46 ab	4.06 a	8.59 c	5.71 bd	7.08 cd
Norway rat					
Rat traps	0	0	0	0	0
Fenn traps	0.09 a	0.28 a	0.22 a	0.15 a	0.15 a
Stoat	0.44 a	0.14 b	0.20 b	0.11 b	0.24 ab
Weasel	0.09	0.04	0.11	0.02	0.06
Ferret	0.04	0.08	0	0.06	0.04
Feral cat	0.05	0.08	0.02	0	0
Hedgehog	1.41 a	1.50 a	1.07 a	1.06 a	0.82 a

Table 6: Seasonal variation in five-year means of capture rates (captures per 100 trapnights) of all species. Values in any row followed by the same letter do not differ significantly at $P=0.05$; rows without letters were not tested because of small sample size. All means are controlled for all other variables using the General Linear Model (GLM).

	SPRING	SUMMER	AUTUMN	WINTER
Mouse	2.99 ab	1.49a	5.33 b	4.88 b
Ship rat				
Rat traps	4.43 a	3.48 a	4.53 a	4.45 a
Fenn traps	7.16 a	3.98 b	6.00 a	6.51 a
Norway rat				
Rat traps	0	0	0	0
Fenn traps	0.27 a	0.16 a	0.16 a	0.12 a
Stoat	0.15 ab	0.37c	0.33 ac	0.07 b
Weasel	0.12	0.10	0.05	0
Ferret	0.03	0.02	0.13	0
Feral cat	0.02	0.05	0.05	0.02
Hedgehog	1.12 a	1.76 a	1.73 a	0.05 b

(RL2) during 1983 and 1984 when these two lines were run concurrently, nor was there any overall difference between capture rates in the interiors of unlogged (RU) and logged (RL2) over the whole five years. Fenn traps through logged and unlogged native forests (FL, FU) also showed that, unlike mice, rats had no preference for logged native forest. Within exotic forest (Fig. 7c), rats were present

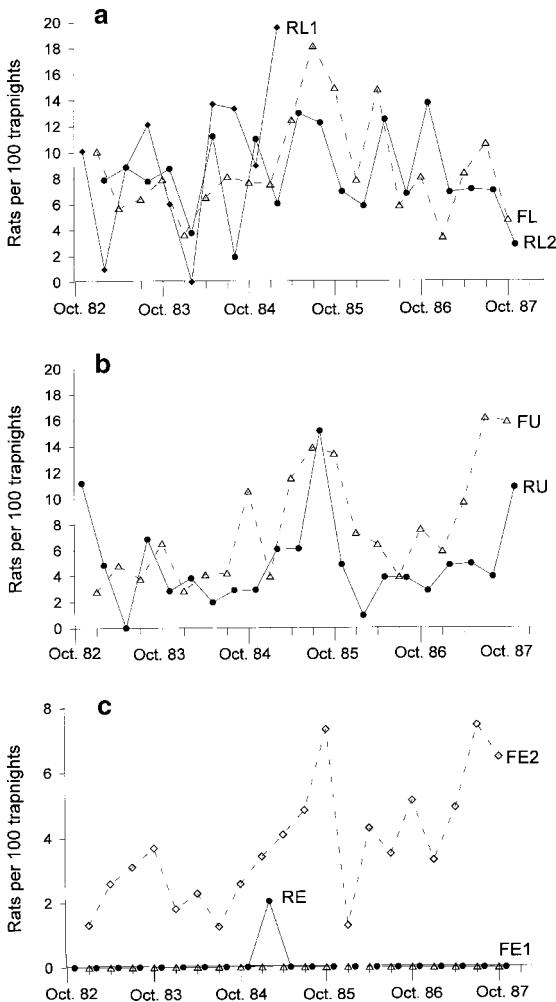


Figure 7: Density indices ($C/100TN$) for ship rats through the five years, in rat traps (prefix R) and Fenn traps (prefix F). (a) Captures in logged native forest, along traplines FL and RL1 (road edge), and RL2 (forest interior); (b) captures in unlogged forest interior along traplines RU and FU; (c) captures in exotic forest along traplines RE and FE2 (in the young plantation illustrated in Fig. 2) and FE2 (in older plantations).

though not abundant in the older plantations (line FE2), but practically absent from the 4-9 year old *P. radiata* block (RE, FE1).

The small number of significant correlations between trap site attributes and trap success for ship rats in indigenous forest (Table 7), suggests that, on the broad scale we sampled, ship rats were more or less evenly distributed throughout the forest. However, more ship rats were trapped on warmer, steeper sites with minimum cold-air pondage, and fewest in early successional disturbed sites (Figs. 3 and 6c).

In exotic forest, only two rats were caught in the young plantation, against 299 in the older compartments (Table 2). The significant positive correlations in exotic forest lines between ship rat captures and canopy cover and height, and negative correlations with 0-0.3m tier vegetation cover and ordination axis 1 (Fig. 8), are therefore due simply to the opposite patterns of abundance of rats in old and young exotics (Table 7, Fig. 7c). The species ordination (Fig. 8) shows that this separation reflects differences both in understorey composition and in exotic canopy. In younger stands the understoreys are dominated by herbaceous species (e.g., *Holcus lanatus*, *Pteridium esculentum*, *Cortaderia fulvida*, *Agrostis capillaris*, *Paesidia scaberula*, *Lotus sp.*, *Hypochaeris radicata*, *Senecio jacobaea*, and *Cirsium vulgare*, all on the right of Fig. 8). With time, these are successively replaced by woody native species (e.g., *Melicytus ramiflorus*, *Weinmannia racemosa*, *Coprosma grandifolia*, *Coprosma tenuifolia*, *Pittosporum eugenoides* and *Elaeocarpus dentatus*, more on the left of Fig. 8). These either invade from adjacent indigenous remnants, or regrow from stumps after mechanical clearance. The ordinations indicate that the traps catching most ship rats in exotic forests tend to be the ones sited near fruiting understorey trees such as *Pseudopanax arboreus*, *Schefflera digitata*, *Coprosma grandifolia* and *Aristotelia serrata* (Fig. 8), which need time to establish.

There was a substantial increase in abundance of ship rats in 1985 (Table 5), most marked in the logged and unlogged native forest (Table 3) and visible in the data from both trap types (Figs. 7a and 7b). Both traplines caught fewer rats in summer, significantly so in Fenns (Table 6). These annual and seasonal differences were less marked in the data from the rodent lines than from Fenn trap lines, probably because the rodent traps were operated for fewer trap-nights per session (Table 2).

We considered the possibility that some of this variation could represent a reaction by the rats to a good crop of tawa seeds in 1984 (*unpubl. data*; Forest Research Institute, Rotorua); but there was a

Table 7: Spearman rank correlation coefficients between site attributes and trap success (expressed as captures per 100 trapnights) for ship rats on all traplines * P<0.05; ** P<0.01.

SITE ATTRIBUTE	RU	FU	RL2	RL1	FL	ALL INDIG.	RE	FE2	ALL EXOTIC
Physiography	-0.20	-0.16	-0.10	-0.18	0.27	0.09	-0.06	0.04	-0.09
Drainage	-0.17	-0.01	0.02	0.22	0.05	0.09	0.06	-0.27	-0.14
Altitude	0.09	-0.55**	0.11	-0.03	0.41**	0.17*	-0.15	0.08	0.05
Slope	-0.12	-0.15	-0.01	0.13	0.26	0.16*	-0.12	-0.08	-0.10
Distance to escape cover	-0.26	-0.09	0.07	0.09	0.16	-0.03	-0.09	-0.20	0.03
Distance to road	-0.03	-0.06	-0.23	0.13	-0.05	-0.13	-0.08	-0.40*	-0.13*
Canopy cover	-0.25	-0.30	-0.31	0.07	0.53**	-0.08	-0.21	-0.07	0.28**
Vascular ground cover	-0.09	0.14	-0.04	-0.21	-0.37*	-0.14	-0.26	0.13	0.06
Canopy height	-0.29	0.14	0.19	0.36	0.44**	0.00	0.08	-0.17	0.55**
2-5m cover	0.18	0.11	0.08	-0.18	0.24	0.10	-0.21	0.46**	-0.15
0.3-2m cover	-0.11	-0.06	0.23	0.03	-0.33*	-0.06	-0.21	0.20	0.19
0-0.3m cover	0.10	0.06	0.16	-0.14	-0.35*	-0.13	0.19	-0.25	-0.24*
Axis 1	0.10	-0.36*	-0.13	0.15	0.45**	-0.09	-0.01	0.30	-0.51**
Axis 2	0.09	-0.32	0.24	0.38*	0.69**	0.16*	-0.08	0.36*	-0.23*

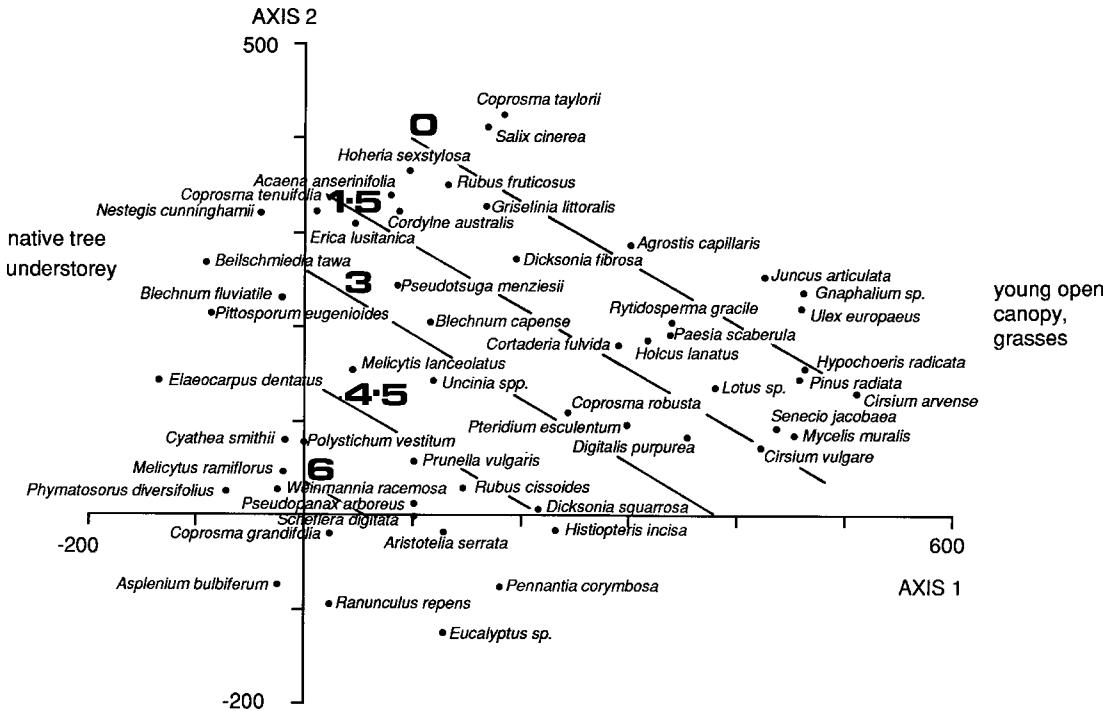


Figure 8: Ordination plot for plant species growing within 15 m of traps set in exotic forests. The diagonal lines show the relationship between the vegetation ordination and the density indices of ship rats (0-6 C/100TN). Species which are closely associated in ordination space will also be closely associated on the ground. The environmental interpretations (e.g., understorey native trees) of Axis 1 are derived from the positions along the axis of species with known site preferences.

concurrent, though smaller, increase in the exotic forest some 3 km from the nearest extensive stand of tawa (Fig. 7c). The rat stomach contents have not yet been analysed, but there is no evidence in the literature that tawa is an important food to rats in any year (Beveridge, 1964; Innes, 1990).

Norway rats

Only 43 Norway rats were collected throughout the study (Table 2). Moreover, they were caught only in Fenn traps, and only in native forest (Table 3). It is not clear whether it was the meat baiting or greater holding strength of Fenn traps, or the particular locations or greater length of the Fenn trap lines, that made them more successful in catching the large Norway rats. Standard rodent trap lines used alone therefore do not necessarily detect Norway rats in forest.

Thirty five Norway rats came from a single trap, FU16, in the Waipapa Ecological Reserve about 1 m from the bank of the Waipapa Stream (Fig. 1); all the rest, a total of eight, came from sites scattered along the Ngaroma Road. None of the 12 401 corrected trapnights recorded in exotic forest caught a single Norway rat. This variation in capture rate between areas was significant (Table 3) even though the sample was very small. But there was no significant annual or seasonal variation in numbers of Norway rats caught (Tables 5, 6).

Stoats

Stoats made up the great majority of the 84 mustelids caught (68% stoats, 19% weasels and 13% ferrets). Half the mustelids came from the traplines in exotic forest, 32% from the cutover forest and 18% from the unlogged forest.

Local variation in capture rate of stoats was significant; they were caught most often in the older exotic plantations (Table 3; Fig. 9), and least often in the 1978 plantation. Native forest, either logged or not, yielded a harvest intermediate between these extremes. However, this variation between areas is not entirely due to differences in the local distribution of stoats.

By far the largest number of stoats was collected in the first year of trapping (Table 5), especially in the first two trapping sessions, January and April 1983. We collected 21 stoats in these two sessions, plus another one from unrelated control work in February 1983, compared with 7, 6, 4 and 5 in the same periods of the following four years. Of the 22 caught in early 1983, 13 came from the older exotic plantations and one from the young *radiata* block; only two came from unlogged forest and six from the cutover forest. This initial bonanza, mostly from one area, was sufficient to account for much of the

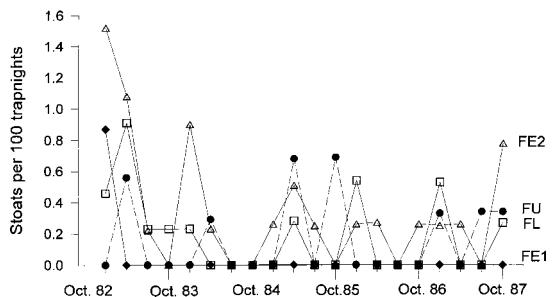


Figure 9: Density indices (C/100TN) for stoats in Fenn traps through the five years, along traplines set at logged forest road edge (FL), in unlogged forest interior (FU), young exotic forest (FE1) and mature exotic forest (FE2).

variation in capture rate between areas (Table 3). In the four years 1984-87, we never collected even one more stoat from the traps in the young plantation - even in 1984, the year that mice were very abundant there.

There was a significant seasonal difference in the capture rate of stoats, lowest in winter and highest in summer and autumn (Table 6).

Weasels

Weasels are by far the least common of the three mustelids in New Zealand. At Pureora, only 16 weasels were caught, all males, and these only in two of the three habitats (Table 3).

Nothing can be said about local, annual and seasonal variation within such a small sample, although the data (Tables 3, 5, 6) are consistent with those from the northern hemisphere (King, 1989) and elsewhere in New Zealand (King, 1990), showing that the population biology of weasels is closely influenced by the distribution and abundance of small rodents.

No weasels were caught in unlogged forest, where ground cover and mice were least abundant. Nine weasels came from the exotic forest, particularly (to 0.14 C/100TN) along the short stretch of the Fenn trap line (10 traps) that ran through the young pine plantation (Fig. 1, line FE1), and especially (to a temporary peak of 1.15 C/100TN) in exotics of all ages during the summer following the mouse irruption, from October 1984 to April 1985 inclusive. The other seven came from the road edge traps along the Ngaroma Road, where mice were more abundant than in unlogged forest but less so than among the young exotics.

Ferrets

The local and annual distributions of the eleven ferrets collected were virtually opposite to those for weasels. Ferrets were caught most often in the unlogged forest (though not frequently even there: the five-year mean capture rate was only 0.08 C/100TN: Table 3) and not at all in the young plantation or in 1985.

Feral cats

The eight feral cats caught came from all areas and all seasons, but only in the first three years. There are two possible reasons why no cats entered the Fenn traps in 1986 or 1987: (1) the wires placed across the trap entrances in 1984 effectively kept them out, or (2) the park rangers' other control operations against cats, which accounted for 7 cats in 1985, temporarily removed cats from the area.

Hedgehogs

Hedgehogs were very scarce in the cutover native forest along the Ngaroma road, but more common in the unlogged forest of the Waipapa Ecological Reserve, and even more so in the older exotic plantations (Fig. 10). Pooled annual means for hedgehogs (Table 5) dropped off slowly over the five years.

Most published data on the distribution of hedgehogs come from road-kill data collected from main highways (Brockie, 1990). This study is the first to document systematic capture records for hedgehogs trapped in forest, both along quiet tracks with little traffic and also in the interior well away from roads of any kind. The data from Waipapa are particularly interesting, since they confirm that hedgehogs range throughout unlogged forest regardless of tracks or any other human assistance.

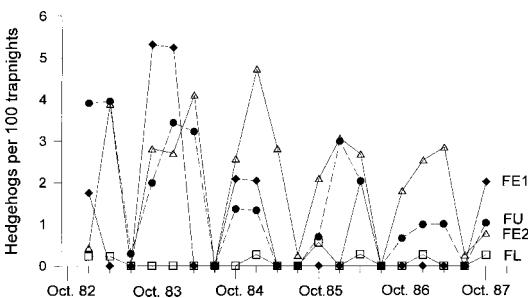


Figure 10: Density indices (C/100TN) for hedgehogs in Fenn traps through the five years, along traplines set at logged forest road edge (FL), in unlogged forest interior (FU), young exotic forest (FE1) and older plantations (FE2).

The decline in overall capture rate through the five years was not significant overall, which suggests that the wires across the trap tunnel entrances, intended to prevent hedgehogs from entering and blocking the traps against mustelids, had only a minor effect, if any. Indeed, in the older exotics and in the cutover native forest - the areas with the highest and the lowest local means, respectively - there was no decline at all. Only in the unlogged forest and in the young plantation were conspicuously more hedgehogs caught in the first two years of the study than in the last three. Since all tunnels were wired at the same time and in the same way, it seems reasonable to conclude that the variations in capture rates between years and areas represent real local and annual differences in hedgehog population density.

The seasonal data for hedgehogs show a pronounced drop in winter capture rates in all areas. In lowland New Zealand, especially in the north, few hedgehogs hibernate, since it is hazardous and can be avoided if the mean earth temperature remains above 10-11 °C, but the winter climate at Pureora is cool enough to make hibernation necessary. On exposed open grassland at Pureora village, the grass minimum temperature (lowest temperature recorded at ground level in the preceding twenty-four hours) was less than 11 °C on an average of 336 days per year. The mean earth temperature (at a depth of 5 cm at 9 am) was below 11 °C for an average of 187 days a year. Under the shelter of the forest canopy, or in a hibernaculum under a thick layer of litter, the number of such days experienced by hedgehogs would be substantially fewer, but still sufficient to discourage most of them from venturing out of their nests in mid winter. As expected, therefore, very few hedgehogs were caught in any habitat in July, the winter quarter (Table 6, Fig. 10).

Relative abundances of small mammals by habitat

The relative abundances of the five most common small mammal species were often significantly different in native versus exotic forests, and in exotic forests of different ages (Fig. 11, Table 3). Most striking was the great abundance of mice and the absence of rats in the young plantation.

Trapping methodology

Escapes

The proportion of traps recorded as "sprung but empty" varied considerably between traplines, years and seasons. It seems reasonable to predict that most of these traps were set off by target animals which

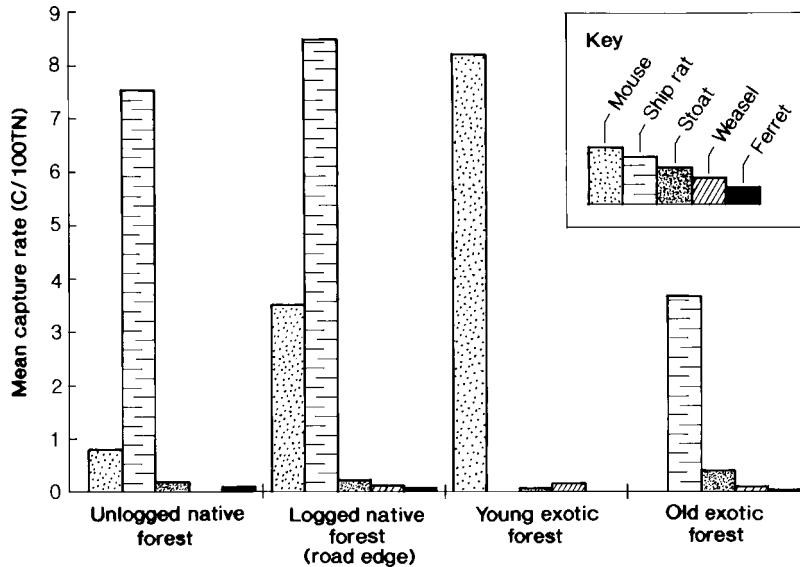


Figure 11: Five-year mean density indices (C/100TN) for five species of small mammals in four habitats at Pureora Forest Park. Data shown are those derived from rodent trap lines for mice, and from the Fenn trap lines for all other species. The interior of the logged native forest is not represented because no Fenn traps were set there. There were no rodent traps in the old exotic forest.

were either not in the right position to be held, or were held for a while but then escaped. If so, there should be a consistent positive correlation between the number of sprung traps recorded and the density indices of the commonest species available to be caught. If there is such a correlation, it would provide grounds for reassurance that the sprung traps were reflecting variations in the abundance of animals as much as were the records of animals caught. In that case, sprung traps can be regarded as normal, even meaningful, rather than as a source of error.

On the other hand, if there is no such correlation, we should consider alternative explanations such as the possibility that the number of sprung traps represents uncontrolled variation (1) in interference from non-target animals, or (2) between individual trappers in the consistency with which they set the traps, or (3) in external conditions such as the weather. Any of these, if proven and significant, would introduce uncertainty about whether density indices really do track variations in real population density.

Table 8 shows that both kinds of rodent traps did tend to be disturbed (recorded as sprung but empty) more often in the habitats where rodents were most numerous. In the young exotic forest and along the logged forest road edge, where the density

indices for mice were highest (Table 3), the proportion of disturbed traps was positively correlated with the overall mean capture rate for mice. A similar pattern is visible, less clearly, in the data for ship rats along the rodent traplines. An ANOVA controlling for season showed that most of the variation in rate of trap disturbance was due to differences between years ($P < 0.001$) and between lines controlling for year ($P = 0.032$). Despite the occasional puzzling exceptions, these data suggest that in general the sprung rodent traps are the work of escaped rodents.

Conversely, disturbance of Fenn traps was negatively correlated with density of ship rats in all areas, significantly so in the unlogged and older exotic forests where ship rats were most common. That is, the fewer ship rats there were, the more Fenn traps were disturbed. Ship rats are by far the most abundant of the species collected by Fenns, and seldom escape from their steel grip, so ship rats often block the traps against other species; perhaps this means that where there were fewer ship rats, there were more unoccupied traps available for some other species to find. In unlogged forest, where the negative correlation between trap disturbance and ship rat density was most pronounced, the same correlation for both feral cats and hedgehogs was positive.

Table 8: Spearman rank correlation coefficients between the proportion of traps recorded as sprung but empty, and the density indices of each species. R: rat traps, M: Mouse traps, F: Fenn traps. * = $P < 0.05$; ** = $P < 0.01$

Line	UNLOGGED	LOGGED		EXOTIC	
	interior RU, FU	interior RL2	edge FL, RL1	1978 RE, FE1	older FE2
Mouse					
M	0.33	0.76**	0.38	0.75**	-
R	0.39	0.59**	0.15	0.76**	-
F	0	-	-0.12	0.12	0
Ship rat					
M	0.66**	0.38	0.92**	0.02	-
R	0.67**	0.49*	0.36	0.24	-
F	-0.64**	-	-0.23	0	-0.45*
Norway rat					
R	0	-	0	0	0
F	-0.05	-	0.10	0	0
Stoat					
F	-0.10	-	0.32	0.37	0.21
Weasel					
F	0	-	-0.24	-0.20	0.17
Ferret					
F	0.22	-	0.44	0	0.03
Feral cat					
F	0.45*	-	0.26	0.05	-0.05
Hedgehog					
F	0.55*	-	-0.11	0.42	0.35

The species most likely to set off Fenn traps without being held is the possum. Possums are numerous, and although they cannot enter the tunnels, they can reach inside them, and sometimes also overturn the tunnels. The wires placed across the tunnel entrances in mid 1984 would have made it more difficult for possums to reach the trap. After that, there was a large and significant reduction in the incidence of disturbance of Fenn traps (Table 9: $P < 0.001$, from an ANOVA analysis treating escapes as a "species" and controlling for line and season). It seems that although the wires were no barrier to hedgehogs, which are a lot more agile than they appear, they were effective against possums and perhaps also cats.

If the rate of trap disturbance varies with season, e.g., higher in summer, we might suspect interference by animals that are more active in summer, such as invertebrates. Traps are often visited by invertebrates, especially ants, beetles, slugs, millipedes and wetas. They eat the bait, and some are large enough to set off the traps (e.g., one millipede was caught in a mouse trap). However, the incidence of disturbance of neither type of trap varied significantly with season in ANOVA tests controlling for line and year ($P = 0.406$ in Fenn traps, $P = 0.126$ in rodent traps: Table 9).

A further source of variation is the difference in setting technique used by individual trappers. All set

the traps carefully and in approximately the same way, but presumably not always to exactly the same degree of sensitivity. It would be impossible to eliminate this factor, and it may not in fact be very important anyway. Experimental studies have shown that even larger differences in technique, e.g., in whether or not the traps were covered with leaves or soil, do not significantly affect the capture rate of stoats (Dilks *et al.*, 1996).

Decline in capture rate through a session

The capture rate for ship rats consistently declined through a trapping session, both in Fenn and in rat traps (Table 10). By the tenth day of trapping, the capture rate was commonly under half the figure recorded on the first day. The same trend appeared separately in all three areas in which rats were sampled by Fenn traps, despite the differences in general density of rats in each shown in Fig. 7.

The decline was steepest over the first four nights of trapping, and then continued but more slowly and rather erratically, even with occasional increases, especially around the 5th to 9th days. We suggest that the traps removed the nearest or most dominant resident animals in the first four nights of each session, which were immediately replaced by dominant neighbours or the next-ranking locals. As trapping continued, these were also removed, and further captures depended on chance immigration of

Table 9: Variation in number of traps recorded as sprung but empty (expressed as "captures" per 100 trapnights) with line, year and season. Values in any row followed by the same letter do not differ significantly at $P=0.05$. All means are controlled for all other variables using the General Linear Model (GLM).

LINE	UNLOGGED	LOGGED		EXOTICS	
	RU, FU	interior	edge	1978	older
Fenn traps	5.86 a	-	4.26 a	2.45 b	6.54a
Rodent traps	4.67 a	6.82 a	7.15 a	4.91 a	-
YEAR	1983	1984	1985	1986	1987
Fenn traps	7.18 a	7.48 a	3.28 b	3.65 b	2.31 b
Rodent traps	2.77 a	6.19 b c	9.02 c	4.35 ab	5.01 b
SEASON	Spring	Summer	Winter	Autumn	
Fenn traps	4.03 a	4.99 a	5.68 a	4.36 a	
Rodent traps	4.62 a	4.35 a	7.91 a	4.99 a	

Table 10: Variation in capture rate (captures per 100 trapnights) through a trapping session. Rr: ship rats, Me: stoats, Ee: hedgehogs * $P<0.05$; ** $P<0.01$.

DAY	1	2	3	4	5	6	7	8	9	10	d.f.; F-ratio
All areas pooled:											
Fenn traps											
Rr	9.51	8.30	6.22	5.07	4.99	3.96	4.37	3.51	3.15	3.61	9, 684; 11.53**
Me	0.2	0.14	0.14	0.18	0.25	0.17	0.28	0.14	0.17	0.26	9, 684; 0.51
Ee	1.12	1.47	1.20	0.99	1.21	1.03	1.39	0.95	1.42	1.28	9, 684; 0.50
Rat traps											
Rr	6.39	5.01	3.89								2, 136; 5.86**
Mm	2.54	2.32	2.08								2, 136; 0.14
Mouse traps											
Mm	3.70	3.81	3.97								2, 352; 1.24
For ship rats collected in Fenns only, by area:											
Logged native (FL)	17.1	15.5	9.88	8.57	8.57	6.91	8.35	5.02	5.77	5.75	9, 171; 6.81**
Unlogged native (FU)	13.5	11.8	10.3	7.35	9.17	6.60	5.73	5.88	4.50	6.00	9, 171; 2.48**
Older exotics (FE2)	7.36	5.76	4.69	4.37	2.23	2.32	3.39	3.12	2.32	2.69	9, 171; 4.61**

dispersing individuals from further afield. It would be interesting to see this suggestion tested.

After ship rats, hedgehogs were the second most frequent captures in Fenn traps, but they showed no trend in numbers caught through the trapping session (Table 10); neither did the rarely-caught stoats. The capture rate for mice in mouse traps showed a slight though insignificant (Table 10) increase on the third day, but the numbers of mice entering rat traps remained roughly constant through each three-day session.

Discussion

Sampling design

Little was known in 1982 about which species of small mammals might be present, or about the

relative distribution of each in various possible sample areas different in gross forest appearance, history and access. Therefore we used a standard non-stratified sampling design, in which traps were positioned systematically by spacing in the three main types of forest but randomly with respect to microhabitat. Such a design was appropriate for the primary objective of this and most similar descriptive studies done in New Zealand so far: but few reports mention the hidden assumption on which it is based, which is that estimates of the local abundance of each species derived by this method will be a function of the local distribution (or absence) of its preferred microhabitats. We had no opportunity to improve the sampling design to take account of this factor, because at the time our procedures were set it was impossible to predict which the important variables would be. For example, we did not detect the significant

differences between younger and older exotics until the analysis stage, well after the field work was finished.

Ideally, this study should be followed up by one that tests the habitat-use patterns we have described, using a stratified random sampling design. This method requires that two sets of data be known in advance: first, the relevant categories of microhabitat, and second, their distribution in the chosen sample area. Representative microhabitats can be defined from our data, at least as a first approximation. Then, a survey of the vegetation would be required to establish sample plots, and a pre-determined sampling effort expended in each. In such a finer-scale study, the trap spacing should be closer than the 50 m we used, and the traps placed precisely (Stewart, 1979; Norton, 1987).

Both stratified and non-stratified methods contain much of the same information, and their results are strongly correlated on the broad scale. The difference between them depends on the level of the comparisons being made and the extent of habitat diversity in the study area. Communities sampled by stratified techniques can be more accurately compared than those sampled by the (hitherto standard) non-stratified methods we used (Price and Kramer, 1984). On the other hand, stratified sampling usually avoids ecotones such as those along road edges, and where these are an important component of the total community, stratified sampling can underestimate the total local density and diversity (Taylor, Friend and Dudzinski, 1984).

Our secondary objective was to explain the apparent habitat choices of the common small mammal species we observed, as inferred from their different abundance records within each forest type. There are two possible ways of doing this. One is to compare the results from sets of replicate traplines in each habitat; but we had only one trapline in each habitat, for reasons explained in Methods. It would be possible to derive inferential statistics from within our very large dataset, but not without incurring the error of pseudoreplication which is particularly common in field studies of small mammals (Hurlbert, 1984).

The alternative method is to record and analyse detailed microhabitat data on every trapping station (Braithwaite and Gullan, 1978; Fox, 1984), as we did at Pureora. The extra work required is modest relative to the total investment of effort required to collect adequate long-term trapping data on small mammals (Gullan and Norris, 1981), but increases their value disproportionately. In the Pureora study these measurements provided quantitative descriptions of, and comparisons between, study

areas originally chosen on purely visual and practical criteria. For example, the areas we selected to represent logged or unlogged forest differed in other ways as well, whose effects we could not predict in advance; the logged forest sampled by lines RL1, RL2 and FL was on warmer, steeper terrain compared with the unlogged forest sampled by lines RU and FU. How then could we identify the causes of the different density indices we observed? Detailed analysis of capture records of rats in relation to trap microhabitat showed that, for ship rats, the difference between these areas was probably due more to slope and to patterns of cold-air drainage than to logging; for the largest single local population of Norway rats we detected, the proximity of running water seemed to be more important. Such analyses provide objective grounds for explaining the habitat choices we documented, and for generalising them to other areas.

Impacts of past logging and conversion to exotics on the distribution and abundance of small mammals

Structural and floristic changes attributable to partial logging and roading in the past are still detectable in the native forests of Pureora. Our data show that the small mammal community remaining after logging is different from that in unlogged forest, but also that not all of these potential predators respond in the same way. Of course the impacts of changes in predator density depend on whether and what native fauna are thereby put at risk.

Effects on rodents of selective logging in native forest

Ship rats and mice are among the world's most successful mammalian 'tramp' species (Clark, 1980; Watts and Aslin, 1981), represented in many different habitats and climates world-wide. Both are ecologically versatile, but at Pureora they reached highest numbers in different habitats. Capture success of mice was significantly correlated with the increased ground cover along the margins of old logging tracks and among the dense regrowth that quickly covers any cleared site, perhaps because their vulnerability to predation confines them to shelter, whereas ship rats were indifferent to the nett effects of the removal of large podocarps and the increase in ground cover after logging. This result confirms the preliminary observations of Hay (1981), who found that mice, but not ship rats, were much more abundant in Pureora blocks logged 3-7 years previously than in unlogged forest. Mice were not more abundant in logged forest at Whirinaki, where logging was still in progress at the time of

Hay's study. Taken together, these observations suggest that thick ground cover, and mice, both develop high densities after disturbance, but take some time to do it.

Ship rats eat a broad range of foods, including arthropods (especially wetas) and fruits (Innes, 1990), so are unlikely to depend on a few species, e.g. merchantable podocarps, for maintenance supplies. However, their lack of response to the removal of podocarps and to the increase in ground cover associated with logging does not mean that they would ignore a concurrent heavy mast seeding of several species of podocarps in unlogged forest at Pureora; their numbers would probably increase in response, as after hardwood seeding in the Orongorongo Valley (Daniel, 1978; Brockie, 1992), although no such event fell during the five years of our study. We have no explanation for the increased numbers of ship rats on all lines in 1985.

Roads are a complicating variable in most studies of the effects of logging, because they introduce a distinctly different linear community of small mammals, due more to roading than to logging but which can seldom be allowed for since nearly all logged forests have roads. Roading alone, with or without logging, will provide good habitat for mice if a permanent, denser ecotone establishes along the road edge verge. By contrast, logging without roads (e.g., by helicopter) would affect mouse numbers only in isolated patches. The characteristic road edge zone through a forest (Adams and Geis, 1983) should be subsampled separately in future studies of small mammals in logged forests. In Australia, roadside and railway verges provide favourable habitat for mice (Mutze, 1991). Roads can become a barrier to small mammals (Barnett, How and Humphreys, 1978; Oxley, Fenton and Carmody, 1974), but the roads in our study areas were only seldom-used gravel tracks.

Ship rats have largely replaced Norway rats, which arrived in New Zealand first but are now much less common than during the last century (Moors, 1990). The only remnant colony of Norway rats we located at Pureora survives near running water, as on Stewart Island (Sturmer, 1988).

Effects on rodents of conversion to exotics

In the young plantation, where by 1984 a thick and undisturbed blanket of grass, herbs, bracken and litter had accumulated over the six years since clear-felling, mice staged a dramatic irruption reaching at least twice the numbers recorded by the same techniques during two post-seedfall irruptions in Fiordland beech forest (20-25 C/100TN; King, 1983). One possible explanation might be that a thick growth of dense browntop, bracken and toetoe

offers plenty of natural escape routes for mice evading most visually hunting predators, except weasels that can follow them along their runways and into their nests.

Alternatively, mice there may be able to escape from social interference or predation by the much larger ship rats. The 1978 plantation was the one habitat which ship rats almost completely avoided (Fig. 11), whereas rats were widespread in the older (>20 year) stands from which mice were apparently absent. This contrast has been observed before: Clout (1980) also found mice absent but ship rats abundant in a 15-year old stand of pines near Tokoroa. Badan (1979) found mice abundant under dense cover in Northland pine forests, both in a 3-year old *P.radiata* plantation (peak density estimate 47.5 C/100TN), and under lupin in mature pines. In the mature pine block, Badan caught mice significantly more often under lupins than in areas with no lupin cover ($\chi^2 = 36.6$, d.f.=2, $P < 0.01$). It was well known to plantation foresters in the central North Island and the Mamaku Plateau that mice were likely to be abundant for a few years in cleared patches of forest of any type, but that they would disappear after the canopy closed (G.W. Hedderwick, *pers. comm.*). Even in the absence of dense ground cover, abundance indices for mice consistently increase after successful poisoning of ship rats (Innes *et al.*, 1995).

Perhaps part of the reason for this habitat difference between ship rats and mice relates to their different use of trees. Mice prefer to forage mostly on the ground, especially in the damp microclimate under thick cover where they can find more food (seeds and invertebrates: Badan, 1979; Murphy and Pickard, 1990). Tree-based traps and radio-tracking show that ship rats are superbly agile climbers and in some places, e.g., Rotoehu Forest, spend most of their time above the ground (Hooker and Innes, 1995). This could be a sufficient explanation in itself, regardless of predation or competition. On Mana Island in 1977-78, in the absence of rats, cats and mustelids, population density indices for mice were very high in thick grass, but low in a stand of kanuka (*Kunzea ericoides*; Efford, Karl and Moller, 1988).

This pattern suggests a hypothesis concerning the differential effects of forestry operations on ship rats and mice. We predict that (1) mice alone will be common in a newly established exotic forest until it develops a high canopy and loses its thick ground cover, but then ship rats will gradually invade and replace mice as resident rodents; (2) conversely, in a logged podocarp-hardwood forest, both will be present at first but, as regeneration proceeds, mice will decline to very low numbers confined to

scattered remaining areas of dense cover, while ship rats will remain abundant and widespread. Either way, the result is that mature forest of either type is likely to have a permanent population of ship rats, and few mice except near areas of dense ground cover. Since forest clearings are successional habitats that could, if left alone, give way to mature forest of either type, less favoured by mice, the same hypothesis predicts that (3) the processes of operating an exotic forest, or sustained-yield harvesting of an indigenous forest, will generate local and temporal variations in the abundance of mice, following each transient patch of early-succession vegetation.

Effects on mustelids of selective logging in native forest

In contrast to most of the sites sampled with the same methods by King and Moody (1982), all three species of mustelids co-existed at Pureora. However, the three mustelid species used the patchwork of habitats available at Pureora in slightly different ways. The capture records (Table 3) suggest that weasels responded to logging in native forest by following the mice into the disturbed road edges; ferrets and stoats did not react.

All three mustelids are usually scarce, except ferrets where rabbits are abundant, and stoats after a mast year in beech forests. At Pureora the differences in density indices for stoats between seasons and years were much less than between masting and non-masting years in beech forests, which suggests that no habitat in Pureora Forest Park supplies quite the same range of feast-or-famine conditions typically induced by the masting cycle in beech forests. In general the abundance of stoats at Pureora was similar to, or lower than, in beech forests during a non-masting year.

Effects on mustelids of conversion to exotics

Mustelids as a group were most abundant, not in the logged forest which supported the largest total biomass of rodents (mainly rats: Fig. 11), but in exotic forests of any age (Table 3, Fig. 11). The reason for this is probably that, especially for stoats and ferrets, rodents are generally a less critical food resource than are rabbits and possums (King and Moody, 1982). We could not include these species in our programme, but observed rabbits more often in exotic than in native forests, especially in grassy clearings and areas disturbed by forestry operations.

Our data on weasels are consistent with the predictable correlation between the distribution and numbers of weasels and of mice, although they are too few to demonstrate this connection formally. Weasels did show a substantial but brief numerical

response to the increased supplies of mice in the plantation in 1984; in leaner times they apparently survive in low numbers only where recently disturbed vegetation favours mice.

By contrast, we detected no comparable response in stoats. This is rather surprising, because mice are among the preferred prey of stoats, so one might have expected a higher catch of stoats in the young pines in or following the winter of 1984. Mice were rapidly increasing in April 1984, when there were still some stoats present in the neighbouring older plantations. Yet the Fenn lines there produced no mustelids at all in July, even though in August the density index for mice was still 20.2 C/100TN. There are several possible explanations.

- (1) In winter, stoats have limited capacity to make a numerical response to a sudden increase in food supply. Unlike weasels, they cannot produce any young until the following September, and their social intolerance inhibits any substantial local aggregative response by stoats from other areas.
- (2) The area of 1978 pines (724 ha) was small relative to the vast area of other habitats that surrounded it, so the bonanza in the young plantation could have had a limited effect on the local stoat population generally.
- (3) Many of the stoats originally resident in the young plantation would also range into nearby older forest and may already have been removed.
- (4) The Fenn lines were operated in different months from the rodent lines, and may have sampled slightly different populations. The calculation of quarterly trapping indices is a crude method of monitoring small mammals, and we had no independent means of confirming them for mustelids. Nevertheless, for ship rats and mice they proved to be reasonably sensitive in detecting real differences in local distributions wherever the trapline indices could be confirmed by comparisons between Fenn and standard rodent lines, or from the vegetation ordination study; we have no reason to suspect they did not do the same for mustelids.

Conclusions on the effects on small mammals of logging and conversion to exotics

Our data show that logging at Pureora has affected only a small part of the total community of small mammals living in the indigenous forests we sampled. Over the five years of our regular field collections (1983-7), there were generally only rather small and not necessarily permanent differences between logged and unlogged native forests in the mammal fauna they supported (Table 3). The increases in numbers of mice and of weasels

were definite but likely to decline as the logged forests regenerate; the record of Norway rats along the Ngaroma Road through logged forest included only eight individuals, apparently all emigrants from the single permanent colony on the edge of the unlogged forest. The smaller number of hedgehogs in logged than in unlogged forest is significant but inexplicable from these data. By contrast, ship rats, stoats, cats and ferrets were largely indifferent to the consequences of the changes in native vegetation induced by logging. Any estimate of the impact of selective logging in indigenous forests must therefore depend on which species of native wildlife is of interest, plus some knowledge of which species of mammals might threaten them. Moreover, logging is a complex operation whose consequences must be variable locally.

The consequences of clearfelling (total conversion) for rodents and mustelids are far greater than are those of selective logging. Native wildlife may be threatened, not only in the clearfelled block itself (although few significant threatened species will live in exotic forest) but also in indigenous forest nearby, even if protected. For example, the 1978 plantation we sampled lies adjacent to a remnant 40 ha stand of unlogged forest along Pikiariki Road in the South Block at Pureora, reprieved from logging in 1979 (Wright, 1980). Rats remained abundant in the remnant block as always (Hay, 1981). Across the road in the 1978 plantation, the forestry operations induced the conditions favouring the 1984 irruption of mice plus the associated increase in weasels. The older exotic forests further back from Pikiariki Road supported fewer rats than do indigenous forests, but more stoats and as many cats and hedgehogs, all of which range very widely and must often have visited the remnant block. In such an environment, the scarcity of Norway rats and ferrets near the remnant block would hardly be much comfort.

The results of this study allow several new conclusions about the distribution of small mammals in New Zealand forests, and also confirm some old ones.

1. Contrary to expectations, we regularly collected both hedgehogs and ferrets throughout the unlogged, unroaded podocarp-hardwood forest in Waipapa Ecological Reserve. Previous studies had concluded that both hedgehogs and ferrets avoid the forest interior (Brockie, 1990; Lavers and Clapperton, 1990).
2. We confirmed that non-commensal Norway rats can still survive in mainland native forests, especially in local colonies near running water. Feral cats were scarce but present in all habitats sampled.
3. House mice strongly preferred areas of dense ground cover, presumably because they found both food and shelter there. A shortlived population irruption of mice in a six-year old plantation far exceeded the average post-seedfall irruption in southern beech forests, but its immediate cause was not determined. The expected strong correlation between the distribution and abundance of mice and of weasels was confirmed.
4. Ship rats were very much more common in podocarp-hardwood forests than in southern beech forests, but stoats were less so than there. Neither was apparently affected by selective logging of native forests; both responded sharply to clearfelling and conversion, but in opposite directions - in exotic plantations stoats were more abundant, whereas ship rats were virtually absent from young plantings and scarce in older ones. These two species are of most concern as potential kokako predators, and the implications of our findings for the kokako recovery programme are explored below.

Comparison with other ecosystems

In beech forest in the South Island, the link between the periodic masting (irregular heavy seedfalls) and the consequent population fluctuations of rodents and mustelids is well known (King, 1983; Murphy and Dowding, 1995). The beech forest to which these data refer is a habitat very different from Pureora, and there is no extensive area of it nearer than 50 km from Pureora Village, on the slopes of Pihanga, Tihia and Kakaramea, in Tongariro National Park. The nearest comparison would be to the first long-term integrated study of forest predators and their prey using these methods, which began in 1971 in mixed beech-podocarp-broadleaved forest of the Orongorongo Valley, southern North Island (Fitzgerald and Karl, 1979). The results of this study are now being analysed, and a preliminary account is given by Fitzgerald *et al.* (1996). North Island podocarp forests are capable of periodic masting, though there was no multi-species synchronous seeding during our study. In general, the masting model explains well the unstable population dynamics of rodents in the feast-or-famine environment of a beech forest, but it is less appropriate in the rich podocarp forests of Pureora with their complex and relatively stable food supplies.

Northern-hemisphere forests have been exploited as extensively and for much longer than those in New Zealand, and the impacts of logging and roading on northern small mammals and birds have been more often investigated than here. Small mammals and

birds in northern forests are abundant, diverse and of conservation interest in their own right, whereas in New Zealand attention has been focussed almost exclusively on native birds, and all mammals are regarded merely as pests. Nevertheless, the northern-hemisphere literature provides some interesting comparisons with New Zealand. Feral house mice and ship rats, the only common species of rodents in New Zealand, occupy many non-commensal habitats here from which they are excluded elsewhere by native voles and fieldmice (King, 1990). Hence feral mice in New Zealand are in some ways the functional equivalents of the common species of *Clethrionomys* and *Microtus* that are abundant in thick cover and grassland, respectively; ship rats here are partly arboreal, and live somewhat like tree squirrels (*Sciurus* sp.).

The patterns we describe in the feral commensal and introduced mammals at Pureora, e.g. more small, terrestrial rodents (more of both individuals and species) plus mustelids in early-succession stands and more larger, arboreal "squirrels" in mature stands, are repeated among the quite different native species in managed northern-hemisphere forests (Harris, 1984; Kirkland, 1990; Yahner, 1992). Kirkland (1990) points out that the ability of north-temperate forest small mammals to exploit the altered environments created by clearcutting is not surprising, since they evolved in an environment characterised by periodic ecosystem disturbances. Ship rats and house mice moved from wild to commensal habitats centuries ago, and ship rats are now rare in any habitat in Britain; in New Zealand both are common in the wild, and both have retained the same abilities and responses as their pre-commensal ancestors.

In Australia, the rich fauna of native rodents (Watts and Aslin, 1981) seems to exclude ship rats and feral house mice from most intact indigenous habitats. These two species tend to invade disturbed areas such as plantations established after clearfelling and burning of the original forest (Barnett, How and Humphreys, 1977; Suckling and Heislars, 1978; Friend, 1979; Watts and Aslin, 1981; Lunney, Cullis and Eby, 1987). However, among irrigated summer crops in the Macquarie Valley, NSW, Twigg and Kay (1994) confirmed our finding that dense ground cover is one of the most important habitat variables determining local variation in the abundance of house mice.

Implications for North Island kokako

Less than 200 years ago the forest at Pureora was a semi-continuous blanket of tall podocarp forest covering the whole of our study area. The only small

mammals present were kiore and bats, and the avifauna was hugely more abundant and diverse than now (Atkinson and Millener, 1991). Conditions of life for the native fauna and flora are now radically different, and it is hardly surprising that so many have disappeared. Against this background, the survival to the present of diminished populations of some ancient and vulnerable species such as the kokako is remarkable, and fully justifies all possible effort to assist the remainder.

Predation of eggs, nestlings and subadults by ship rats, mustelids (especially stoats), possums, and perhaps cats and mice was perceived as the most damaging interaction between small mammals and North Island kokako (*unpubl. data*; J.R. Hay, Department of Conservation, Wellington); competition from possums was an overlooked factor in kokako decline until Leathwick *et al.* (1983) suggested it. More recent evidence confirms that possums are important predators of kokako eggs, chicks and probably adults (Brown, Innes and Shorten, 1993), as suspected by J.R. Hay (*unpubl. data*).

Of the possible kokako predators (except possums, which were not included in this study), only mice and weasels were more abundant in logged forest at Pureora, and then only along road edges. Therefore it is unlikely that the predation risk to kokako is higher in logged forest compared with unlogged forest, and predator control (if required) should be applied equally in logged and unlogged kokako habitat. While at present virtually nothing is known of the importance of stoats, ferrets and cats as predators of kokako, these species are at least as abundant in unlogged as logged indigenous forest.

The significance of predation by the various small mammal species, and the effects of controlling them, can be determined only by studying the kokako themselves, and this picture is only slowly emerging. Nest predators confirmed by video-filming at 19 kokako nests at Rotoehu Forest (which has a very similar logging history to Pureora) in the Bay of Plenty during 1991-94 included ship rats, possums and kahu (*Circus approximans*; J.G. Innes *et al.*, *unpubl. data*). No mice, feral cats or mustelids - all present in the area - were filmed at nests, although cats and/or mustelids could account for losses of fledged juveniles and adults. The Department of Conservation's Kokako Recovery Plan (Rasch, 1992) includes integrated control operations against all mammalian predators and browsers in several mainland forests inhabited by kokako. Two kokako populations protected in this way since 1989 have thrived under management: the number of territorial adults at Mapara (King Country) increased from 52 to 66 during 1989-95,

and at Kaharoa (Bay of Plenty) from 22 to 36 during 1990-93 (J.G. Innes *et al.*, unpubl. data).

Results from Pureora assist such operations by showing that many potential predator species live in the interior of tawa-podocarp forest where most kokako survive, and that the numbers of these predators are characteristically stable from year to year rather than irruptive. The small mammal communities in beech and tawa-podocarp forest are very different, so although pest control to protect threatened fauna in beech forests can be confined to years of predictably high risk, as for yellowheads after a heavy seedfall (King, 1981; O'Donnell and Phillipson, 1996), threats to kokako are probably constant in all years.

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Appendix 1: Mean values of environmental factors and vegetation attributes at each trap site, by trapline

Definitions:

Canopy cover: Proportion of sky blocked by vegetation over 1.35 m high, estimated by eye to the nearest 10%

Mean top height: Mean height of the emergent trees, or, in their absence, of the dominant canopy trees, estimated by eye to the nearest metre

Mean vegetation abundance: Mean values (Bailey and Poulton 1968) of visually estimated vegetation abundance classes, noted as percent cover (see Methods)

Ground cover: Estimated proportion over the plot area of top intercepts below 1.35 m above ground level, to the nearest 5%

Trapline	Unlogged native		Logged native			RE	Exotic FE1	FE2
	RU	FU	RL2	RL1	FL			
Altitude (m)	573	536	629	597	552	604	614	619
Slope (deg)	5.0	6.9	15.1	12.0	10.9	3.4	5.3	4.7
Dominant aspect	41%N	50%N	36%S	36%N	33%E	57%N	30%N	49%N
Distance to road (m)	464	1225	416	6	12	9	8	9
Canopy cover (%)	81	78	68	79	64	49	42	72
Mean top height (m)	32	32	19	15	15	6	6	14

Mean vegetation abundance in height tiers

Tier 1, 20 m+	1.7	2.1	0	0	0	0	0	0
2, 12-20 m	4.2	3.5	3.0	2.4	2.0	0	0	2.3
3, 5-12 m	4.7	4.2	3.3	3.4	2.9	0	0	3.2
4, 2-5 m	3.9	3.8	4.2	4.5	4.3	4.5	4.1	2.8
5, 0.3-2 m	3.4	3.5	2.9	3.7	4.1	3.6	3.5	4.1
6, <0.3 m	3.3	3.8	2.8	2.6	2.5	3.4	3.0	2.2

% Ground cover

Live vascular vegetation	42	51	36	33	50	58	40	44
Non-vascular vegetation	5	2	4	<1	<1	0	0	0
Litter	53	45	60	66	49	42	58	56
% with escape cover <1m	58	22	36	61	69	88	80	58
>3m	22	41	17	6	5	3	0	7