

Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*), in relation to seedfall of southern beech

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Abstract After good seedfalls by southern beech (*Nothofagus* spp.), density indices for mice increased, the breeding season for adult females was brought forward, and winter breeding was observed. The end of the breeding season of the following summer was brought forward only slightly if the maximum density achieved was not great; incomplete data on 2 very high-density populations suggested a much earlier end to breeding. In early winter following a good seedfall the recruitment of juveniles was temporarily increased. After spring, few young mice entered the population, though breeding continued. The distribution of age classes shifted steadily upwards as population density rose. The peak population of 1976-77 comprised mainly old mice, still breeding, but without significant recruitment. No effects of density on sex ratio, litter size, or body weight could be detected from these data. In all populations studied, density decreases were ultimately due to failure of recruitment and the disappearance of ageing, non-breeding mice. The proximate causes of this mortality were probably the onset of cold weather in 1976-77 and predation by stoats in 1979-80.

Keywords *Mus musculus*; feral house mice; reproduction; recruitment; age structure; density index; predation; *Nothofagus* spp.; beech seedfall.

INTRODUCTION

Field populations of feral *Mus musculus* L., the house mouse, are capable of remarkable irruptions or 'plagues'. Such outbreaks have been correlated with periods of unusually favourable weather and/or the associated flush of vegetation, by Pearson (1963) in California and by Newsome & Corbett (1975) in Australia. *M. musculus* is uncommon in temperate

forests, except in New Zealand, where Fitzgerald's (1978) survey—including some of the present data up to 1976—noted population increases after seedfalls from southern beech, *Nothofagus* spp. King (in press) has documented moderate to heavy seedfalls in 3 South Island forests, and the increases in population density of mice which followed. The population structure and reproduction observed in the mice collected during 'seed years' and 'non-seed years' are compared in the present paper.

STUDY AREAS

Eglinton Valley, northern Fiordland National Park (44°50'S, 168°05'E). Length approx. 40 km; aspect NNE-SSW; altitude of valley floor 270-550 m; mean annual rainfall in centre section 2300 mm; range of monthly mean temperatures about 0-8°C; years sampled 1973-80. A glaciated valley with steep sides and flat floor about 0.5-1.0 km wide; continuous evergreen *Nothofagus* forest up to treeline at 1000-1100 m; surrounded by mountain peaks reaching 1500-1800 m.

Lower Hollyford Valley, northern Fiordland National Park (44°45'S, 168°10'E). Length approx. 35 km; aspect mostly N-S; altitude of valley floor 90-370 m; mean annual rainfall at least 4250 mm; range of monthly mean temperatures about 1-10°C; years sampled 1975-80. Steep-sided, but narrower than Eglinton; continuous diverse evergreen forest up to treeline at 1000-1100 m; separated from Eglinton by a pass at 530 m across the Main Divide of the Southern Alps.

Craigieburn Forest Park, Canterbury (43°10'S, 171°40'E). Area approx. 4500 ha; aspect NW-SE; altitude of trapline 790-1340 m; mean annual rainfall at field station 1450 mm; range of monthly mean temperatures 1-13°C; years sampled 1973-78. Contains a 1300 ha remnant of high-altitude evergreen *Nothofagus* forest perched on the flank of a range of foothills of the Southern Alps, adjacent to very large areas of cleared pastoral country and semi-natural grasslands.

Grebe and Borland valleys, southern Fiordland National Park (45°45'S, 167°30'E). Two forested valleys similar in appearance to the Eglinton and situated about 100 km south of it, sampled only in September and November 1979.

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METHODS

Rodent trapping

Rodent traplines were set out in accordance with a standardised procedure (Fitzgerald 1978). Each line comprised 36 stations at 50 m intervals, and each station was furnished with 2 snaptraps. At Craigieburn the stations were wooden tunnels with the ends wired to exclude possums, *Trichosurus vulpecula* (Kerr); a rat trap and a mouse trap were set, facing in opposite directions. In the Eglinton and Hollyford valleys the stations were wooden boxes with a single access hole, and the 2 traps were set side-by-side facing it. There was no difference in capture rate between tunnels and boxes in 2 trials run in November 1979.

Traplines of 36 stations may be regarded as rather too short, and likely to yield samples which are too small for precision in population estimates. However, Hayne (1978) points out that it is better to distribute one's effort into replicate observations of different populations than to concentrate on attaining precision within a single population, unless no general conclusions applicable outside that population are required.

Traps were set, without pre-baiting, for 3 consecutive nights in the last week of February, May, August, and November. The bait, peanut butter and rolled oats, was renewed as necessary. Results were expressed as captures of mice or rats per 100 trap-nights (C/100 TN), corrected for unavailable traps (Nelson & Clark 1973). The frequency of captures was taken to be significantly linearly related to population density, a fair assumption at frequencies below 20 C/100TN (Tanaka 1960, Caughley 1977). For purposes of density estimation, severed tails or feet were counted as a capture unless a mouse with the same part missing was caught in the same trap within the next 2 days. Tufts of fur were not so counted.

Rodent autopsies

Autopsy data were concentrated on size, reproductive condition, and age. The presence of embryos (visible for 2 of the 3 weeks of gestation - Berry 1970) was the only accepted criterion of reproductive activity in females. The condition of the vagina (perforate or imperforate) is an unreliable indicator of breeding condition (Laurie 1946), especially in mice not autopsied on the day of capture. Corpora lutea from successive cycles overlap, and since they cannot be distinguished without resorting to histology they were not counted. Age classes were assigned from examination of the wear of the upper molars, as described by Lidicker (1966). Actual ages were not known, so ages are referred only to classes (which are not necessarily equal), not to chronological intervals; but for present purposes mice in age

classes 1-3 are called 'young' and considered to be 3 months old or less (Lidicker 1966, Bellamy et al. 1973). Classification should be decided by agreement between 2 independent observers; failing that, I made 2 attempts to classify the material, separated by a long interval, and compared and reconciled the results.

Trapping history

Routine quarterly rodent trapping begun in November 1973 in the Eglinton was continued for 4½ years; trapping begun in February 1975 in the Hollyford was continued for 3½ years. Originally there were 2 trap lines in the Eglinton, in forest and on a wide, grassy flat, but after a year the grassland line was dismantled and the traps were shifted to the Hollyford. The study was considered to be finished in February 1978, and trapping on both lines stopped, though the stations were not removed. However, after a good seedfall in 1979 the lines were re-opened for a further 4 samples (September 1979 - May 1980). At Craigieburn trapping was done for 2½ years, finishing in May 1976. In February 1977 E. B. Spurr, of the New Zealand Forest Service, relocated the traps and operated them for a single session, but the mice caught were not autopsied.

In the summer of 1979-80, in conjunction with another study, rodent trap lines were operated in the Grebe and Borland valleys, in southern Fiordland. Traps were set in the usual way, but in tunnels of bent aluminium sheet, about 80 cm long, normally used to house stoat traps. Because the additional trapping in 1979-80 was done in 4 areas and in conjunction with other work, it was not possible to keep exactly to the usual dates. Trapping was 2 weeks later than usual in August 1979, 1 week later than usual in February and May 1980, and 2 weeks earlier than usual in November 1979. These data have been analysed as if they were obtained on the usual dates.

RESULTS

1. Density indices for mice in relation to seedfall

The study spanned 2 seedfalls in northern Fiordland (1976 and 1979), each observed in 2 areas, and 2 at Craigieburn (1974 and 1976), the second observed incompletely. There was a highly significant relationship between seedfall and density indices ($r_s = 0.73$, $P < 0.01$; $N = 11$ - Fig. 1) that is further discussed by King (in press). Most of the seed fell from March to June, and the sequence of changes observed in the mouse populations lasted about a year. 'Seed-year populations' are here defined as those sampled from May to May inclusive after a seedfall.

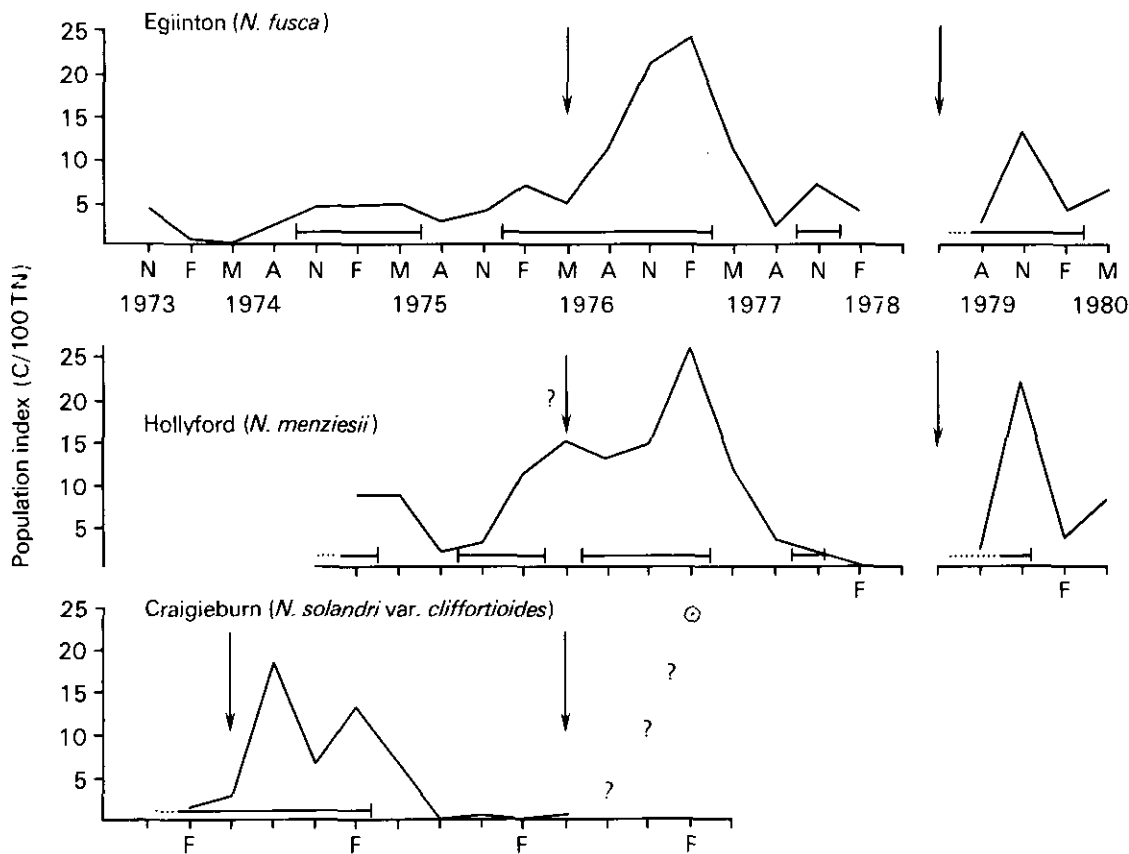


Fig. 1 Population indices (captures per 100 trap nights) for *Mus musculus* recorded in 3 South Island study areas. Arrows denote major seedfalls of southern beech (*Nothofagus* spp.); one is queried, for reasons explained by King (in press). Horizontal bars denote periods when pregnant females were found.

The 2 sessions of trapping in the Grebe and Borland valleys in spring 1979 would not be worth mentioning but for the extremely high density indices recorded in November—77 and 69 C/100TN, about 3 times higher than any previously recorded in New Zealand mainland forests (Fitzgerald 1978), at any season. Actual densities were probably nearer 6 times higher, if allowance is made for the declining correlation between density and frequency of captures (Caughley 1977). These samples provided an especially interesting opportunity to calculate pregnancy rates in populations which, for reasons unknown but probably related to seedfall (King, in press), were at very high density.

2. Changes in mouse population statistics with density

During the seed years, from May to May of 1976–77 and 1979–80 in Fiordland and 1974–75 at Craigieburn, the samples of mice collected each quarter were large enough to analyse separately; at

other times they were not. In the following analysis, the seed year of 1976–77 in Fiordland is compared with the non-seed years pooled and with the 1979–80 data treated separately. When samples are small the Eglinton and Hollyford data are pooled, since the population changes observed in the 2 areas were generally similar (Table 1a, b). For these purposes the data from Craigieburn are of limited use, since there were virtually no data from a non-seed year for comparison (only 2 mice were caught from August 1975 to May 1976 inclusive: Table 1c).

2.1 Proportion of adult females pregnant

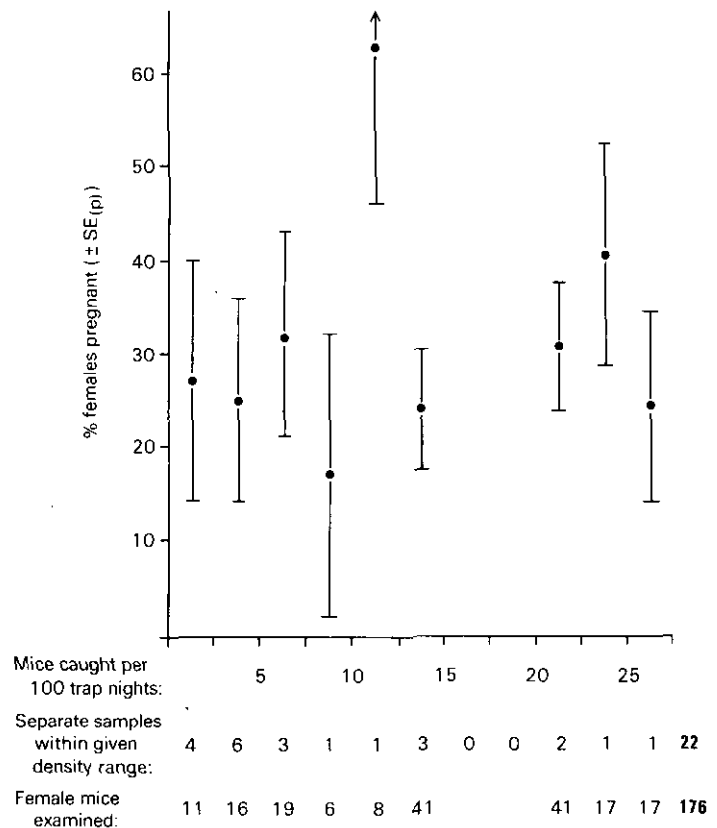
In Table 2 are recorded the observed changes in density and in the proportion of adult females (age classes 4–8 only) bearing visible embryos; seed years are compared with other years pooled.

The proportion of females pregnant in summer (November and February) was similar in seed years and non-seed years (35–50%), but the timing of the whole breeding season was different. In non-seed

Table 1 Mouse population data from 5 beech forest traplines in southern New Zealand (TN, trap nights).

	Corrected total TN	Total captures ^a	Age classes ($\delta + \text{♀}$)										8	9 ^b	?	'Extras' ^c	Females visibly pregnant	Females classified for reproductive condition	
			1	2	3	4	5	6	7	8	9	10							
(a) Eglinton																			
1973 Nov	210	9										2+1	4+1	1+0				0	2
1974 Feb	214	1																—	0
May	216	0																—	0
Aug	213	5				2+1												0	3
1975 Nov	210	9			4+1	2+1	2+0					2+1	2+1	0+1				2	4
Feb	210	9			1+0	3+1	1+0					1+0	1+0					1	1
May	211	10				1+0	2+2	1+0				1+0	2+2	1+0				1	4
Aug	214	6				0+1	1+0	3+2	1+0			1+0	1+0					0	2
Nov	210	8				0+2	1+0	2+0	1+1			1+2	3+1					0	3
1976 Feb	208	14				2+0	2+0	2+2	1+1			1+0	1+0					1	6
May	210	10				2+0	2+0	2+2	1+1			1+0	1+0					1	1
Aug	201	21				2+2	6+2	0+2	1+1			1+1	1+1					1	8
1977 Nov	191	40				3+2	9+7	8+4	14+7			4+2	0+1					13	10
Feb	180	43	1+0			2+3	6+5	1+3	2+0			4+5	4+1				4	3	15
May	200	22				1+3	2+0	0+1	0+1			1+3	2+0	1+0				7	17
Aug	210	4				0+3	2+0	1+1	2+1			0+1	0+1	1+0				0	2
Nov	207	14					1+0	2+1	1+0			2+4	2+1	1+0				0	2
1978 Feb	207	8				2+0	1+1	2+1	1+0			1+0	1+0					3	9
Aug ^d	200	5				1+0	7+4	2+0	1+0			0+1	1+1					0	2
1979 Nov	195	25	0+1			5+4	0+1	2+2	1+2			2+0	1+0	1+0				21	16
Feb	206	8					1+0	3+2	2+1			2+1	2+1					1	5
May	207	12																0	4
		283																26	126
(b) Hollyford																			
1975 Feb	202	17	0+1	2+1	2+1	4+1	1+0	1+1	1+1			1+0	1+1	1+1				1	6
May	201	17			4+2	4+3	2+1	2+1	1+0			2+1	1+0					0	6
Aug	213	4			1+0		1+0	0+2	1+0			0+2						0	2
Nov	211	6				0+1	2+1	0+2	2+0			2+1	0+2					1	4
1976 Feb	196	22				3+2	1+0	3+2	5+4			5+4	2+0					5	8
May	185	27	0+1	1+1	3+5	2+2	5+3	3+0	1+1			1+1	2+0					0	13
Aug	189	24			8+6	1+0	3+0	3+0	1+1			3+0	1+1					1	10
Nov	189	27			1+1	1+1	1+2	12+7	1+1			1+1	0+1					6	12
1977 Feb	177	45				0+1	16+11	6+4	5+1			6+4	5+1					4	17
May	198	22			0+2	1+0	4+6	6+2	1+0			6+2	1+0					0	10
Aug	211	7					4+1	1+1	1+1			4+1	1+1					0	2
Nov	212	4				0+1	1+0	1+1	1+1			0+1	1+0	1+1				1	2
1978 Feb	214	0																—	0
Aug ^d	100	2				2+0												—	0
1979 Nov	187	40	0+1	0+1	3+0	4+4	10+11	3+1	1+1			10+11	3+1	1+1				10	26
Feb	210	6				3+1	1+0	0+1	0+1			3+1	1+0	0+1				0	2
May	195	14				1+1	0+1	5+3	2+1			1+1	5+3	2+1				0	6
		284																29	126

Fig. 2 Percentage female mice pregnant in relation to density index, all November and February samples and all age classes pooled (cf. Fitzgerald 1978); mean \pm SE_(p) ($r_s = 0.07$, NS; $N = 9$).



years, in the Eglinton/Hollyford areas breeding did not start until after August, and was most intense in February; some individuals were still pregnant in May. In seed years, in the Eglinton/Hollyford and Craigieburn areas breeding was well established in August, was most intense in or before November, and had stopped by May. In the Grebe/Borland areas, where density indices were extremely high by November, the intensive breeding observed in September had greatly declined by November. The overall impression is of earlier starting and earlier finishing to the breeding season in proportion to the density attained at the peak.

The difference between the seed year of 1976-77 and the non-seed years pooled in distribution of pregnancies in the Eglinton/Hollyford mice was not significant, either through the entire season or in August, the month of greatest apparent difference (Table 2). For the Grebe/Borland area there appeared to be a forward shift in season, with early curtailment of breeding; but this could be confirmed only with several years' trapping. These data are, however, useful in suggesting that the densities achieved in the Eglinton/Hollyford were less than house mice are capable of in mainland New Zealand forests, and probably less than would have been

required to induce, by themselves, any drastic density-dependent changes in breeding rate in the Eglinton/Hollyford during the seed year of 1976-77.

Fitzgerald (1978) presented a data plot which suggested that pregnancy rates in mice declined in summer populations with density indices over 7.5 C/100TN. I have made the same calculations as he did, pooling all 22 November and February samples for Eglinton, Hollyford, and Craigieburn, and including female mice of all ages (the data can be retrieved from Table 1), but could not repeat his result—compare Fig. 2 with his fig. 3. However, if the comparison is confined to adult females (age classes 4-8), and the November and February data are plotted separately (Fig. 3), the result does suggest a decline in the proportion of females pregnant in November at very high densities. In August, the proportion of females pregnant tended to increase with density (in 1979 the 'August' density index data were acquired in September, and the index for Eglinton/Hollyford was probably an underestimate: see Section 3). These data conform to the suggestion made above that in these study areas a good seedfall usually affects the timing of the following breeding season, rather than the intensity of breeding.

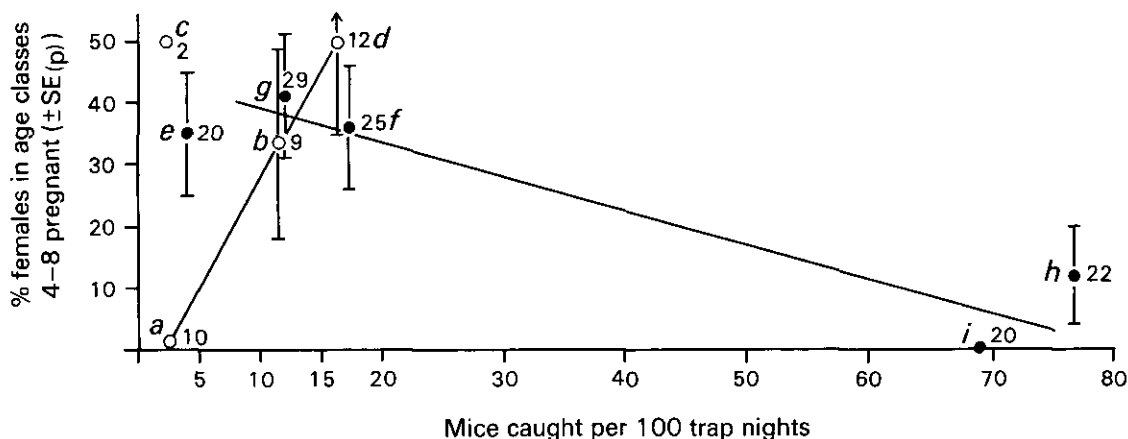


Fig. 3 Percentage of adult (Lidicker's age classes 4-8) female mice pregnant in relation to density index, controlled for season and study area (○, August; ●, November). Lines fitted by eye.

Key to data points

- a August, Eglinton/Hollyford, non-seed years, n adult ♀♀ examined = 10
- b August, Eglinton/Hollyford, seed year 1976, n = 9
- c August, Eglinton/Hollyford, seed year 1979, n = 2
- d August, Grebe/Borland, seed year 1979, n = 12
- e November, Eglinton/Hollyford, non-seed years, n = 20
- f November, Eglinton/Hollyford, seed year 1976, n = 25
- g November, Eglinton/Hollyford, seed year 1979, n = 29
- h November, Grebe, seed year 1979, n = 22
- i November, Borland, seed year 1979, n = 20

2.2 Recruitment

Recruitment is here defined as the addition of young mice (age class 3 or below) to the trappable population, and this usually starts soon after the beginning of each breeding season. A cumulative plot of young mice caught against time is a stepwise curve, the height of each step or annual increment reflecting the success of recruitment of young mice born in that season. The curve levels off when recruitment stops, which happens when mice cease breeding or the mice that are conceived do not enter the population. In homogeneous habitat, an increase in recruitment usually reflects an increase in survival of juveniles, but a decrease in recruitment may be due to acceleration of either mortality or dispersal of juveniles.

The seedfall most completely observed (marked by an arrow in Fig. 4) was followed by rather similar events in all 3 study areas. From May to August all curves have steep upward slopes, showing that many young mice were recruited in the 3 months after the seedfall. Thereafter all 3 levelled off, and over the next 6 months few young mice were added, although

breeding continued until February. Whether the 'missing' young mice died or emigrated is unknown, but for present purposes this is irrelevant. The important point is that they did not join the trappable population in the summers of seed years, when density was high, whereas they did so in the summers of non-seed years.

Recruitment increased in the Hollyford Valley early in the summer of 1976-77, before the beech seed fell (Fig. 4). The Hollyford forest is alone among those studied in containing a rich variety of fruiting trees and shrubs other than beech (see Appendix). Some of these produce large crops at irregular intervals, often earlier in the year than beech; however, such additional food supplies were not monitored in this study.

The data for Fiordland in 1979-80 do not cover the complete cycle of events, as there was no trapping in May 1979. From November 1979 to May 1980, as in 1976-77 but not in non-seed years, there was no recruitment at all, although breeding continued past November at least in both areas, and up to February in the Eglinton.

2.3 Age structure

The different patterns of breeding and recruitment in seed years and non-seed years led, as expected, to different observed age structures (Fig. 5). In seed years there was virtually no recruitment after August (see above), and hence, in all 4 seed-year samples from Eglinton/Hollyford, the frequency distribution of age classes shifted steadily upwards from then on. By February, very few of the mice were found to be in age classes 2-4. In non-seed years, by contrast, the heaviest recruitment was in February and May, when the samples included many mice in age classes 2-4. Differences in the frequency distribution of age classes were significant for both valleys in August and February, and for the Eglinton in November (separate Kolmogorov-Smirnov 2-sample tests).

For Craigieburn, the pattern in the seed year of 1974-75 was similar, though there are no data from non-seed years for comparison (Table 1c).

2.4 Sex ratio

The numbers of males and females in each age class in the 1976-77 seed year and in the non-seed years pooled (Table 1) were analysed by signs test (omitting the incomplete data from 1979-80). Seventy-six cells showed a difference in the numbers of males and females caught in a given season, area, density range, and age class. Of these, 53 showed an excess of males and 23 an excess of females; this overall difference is significant at the 0.001 level (Siegel 1956, p. 74). For the Eglinton/Hollyford areas pooled there is no significant difference in the proportion of males at high density relative to low density in either November ($\chi^2 = 0.33$) or February ($\chi^2 = 0.42$).

2.5 Litter size

The winter (August) litters recorded in the Eglinton/Hollyford after the seedfall were practically the same size as those during the normal breeding season in the following November-February (Table 3A). Recruitment was heaviest from autumn pregnancies just after a seedfall, but there are too few data to say whether litter size was larger in May of seedfall years. Summer litters averaged slightly larger in non-seed years than in seed years, but the difference in frequency distribution of litter sizes between November 1976 and November of non-seed years was not significant (Kolmogorov-Smirnov 2-sample test).

The frequency distribution of litter size by age classes shows no definite pattern of increase or decrease. The modal litter size was 6, and the modal age class for pregnant females was 5 (Table 3B).

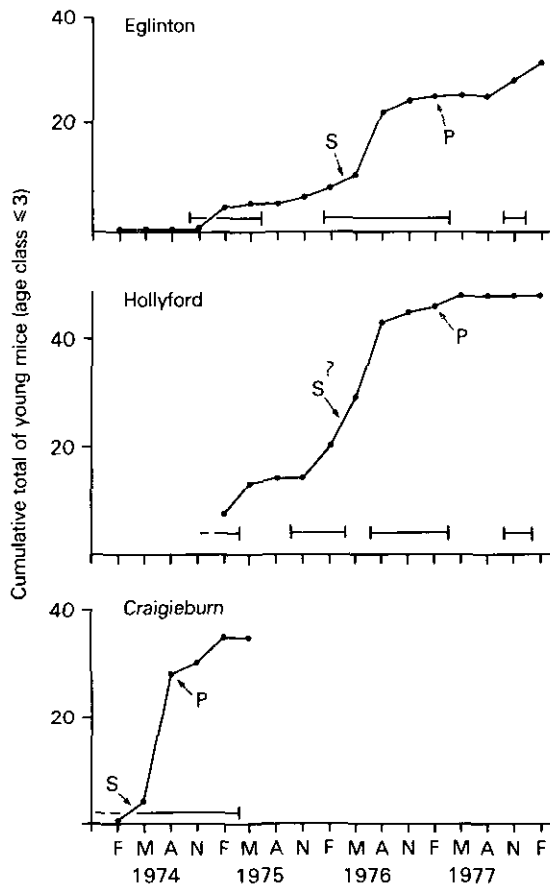


Fig. 4 Cumulative totals of young mice (age classes ≤ 3) added to trappable populations at 3-month intervals. S, major seedfall; P, peak of population density reached. Horizontal bars denote periods when pregnant females were found.

2.6 Body weight

Male mice weighed slightly more than females, and in both sexes mean weight increased through all the age classes (Table 4). There was no sign of any decline in weight in the older age classes such as was reported by Bellamy et al. (1973). Mice from the Eglinton Valley were consistently larger than those from the Hollyford, in all age classes of both sexes, and Craigieburn mice were intermediate. These geographical differences were significant for both sexes in age classes 5 and 6, and for males only in age classes 3 and 4.

The effect of population density on body weight, though difficult to test, was apparently slight. The age structures of high- and low-density populations were so different that few pairs of samples matched for both age class and season could be obtained.

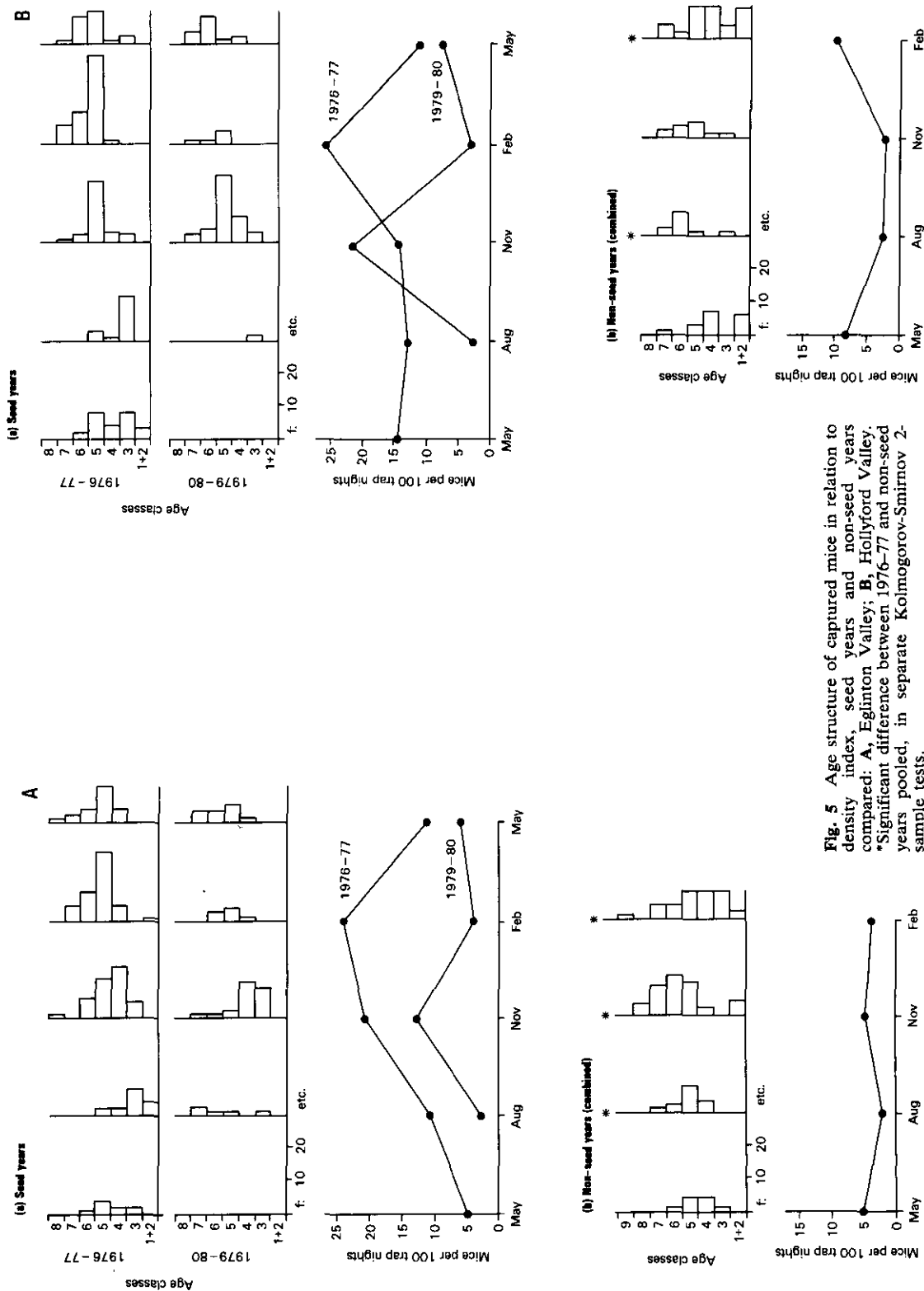


Fig. 5 Age structure of captured mice in relation to density index, seed years and non-seed years compared: **A**, Eglinton Valley; **B**, Hollyford Valley. *Significant difference between 1976-77 and non-seed years pooled, in separate Kolmogorov-Smirnov 2-sample tests.

Table 3A Mean litter sizes† (sample sizes in parentheses). Standard error given for samples >5.

	May	Aug	Nov	Feb
Eglinton & Hollyford				
Seed year 1976-77	8 (1)	5.3 (4)	5.6±0.38 (9)	5.5±0.41 (11)
Seed year 1979-80	—	7 (1)	5.5±0.31 (12)	6 (1)
Non-seed years	7 (1)	—	6.3±0.57 (7)	6.3±0.41 (8)
Craigieburn				
Seed year 1974-75	6.0 (3)	5.4±0.40 (5)	6.0 (2)	5 (1)
Borland/Grebe				
Seed year 1979-80	—	6.4±0.65 (7)	5.0 (3)	

†Including resorbing embryos, as often they cannot be accurately distinguished

Weight continued to increase through all age classes; therefore, mean weight could not be related to density without controlling for age. Simple plots of mean weight and of mean age with time elapsed since the seedfall both followed population age structure. The only controlled comparisons that could be made were between groups of males in age classes 5 and 6 caught in November (Table 5). The highest mean weights were recorded when densities were highest in the Grebe/Borland, but this could have a purely geographic explanation, since we have no data on body weight of mice from low-density populations in that area. The Eglinton was the only area with reasonably good samples for both high-density (1976 and 1979) and low-density populations, and there was no significant change in body weight across the range of densities observed (Kolmogorov-Smirnov 2-sample test; $D = 3.93$, NS).

3. Differences between seed-year populations, Eglinton/Hollyford

In two important respects the 1979-80 seed-year population did not duplicate the 1976-77 one. First, in late winter of 1979 the density index was much lower than in 1976; very few mice were caught, though they included class 3 young in both valleys (Table 1a, b). Second, the summer peaks in 1979-80 were much earlier and much lower than in 1976-77, though with a slight recovery in May 1980.

The low population density estimates for both valleys in September 1979 could be attributed to: (a) new traps; (b) trap-shyness (available seed was still abundant, as most does not germinate till November); (c) no winter breeding, and/or enhanced survival of young mice between May and August 1979, in contrast to the same period in 1976. In November, however, only 2 months later, the expected high population density and high proportion of young mice did appear, and both populations gave every indication of increasing to a peak in February 1980 at least as high as that in February

Table 3B Frequency (f) distribution of litter size by age class, November and February only, Eglinton and Hollyford pooled, all densities.

No. of embryos	Age class:	4	5	6	7	8	f litter sizes
2							
3			1				1
4			5	1		1	7
5		3	4	4			11
6		5	8	2	1		16
7		1	4	1	3		9
8		2	2				4
f age classes:		11	24	8	4	1	48

1977. The increase in number of young mice caught in November 1979 was very large relative to the number of breeding females examined 2 months previously (Table 1a, b), and at that time of year was unlikely to be due to immigration. I consider the simplest and most feasible explanation to be that the September 1979 density index is an underestimate. The 1979 seed crop was considerably greater than that of 1976 in both valleys, so enough seed could still have remained by September for mice to be uninterested in baited traps. The November 1979 density index is less suspect, as it was estimated twice, from data collected at or after the time of germination (see Methods). By February 1980 both populations comprised only old, non-breeding mice, and were similar to those of February 1977 (except only in density), in contrast with non-seed-year populations (Fig. 5). In demographic character the 1979-80 populations were consistent with the suggestion that both responded to the 1979 seedfall in a manner comparable with the populations in 1976. Hence, the mice were probably prevented from reaching high densities in summer 1979-80 by some extrinsic factor operating after November, probably predation by stoats (King, in press).

Table 4 Mean whole-body weights in grams (seasons and densities pooled), with standard errors, sample sizes, and values of *H* (Kruskal-Wallis analysis of variance by ranks).

	Age classes								Value of <i>H</i>
	1 and 2		3 and 4		5 and 6		7 and 8		
Eglinton, Hollyford, Craigieburn									
MALES									
Eglinton	10.2	(4)	18.0±0.40	(68)	20.8±0.29	(86)	21.8±0.53	(26)	40.6***, 2 d.f.
Hollyford	7.6±0.66	(11)	15.0±0.32	(55)	18.1±0.21	(98)	19.4±0.62	(15)	56.9***, 2 d.f.
Craigieburn	—		14.4±0.67	(27)	19.3±0.48	(23)	20.4	(1)	18.9***, 2 d.f.
<i>H</i> :	—		28.1***, 2 d.f.		55.2***, 2 d.f.		—		—
FEMALES (excluding visible pregnancies)									
Eglinton	8.9±0.67	(12)	15.1±0.48	(30)	18.6±0.41	(47)	19.4±0.87	(7)	50.9***, 3 d.f.
Hollyford	8.3±0.80	(9)	13.5±0.48	(34)	16.8±0.34	(44)	18.8	(5)	42.0***, 3 d.f.
Craigieburn	6.4	(1)	14.4±0.79	(16)	17.5±0.89	(14)	—		8.1*, 2 d.f.
<i>H</i> :	—		1.71 NS, 2 d.f.		12.9**, -2 d.f.		—		—
Grebe/Borland									
MALES									
Grebe	8.8±0.72	(10)	17.8±0.53	(51)	23.6±0.61	(7)	—		
Borland	—		17.3±0.42	(68)	22.8±0.66	(10)	25.1	(1)	
FEMALES									
Grebe	8.4±0.68	(5)	15.5±0.57	(33)	22.3±1.36	(8)	—		
Borland	9.1	(3)	16.4±0.66	(31)	24.8±0.75	(8)	24.8	(2)	

Table 5 Variation with density of body weight in male mice, age classes 5 and 6, collected in November.

Density:	Mean body weight (<i>n</i>)			
	Very high 1979	Moderately high 1976	Low 1979	Low 1973-77
Grebe	24.1 (6)			
Borland	23.3 (9)			
Eglinton		20.2 (11)	23.1 (6)	22.5 (12)
Hollyford		19.8 (13)	18.8 (22)	18.1 (3)

DISCUSSION

The population increases of mice in the Eglinton and Hollyford after the seedfall in 1976, and at Craigieburn after the seedfall in 1974, were associated with substantial increase in recruitment of young in early winter, so that by spring a large number of young parents were already producing the first of the summer generations. At least some pregnant females were present during the winter also. Their distribution was not significantly different from that in non-seed years; but the samples were taken only every 3 months, and numbers are small in the winter quarter (August) in any year. It is quite probable that breeding by overwintering females was extensive, and made an important contribution to the peak, as indeed would be expected from the reproductive ecology of house mice (Bronson 1979). It seems less likely that daylength, temperature, litter size, or a change in sex ratio were involved. The improved juvenile

survival and youthful age structure in spring appeared consistently just before population peaks in every study area, as in many previous field studies of *Mus* (reviewed by Berry (1981)).

If the observed changes are in fact stimulated by the beech seedfall, the exact mechanism of the response remains to be worked out. For example, since the most spectacular accelerations of the density index were usually delayed until spring, it could be suggested that the mice may be influenced more by the germinating sprouts than by the overwintering seed. This does not explain the sudden increase in recruitment of juveniles in early winter, immediately after the seedfall (Section 2.2).

The ultimate cause of the decline of every seed-year population observed was failure of recruitment—only partial at first, in late winter and spring, but almost total by February, when, in non-seed years, most young mice appeared (Fig. 5). Lack of recruitment would follow a cessation of breeding, or an increase in losses of young before or after birth. In the Eglinton/Hollyford in 1976-77 there was no significant reduction in the proportion of pregnant females, from which it may be inferred that breeding was not impaired by density at that level and that food was not limiting (Berry et al. 1973). Total resorption of embryos has been recorded in captive *Mus* at high densities (DeLong 1978), but seems not to occur to any great extent; generally the incidence of post-implantation loss in *Mus* is low (Berry 1981; but cf. Lidicker 1966), and the Bruce effect does not explain important variations in the reproductive behaviour of field populations (DeLong 1967). This

leaves only postnatal mortality, emigration, or trap avoidance as possible explanations. From the present data it is not possible to distinguish between these. However, the unknown factor was extremely age-specific: very few young mice were caught after early summer in seed years, though they were caught in large numbers earlier in such years, and in mid and late summer in non-seed years. Trap avoidance is thus less likely than increased mortality or emigration. Predation may have been a proximate cause of the 1979–80 decline, but only after some other factor had already prevented further recruitment. Pearson (1963) considered emigration to have been more important than mortality during a monitored decline of *Mus* in California. His data and mine are most consistent with what Lidicker (1975) has called "pre-saturation emigration", which is especially characteristic of colonising species such as *Mus musculus*. In this type of dispersal, in contrast with the saturation or 'last resort' type, social pressures motivate dispersal—including many mice which are young or subordinate (Butler 1980), but still in good condition—long before economic saturation of the core habitat is reached. The same pressures act against the settlement of immigrants. The effect is to increase the proportion of old mice in the population, as observed in every decline described here and by DeLong (1967).

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Appendix Report on vegetation at Hollyford and Eglinton rodent traplines, May 1978

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Vegetation along rodent traplines in the Hollyford and Eglinton Valleys was examined at the request of the Fiordland National Park Board on 9–10 May 1978. My aim was to briefly describe the vegetation at each site and to record plant species which might offer food sources to rodents.

I recorded the dominant plants within 20 m of each trap site. The following generalised descriptions are based on the frequency of dominant species at each of the 36 sites in the Eglinton and 31 sites in the Hollyford (where 5 trap sites could not be located).

Hollyford

The forest canopy around 20 m high is mostly silver beech, *Nothofagus menziesii* (26 sites) and kamahi, *Weinmannia racemosa* (19) with much less red beech, *Nothofagus fusca* (3), and with scattered emergent podocarps (rimu, *Dacrydium cupressinum* 8; kahikatea, *Podocarpus dacrydioides* 4; miro, *Podocarpus ferrugineus* 2; matai, *Podocarpus spicatus* 2). There is a diversity of small trees either beneath the larger ones or themselves forming a lower canopy in much of the forest; treeferns *Cyathea smithii* and *Dicksonia squarrosa* (both 26); marble leaf, *Carpodetus serratus* (19); *Coprosma rotundifolia* (16); *Fuchsia* sp. (14); wineberry, *Aristotelia serrata* (9); broadleaf, *Griselinia littoralis* (8); pepper tree, *Pseudowintera colorata* (8); kaikomako, *Pennantia corymbosa* (7); mahoe, *Meliccytus ramiflorus* (7); and lancewood, *Pseudopanax crassifolius* (3). Smaller plants of the above, especially treeferns, are also common in the shrub layer, along with *Coprosma rhamnoides* (8). There is a dense ground cover of ferns and large herbs: shield fern, *Polystichum vestitum* (21); crown fern, *Blechnum discolor* (10); *Microlaena* (12); *Uncinia uncinata* (8); hen and chickens fern, *Asplenium bulbiferum* (6); *Blechnum capense* (5); *B. minus* (5); *B. fluviatile* (4); and *Astelia fragrans* (4). Lianas are common, mainly *Metrosideros diffusa*, *Rubus cissoides*, and *R. schmidelioides*.

The Hollyford roadside provides a habitat for many species not found in the forest, especially grasses, herbs, and weeds. Typically there is a verge where browntop (*Agrostis tenuis*), ragwort (*Senecio*

jacobaea), lotus (*Lotus* sp.), and bidibidi (*Acaena* sp.) are common, backed by ferns (shield fern, *Paesia* sp. and *Blechnum capense*), then by small trees of wineberry and *Fuchsia* or by shrubs of *Comprosmia parviflora* and *C. propinqua* in more open places.

Eglinton

Red beech is by far the commonest species, large trees (to c. 30 m) forming an even canopy at all 36 sites. It is abundant also as poles, saplings, shrubs, and seedlings. Silver beech reaches the canopy at 4 sites but is more common as small trees (10 sites) along with a few small lancewood (9), broadleaf (7), and wineberry (4). Among the shrubs *Coprosma rhamnoides* is most common (26), with *C. foetidissima* (6), *C. astonii* (5), and *C. colensoi* (3). The forest understorey is generally very open, and the ground is rather bare. Litter cover is 56% on average, most of the rest being bryophytes and scattered plants of shield fern (23), *Uncinia uncinata* (20), *U. gracilentata* (9), filmy ferns, *Hymenophyllum* sp. (9), *Microlaena* (6), *Blechnum minus* (5), and *B. vulcanicum* (4).

The Eglinton roadside holds scattered herbs, grasses, weeds, and ferns, but there is no forest-edge shrub layer comparable to that in the Hollyford.

Plants as rodent foods

A species list for each trapline was compiled, with annotations indicating those species which have fleshy fruits, seeds of reasonable size, or rhizomes that might be used as foods by rodents. Species which seem to offer a lot of food (either because they fruit heavily or because they are abundant) were distinguished from those offering only small amounts.

Total flora is 124 species in the Hollyford, as against 104 in the Eglinton. There are very few common species in the Eglinton, so the forest there is much less diverse. In the Hollyford, 28 species appear to be major potential food sources to rodents; in the Eglinton only 8 species, of which red beech is the main one, but also the most fickle because of marked periodicity of seed years. The Hollyford trapline appears to occupy the richer of the two habitats, partly because of the variety of habitats, not only within the forest but also because of the close proximity of the roadside and the riverbed.

Full species lists may be obtained from P. N. Johnson or C. M. King.