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POPULATION BIOLOGY OF SMALL MAMMALS IN PUREORA FOREST PARK: 2. THE FERAL HOUSE MOUSE (*MUS MUSCULUS)*

Summary: Over five years from November 1982 to November 1987, we examined 495 mice collected from unlogged and logged native forest and from exotic forest at Pureora Forest Park, in the central North Island of New Zealand. Sex ratio, litter size, and breeding effort (pregnancy rate in females, proportion of males with visible tubules) were similar in all samples. By contrast, both density (captures per 100 trap-nights = C/100TN) and recruitment (proportion of young mice of age classes 1-3) were higher in densely vegetated habitats (along the road edge or in a young exotic plantation) than in the forest interior, whether logged or not. The age structures of the road edge and interior forest samples were significantly different (road edge, 33-35% young; interior, 10-11% young, means adjusted for sex, season and year by GLM). Mice of a given age caught in summer were larger, especially the females, implying that young mice grew faster in summer than at other seasons, and that older mice, especially females, also put on extra weight in summer.

Most pregnant mice were found in spring and summer, but there was no winter quiescence in mature mice of either sex, and three of 29 pregnant females were collected in August. In five of 29 litters of embryos, at least one embryo was resorbing, totalling 12 of 161 embryos (7.4%). Litter size (viable embryos only) ranged from 5 to 8 (average 6) in 23 spring and summer pregnancies, but only 1-5 in four autumn and winter pregnancies.

At high densities during 1984 in the young plantation (41.1 C/100TN in May) mice were significantly smaller in autumn, though somewhat larger in spring, and fewer young were recruited in 1984 and 1985. In these years we found significantly fewer males fertile, litters smaller and pregnancy rates lower, both in the plantation and in other habitats. The population peak was much higher than most apparently similar post-seedfall peaks in beech forest documented by the same methods, but it was different because (1) it developed very suddenly in autumn rather than building up slowly over winter and spring and peaking in summer; (2) it was not preceded by winter breeding; and (3) it was made up mostly of mice born in the previous summer, whereas peak populations in beech forests are usually made up of mice born during the previous winter and spring.

Keywords: Feral *Mus musculus*; New Zealand; population structure; age; reproduction; measurements; recruitment; growth; habitat effects; irruption.

Introduction

Pureora Forest Park, on the volcanic plateau of the central North Island of New Zealand, is a mosaic of indigenous and exotic forests of various ages and types. From November 1982 to November 1987 we studied the introduced small mammals resident in the Park, to provide background information relevant to the control of predators of declining endemic forest fauna such as the kokako (Aves; *Callaeas cinerea wilsoni* Gmelin). Because population irruptions of mice in beech forests can set off episodes of increased predation on forest fauna (O'Donnell and Phillipson, 1996), we were concerned to discover whether the same might apply in the podocarp-hardwood forests at Pureora. We included in our survey the three mustelids present in New Zealand (*Mustela erminea*[1]*, M. nivalis* and *M. furo),* both European rats *(Rattus rattus* and *R. norvegicus),* and the feral cat (*Felis catus)*, hedgehog (*Erinaceus europaeus*) and house mouse*, (Mus musculus)*. King *et al.* (1996) have described the field data on abundance, distribution and habitat preferences of the eight species regularly monitored.

There were significant distinctions between habitats in distribution and abundance of mice. Fewest mice lived in the native forest interior, whether logged or not; more along the road edge in logged native forest; and by far the most in the 1978 *Pinus radiata* plantation (Fig. 1). The environmental conditions most favouring a high density of mice

[1] *Mammal names follow King (1990)*

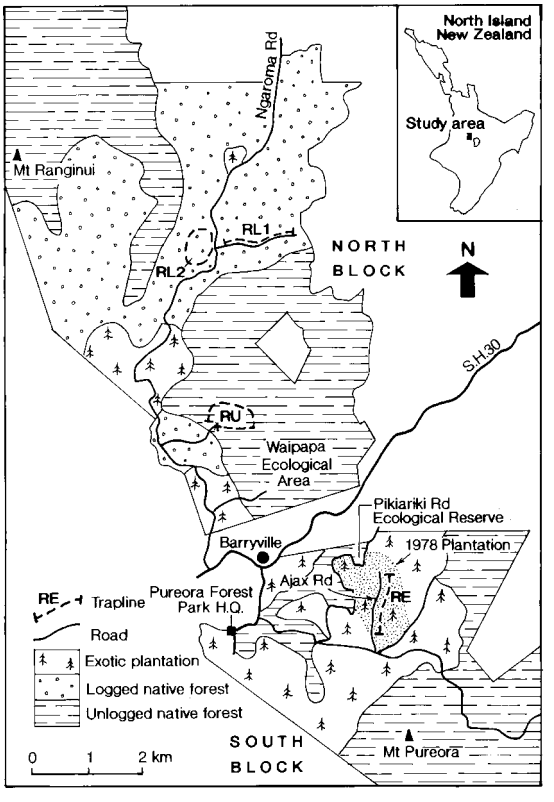

Figure 1: *Map of the study areas. Rodent traplines of standard length, 1.8 km (prefixed R, using rodent break-back traps) were set with traps at 50 m intervals to sample both disturbed habitats (RE, in a plantation of Pinus radiata established in 1978, and RL1, along an overgrown track in logged forest) and forest interiors, either logged (RL2) or not (RU). For fuller description, see King et al., 1996.*

included a sparse canopy and thick vascular ground cover (mostly grass and weeds). These conditions are best met in recently disturbed sites such as temporary forest clearings, and along permanent road edge verges in any kind of forest. Two of our traplines, one in logged native forest and the other in the young plantation, sampled road edge habitats, whereas on the other two lines, in unlogged forest and in logged forest, the traps sampled forest interiors.

The density indices for mice also varied substantially from year to year. The peak capture rate of 41.1 C/100TN in the young plantation in May 1984 (Fig. 2) 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 in density indices between areas was still significant even when controlled for year. Mice were significantly more abundant in autumn and winter than in summer (King *et al.*, 1996).

This is one of three companion papers describing the results of systematic necropsy of the trapped animals. The aim of this study was to record the measurements, population structure and reproduction of mice at Pureora in relation to habitat, season and year.

Previous studies of the biology of feral house mice in New Zealand forest environments have been well summarised by Murphy and Pickard (1990) and Brockie (1992).

Methods

Study areas

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

In the logged and unlogged indigenous forest, rodent traplines sampled both the the narrow strip (6-12 m) of dense cover along road edges and the forest interior >400m from the nearest road. The "roads" were single-lane gravel tracks carrying about 0-10 vehicles per day. In the exotic forest, we concentrated on a large (724 ha) homogenous area of one type, a young plantation of *Pinus radiata* established in 1978, which lay adjacent to the Pikiariki Ecological Reserve where kokako were known to survive. We set a rodent trapline along a road-edge in this block, but not in the older plantations east and south of it. The young trees grew rapidly throughout the study, and were thinned in March 1985 and November 1986 (to 245 stems ha^{-1}), and pruned in October 1986 to 4 m above ground level.

Rodent traplines

Four rodent traplines of standard length, 1.8 km (using "Supreme Eziset" rodent break-back traps) sampled both road edge habitats (in the young

plantation, trapline RE) and along an overgrown track in logged forest, (trapline RL1) and forest interiors, both logged (trapline RL2) and unlogged (trapline RU). One rat trap and one mouse trap were set at 36 trap stations spaced at 50m intervals, and baited with peanut-butter and rolled oats, according to the standard method established by B.M. Fitzgerald (Fitzgerald and Karl, 1979; Innes, 1990).

After a pilot trapping session in November 1982, all lines were set and inspected daily for three days during four trapping sessions a year, in the last weeks of February, May, August and November of 1983-87 inclusive. One line (RL1, logged forest road edge) was closed after February 1985 (Fig. 2). The wooden bases of all traps were soaked in linseed oil before first use, and the springs were oiled periodically. We inspected all traps daily and recorded their condition.

Laboratory procedures

All animals caught were returned to the laboratory frozen, and later examined for a standard list of physical attributes. The dissection records were compiled into the standardised DSIR Ecology Division file format for the national database on rodents (Karl *et al.,* 1984), and linked to the field records by the trap number. The sample for August 1984 was poorly preserved, because of a temporary freezer breakdown at the field station, but most information needed from it other than reproductive condition could still be recorded.

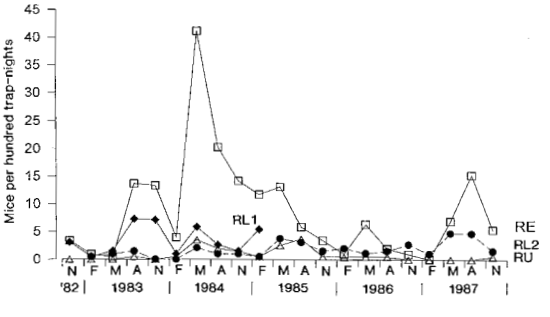

Figure 2: *Density indices (captures per 100 trap-nights) recorded on the four traplines over the five years of the study. Key: Line RL1, logged native forest road edge (closed after February 1985); RL2, logged native forest interior; RU, unlogged native forest interior; RE, exotic plantation road edge.*

Measurements

We recorded whole body weight, paunched weight (after removal of stomach), total length and tail length (by the "hanging tail" method), omitting mice that had been chewed in the trap or were missing tails or feet. In analyses of weight we excluded the pregnant females, and in analyses of length we excluded any mouse with a damaged spine or tail.

Age determination

We classified all mice according to Lidicker's categories of molar toothwear, as illustrated from New Zealand material by Murphy and Pickard (1990). This method gives consistent results open to comparison with other New Zealand studies, and has been calibrated against a collection of 44 known-aged, wild-caught mice by Murphy (1989). Murphy found some disagreements between Lidicker's age classes and the actual ages of mice in classes 5 and 6, but the broad correlation was confirmed (Appendix 1). Badan (1979) deduced the ages represented by each of Lidicker's defined categories by calculating the number of months since the last breeding season that mice of each class appeared, and then disappeared, from the population. He arrived at a similar broad confirmation (Appendix 1). Therefore, although Lidicker's age classes cannot strictly be related to chronological age in any new population without local calibration, they do give useful and generally reliable relative rankings. A more detailed study would be desirable, since similar patterns of wear were assigned to different ages by Keller (1974). For certain purposes we grouped the age classes into two categories, young mice (classes 1-3) and old mice (classes 4-8). From Appendix 1 we estimate that the young mice were all under 3-4 months old.

Criteria for assessing reproductive activity

The condition of the vagina (perforate or imperforate) is not presented because it is an unreliable indicator of reproductive condition (Pye, 1993).

We took active pregnancies and lactations to define present breeding, although the number of actively breeding females is thereby underestimated (embryos are not visible to the naked eye for the first 5 days of the 20-day gestation period: Laurie, 1946). Females that had bred at some time in their lives, though not necessarily during the sample period in which they were collected, were defined as those that were pregnant, lactating, or with uterine scars. Uterus condition was classified into one of three standard categories of relative thickness. Those classed as "thread" could be either immature or mature but quiescent; enlarged uteri associated with ovarian activity were classed as "string" or "cord".

Litter size was estimated as the mean number of viable embryos (excluding resorptions) per pregnant female. The traditional criterion indicating breeding condition in males, the position of the testes (scrotal or abdominal), is not presented because it is unreliable (Badan, 1979; Efford, Karl and Moller, 1988); we determined male breeding condition mainly from whether or not the tubules in the epididymides were visible. We also tried a new method, based on the length and width of the testes in mm. By assuming that width and depth were equal, we derived a rough estimate of testis volume (length x width x depth = volume in mm^3). We define recruitment as the addition of young mice (age classes 1-3) to the trapped samples. Indicators of recruitment include: high proportions of young mice of both sexes, an increase in the ratio of females classed as never having bred, and a drop in the mean age of the population. The category "young" refers to chronological age as reflected by tooth wear, not to reproductive maturity. Analyses of female reproductive output did not include any mice of category 1 (the only ones that were certainly all immature).

Statistical analysis

After cross-checking the input files, we analysed the data using the statistical packages SAS and GENSTAT.

We first used nonparametric statistics, because the samples were often small and not always normally distributed. However, many of the parameters we were interested in were influenced by several sources of variation at once, e.g., season, age, year and trap line. Non-parametric tests are rather poor at handling more than one variable at a time, so we turned to the General Linear Model Procedure (PROC GLM) of SAS and the generalised linear model procedures in GENSTAT.

We used these programmes to perform a split-plot analysis of covariance on each of the variables of interest (age, sex, 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. Percentage variables were handled by GENSTAT's generalised linear models with logit link function and binomial error function, and by using deviance ratios to test the significance of each factor. All other variables were handled by PROC GLM. In all tables, significant differences were assumed if $P<0.05$.

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 x year interaction term was used as the error term for testing differences between lines. This procedure will detect differences between habitats that remained consistent over the five years covered by the study. Similarly, season was tested against the season x line interaction. Other factors were tested against the residual error. Where appropriate, adjustments were made for age by fitting both age and age-squared as co-variates. Least significant differences (LSDs) were used to detect significant differences between adjusted means. The raw data are available on request from MOK.

Data from the pilot trapping session in November 1982 were omitted from the analyses involving comparisons between years and seasons, since they represented only one season of that year. Separate analyses of the large sample from the young plantation allowed closer examination of the effects of density on population parameters.

Results

Distribution of samples

Of 518 captures recorded in rodent traps (King *et al.,* 1996), we excluded 23 fragmentary or damaged specimens, leaving 495 carcases in good condition. About one third of them came from the three indigenous forest lines together and two thirds from the young plantation of exotic forest (Table 1) - of which 135 were collected during the 1984 population irruption. Not all the mice examined were included in every analysis.

Rat traps have a heavier spring than mouse traps, but all traps were set very finely and there were no differences in the weights, lengths, ages or sexes of the mice collected from rat traps (n=159) and mouse traps (n=359). We recorded only one multiple capture, in a rat trap in the young plantation during the population irruption of May 1984, as illustrated by Innes (1990). Both were non-breeding males, one of age class 3 and the other of age class 4.

Population structure

Table 1 shows the distributions of age classes and sexes by habitat, season and year. All the mean values for each variable shown are automatically adjusted for the effects of all the other variables, whether significant or not.

Males outnumbered females in the capture records from all traplines, all years, in both road edge and interior forests of both types, and in all age classes. None of these differences were significant

Table 1: *Age structure and sex ratio (percentage of males) among 495 mice collected from Pureora (individuals with incomplete data excluded from certain tabulations). For definitions of the habitats sampled by each trap line, and of age groups and statistical tests, see text. Every mean percentage value shown is adjusted for all other appropriate variables and tested by the generalised linear model of GENSTAT. Cells labelled with the same letter are not significantly different (at P=0.05) from other cells with the same letter: n = the total number of mice from which each percentage value was derived.*

		Percent male			Percent young		
		n	%	sig	n	%	sig
Line	RU Unlogged interior	33	63	a	32	10	b
	RL2 Logged interior	64	59	a	63	11	b
	RL1 Logged road edge	57	69	a	54	35	a
	RE Exotic road edge	328	65	a	322	33	a
Season	Spring	106	63	a	102	3	c
	Summer	53	35	b	53	46	a
	Autumn	161	63	a	158	44	a
	Winter	162	67	a	158	24	b
Year	1983	92	64	a	86	48	ab
	1984	173	59	a	170	22	b
	1985	102	62	a	100	16	b
	1986	38	55	a	38	30	ab
	1987	77	65	a	77	39	a
	All	482	61	-	471	27	-
Age classes	1-2	25	70	a	-	-	-
	3	104	55	a	-	-	-
	4	210	59	a	-	-	-
	5	118	63	a	-	-	-
	6-8	27	80	a	-	-	-
Age groups	Young	129	58	a	-	-	-
	Old	355	62	a	-	-	-
Sex	Male	-	-	-	287	28	a
	Female	-	-	-	184	30	a

overall (by χ^2 tests or GLM). However, significantly fewer males were caught in summer (Table 1).

Most mice collected were classified into age groups 3, 4 and 5 (Table 1). The two youngest and the three oldest age groups were poorly represented; class 1 contained only five males, class 2 eight females and 12 males, class 6 four females and 14 males, class 7 four males, and class 8 one female.

The relative proportions of young mice were significantly lower among samples collected from the interior of native forest (10% in unlogged and 11% in logged forest) than among samples collected from the road edge, either in logged native forest (35%) or in the young plantation (33%) even after the comparisons were controlled for all other relevant variables (Table 1). In logged forest, the density indices from the forest interior lines were also lower than those from the road edge lines taken at the same times (Fig. 2). Of 46 mice from the road edge collected between February 1983 and February 1985 inclusive, 32% were young, against 9% of 12 from the interior over the same period (or 11% of 63 over the whole five years). Therefore, whenever it was useful to pool samples in the following analyses, we did so by distance to road edge rather than by forest composition.

There were significant (Table 1) differences in age distributions with season which, at Pureora, were strongly influenced by distance to the road edge (Fig. 3). In the two interior forest traplines, all mice caught in the spring (November) sample were classed as old, i.e., fully mature breeding adults (age classes 4-8) born in the previous season. Their newly emerged offspring (class 2) appeared only in summer, and by autumn, mice born in the current season had reached classes 3 and 4. Breeding stops

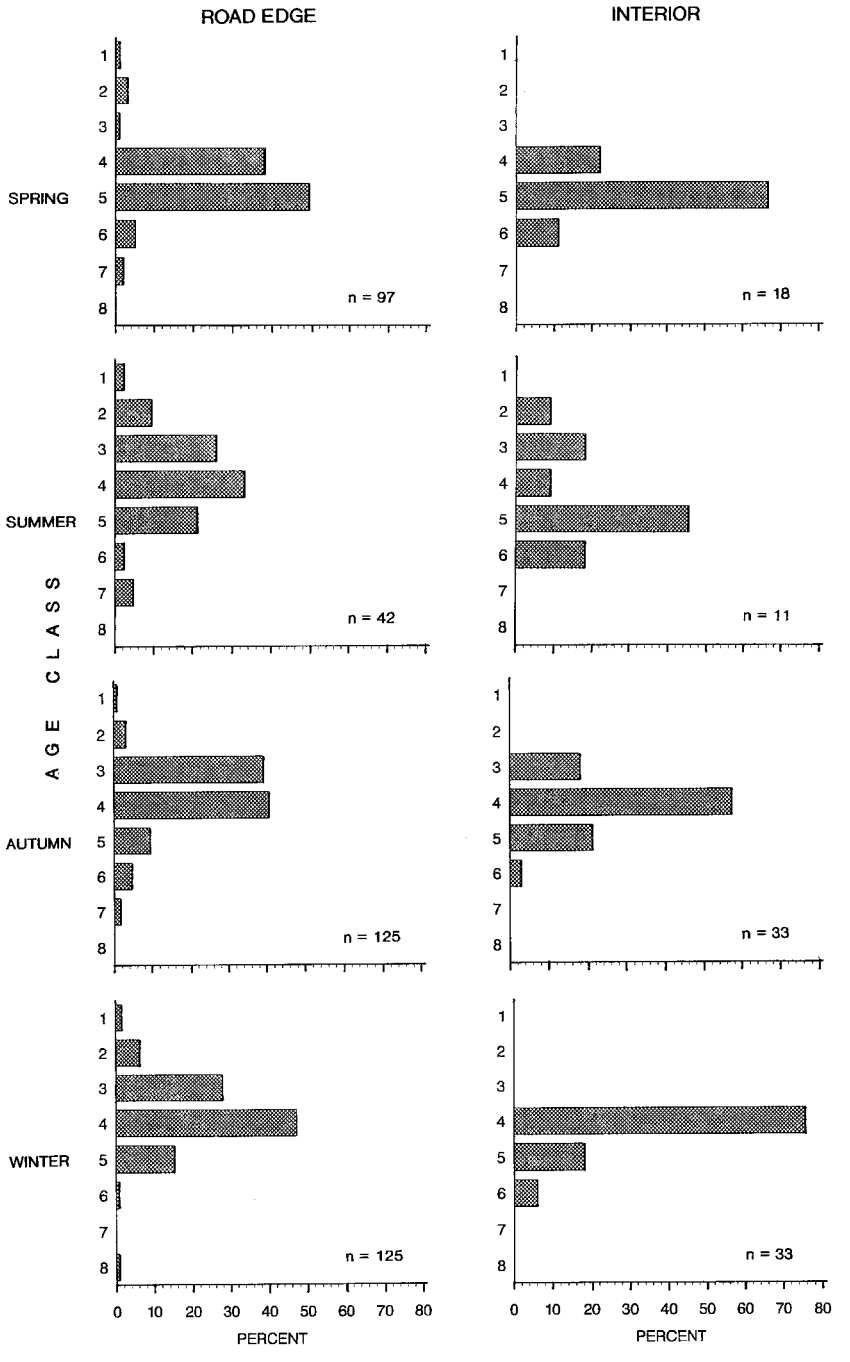

Figure 3: *Age structures of mouse populations by season from road edge traplines (logged native plus exotic forest) compared with forest interior (logged and unlogged native forest) traplines. Samples pooled by distance to road edge rather than by forest composition for reasons explained in text.*

as the weather cools, so the autumn and winter samples were again composed almost entirely of old, non-breeding adults of classes 4-6.

By contrast, in the two road edge communities all age classes, including very young mice of classes 1-2 and very old ones of classes 7-8, were caught at any season of the year. The apparent shortage of very old mice (classes 6+) in the forest interior is not a sampling error: although such old mice are rare, so appear most often in the largest samples, there were no significant differences between lines in the distribution of old mice ($P = 0.67$).

Measurements

Table 2 shows that there were no significant differences between trap lines in the distributions of any measurements (means adjusted for age and sex), so all lines were pooled in the following analyses. Whole body weight (excluding pregnant females) and paunched weight gave similar seasonal variation (Table 3). Whole body weight is a reliable measure taken alone, and allows comparisons with studies of live-trapped mice, so we suggest that separate records of paunched weight are no longer necessary. Annual variations in head-and-body length and tail length did not match those shown by the weight data.

Fig. 4 shows the unadjusted mean whole weights of each sex by age class. Mice continue to grow throughout life, but the increase in body weight with age in the two sexes is not the same in all seasons; male and female mice of a given age were significantly larger in all dimensions in summer than at any other time of year (Table 3), especially the females ($P<0.0001$). These data imply that juvenile mice grew faster in summer than at other seasons, and that mature mice, especially females, put on extra weight during breeding.

Reproduction

No indicators of reproductive activity showed any significant variation with habitat (forest type, line or

Table 2: *General distribution of body measurements of Pureora mice, excluding pregnant females and all mice with any physical damage. All means adjusted for age, sex, season and year by GLM. Cells labelled with the same letter are not significantly different (at* P=*0.05) from other cells with the same letter.*

		Whole body weight (g)			Paunched weight (g)			Total length (mm)			Tail length (mm)		
		n	$\bar{x}$	sig	n	$\bar{x}$	sig	n	$\bar{x}$	sig	n	$\bar{x}$	sig
Line	RU Unlogged interior	30	16.9	a	29	15.8	a	29	158.9	a	29	80.3	a
	RL2 Logged interior	60	16.0	a	60	14.9	a	59	158.4	a	60	80.0	a
	RL1 Logged road edge	49	15.9	a	49	15.1	a	48	159.0	a	48	79.3	a
	RE Exotic road edge	301	16.2	a	292	15.3	a	290	159.8	a	292	80.3	a
Season	Spring	89	15.7	b	84	14.6	b	92	158.6	b	92	80.0	a
	Summer	41	18.3	a	41	17.3	a	46	162.7	a	48	81.2	a
	Autumn	155	15.3	b	154	14.4	b	141	158.3	b	143	79.4	a
	Winter	155	15.8	b	151	14.8	b	147	156.5	b	147	79.4	a
Year	1983	77	17.1	a	77	16.0	a	80	158.8	a	80	79.3	a
	1984	162	15.6	bc	154	14.7	bc	151	157.7	a	152	80.4	a
	1985	92	15.3	c	91	14.4	c	86	159.1	a	88	79.3	a
	1986	35	16.7	a	35	15.5	ab	38	160.5	a	38	81.4	a
	1987	74	16.6	ab	73	15.8	a	71	159.0	a	72	79.7	a
All		440			430			426			430		
Sex	Male	283	16.7	a	278	15.7	a	261	160.6	a	264	80.8	a
	Female	157	15.4	b	152	14.4	b	165	156.6	b	166	78.8	b
Age class	1-2	23	10.8	d	23	10.2	d	22	140.4	e	23	69.8	e
	3	99	13.9	c	98	12.9	c	90	151.9	d	91	76.9	d
	4	193	16.3	b	188	15.4	b	194	159.5	c	196	80.3	c
	5	103	18.2	a	99	17.0	a	99	164.6	b	99	82.7	b
	6-8[1]	22	19.2	a	22	17.9	a	21	170.2	a	21	85.4	a

[1] For comparison with other areas, see Murphy and Pickard (1990:Table 40).

Table 3: *Seasonal variation in body measurements in each sex. Adjusted means generated by GLM controlling for age, line and year. Unadjusted whole weights ± SE (n) plotted by age class in Fig. 4.*

	Whole weight (g)	Paunched weight (g)	Total length (mm)
Males			
Spring	16.1 ± 0.31 (75)	15.0 ± 0.29 (72)	159.8 ± 1.27 (69)
Summer	17.5 ± 0.58 (18)	16.6 ± 0.53 (18)	160.4 ± 2.36 (17)
Autumn	15.7 ± 0.29 (94)	14.8 ± 0.27 (94)	160.8 ± 1.20 (86)
Winter	16.3 ± 0.27 (105)	15.3 ± 0.25 (103)	158.1 ± 1.11 (97)
All year	16.4 ± 0.23 (292)	15.4 ± 0.21 (287)	159 8 ± 0.93 (269)
Females			
Spring	14.5 ± 0.47 (26)	13.3 ± 0.44 (24)	156.4 ± 1.64 (35)
Summer	18.7 ± 0.53 (23)	17.4 ± 0.49 (23)	163.1 ± 1.88 (29)
Autumn	14.4 ± 0.35 (61)	13.6 ± 0.32 (60)	154.8 ± 1.44 (55)
Winter	14.5 ± 0.37 (50)	13.4 ± 0.34 (48)	153.5 ± 1.44 (50)
All year	15.6 ± 0.25 (160)	14.4 ± 0.23 (155)	157.0 ± 0.94 (169)
GLM Season x sex	F = 4.55, *P* <0.004	F = 4.41, *P* <0.005	F=2.54, *P* <0.056

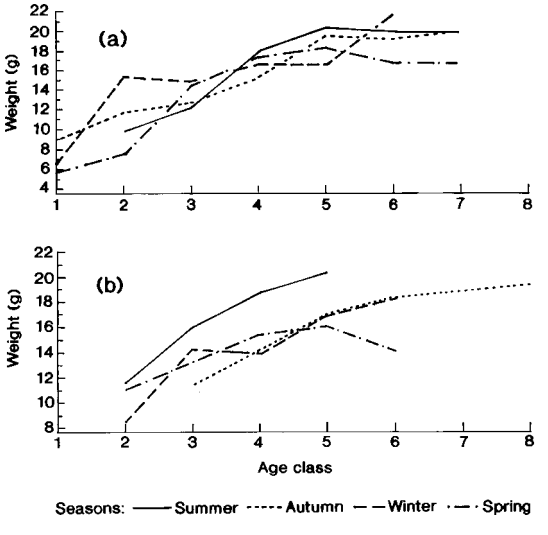

Figure 4: *Unadjusted mean weights of mice by age class and season in (a) males and (b) females. For standard errors, sample sizes and tests, see Table 3. The greater weight for age in summer was significant in both sexes.*

distance to road: Tables 4 and 5). Variation between years in these characters was also non-significant for females, but not for males.

Two of eight females assigned to age class 2, weighing 10-12 g (Table 2), had enlarged uteri, and one was pregnant. Two of 11 males of the same age had visible tubules, although all had abdominal testes. We therefore assumed that any mouse of category 2 or above could have been sexually mature.

The categories of uterus condition showed the expected seasonal variation. "Thread" uteri characteristic either of very young or of mature but sexually inactive females dominated the samples in autumn and winter, although they comprised at least 25% of females (young or old) at any season. There were signs of ovarian activity all the year round, even in young mice (Fig. 5).

Pregnancies and active lactations were recorded most often in spring (old mice only) and summer (old and young equally): virtually all female mice caught in summer had bred (Table 4). Only 29 of 168 females were scored as definitely pregnant (and two were omitted from Table 4 because some data were missing), but they were more or less evenly divided between the trap lines. The pregnancy rate ranged from 20% to 25% in most subsamples except in the logged forest interior, which was lower (6%) but not significantly so. Three pregnant females were collected in winter, despite the high altitude and cool climate of the Pureora district - one each from unlogged, logged and exotic forest, one young, two old (Fig. 5). Two of them were caught in August 1983, one along a track in the logged forest and one in the young plantation. The third came from the unlogged forest in the following August. The fewest pregnancies were recorded in autumn, coinciding with the season of least sexual activity among males (Table 5). Age class made no difference to litter size, but older mice were more likely to be pregnant or lactating when caught, and to carry uterine scars.

In two of the five years observed, active reproduction had ceased by May (Fig. 6a), and in the other three years only a minority of females was still lactating by then. In 1985 and 1986, breeding did not start again until after August; in 1983 and 1987

Table 4: *General distribution of female reproductive characters. All means adjusted for age, line, season and year by GLM. Definitions: "Young", mice of age classes 1-3; "Present breeding rate", percent females of all ages pregnant or lactating or both; "Past breeding rate", percent females of all ages showing any sign of ever having bred, ie pregnant, lactating or with uterine scars. Cells labelled with the same letter are not significantly different (at* P=*0.05) from other cells with the same letter.*

		% pregnant			Mean no. viable embryos			Mean no. uterine scars			Present breeding rate (% preg/lact)			Past breeding rate (% bred)		
		%	n		$\bar{x}$	n		$\bar{x}$	n		%	n		%	n	
Line	RU Unlogged	25	10	a	3.3	2	a	-		a	12	7	a	29	7	a
	RL2 Logged interior	6	22	a	5.5	2	a	6.6	9	a	18	20	a	34	22	a
	RL1 Logged road edge	20	17	a	5.1	4	a	7.0	6	a	28	16	a	51	19	a
	RE Exotic road edge	20	111	a	4.3	19	a	5.8	26	a	27	104	a	39	111	a
Season	Spring	28	35	a	6.0	13	a	3.2	6	b	23	29	b	34	34	b
	Summer	50	32	a	6.4	10	a	9.3	18	a	84	27	a	99	32	a
	Autumn	2	59	b	1.0	1	a	7.1	12	a	6	59	b	18	58	b
	Winter	7	34	b	4.9	3	a	6.1	5	a	11	32	b	24	35	b
Year	1983	29	28	a	4.3	9	a	5.6	4	a	32	31	a	46	31	a
	1984	18	51	a	3.2	7	a	5.2	9	a	16	42	a	36	48	a
	1985	9	39	a	4.2	6	a	7.6	13	a	20	33	a	26	38	a
	1986	20	18	a	4.1	3	a	5.6	9	a	38	18	a	59	18	a
	1987	20	24	a	6.9	2	a	8.0	6	a	29	23	a	42	24	a
Age group	Young (Cl. 1-3)	14	50	a	3.6	5	a	2.9	8	a	16	48	a	23	50	a
	Mature (Cl 4+)	20	110	a	4.9	21	a	7.6	33	b	31	95	b	52	105	b
All		16	160			27			41		27			45		

Table 5: *General distribution of male reproductive characters. All means adjusted for age, line, season and year by GLM. Cells labelled with the same letter are not significantly different (at* P=*0.05) from other cells with the same letter.*

		% with visible tubules			Mean testis volume (mm^3)		
		%	n		$\bar{x}$	n	
Line	RU Unlogged interior	65	15	a	105	20	a
	RL2 Logged interior	38	39	a	83	40	a
	RL1Logged road edge	27	28	a	79	31	a
	RE Exotic road edge	34	156	a	80	186	a
Season	Spring	69	55	a	92	65	a
	Summer	85	16	a	118	18	b
	Autumn	19	92	b	57	94	c
	Winter	28	75	b	80	100	d
Year	1983	58	57	a	103	56	a
	1984	40	60	ab	76	96	b
	1985	17	52	c	60	54	c
	1986	20	20	bc	91	20	ab
	1987	41	49	ab	105	51	a
Age group	Young (classes 1-3)	25	69	a	58	70	a
	Old (Classes 4+)	43	169	b	96	207	b
All		37	238		87	277	

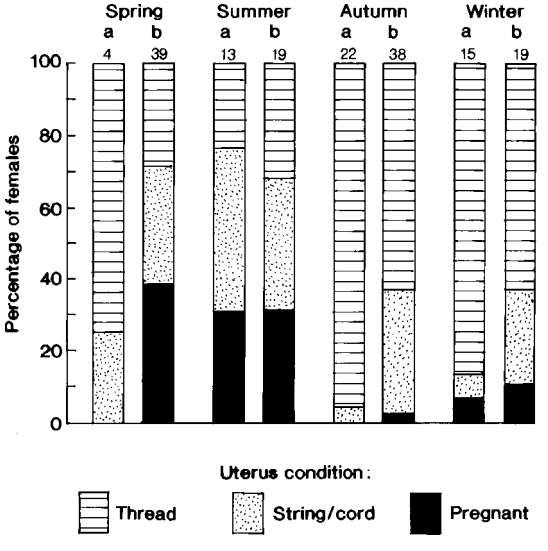

Figure 5: *Seasonal distribution of uterus condition in (a) young (age classes 1-3) and (b) older (4+) females, with sample sizes.*

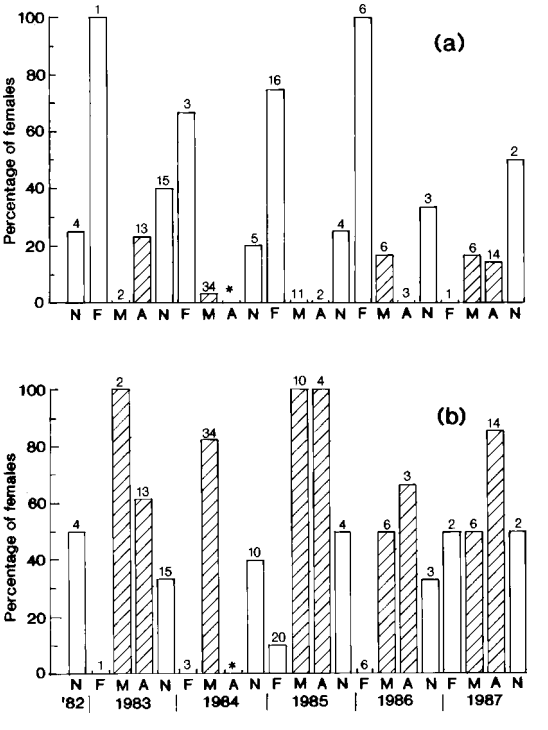

Figure 6: *(a) Proportion of females pregnant, lactating or both through the five years. Parous females were most numerous in spring and summer (clear bars), but often also present in autumn and winter (hatched bars). The sample for August 1984 (starred) contained 18 females, all too poorly preserved to be assessed for reproductive condition, although at least one was pregnant.*
(b) Proportion of females scored as never having bred (i.e., not pregnant or lactating and with no uterine scars). The largest numbers of non-parous females appear in the autumn and winter (hatched bars), rather than in spring and summer (clear bars) - i.e., the opposite to Fig. 6a.

breeding had already begun by August. Of the 18 poorly preserved females collected in August 1984 and recovered after the freezer breakdown, at least one was pregnant.

The seasonal distribution of viable embryos and the mean litter size are shown in Fig. 7. The seasons of 1983-4 and 1984-5 started early (viable embryos recorded in August) and continued to February; the season of 1986-7 ended late (after May), but breeding had started again by the time of our last trapping session in November 1987. Litter size ranged from 5 to 8 viable embryos (average 6) in 23 spring and summer pregnancies, but was smaller in autumn and winter (range 1-5 in 4 pregnancies) though samples were too small to tell if the difference was significant (Table 4). Scars from several previous litters can accumulate with time, so counts of scars were generally higher and correlated with age.

Resorbing embryos were found in five of 29 litters counted, totalling 12 of 161 embryos (7.4%). One embryo was being resorbed out of five litters ranging from 4 to 7 embryos in total; two out of one litter of eight; and in one case the whole litter was being resorbed - five out of five. The single case of total resorption, plus one of the single resorptions, were recorded in the young plantation during the summer of 1984/5, ie following the population peak.

Least squares means for indices of reproductive activity in males adjusted for all other variables were similar in all habitat types (Table 5). Trends in the figures for testis volume followed those for proportion with visible tubules (Tables 5, 6). Mean indices of breeding activity declined in autumn and winter, mostly due to the annual influx of immature young males, but some mature males remained in breeding condition all year. The decline in reproductive activity of both sexes in 1985 was most pronounced in the sample from the young plantation (see Table 6b), but also appeared in the other lines.

Recruitment

Recruitment was strongly seasonal. The percentage of the population classed as young was highest in the summer and autumn on all lines (Table 1, Fig. 3).

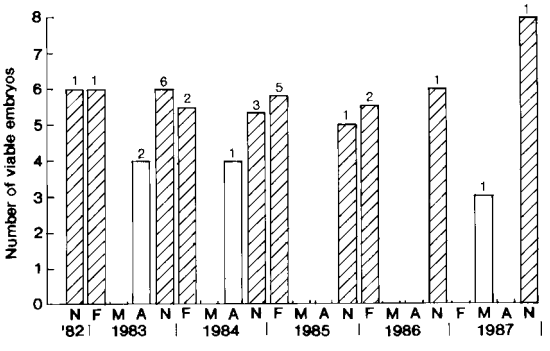

Figure 7: *The distribution of viable embryos (as mean counts per pregnant female) through the study. Autumn and winter litters (clear bars) tended to be smaller. The single litter shown for August 1984 is a minimum (see text).*

The proportion of females classed as never having bred was always under 50% in spring and summer but 50-100% in autumn and winter (Fig. 6b). However, although breeding effort was apparently similar in all habitats (Tables 4 and 5), these criteria suggest that recruitment was higher in the road edge habitats, both in native forest where indigenous woody species were recolonising the edge of an old logging track, and in the young plantation. On these two trap lines, over a third of all mice collected were young (Table 1). By comparison, only about one tenth of the mice collected on the two native forest interior lines were young, whether the forest was logged or not. These differences were significant, both as frequency distributions of age groups (Fig. 3) and in an analysis of variance of age controlling for distance to road, season and sex ($P<0.001$).

The road edge females did not have higher counts of viable embryos or uterine scars (Table 4), and both habitats can support winter breeding, but the road edge females were much more likely to start breeding at or before age class 3 than females of the same age in the interior forest (Kolmogorov-Smirnov 2-sample test, $P=0.001$: n=48, 7 young females, respectively). Therefore the higher productivity and numbers of the road edge populations appear to be due mainly to better recruitment and earlier breeding.

Effects of density on size and reproduction in the young plantation

Mice collected from the very dense population in the young plantation during 1984 were significantly lighter (but not shorter) than other mice of the same age collected in other years (Table 6a). The effect persisted into 1985, the year of steady decline that followed (Fig. 2). This is not due to an influx of young mice; on the contrary, over the same periods the proportions of young mice significantly *de*creased (Table 6a). GLM analyses of variance of weight controlling for age, sex and season confirmed that the overall difference was significant in both years (Table 6a). Fig. 8 plots the mean weights of

Table 6a: *Annual variation in density, population structure, measurements and reproductive activity of mice collected from the RE line in the young plantation. Cell means calculated by GLM adjusting for all other relevant variables. Definitions: "Young", mice of age classes 1-3; "Present breeding rate", percent females of all ages pregnant or lactating or both; "Past breeding rate", percent females of all ages showing any sign of ever having bred, ie pregnant, lactating or with uterine scars. Cells labelled with the same letter are not significantly different (at* P=*0.05) from other cells with the same letter.*

Year	Density (c/100TN)	n	% Male %		n	% Young %		n	Whole weight $\bar{x}$		n	Paunched weight $\bar{x}$		n	Total length $\bar{x}$		n	Tail length $\bar{x}$	
1983	7.1	56	65	a	53	58	a	47	17.3	a	47	16.3	a	50	160.6	a	50	80.4	a
1984	19.8	135	57	a	132	25	b	127	15.0	b	127	14.2	b	115	156.5	a	116	79.7	a
1985	8.5	62	58	a	62	18	b	55	14.6	b	55	13.9	b	52	157.9	a	53	78.7	a
1986	2.5	21	64	a	21	34	ab	20	16.4	a	20	15.4	a	21	159.4	a	21	80.3	a
1987	6.9	54	60	a	54	45	a	52	16.9	a	52	16.0	a	52	160.9	a	52	80.3	a

Year	% Pregnant n	%		Mean no. viable embryos n	$\bar{x}$		Mean no. uterine scars n	$\bar{x}$		Present breeding rate n	%		Past breeding rate n	%		% visible tubules n	%		Mean testis volume n	$\bar{x}$	
1983	18	22	a	6	4.4	ab	4	6.3	a	18	24	a	18	51	a	35	67	a	35	95	a
1984	40	11	a	4	3.0	c	7	3.2	a	36	10	a	38	24	a	44	23	bc	72	64	b
1985	26	12	a	6	3.8	bc	8	5.3	a	21	24	a	26	20	a	32	10	c	32	50	b
1986	8	15	a	1	4.9	ab	3	3.5	a	8	26	a	8	52	a	13	31	abc	13	89	a
1987	19	30	a	2	6.9	a	4	10.4	b	19	29	a	19	43	a	32	43	ab	34	100	a

Table 6b: *Annual variation in density, population structure, measurements and reproductive activity of mice collected from indigenous forest , i.e., all lines other than the RE line in the young plantation. Cell means calculated by GLM adjusting for all other relevant variables. Definitions: "Young", mice of age classes 1-3; "Present breeding rate", percent females of all ages pregnant or lactating or both; "Past breeding rate", percent females of all ages showing any sign of ever having bred, ie pregnant, lactating or with uterine scars. Cells labelled with the same letter are not significantly different (at* P=*0.05) from other cells with the same letter.*

Year	% Male			% Young			Whole weight			Paunched weight			Total length			Tail length		
	n	%		n	%		n	$\bar{x}$		n	$\bar{x}$		n	$\bar{x}$		n	$\bar{x}$	
1983	36	67	a	33	46	a	30	16.5	a	30	15.4	a	30	157.7	a	30	78.1	a
1984	38	64	a	38	16	a	35	16.3	a	34	15.2	a	36	159.8	a	36	80.9	a
1985	40	68	a	38	10	a	37	15.9	a	37	14.9	a	34	160.6	a	35	80.3	a
1986	17	43	a	17	7	a	15	16.8	a	15	15.5	a	17	161.5	a	17	82.6	a
1987	23	75	a	23	13	a	22	15.9	a	22	15.1	a	19	156.4	a	20	79.6	a

Year	% Pregnant			Mean no. viable embryos			Mean no. uterine scars			Present breeding rate			Past breeding rate			% visible tubules			Mean testis volume		
	n	%		n	$\bar{x}$		n	$\bar{x}$		n	%		n	%		n	%		n	$\bar{x}$	
1983	10	41	a	0	-	-	0	-	-	10	50	a	10	48	ab	22	42	b	21	102	a
1984	11	58	a	3	5.7	a	2	9.5	a	5	40	a	9	72	a	16	79	a	24	92	a
1985	13	0	a	3	5.0	a	5	6.6	a	12	19	a	12	33	b	20	28	bc	22	65	b
1986	10	7	a	2	5.5	a	6	7.5	a	10	42	a	10	64	ab	7	12	c	7	86	ab
1987	5	0	a	0	-	-	2	7.5	a	4	0	a	5	32	b	17	31	bc	17	97	a

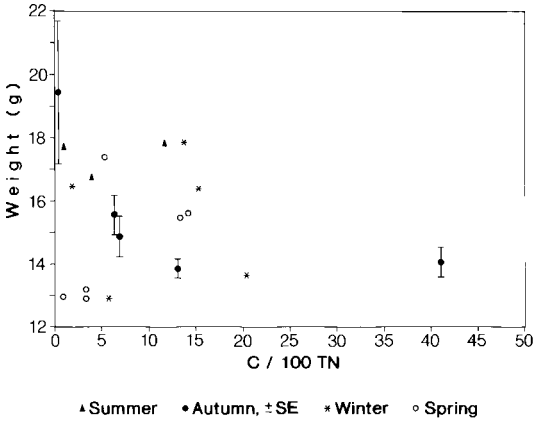

Figure 8: *Mean body weight (adjusted for age and sex) of mice collected in the young plantation in relation to density and season. Mice collected in autumn were significantly lighter (P=0.037) at high densities; those collected in spring tended to be heavier.*

the plantation mice (adjusted for age and sex) by season against capture rate. In autumn, mice were significantly smaller at higher densities (Spearman's rank correlation coefficient r_s=-9.0, *P*=0.037). In spring, they tended to be larger at high densities, though not significantly (r_s=0.77, *P*=0.072).

In 1984 and, even more so in 1985, there was a substantial decline in male breeding condition. Of 33 males collected in the plantation throughout 1985, only 10% had visible tubules. Spearman's rank correlation coefficient found no correlations between capture rate and breeding activity in either sex (pregnancy rate or proportion of males with visible tubules), and none with mean age.

Causes of the 1984 population peak in the plantation

We had no information on when the favourable conditions stimulating the Pureora peak began, so we analysed the data by calendar years. Fig. 2 shows that calendar 1984 spanned the period of highest densities recorded, and calendar 1985 the long decline that followed.

Winter breeding, which often precedes population increases in mice, was practically absent in the plantation in 1983 (none of 29 females from there had viable embryos in May, and only one of nine in August).

The peak population itself (May 1984) comprised mostly mice of age classes 3 and 4, i.e., roughly 2-5 months old, born over the previous summer. Breeding stopped as usual after February 1984; in May we collected only two very young mice of classes 1 and 2, and out of 62 older mice, not one female was pregnant or lactating, and only one of class 4 and three of class 5 had ever bred at

all. The population peak in the plantation must therefore have been produced by normal breeding plus improved recruitment over summer, rather than, as in beech forests, extended breeding plus improved recruitment over the previous winter.

Discussion

Trapped samples are known to give an inaccurate view of a total population. Laurie (1946) compared trapped samples with total population counts obtained by physically dismantling corn ricks. He concluded that trapping with break-back traps provides a biased sample, because larger mice are caught more easily than smaller ones. In addition, Berry and Jakobson (1971) estimated (from foetal counts and pregnancy rates) that about half the young born fail to enter the trappable population at all. The extent of these biases in New Zealand studies should be investigated; meanwhile, the present results may be validly compared with previous studies in New Zealand that have used the same methods. However, because the spacing and baiting of traps, and the frequency and months of setting, also affect the level of sampling, results from studies that have used different field regimes (such as that of Badan, 1979; Pickard, 1984; Murphy, 1992; Miller and Miller, 1995) can be compared with ours only in general terms.

"The house mouse is a weed: quick to exploit opportunity, and able to withstand local adversity and extinction without harm ... to breed rapidly, tolerate a wide variety of conditions, and adjust quickly to changes in its environment" (Berry, 1981). The feral house mice at Pureora fit Berry's description well. They live independently of direct association with human activities, but swiftly take advantage of any human modification of the landscape - in short, they are the animal world's equivalent of the plant weeds that follow the loggers' chainsaws and bulldozers everywhere.

Previous studies have reported higher densities of mice in disturbed habitats (Hay, 1981; Fox and Fox, 1986; Murphy, 1989), or have documented links between the density and the population dynamics of feral mice and the patches of weeds and thick ground cover along fencelines and road verges in agricultural lands, called "donor habitats" by Singleton (1989) or "refuge habitats" by Mutze (1991) and Twigg and Kay (1994). Mice living in such favourable places supply colonists to surrounding habitats in which the maintenance of a permanent population is more difficult. This study suggests that the same pattern of distribution may be observed in forests after disturbances such as logging and roading.

Reproduction

In Britain (Berry and Jakobson, 1971), in Woodhill Forest (Badan, 1979), and on Mana Island (Efford *et al.,* 1988), mice reach sexual maturity at about six weeks, i.e., during Lidicker's age class 2. On Mana Island, there was a definite anoestrous period over winter, and young mice remained sexually immature until about 16 g even in midsummer (Efford *et al.,* 1988), but at Pureora there were signs of at least some ovarian and testicular activity all the year round, and young mice could be sexually mature at 12 g.

It would be interesting to know the cause of the drastic decline in breeding condition among male mice in 1985, especially as there was a corresponding drop in the proportions of females having bred and also (from 1984) in their mean litter size. The young trees in the plantation were thinned in March 1985, and the resulting extra cover provided by the discarded slash should have favoured the mice. A possible explanation might have been a poisoning or spraying operation conducted against pests of production forests, if it were not for the fact that the same decline in reproductive activity of both sexes, though not in age structure or body size, is visible in the data from indigenous forests (Table 6b).

Multiple captures, reviewed by Taulman, Thill and Williamson (1994), are indirect evidence of the close association between foraging pairs of small mammals, even though the proportion of double captures to total captures in snap-trapping studies probably underestimates the frequency of social travelling. Contrary to what one might expect, the pairs are not necessarily interested in mating. Taulman *et al.* (1994) found four records of double captures in 81 311 trapnights over four years. Two were male-female adult pairs of *Ochrotomys nuttali,* and two were juvenile male pairs of *Peromyscus* sp. Our single record from 14 502 corrected trapnights over five years was of a pair of juvenile males.

The key role of recruitment

The field data (described by King *et al.,* 1996) documented the considerable effect of forest disturbance on the density of mice at Pureora; mice reached greatest abundance in habitats with thick ground cover and open canopy - i.e., those least like the original forest. This paper suggests that the difference in local abundance was not due to any failure in productivity by the mice living in the forest interior, since (unlike Singleton, 1989) we could find no variation with habitat in any of the usual indicators of reproductive effort, such as fertile season, pregnancy rate, male fecundity, or litter size

(Tables 4 and 5). Rather, there seems to have been a systematic failure in recruitment of the young mice produced in forest interior habitats, which was not matched in the thick vegetation along the road edges and in the young plantation. Hence, normal breeding produced far larger local populations of mice, of a completely different age structure, in habitats disturbed in various ways by human activities than in tall forest. Moreover, the mice were apparently insensitive to forest type as such - so long as the ground cover was thick enough, it seemed to make little difference whether the nearest trees were native or exotic species.

These data suggest that the distance to the road edge has a greater effect on the density and age structure of a local population (which may reflect productivity and population dynamics) than does forest composition (reflecting site characters and logging history) *per se*. It could be argued that the effects of roading were confounded with those of forest composition in the main data set. We can test this suggestion, because we had two subsets of mice collected simultaneously from the road edge and from the forest interior of the same habitat, logged native forest. In them the difference in age structure was confirmed.

Dense ground vegetation provides a damp microclimate and offers the shelter, escape cover and rich supplies of food (fruits, seeds, and invertebrates) favoured by mice (Badan, 1986; Mutze, 1991). Invertebrates such as insects are especially important, and in some habitats they are the main item of diet (Miller and Miller, 1995). Insects supply concentrated protein, which significantly improves breeding performance (Bomford, 1987) and survival especially of the young (White, 1993). In turn, this may explain why Berry and Bronson (1992), after an extensive review of the literature, concluded that mice apparently prefer insect to plant food.

Since recruitment rate is generally determined by food supply, recruitment can be periodically increased by local and annual increases in some highly nitrogenous foods. For example, in a young plantation at Woodhill Forest, Badan (1986) recorded a population irruption of mice at about the same season (April/May 1977) that we did at Pureora (May 1984), which reached a peak density index of 47.4 C/100TN; a few months earlier, almost every mouse examined had been eating larvae of the variable bell moth (*Capua semiferana*) and/or the kowhai moth (*Uresiphita polygonalis maorialis*). In beech forest in the Orongorongo Valley, Fitzgerald *et al.* (1996) have shown a strong correlation between the numbers of emerging *Tingena epimylia* and of mice after heavy beech seedfalls, and that litter-feeding caterpillars provided a very important source of food for mice. We therefore suggest that, at Pureora, the sudden sharp acceleration in recruitment in the young plantation in autumn 1984 could have been set off by a temporary flux of high-quality protein food for the growing young mice, such as would be provided by a mass emergence of insects, over the summer of 1983/84. If insects and seeds are always more abundant in disturbed and roadside vegetation, the generally higher recruitment of mice along the roadedge line in normal years could be explained by the same correlation. Entomological surveys and analysis of the guts of the mice we collected at Pureora (still available) could be used to test this hypothesis.

Mice were most abundant in the young plantation, the only habitat we observed in which ship rats were practically absent (King *et al.*, 1996). We therefore propose a second hypothesis, which does not exclude the first, that thick ground cover (both live vegetation and accumulated humus) provides excellent burrowing conditions and protection for mice from predation by, or competition with, ship rats. In open-floored forest, mice would have greater difficulty in concealing their scent trails and nest-sites from the abundant and ubiquitous rats, which would therefore be more likely to find the breeding nests and eat the nestling mice. Hence the opportunity to escape from rats afforded to mice by thick cover could well be sufficient to increase recruitment, even without the additional food available under thick, damp cover. At present this idea rests only on circumstantial evidence, though it is greatly strengthened by the parallel observations made by Innes *et al.* (1995) after poison operations against ship rats. Whenever the rat kill exceeded 90%, tracking tunnels detected increased numbers of mice starting 3-6 months after poisoning, reaching a maximum 7-9 months after poisoning, and then declining to previous levels as the rats recovered. Several other cases of apparently reciprocal distributions of the two species in pine plantations were listed by Clout (1980). On Rangitioto Island, Miller and Miller (1995) caught mice more often on broken lava than in open-floored kanuka forest, and speculated that the lava might offer the mice protection from predation by, or competition from, ship rats.

Causes of population irruptions of mice in New Zealand

In beech forests in the Eglinton and Hollyford Valleys, Fiordland National Park, peak populations of mice followed the heavy seedfalls of 1976 and 1979. The peak populations, defined by King (1982) as comprising the five samples taken from the May immediately after the seedfall to the following May

inclusive, were significantly different from other beech forest samples taken in the same seasons, both in age structure and in breeding pattern. They were produced by a combination of extended breeding by adults and enhanced recruitment of young into the population, both most pronounced over the winter following the autumn seedfall and before the population peak in the following spring and summer (King, 1982). Recruitment of young levelled off in spring, well before the population peak in February 1977. Very few of the young mice born in the November after the seedfall entered the population in February.

There were important differences between the peak populations observed by the same methods in beech forests and in the young pine plantation at Pureora. First, the Fiordland beech forest peak populations built up during winter and spring, peaked in summer and were already steeply declining by autumn, whereas the peak population at Pureora developed very suddenly in autumn (Fig. 2), reversing an apparent decline over summer. Second, the extensive winter breeding that characteristically preceded mouse population peaks in beech forest was absent in the Pureora plantation. Third, recruitment in beech forests declined after August and virtually stopped by November, whereas the young born at Pureora in November 1983 and February 1984 had entered the population in substantial numbers by May.

These comparisons confirm Murphy's (1992) suggestion that several different factors are important in regulating mouse numbers. The most obvious precursor of an irruption is a sudden increase in the supply of nitrogenous food, which has different effects if it is added in winter, as after a beech seedfall (Fitzgerald *et al.,* 1996) or in summer, as after a flush of insects in a pine forest. Regular removal of stoats probably enhanced the 1976 Fiordland peak (King, 1985). In Australia, different factors, especially rainfall, are critical (Singleton, 1989).

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References

Badan, D. 1979 (unpublished). *The Ecology of Mice* (Mus musculus L.) *in Two Forests near Auckland*. MSc thesis, University of Auckland, Auckland, N.Z. 175 pp.

Badan, D. 1986. Diet of the house mouse (*Mus musculus* L.) in two pine and a kauri forest. *New Zealand Journal of Ecology 9*: 137-141.

Berry, R.J. 1981. Population dynamics of the house mouse. *Symposium of the Zoological Society of London 47*: 395-425.

Berry, R.J.; Bronson, F.H. 1992. Life history and bioeconomy of the house mouse. *Biological Reviews 67*: 519-550.

Berry, R.J.; Jakobson, M.E. 1971. Life and death in an island population of the house mouse. *Experimental Gerontology 6*: 187-197.

Bomford, M. 1987. Food and reproduction of wild house mice. III. Experiments on the breeding performance of caged house mice fed rice-based diets. *Australian Wildlife Research 14*: 207-218.

Brockie, R.E. 1992. *A Living New Zealand Forest*. Bateman, Auckland. N.Z. 172 pp.

Clout, M.N. 1980. Ship rats (*Rattus rattus* L.) in a *Pinus radiata* plantation. *New Zealand Journal of Ecology 3*: 141-145.

Efford, M.G.; Karl, B.J.; Moller, H. 1988. Population ecology of *Mus musculus* on Mana Island, New Zealand. *Journal of Zoology (London) 216*: 539-563.

Fitzgerald, B.M.; Karl, B.J. 1979. Foods of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington. *New Zealand Journal of Zoology 6*: 107-126.

Fitzgerald, B.M.; Daniel, M.J.; Fitzgerald, A.E.; Karl, B.J.; Meads, M.J.; Notman, P.R. 1996. Factors contributing to fluctuations in house mice (*Mus musculus*) populations in hard beech (*Nothofagus truncata*) forest. *Journal of the Royal Society of New Zealand 26*: 237-249.

Fox, M.D.; Fox, B.J. 1986. The susceptibility of natural communities to invasion. *In*: Groves, R.H.; Burdon, J.J. (Editors), *Ecology of Biological Invasions: an Australian perspective*. Australian Academy of Sciences, Canberra. 166 pp.

Innes, J.G. 1990. Ship Rat. *In:* King, C.M. (Editor), *The Handbook of New Zealand Mammals*, pp. 206-225. Oxford University Press, Auckland, N.Z. 600 pp.

Innes, J.; Warburton, B.; Williams, D.; Speed, H.; Bradfield, P. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *New Zealand Journal of Ecology 19:* 5-17.

Hay, J.R. 1981. *The kokako*. Unpublished report, Forest and Bird Research Group, Rotorua. 168 pp.

Karl, B.J.; Moller, H.; Thomas, B.W.; Tilley, J.A.V. 1984. A standardised data file for rodent autopsies. DSIR Ecology division, Unpublished report.

Keller, A. 1974. Détermination de l'âge de *Mus musculus* Linné par l'usure de la dentition. *Revue Suisse de Zoologie 81*: 839-844.

King, C.M. 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*), in relation to seedfall of southern beech. *New Zealand Journal of Zoology 9*: 467-480.

King, C.M. 1985. Interactions between woodland rodents and their predators. *Symposium of the Zoological Society of London 55:* 219-47.

King, C.M. 1990 (Editor), *The Handbook of New Zealand Mammals*. Oxford University Press, Auckland, N.Z. 600 pp.

King, C.M.; Innes, J.G.; Flux, M.; Kimberley, M.O.; Leathwick, J.R.; Williams, D.S. 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *New Zealand Journal of Ecology 20:* 215-240.

Laurie, E.M. 1946. The reproduction of the house-mouse (*Mus musculus*) living in different environments. *Proceedings of the Royal Society of London, series B 133*: 248-281.

Miller, C.J.; Miller, T.K. 1995. Population dynamics and diet of rodents on Rangitoto Island, including the effect of a 1080 poison operation. *New Zealand Journal of Ecology 19:* 19-27.

Murphy, E.C. 1989 (unpublished). *The Demography of an Island and Mainland Population of House Mice in the Marlborough Sounds, New Zealand.* PhD thesis, Victoria University of Wellington, N.Z. 150 pp.

Murphy, E.C. 1992. The effects of a natural increase in food supply on a wild population of house mice. *New Zealand Journal of Ecology 16*: 33-40.

Murphy, E.C.; Pickard C.R. 1990. House Mouse. *In:* C.M. King, (Editor), *The Handbook of New Zealand Mammals,* pp. 225-242. Oxford University Press, Auckland, N.Z. 600 pp.

Mutze, G.J. 1991. Mouse plagues in South Australian cereal-growing areas. III. Changes in mouse abundance during plague and non-plague years, and the role of refugia. *Wildlife Research 18*: 593-604.

O'Donnell, C.F.J.; Phillipson, S.M. 1996. Predicting the occurrence of mohua predation from the seedfall, mouse and predator fluctuations in beech forest. *New Zealand Journal of Zoology 23*: in press.

Pickard, C.R. 1994 (unpublished). *The Population Ecology of the House Mouse (Mus musculus) on Mana Island.* MSc thesis, Victoria University of Wellington, N.Z. 234 pp.

Pye, T. 1993. Reproductive biology of the feral house mouse (*Mus musculus*) on subantarctic Macquarie Island. *Wildlife Research 20*: 745-758.

Singleton, G.R. 1989. Population dynamics of an outbreak of house mice (*Mus domesticus*) in the mallee wheatlands of Australia - hypothesis of plague formation. *Journal of Zoology (London) 219:* 495-515.

Taulman, J.F.; Thill, R.E.; Williamson, J.H. 1994. Double captures of small mammals in single-capture traps: random encounters or social travelling? *Southwestern Naturalist 38*: 358-363.

Twigg, L.E.; Kay, B.J. 1994. The effect of microhabitat and weather on house mouse (*Mus domesticus*) numbers and the implications for management. *Journal of Applied Ecology 31:* 651-663.

White, T.C.R. 1993. *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer Verlag, Berlin. 425 pp.

Appendix 1: *Classes of age assigned to house mice from molar toothwear, and the actual ages in months represented by each class, as estimated by four authors.*

Age class	Brooks Is, CA	Woodhill, NZ	Marlborough Sounds, NZ	France Class	Age
1	0-1	<1	-	1	0.75
2	1-2	1-2	-	2	1-2
3	2-4	2-3	3.2 ± 0.2 (3)		
4	4-6	3-5	4.3 ± 0.8 (14)	3	3-5
5	6-8	5-8	6.5 ±2.1 (5)		
6	8-10	8-11	11.3 ±2.8 (10)	4	6-10
7	10-14	11-13	12.6 ± 1.0 (11)		
8	>14	>13	15 (1)	5	>11
9	-	-			
Author	Lidicker 1966[1]	Badan 1979	Murphy 1989[2]	Keller 1974[3]	

[1] Lidicker's categories are illustrated from New Zealand material classified by B.M. Fitzgerald and B.J. Karl in Murphy and Pickard (1990)

[2] Based on 44 known aged mice livetrapped in the wild (numbers in each age class given in parentheses)

[3] Keller provided drawings of nine stages of wear similar to the nine categories used by Lidicker, but defined only five categories of age, which disagreed substantially with those of all the other authors