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THE RELATIONSHIPS BETWEEN BEECH (*NOTHOFAGUS* SP.) SEEDFALL AND POPULATIONS OF MICE (*MUS MUSCULUS*), AND THE DEMOGRAPHIC AND DIETARY RESPONSES OF STOATS (*MUSTELA ERMINEA*), IN THREE NEW ZEALAND FORESTS

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SUMMARY

(1) There was a significant relationship between seedfall and populations of mice in all forests studied. Good seedfalls were followed by increases in density of mice and changes in population structure not seen in years when the seedfall failed. Predictability of these changes decreased with increasing diversity of forest composition.

(2) Stoats responded both numerically and functionally to increases in mice. There was a significant relationship between the densities of mice and of stoats in summer in two forests. (In a third, this relationship was modified by the presence nearby of many lagomorphs, an important alternative prey for stoats.) The numerical response was due to increased survival, in the uterus or the nest, of young stoats born in spring when mice were abundant, not to increased fecundity of adult female stoats. In all three forests, stoats ate significantly more mice in the summers that mice were abundant.

(3) Ship rats (*Rattus rattus* (L.)) were most abundant in the most diverse of the three forests. The density index for *R. rattus* increased there after the 1976 seedfall, but not after that of 1979. A few kiore (*R. exulans* (Peale)) coexisted with *R. rattus* in this forest.

(4) Stoats did not eat significantly fewer birds when there were plenty of mice, either in summer or autumn, but nevertheless there was a significant negative correlation between the proportions of birds and mice in the diet in autumn. In summer this correlation was very weak and probably non-existent.

(5) A 'bird predation index', which takes into account both the numbers of stoats present and what they ate, suggests that more birds are eaten in summers of peak numbers of mice and stoats, because of the strong numerical response by stoats to mice and lack of 'buffering' of birds by mice. In autumn this effect is weakened by a regular seasonal switch by stoats from birds to mice, especially in the autumn of a mouse peak year.

(6) The indirect effects of mouse irruptions on populations of forest birds in New Zealand should be further examined. Control of stoats in mouse peak summers could prevent a temporary increase in predation on birds by stoats during the highest risk period, though whether this would benefit the birds is unknown.

INTRODUCTION

Many studies in the northern hemisphere have shown that the occasional heavy seed crops of certain forest trees cause increases in the productivity, survival and numbers of forest rodents during the following months (e.g. Smyth 1966; Hansson 1971; Vincent 1977;

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Jensen 1978; Flowerdew & Gardner 1978; Gashwiler 1979). Likewise, there is mounting evidence that increases in numbers of rodents may cause functional and/or numerical responses in their predators (Southern 1970; Pearson 1971; Goszczynski 1977). All three trophic levels were linked by Edson (1933), who noted increased numbers of mice and *Mustela frenata* after a heavy crop of vetch seeds in autumn 1931. The direct relationships between seedfall, rodents and predators are relevant both to predation theory, and, in certain habitats, to the conservation and the protection of birds. Lack (1954) suggested that the cyclic declines of some Palaearctic game birds may be caused by increased predation on them by rodent-predators after a decrease in their usual prey. Although he later withdrew this as an explanation of cycles in game birds (Lack 1966), the idea that increased predation on birds could follow the declines of occasional irruptions of rodents has remained.

This study examines the hypothesis linking beech seedfall, population biology of mice, and predation by stoats on birds as applied to New Zealand by Riney *et al.* (1959)... 'there are indications that the mouse and kiore [*Mus musculus* and *Rattus exulans*] may occasionally increase tremendously in numbers, perhaps in response to an unusually heavy seeding of beech. If this happened, it would provide the stoats with a greatly increased food supply, resulting in better survival of young and a build-up of the stoat population. When the mice declined to normal densities there might be increased predation on birds, including rare species near the threshold of minimum density'. New Zealand has suffered devastating losses of native birds over the last thousand or so years, since the arrival of Polynesian and, later, European man, accompanied by various terrestrial predators. Stoats could have contributed, to an unknown degree, to part of this historic loss; and it is possible (though so far unproven) that they may limit the present densities of at least some species of birds in at least some years. General control of stoats is impossible, but if the hypothesis of Riney *et al.* is correct, we would be able to identify periods of increased risk to beech forest birds and concentrate control efforts then.

The difficulties of investigating these complex relationships in the field are daunting, though eased somewhat by the absence in New Zealand of certain complicating factors. There are large areas of native beech (*Nothofagus* spp.) forest of relatively simple composition, where the annual fall of seed varies greatly in size and quality. These forests harbour a small fauna of terrestrial mammals, all introduced, among which the house mouse (*Mus musculus* L.) and ship rat (*Rattus rattus*) are the only common small rodents, and stoats (*Mustela erminea* L.) are usually the commonest, and often the only carnivores. Few undisturbed forests in Fiordland support more than 10–15 species of breeding birds, with summer densities usually < 200 pairs/40 ha (Kikkawa 1966). This situation contrasts with the complex predator-prey communities described by Keith *et al.* (1977); Goszczynski (1977) and Andersson & Erlinge (1977). The full sequence of events from seedfall to predators can therefore be observed, seldom much influenced by competition at any level.

STUDY AREAS (Fig. 1)

Eglinton Valley, northern Fiordland National Park (44° 50' S, 168° 05' E)

Length c. 40 km; aspect NNE–SSW; altitude of floor 270–550 m; mean rainfall in centre section 2300 mm/year; 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 forest up to treeline at 1000–1100 m; surrounded by mountain

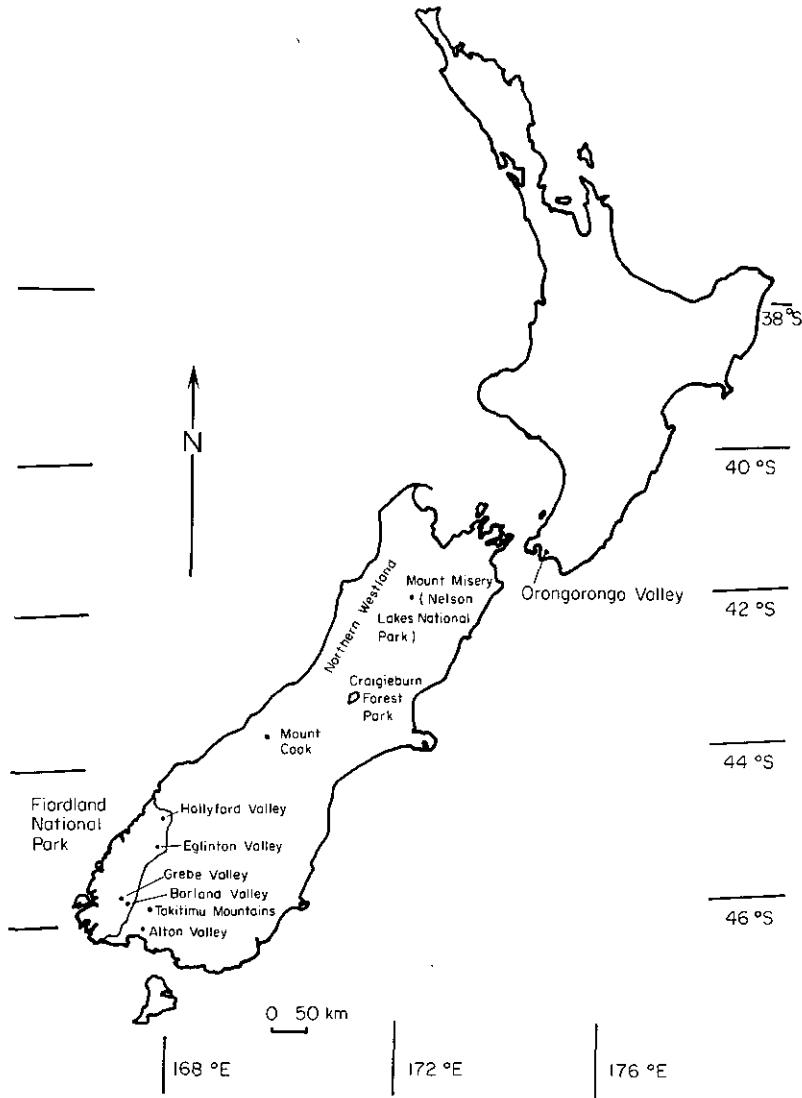


FIG. 1. Sketch map of New Zealand showing locations mentioned in the text.

peaks reaching 1500–1800 m. A vegetation survey near the rodent trapline identified eight species of seedbearing plants as major sources of food for rodents, of which red beech (*Nothofagus fusca*) is the dominant.

Lower Hollyford Valley, northern Fiordland National Park (44°45'S, 168°10'E)

Length c. 35 km; aspect mostly N–S; altitude of floor 90–370 m; mean rainfall at least 4250 mm/year; 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 the Eglinton by a low pass at 530 m across the Main Divide of the Southern Alps. A vegetation survey along the rodent trapline identified twenty-eight species of seedbearing plants as major sources of food for rodents, including scattered silver beech (*N. menziesii*).

Craigieburn Forest Park, Canterbury (43°10'S; 171°40'E)

Total area c. 4500 ha; aspect SE; altitude of trapline 790–1340 m; rainfall at field station 1450 mm/year, range of monthly mean temperatures 1–13 °C; years sampled 1973–78. Contains a remnant (1300 ha) of high-altitude evergreen forest perched on the flank of a range of foothills of the Southern Alps, adjacent to very large areas of cleared pastoral country and natural but damaged alpine grasslands. Mountain beech (*N. solandri* var. *cliffortioides*) is the only major seedbearing plant in the forest.

Grebe and Borland Valleys, southern Fiordland National Park (45°45'S; 167°30'E)

Two forested valleys, similar in appearance to the Eglinton and about 100 km south of it, sampled only in September and November 1979. Vegetation (not surveyed) dominated by mountain and silver beech.

METHODS

Beech seedfall

Seedfall was estimated according to the method used by the New Zealand Forest Service (Wardle 1970). The Eglinton and Hollyford Valleys each had a line of eight Beveridge seed trays (area 0.28 m²) set out at 50-m intervals and cleared monthly throughout the year. The total fall of sound seed/m² for the year (March–February) in each area was first estimated from the mean count (\pm S.D.) of sound seeds/tray/year divided by 0.28, in order to allow comparison with New Zealand Forest Service data. But because there was considerable variation in counts between trays, the confidence intervals and coefficient of variation for each annual estimate were calculated after transformation of the data to a scale of log base 10 of $x + 1$.

In the Hollyford Valley study area, where beech does not form a continuous canopy, three trays were not under beech trees and rarely contained any beech seeds. However, the average number of seeds per tray in the Hollyford was still calculated from eight trays, not five, since the aim was to estimate the seedfall over the study area generally, not just the parts of it that were under beech trees. There was no guarantee that the seedfall along the particular 400 m chosen for tray sites was typical of the rest of the forest, except in years of universal seed failure (1977) or universal bonanza (1979). In all years, there was much local variation among the individual trees near the Hollyford seed trays.

Seedfall data for Craigieburn and the Alton Valley (southern Fiordland), were supplied by New Zealand Forest Service (J. A. Wardle 1970 and unpublished; D. A. Franklin unpublished). The Alton data are included as a comparison with the Hollyford Valley, and also because some rodent trapping was done in southern Fiordland in 1979/80.

Rodent trapping

Rodent traplines were set out according to a standardized procedure (Fitzgerald 1978). Each line comprised thirty-six stations at 50 m intervals. In Fiordland, eight of the stations, near the middle of each line, also had a seed tray nearby; at Craigieburn, stations were about 100 m from the seed trays.

Traps were set, without prebaiting, for three consecutive nights in the last weeks of February, May, August and November. Bait was peanut butter and rolled oats, renewed as needed. Results were expressed as the number of mice or rats caught 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 density of mice, a fair assumption

at frequencies below 20 C/100 TN (Tanaka 1960; Caughley 1977). Severed tails or feet were counted as a capture, for the purposes of density estimation, unless a mouse with the same part missing was caught in the same trap within the next two days. Tufts of fur were not so counted.

Stoat trapping

Fenn (steel) traps were set for stoats as described by King & Edgar (1977) and King (1980). In the Eglinton, twenty traps were left permanently set from November 1972 to June 1974; fifty traps (later forty-eight) for 14 days a month from June 1974 to March 1976; and forty-eight traps for 10 days a month from April 1976 to April 1978. In the Hollyford, forty traps were set for 14 days a month from February 1975 to March 1976, and 10 days a month from April 1976 to April 1978. In 1979–80, thirty-five to forty live traps (also described by King & Edgar 1977) were set in each valley, for 4 days a week for 9 weeks between 20 November and 1 February. Spacing of traps was variable up to March 1976 (King 1980), and thereafter always at about 400 m. All traps were baited and visited daily by Fiordland National Park Board staff. Whereas all stoats caught in Fenn traps were killed and removed, most stoats caught in live traps were tagged and released (King & McMillan 1982). Recaptures of marked individuals were omitted when calculating density estimates from live-trapped stoats. At Craigieburn, fourteen, later eighteen, Fenn traps at about 400-m intervals were left permanently set, unbaited, and checked every few days by New Zealand Forest Service meteorological officers from April 1973 to August 1978. Unbaited stoat traps catch at a significantly lower rate than baited ones (King & Edgar 1977), so the stoat traps in Fiordland and at Craigieburn probably sampled the populations differently. The frequency of captures (number of stoats caught per 100 trap-nights) was always less than nine, so may be taken to be linearly related to density throughout the range observed.

Stoat autopsies

Dead stoats were sent in frozen; methods and full data from 1599 individuals autopsied up to March 1976 are given by King & Moody (1982). Data obtained since then on food habits are reported herein, and on age distribution and reproduction in King (1981).

Age was determined from the cleaned skull and baculum. In summer (December–February inclusive), young stoats of both sexes could be reliably distinguished from adults, though adults could not be further subdivided. Young females were indistinguishable from adults after March, and subadult males after August, of the year following that of their birth (King & Moody 1982).

RESULTS

The following results are based on analysis of twelve seasons' beech seedfall, 1138 captures of rodents, 905 carcasses and 162 scats of stoats.

Beech seedfall (Table 1)

Production of seed by beech of all species is erratic, ranging from nil to thousands of sound seeds/m² for the season. Different species do not all seed in the same year, except in major mast years such as 1979, when good production was practically universal (Table 1(a)). In the intervening years, there may be variation between and within localities. For example, in 1974, the mountain beech produced a moderate fall at Craigieburn, but the red

TABLE I(a). Beech seedfall (sound seed/m²), arithmetic scale

	Eglinton		Northern Fiordland		Hollyford		Southern Fiordland		Canterbury	
	seed $\bar{x} \pm 1$ S.D.	% sound	seed $\bar{x} \pm 1$ S.D.	% sound	seed $\bar{x} \pm 1$ S.D.	% sound	\bar{x} seed	% sound	Craigieburn 'C' line	% sound
1973	NR	—	NR	—	NR	—	0.5	2	0	—
1974	5.3 ± 3.6	7	NR	—	NR	—	1250	37	1814	43
1975	14.7 ± 9.04	10	514.7 ± 591.54†	16	—	—	0.5	2	5	2
1976	22.3 ± 22.32	8	290.2 ± 305.30	31	—	—	3150	63	2165	56
1977	0	—	0	—	—	—	9	8	0.5	8
1978	NR	—	NR	—	—	—	0.5	1	35	7
1979	104.0 ± 44.99	15	998.7 ± 1581.81	38	—	—	900	48	3427	69
Major species present	<i>Nathofagus fusca</i> (red beech)		<i>N. menziesii</i> (silver beech)		<i>N. menziesii</i> (silver beech)		<i>N. menziesii</i> (silver beech)		<i>N. solandri</i> var. <i>cliffortioides</i> (mountain beech)	
Collection	March–February		March–February		February–June		February–June		March–July	
Number of trays	8*		8		12		8		8	
Altitude	480 m		120 m		290 m		1036 m		1036 m	
Reference	present study		present study		D. A. Franklin, personal communication		D. A. Franklin, personal communication		J. A. Wardle, personal communication	

NR = not recorded.

* 4 in 1974, starting in April.

† See beech seedfall Results, p. 147.

TABLE 1(b). Transformed data on beech seedfall ($\log_{10} x + 1$, $x = \bar{x}$, number of sound seeds per tray), northern Fiordland only

	Mean \pm S.D.	95% Confidence range	Coefficient of variation
Eglinton Valley			
1974	0.376 \pm 0.151	0.136–0.616	40.0
1975	0.651 \pm 0.260	0.437–0.865	39.3
1976	0.674 \pm 0.462	0.288–1.060	68.5
1977	0		
1979	1.44 \pm 0.203	1.272–1.611	14.1
Hollyford Valley			
1975	1.419 \pm 1.203	0.413–2.426	84.8
1976	1.298 \pm 1.085	0.391–2.206	83.6
1977	0		
1979	1.494 \pm 1.313	0.396–2.592	87.9

beech in the Eglinton did not. In 1975 the silver beech in the Hollyford (northern Fiordland) produced much more seed, at least in the area sampled, than in the Alton (southern Fiordland). In 1972 the silver beech in the Takitimu Mountains, just east of Fiordland, produced seed when those in the Alton did not (Manson 1974; D. A. Franklin, personal communication); the reverse happened in 1974 (L. E. Burrows, personal communication).

In the Hollyford, there was considerable variation in the number of seeds collected from each tray in a given year, and also from year to year in a given tray. The coefficients of variation for the Hollyford counts were much greater than in the Eglinton (Table 1(b)). The Hollyford beech trees sampled were scattered and interspersed with other species, and apparently did not all seed together in any year. The behaviour of individual trees near the trays probably influenced the counts, especially in 1975, not necessarily in a way representative of the whole forest. The other study areas were all more or less homogeneous stands of beech trees.

In all the study areas, the bulk of the seed crop falls from March to June or July and lies on the ground all winter, germinating in October–November. In 1979 many seeds could still be found lying in the litter in November, in all four areas sampled then (Grebe, Borland, Eglinton and Hollyford).

Changes in density and population indices for mice

Figure 2 shows that moderate or heavy seedfalls in 1974, 1976 and 1979 were followed by increases in the density indices for mice. King (unpublished) describes the changes in age structure and reproduction of the mice collected in seed years. In all the populations studied, the density increases were associated with improved recruitment of young in the autumn and early winter of a seed year, and also with winter breeding by adults. Few young mice entered the populations after spring, though breeding continued; the age structure shifted steadily upwards, and population decreases were ultimately due to failure of recruitment and the disappearance of the ageing adults. Sample sizes are given in Table 2.

Relationship between mouse density and beech seedfall

Figure 3 plots the relationship between the seedfall (sound seeds/m² for the season, Table 1(a)) and the density of mice over the four samples (August–May inclusive) following the main period of the fall. These four quarterly samples are pooled, because the

Beech seedfall, mouse and stoat populations

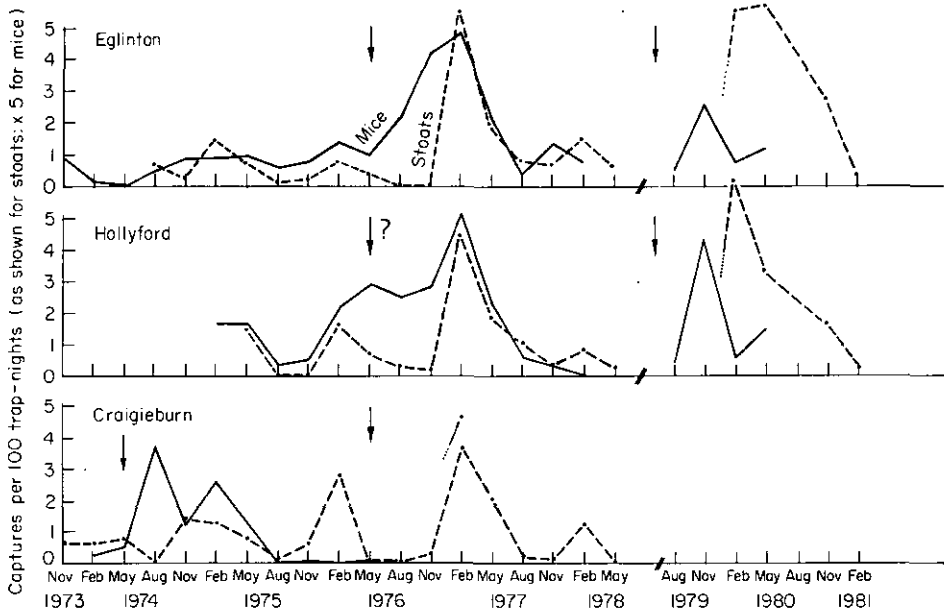


FIG. 2. Seasonal and annual variation in the capture rate ($C/100\text{ TN}$) of stoats and mice, each 3 months (monthly data for stoats, 1973–78, given by King 1980). (—), mice; (---), stoats. Arrows mark centre of period of major seedfalls.

highest number of mice caught per 100 trap-nights was recorded in different quarters (August or November or February), and the actual peaks of these populations could in fact have been in the intervening months. For the pooled data, the Spearman rank correlation coefficient was highly significant ($r_s = 0.73$, $P < 0.01$, $n = 11$). (Coefficients for individual forests varied in degree of significance with the amount of rodent food available other than beech seed.) Other records of high density populations of mice, not included in Fig. 3, were also associated with good beech seedfalls, e.g. at Craigieburn in

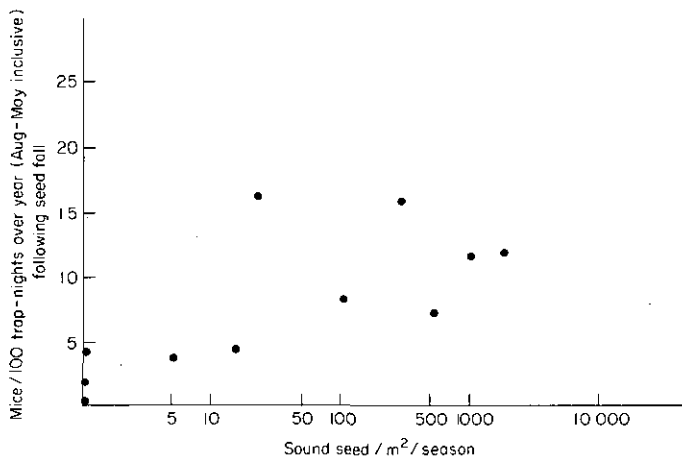


FIG. 3. Relationship between seedfall (number of sound seeds/m²) and the total number of mice caught/total number of trapnights $\times 100$ over the four samples (August to May inclusive) following the end of the fall. $r_s = 0.73^{**}$, $n = 11$.

TABLE 2. Rodent population data (mice, *Mus musculus*; rats, *Rattus rattus* and *R. exulans*)

	Mice*		Eglington		Rats†		Mice		Hollyford		Rats		Craigieburn‡	
	n	C/100 TN	n	C/100 TN	n	C/100 TN	n	C/100 TN	n	C/100 TN	n	C/100 TN	n	C/100 TN
1973	9	4.3	0	—	—	—	—	—	—	—	—	—	—	—
1973/4	1	0.5	0	—	—	—	—	—	—	—	—	—	—	—
	0	0	0	—	—	—	—	—	—	—	—	—	—	—
	5	2.3	0	—	—	—	—	—	—	—	—	—	—	—
1974/5	9	4.3	0	—	—	—	—	—	—	—	—	—	—	—
	9	4.3	2	0.10	17	8.4	0	—	0	—	—	—	—	—
	10	4.7	0	—	17	8.5	2	1.0	2	1.0	0	0	0	0
	6	2.8	0	—	4	1.9	1	0.47	1	0.47	0	0	0	0
	8	3.8	2	0.95	6	2.8	3	0.16	3	0.16	1	0.5	1	0.5
1975/6	14	6.7	2	0.10	22	11.2	2	0.16	3	0.16	0	0	0	0
	10	4.8	0	—	27	14.6	8	0.52	8	0.52	1	0.5	1	0.5
	21	10.5	0	—	24	12.7	20	1.56	20	1.56	NT	—	NT	—
	40	20.9	1	0.52	27	14.3	22	1.60	22	1.60	NT	—	NT	—
1976/7	43	24.0	9	0.58	45	25.4	7	0.54	7	0.54	48	23.4	48	23.4
	22	11.0	14	0.99	22	11.1	20	1.70	20	1.70	—	—	—	—
	4	1.9	2	0.14	7	3.3	9	0.64	9	0.64	—	—	—	—
	14	6.8	0	—	4	1.9	1	0.08	1	0.08	—	—	—	—
1977/8	8	3.9	10	0.62	0	0	11	0.93	11	0.93	—	—	—	—
	5	2.5	0	—	2	2.0	1	1.00	1	1.00	—	—	—	—
1979	25	12.8	0	—	40	21.4	0	—	0	—	57	15.8	57	15.8
1979/80	8	3.9	0	—	6	2.9	0	—	0	—	211	73.3	211	73.3
	12	5.8	1	0.38	14	7.2	0	—	0	—	NT	—	NT	—
Totals	283		43		284		108		416		4		416	4

NT No trapping.

* Rat and mouse traps (standard lines, total 216 trap-nights per quarter per line).

† Rat and mouse traps (*R. exulans* often caught in mouse traps), plus Fenn traps (standard lines, average total c. 1500 trap-nights per quarter per line).

‡ No rats caught at Craigieburn.

Grebe and Borland

Mice Rats
15.8 1 0.28
73.3 3 1.04

February 1977, and in the Grebe and Borland Valleys (35 km north of the Alton Valley in southern Fiordland) in November 1979 (Table 2). After the 1974 seedfall in southern Fiordland (Table 1(a)), mice were so numerous that they could be seen running about in the forest by day, and the local newspaper reported a plague (Southland Times 18 November 1974, 'Monowai Mouse Nuisance').

Unlike beech trees, the grasses on the river meadow flats in the Eglinton Valley seed every year. From February to November inclusive of 1974 (a poor seed year in that area, Table 1(a)), a thirty-six station trapline was operated in the meadows to see if mice would survive better there, or even migrate from the forest, when the beech trees failed to seed. Only one mouse was caught, and that in the trap nearest the edge of the forest.

Changes in density indices for stoats

Figure 2 shows the number of stoats caught per 100 trap-nights, each 3 months. In all three study areas there was a regular seasonal pattern: more stoats were caught in the summer (December–February) than at any other season of the same year. Superimposed on this regular variation, there was also an irregular variation in the size of the summer peak. In Fiordland, the highest peaks in the summers of 1976/77 and 1979/80 were four-to-five times higher than in other years. The density index figures for the unbaited Craigieburn traps were lower, but in 3 of the 5 years they also showed a summer peak of variable height. The Craigieburn data help to dispel any suggestion (e.g. by Teplov 1952), that this regular pattern could be due to variation between years in the hunger and hence willingness of stoats to enter baited traps. In 1979/80 stoats were live-trapped and released during the summer; in the Eglinton the summer peak declined later than that of 1976/77, when stoats were removed at first capture (Fig. 2 and King & McMillan 1982). This effect was less pronounced in the Hollyford.

No regular density indices for stoats were obtained in the Grebe/Borland areas in southern Fiordland, but over the summer of 1979/80 an intensive trapping effort produced only 11 stoats in all (density indices 1.0 and 0.8 C/100 TN, respectively).

Relationship between the densities of stoats and of mice

In Fiordland the correlation between the summer density indices for mice and for stoats was good (Fig. 4). At Craigieburn, in 1974/75 fewer stoats were caught there than would be expected from the peak in mice, while in 1975/76 many stoats were caught in a season when mice were virtually absent. In 1976/77 the data are incomplete, but suggest as good a response at Craigieburn as in Fiordland. Craigieburn is an isolated remnant of forest surrounded by vast areas of open country where lagomorphs are common. Lagomorphs are favoured prey of stoats, and are frequently eaten by them at Craigieburn (King & Moody 1982). It is possible that in 1974/75 and 1975/76 there were many lagomorphs on the grasslands surrounding the forest, so that stoats spent more time hunting them than the mice inside the forest. In 1976/77, on the other hand, lagomorphs may have been scarce, so more stoats came to the forest to feed on mice and were caught there. Unfortunately the population of lagomorphs was not indexed, so this suggestion remains speculative. It is supported, however, by the drop in frequency occurrence of lagomorphs in the guts of the Craigieburn stoats after summer 1975/76 (Table 7).

It could be argued from Fig. 2 that the three simultaneous peaks in populations of mice and stoats in 1976/77 were coincidental, caused by some common external factor, perhaps meteorological. Might the stoats have increased that summer anyway, even if the mice had not?

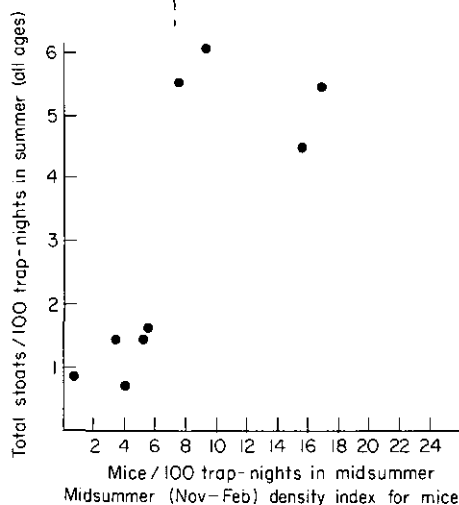


FIG. 4. Relationship between density indices for mice and stoats in Fiordland in summer. $r_s = 0.77^*$, $n = 9$. The summer density index for mice is the mean of the November and February indices.

At Mount Cook National Park (230 km north of the Eglinton, and 140 km south of Craigieburn), the number of stoats caught per 100 trap-nights in twenty to thirty unbaited traps was recorded by M. Clarbrough from December 1974 to November 1977 (Table 3). There was the same variable summer peak in capture rate, which reached 3.0 C/100 TN in summer of 1975/76, but only 1.8 C/100 TN in 1976/77. There is little beech forest and few mice near the traplines at Mount Cook, and the main prey of stoats there are lagomorphs. This exception suggests that the correlation between population fluctuations of mice and stoats in beech forests is causal. However, it may be weaker in forests, such as Craigieburn, which also offer substantial food resources for stoats other than mice.

Changes in age structure and breeding of stoats

The summer peak in capture rate of stoats (Fig. 2) coincides with the dispersal of the single annual crop of young. Calculating the capture rates of adults and young separately shows that in peak years, many young stoats are caught, but in other years, very few (Table 3). In Fiordland there was a significant correlation ($r_s = 0.72$, $P < 0.05$) between the density index for mice in November and the number of young stoats caught per 100 trap-nights in the following December–February. (At Craigieburn the production of young is probably also influenced by the availability of lagomorphs.) The annual variation in fecundity of female stoats (Table 4) is much less than that in age structure: King (1981) gave further details, and suggested that the productivity of stoats is controlled by mortality at various stages between implantation and independence, which is in turn strongly influenced by the density of mice.

Food habits of stoats

The general food habits of stoats in the New Zealand National Parks are described in detail by King & Moody (1982). They analysed the contents of 1250 guts (including those from Fiordland and Craigieburn collected up to March 1976) and found a total of 2643 prey items. There were no general and consistent differences in food habits with age. In all seasons female stoats ate significantly more mice and ground wetas (large, native

TABLE 3. Stoat population data

Date	Eglington			Hollyford			Craigieburn			Mount Cook n C/100 TN
	Total carcasses* ♂	♀	C/100 TN† Total Young	Total carcasses ♂	♀	C/100 TN Total Young	Total carcasses ♂	♀	C/100 TN Total Young	
1972/73	Su	13	1				4	5	1.28	
	A	0	2				6	3	0.70	
	W	25	14				7	2	0.72	
	Sp	23	4				2	6	0.72	0.45
1973/74	Su	17	4				6	5	0.85	
	A	6	6				0	1	0.08	
	W	14	10	0.68			19	0	1.49	
	Sp	4	5	0.24			6	11	1.35	1.03
1974/75	Su	14	16	1.46	23	39	9.28	5.30	0.82	0.87
	A	9	6	0.70	12	17	1.50	7	17	0.82
	W	0	2	0.10	0	1	0	0	0.18	0.94
	Sp	2	1	0.15	3	0	0	2	0.90	0.21
1975/76	Su	3	10	0.70	9	16	1.63	0.96	2.86	0.22
	A	0	4	0.37	3	4	0.67	0	1	2.97
	W	0	0	0	1	2	0.27	0	1	0.57
	Sp	0	0	0	2	0	0.17	3	1	0.30
1976/77	Su	47	25	5.43	29	21	4.45	3.64	3.68	0.80
	A	15	11	1.91	12	10	1.87	1.07	2.01	1.80
	W	2	6	0.71	6	2	1.07	0.67	0.33	0.63
	Sp	6	3	0.64	3	1	0.34	2	0	0.19
1977/78	Su	6	14	1.42	7	3	0.84	0.51	1.25	0.30
	A	5	0	0.53	1	1	0.25	0	1	0.07
	W	—	—	—	—	—	—	—	—	—
1979/80 (live captures)	Su	(37)	(29)	5.49	(44)	(28)	6.19	5.26	0.07	0.07
	A	11	4	5.66	7	2	3.38	—	—	—
	W	—	—	—	—	—	—	—	—	—
1980/81	Sp	11	2	2.79	7	2	1.66	—	—	—
Sex unknown	Su	3	1	0.43	0	1	0.22	—	—	—
	Sp	3	—	—	3	—	—	—	—	—
Total carcasses examined		390		250		265				

* Including extras (stoats caught off standardized traplines).

† Excluding extras. Calculated from the beginning of standardized trapping only (June 1974). Total capture rate includes damaged carcasses with age or sex unknown: capture rate for young excludes these.

TABLE 4. Annual variation in fecundity of stoats

Mating season of	Corpora lutea per female, $\bar{x} \pm$ S.E. and (n)*		
	Eglinton	Hollyford	Craigieburn
1972	9.6 \pm 0.36 (16)	—	9.1 \pm 0.55 (8)
1973	10.2 \pm 0.43 (16)	—	8.6 \pm 0.81 (5)
1974	9.7 \pm 0.33 (24)	9.4 \pm 0.24 (50)	0.6 \pm 0.70 (24)
1975	9.7 \pm 0.64 (7)	8.3 \pm 0.62 (10)	9.1 \pm 0.40 (21)
1976	10.2 \pm 0.47 (35)	10.3 \pm 0.41 (26)	8.7 \pm 0.38 (33)
1977	8.9 \pm 0.63 (12)	8.7 (3)	8.4 \pm 0.61 (7)
1979	10.6 \pm 0.42 (8)	13.6 \pm 1.40 (5)	—
Kruskal-Wallis analysis of variance	$H = 5.51$ (NS)	$H = 17.96$ 0.01 > $P > 0.001$	$H = 5.76$ (NS)
Years of high density mice	10.3 \pm 0.39 (43)	10.8 \pm 0.45 (31)	10.6 \pm 0.70 (24)
Years of low density mice	9.7 \pm 0.23 (59)	8.4 \pm 0.47 (13)	9.1 \pm 0.39 (21)
			Kruskal-Wallis analysis of variance $H = 1.40$ (NS) $H = 6.64$ ($P < 0.05$)

* For frequency distributions, see King (1981).

Orthoptera), and males ate more opossums (*Trichosurus vulpecula* Kerr 1792); both sexes of stoats ate birds to about the same extent. When prey categories were grouped as small (insects), medium (birds, mice, lizards) or large (lagomorphs, opossums, rats) females were found to eat significantly more small prey, and males significantly more large prey. There were also differences in diet between forest types and seasons, of which at least some probably reflected changes in availability of prey. Large prey supplied most of the biomass eaten by stoats; insects, though found in about 40% of guts, contributed only about 10% of the volume of prey ingested. The present analysis goes on from this basis to consider whether variations in density of mice affect the consumption by stoats of mice and birds. Data are subdivided by season and area, but not by age or sex except in respect of mice.

Changes in food habits of stoats with changes in the density of mice

Tables 5–7 show the frequency of occurrence of the major prey types and the sample sizes for each season through the study. There were considerable variations between years in the occurrence of mice, birds, and the main alternative prey (larger mammals) in each season. Differences in the occurrence of given prey in years of known high and of low density of mice, pooled, were tested by a series of 2×2 Chi-squared tests (Table 8). Because many samples were rather small, it was not possible to test for differences between individual years. There were few data for the winter and spring seasons in any year, so the tests are confined to the summer and autumn seasons.

In the two Fiordland areas, the pattern is similar. In both, more mice were eaten in summer and autumn of high mouse-density years, significantly so in three of four comparisons. In both, there were no significant differences in the occurrence of either birds or the larger mammals (rats, lagomorphs and opossums pooled) with density of mice in either season.

At Craigieburn, Table 7 shows two interesting special points. First, in winter and spring of 1975 when, according to the rodent density index lines (Table 2), mice were at a very low density, stoats were still able to catch some. Secondly, from spring to autumn during the 1974/75 mouse peak, lagomorphs were found as well as mice; but over the same period during the 1976/77 mouse peak, few lagomorphs were found, and an especially high

TABLE 5. Seasonal distribution of prey* of stoats in the Eglinton Valley (sexes and ages pooled)

Mouse density	Year	Season	Total guts with contents	Mice <i>n</i>	Guts containing Larger			
					Birds‡ <i>n</i>	mammals† <i>n</i>	Insects <i>n</i>	
?	1972/3	Su	6	4	2	1	4	
	1973	A	2	0	1	1	2	
Low	1973	W	37	13	18	19	18	
	1973	Sp	21	6	11	8	12	
	1973/4	Su	17	3	6	8	8	
	1974	A	9	2	4	4	7	
	1974	W	24	4	14	7	19	
	1974	Sp	9	4	8	0	7	
	1974/5	Su	27	9	15	6	16	
	1975	A	13	5	3	2	7	
	1975	W	2	0	2	0	1	
	1975	Sp	2	1	0	1	1	
High	1975/6	Su	11	3	6	3	7	
	1976	A	4	1	1	1	2	
	1976	W	0					
	1976	Sp	0					
	1976/7	Su	63	22	44	6	21	
	1977	A	24	17	3	4	3	
	Low	1977	W	7	5	3	1	1
		1977	Sp	7	1	3	2	3
		1977/8	Su	17	1	12	1	10
	High	1978	A	3	0	3	0	0
1979/80		Su	88§	42	46	27	19	
	1980	A	12	6	4	3	3	

* Principal prey only. Some guts had contents not listed here, e.g. lizards, carrion.

† Larger mammals = Lagomorphs + rats + opossums + unidentified mammals pooled.

‡ Excluding eggs (very few found).

§ Live-trapping in summer 1979/80: scats with contents defined as those containing foods other than bait (white mice) provided.

TABLE 6. Seasonal distribution of prey of stoats in the Hollyford Valley (see Table 5 for annotations)

Mouse density	Year	Season	Total guts with contents	Mice <i>n</i>	Guts containing Larger		
					Birds <i>n</i>	mammals <i>n</i>	Insects <i>n</i>
Low	1975*	Su	57	5	33	13	30
	1975	A	25	6	7	10	11
	1975	W	1	1	0	0	0
	1975	Sp	3	0	1	1	0
	1975/6	Su	21	2	12	5	9
	1976	A	7	4	2	1	0
	1976	W	3	1	2	1	1
High	1976	Sp	1	0	1	0	0
	1976/77	Su	44	20	23	6	20
Low	1977	A	22	7	4	8	8
	1977	W	8	2	2	4	1
	1977	Sp	2	1	1	1	1
	1977/8	Su	8	0	4	2	4
	1978	A	2	0	2	0	0
High	1979/80	Su	74	20	44	23	16
	1980	A	6	4	0	0	2

* February 1975 only.

TABLE 7. Seasonal distribution of prey of stoats at Craigieburn (see Table 5 for annotations)

Mouse density	Year	Season	Total guts with contents	Guts containing				
				Mice <i>n</i>	Birds <i>n</i>	Lagomorphs <i>n</i>	Other larger mammals* <i>n</i>	Insects <i>n</i>
? Low	1973	A	9	2	2	1	4	9
	1973	W	7	1	1	1	3	5
	1973	Sp	7	0	1	3	1	4
Low	1973/4	Su	8	0	6	4	1	2
	1974	A	10	3	2	3	5	3
High	1974	W	0					
	1974	Sp	17	5	4	7	1	2
	1974/5	Su	17	7	11	4	1	8
Low	1975	A	21	6	2	12	3	5
	1975	W	6	2	3	2	0	3
	1975	Sp	13	2	5	6	1	1
	1975/6	Su	39	0	27	17	5	11
	1976	A	1	1	0	0	0	0
?	1976	W	1	0	1	1	0	0
	1976	Sp	4	0	3	0	2	0
High	1976/7	Su	40	16	15	9	1	12
	1977	A	22	16	7	0	1	6
? Low	1977	W	4	2	3	0	0	0
	1977	Sp	1	0	1	0	0	0
	1977/78	Su	13	3	8	1	0	3
	1978	A	1	0	0	0	0	1
	1978	W	0					

* Opossums and 'unidentified mammals' only: Rats absent.

TABLE 8. Comparison of frequency of occurrence of mice, birds and larger mammals† in the diet of stoats in seasons of high (H) and low (L) density of mice.

	Percentage frequency of occurrence							
	Mice		Birds		Larger mammals		Guts examined	
	H	L	H	L	H	L	H	L
Eglington								
Summer	42**	22	60	54	22	25	151	72
Autumn	64**	28	19	38	19	24	36	29
Hollyford								
Summer	34***	8	57	57	25	23	118	86
Autumn	39	29	14	32	29	32	28	34
Craigieburn					Lagomorphs			
Summer	40***	5	46*	68	23	37	57	60
Autumn	51	30	21	20	28	20	43	20

The difference between pairs of frequencies were tested by 2×2 chi-squared tests, with results shown in the H column as * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Lagomorphs, rats, opossums, and 'unidentified mammals' (mainly opossums and rats) in Eglington and Hollyford: lagomorphs only at Craigieburn.

proportion of mice in autumn 1977. It seems likely that at Craigieburn, the rate at which stoats ate mice was influenced by the availability of not only the mice inside the forest but also the lagomorphs outside. Nevertheless, at Craigieburn as in Fiordland, more mice were eaten in summer and autumn of high density years, though only the summer difference was

significant (Table 8). Birds were eaten significantly less in summer of high density years and about the same in autumn, in contrast to Fiordland. The number of lagomorphs eaten (calculated alone, as the other larger mammals were rarely found) did not vary significantly with mouse density.

These contrasts can be presented in more detail by plotting the frequency of occurrence of the two prey of greatest interest, birds and mice, against the density index for mice. Figure 5 shows that, in summer, the proportion of mice found increased significantly with the density index for mice; in autumn, there was no correlation. Since mice were found more frequently in the females examined in the general survey (King & Moody 1982), the correlation was tried again using females only, but this did not alter the result in either season (summer, $r_s = 0.58$, $n = 15$, $P < 0.05$; autumn, $r_s = 0.04$, $n = 11$, $P > 0.05$). Figure 6 shows no correlation between the frequency of occurrence of birds in the guts and the density of mice in either summer or autumn. These results (Table 8, Figs 5 & 6) show that the only consistent difference in food habits of stoats in summer and autumn, in relation to the mouse density index, was the apparent functional response by stoats to increased availability of mice in summer.

However, the correlation between incidence of mice and of birds is marginally or definitely inverse in both seasons (Fig. 7). In summer the negative correlation is still

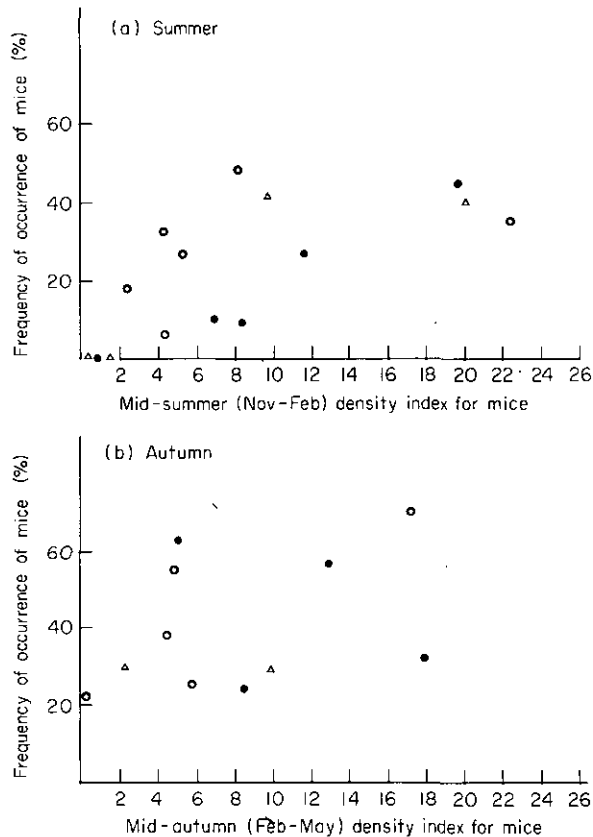


FIG. 5. (a) Frequency of occurrence of mice in guts of stoats in summer in relation to density index for mice, sexes pooled. $r_s = 0.74^{**}$, $N = 15$. (In females only, $r_s = 0.58^*$, $n = 15$. (b) Same, in autumn. $r_s = 0.36$, NS, $n = 11$. (In females only, $r_s = 0.04$, NS). ○ Eglinton; ● Hollyford; △ Craigieburn.

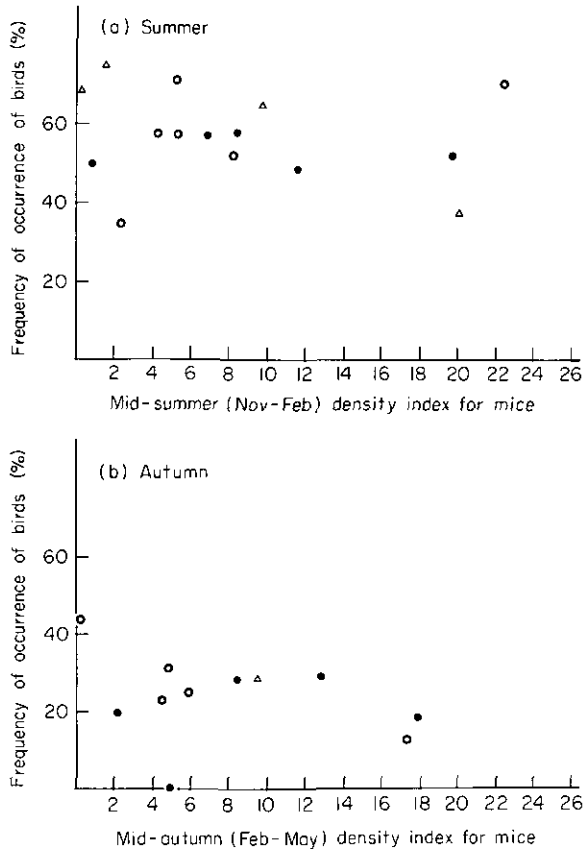


FIG. 6. (a) Frequency of occurrence of birds in guts of stoats in summer, in relation to density index for mice, sexes pooled. $r_s = -0.04$, NS, $n = 15$. (b) Same, in autumn. $r_s = -0.39$, NS, $n = 11$. ○ Eglinton; ● Hollyford; △ Craigieburn.

significant if data from females only are used, but not in autumn, probably because the small samples of females contain too much random error. However, in summer (sexes pooled), the significance of the inverse correlation depends on the point for the Eglinton in the summer of 1972/73 (without this point, $r_s = -0.33$, $n = 16$, $P > 0.05$). Since the sample of guts with contents examined in that summer was only six (Table 5) and the density of mice then was not known, the correlation must be regarded as weak, and may not really exist. By contrast, in autumn, the inverse correlation was much stronger ($r_s = -0.64$, $n = 16$, $P < 0.01$, sexes pooled), and is still significant even without the two outlying points for Eglinton and Hollyford 1978 ($r_s = -0.49$, $n = 14$, $P < 0.05$). The earlier general analysis showed an apparently regular seasonal switch by stoats from birds to mice in the autumn, and Fig. 7 suggests that this tendency is especially pronounced in the autumn following a good seedfall (i.e. 12 months later), while mice are still relatively abundant.

Effects of predation by stoats on mice

Predation by stoats was probably not the reason that young mice, born in late winter and spring of seed years, failed to enter the trappable population (C. M. King unpublished). The density of stoats is low until early summer (mid-December), whereas the

Beech seedfall, mouse and stoat populations

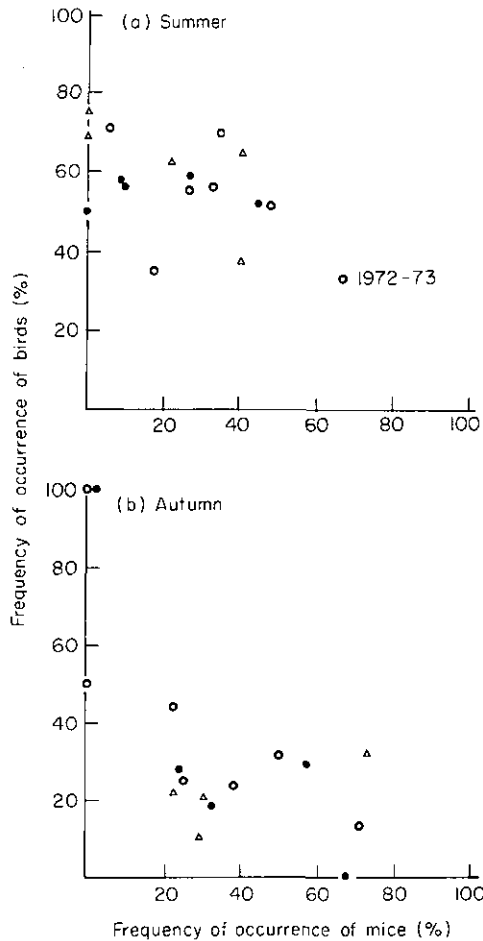


FIG. 7. Correlation between incidence of mice and of birds in the guts of stoats of both sexes. (a) in summer, $r_s = -0.44^*$, $n = 17$ (but without \circ 1972-73, $r_s = -0.33$, NS); and (b) in autumn, $r_s = -0.64^{**}$, $n = 16$. In females only, summer $r_s = -0.45^*$, $n = 15$; autumn $r_s = -0.24$, NS, $n = 13$. \circ Eglinton; \bullet Hollyford; \triangle Craigieburn.

decline in recruitment of mice began between August and November (late winter to spring).

By contrast, predation could have affected the size and timing of the peaks in populations of mice in summer. In 1976/77, in Eglinton/Hollyford, many stoats were caught but were all immediately removed. Although it is unlikely that more than about half the stoats present were killed, the effect was to hasten the expected declines in the stoat density indices over the autumn and winter of 1977, compared with that in 1980, significantly in the Eglinton (King & McMillan 1982). The density indices for mice reached their peaks in both valleys in February 1977, and then the declines in the two ageing, non-recruiting populations of mice was clearly inevitable, with or without predation. The most likely cause was the onset of cold weather, as Berry (1981) states that a drop in temperature is fatal for ageing mice. However, in summer 1979/80, about the same number of individual stoats appeared in the traps, and at about the same time (beginning in late December) as in 1976/77, but they were released alive. By that time the mouse populations had probably reached high densities; but recruitment had already

almost or completely stopped (C. M. King unpublished). Intense predation by the large number of stoats present after early January could have reduced this non-renewable standing crop of mice to the low density observed by the end of February 1980, thereby bringing forward the expected decline in mice by about three months compared with 1976/77.

Rats

Rats were caught both in rodent traps and in Fenn (stoat) traps, more commonly in the latter. Fenn traps were operated much more often (14, later 10, nights per month) than rodent traps (3 nights per quarter), and rats were attracted to the strong-smelling fish-based cat-food used as bait in Fenns. Of the 119 rats from Fiordland which were returned to the laboratory and identified, 108 were ship rats, *R. rattus*, and eleven were kiore, *R. exulans* (ten from the Hollyford and one from the Borland). The kiore comprise the remnants of a previously abundant population apparently displaced by ship rats (and/or stoats) throughout the South Island about the turn of the century (Atkinson 1973). No rats were caught at Craigieburn.

In the Eglinton, most of the rats caught in either kind of trap (six in rodent traps, thirty-seven in Fenns) were collected from spring (November) 1976 to summer 1977/78 inclusive, i.e., after the March–June 1976 seedfall (Table 2). This could represent a somewhat delayed response by rats to the seed, though the samples were small at any time. In the Hollyford, many more rats were caught (fifteen in rodent traps, ninety-three in Fenns), and the increase in *R. rattus* after autumn 1976 was more definite. *R. rattus* was infrequently caught by the rodent traps, and the increase in *R. rattus* may not have been detectable from the standard rodent trap-line alone. Conversely, the smaller *R. exulans* appeared in the rodent traps regularly, but no more often after the seedfall than before.

In 1979/80, no Fenn traps were set until April 1980, and few rats were caught in the stoat live-traps in either valley in December/January. Only two rats were caught in a total of 1885 rodent trap-nights and 531 Fenn trap-nights in the two valleys (one in each) from September 1979 to May 1980. Few rats were found in the eighty-eight and seventy-four stoat scats collected from the two valleys during the summer live-trapping. It appears that rats, like mice (Fig. 2) did not increase as much after the 1979 seedfall as they had after the 1976 fall.

In the Eglinton, stoats ate rats only in seasons where the traps showed rats to be present, but never frequently even then. Most of the rats identified were found in the largest samples of guts. In 1977/78 no rats were identified in seventeen stoats' guts, though rats were still present in the Eglinton, and the mice had by that time reached rather low densities. Only one mouse was identified, in a female stoat. Stoats apparently did not, as might have been expected, switch from mice to rats in that summer. Conversely, some rats were still eaten even when mice were at their peak in 1976/77.

In the Hollyford, stoats ate rats in all seasons, but only in summer and autumn were the samples large enough to analyse. In the summers of 1976/77 and 1977/78, when rats were relatively abundant, stoats ate rats no more often than the 1974/75, 1975/76 and 1979/80 summers ($\chi^2 = 0.018$, NS); in the autumns of 1977 and 1978, stoats ate rats no more often than in the autumns of 1975, 1976, and 1980 ($\chi^2 = 0.22$, NS).

DISCUSSION

The three-stage link between beech seedfall and population changes of mice and of stoats has long been suspected (Riney *et al.*, 1959). Marshall (1963) states that in January 1961

in North Westland, both stoats and mice were unusually numerous: Kirkland (1961) records a good seedfall of red beech in that area in 1960. However, the present study is the first which has attempted to document the sequence of events in detail through all three trophic levels over several years. The evolutionary ecology of mast seeding in trees (mostly Northern Hemisphere species) is discussed by Silvertown (1980).

Seedfall and population density of mice

These data support the general hypothesis that there is a strong correlation between seedfall and mouse population density in *Nothofagus* forests. Changes in the reproduction and age structure of the mice in seed years are further discussed by C. M. King (unpublished). At present, we can only assume that these relationships are causal, since no gut analyses of the mice have yet been done to confirm that mice do eat beech seeds. In theory, the same results would be observed if the mice were responding to some other fruit or seed that produced heavily at the same time as beech. In the Hollyford, silver beech was only one of twenty-eight plant species identified as major sources of food for rodents: but in the Eglinton, red beech was by far the most important of only eight food species, and at Craigieburn, mountain beeches were practically the only seedbearing plants present in the forest trapping area. The idea that beech seedfall was not responsible for the behaviour of the mice is plausible in the Hollyford, but less and less so in the other two areas.

On the other hand, correlation over several past years, even if causal and significant, does not necessarily allow predictions concerning a specific future year, for two reasons. First, seeding may be patchy in moderate seed years, especially in heterogenous forests, and the response of the mice localized or more variable, and perhaps more easily influenced by other factors important in their environment or populations at the time. Second, even after a heavy seedfall the extent and timing of the maximum response achieved may be influenced by external agents, such as predators. The seed always falls at about the same time of year, but the subsequent peak has been observed at various times and is sometimes much lower than expected. If predation is the explanation for the difference between the Fiordland mouse peaks of 1976/77 and 1979/80, the distribution of predators could explain variations in mouse peaks elsewhere too. Perhaps mice are able to reach especially high density (> 24 mice/100 TN) as late as February only where predators are removed, as in northern Fiordland 1977, or naturally few, as in southern Fiordland 1979. Elsewhere (Craigieburn, and northern Fiordland 1979; also Orongorongo Valley and Nelson Lakes: Fitzgerald 1978 and unpublished) mouse peaks have been either earlier, or lower, or both. In Sweden, the relationship between seedfall and rodent populations can be modified by predators (Hansson 1979).

Functional and numerical responses by stoats to mice

These terms both include two components. A predator is said to show a functional response if (a) its diet comprises proportionately more of a given prey as that prey increase in density, or if (b) its total intake increases as a result of eating more of that prey, both per unit time. A predator shows a numerical response if, as a result of a local increase in prey density, (a) the resident predators produce more young or (b) non-resident ones immigrate. The terms refer only to the biology of the predators, not to their effect on the prey (Hassell 1966). In this study we have data on relative changes in percentage of mice in the diet, and on the productivity of the stoats sampled. Whether the changes in diet or reproductive success of stoats were proportionate to the increase in mice is unknown. For brevity, they

are described as functional and numerical responses, although the changes observed were only in the indices used to reflect diet and productivity.

The data were adequate to compare the summer and autumn seasons of seed and non-seed years in Fiordland. Stoats responded both functionally and numerically to increased densities of mice in summer, with very little lag. Female stoats have great latent reproductive capacity and a sensitive mechanism for adjusting reproductive effort to the chances of success (King 1981). Hence, in a spring when the density of mice is rising, they can immediately produce large litters (potentially averaging eight to nine young), which are then weaned at the time the mice are reaching their peak. (In habitats with few mice, variations in other important prey, e.g. lagomorphs, could have the same effect). The proportion of adult stoats in a peak population is small, so by far the greater part of the collective functional response at this time is due to the young. The numerical response is therefore due to one generation, the bulk of the functional response to the next. Both responses were shortlived: the whole sequence of events was complete in less than a year, from the autumn of the seedfall to the next autumn, when the additional young stoats produced were independent and the functional response was no longer significant. The number of young produced had no great effect on the number of breeding adults next season (King 1981). As in the tawny owls observed by Southern (1970), reproductive success was determined by the abundance of prey, but did not itself determine the size of the subsequent population of predators.

Since neither the functional nor numerical responses shown were necessarily proportional to the increase in mice, neither proves that stoats had any effect on them. However, the differences between the two seed years of 1976 and 1979 in Fiordland (p. 158) provides strong circumstantial evidence that the combined functional and numerical responses of stoats could have had a considerable effect on the mice. Fortunately, this idea can be easily tested, by observing the consequences of the next large seedfall using both Fenn and live traps. If true, it implies that the high 1976/77 population peak of mice was not the norm, but quite unusual, since stoats are not normally trapped with the amount of effort that was put in during that period.

The theoretical ideas most relevant to these data are those of White (1978). He suggests that populations of both rodents and predators are normally restrained by a relative shortage of nitrogenous food for the very young. As he predicts, temporary abundance of such foods—seeds for female mice, and mice for female stoats—allowed improved survival of young, and subsequent population increase, in both species (C. M. King 1981, and unpublished). The events observed therefore support the first part of the Riney *et al.* (1959) hypothesis quoted in the Introduction, except that kiore (*R. exulans*), found mainly in the Hollyford Valley, were not caught more often after the seedfalls than before.

In parts of Eurasia, water voles (*Arvicola terrestris*) are important prey for stoats. Aspisov & Popov (1940) calculated a significant correlation between numbers of voles and of stoats trapped in U.S.S.R.; Erlinge (1981) showed a functional response by male stoats and increased breeding success by female stoats, in relation to the density of water voles in southern Sweden.

Rats

Daniel (1978) summarized what was known of the population ecology of ship rats in New Zealand up to 1976, including early data from the present study. The full results support his conclusions that ship rats are generally more abundant in more mixed forests (e.g. the Hollyford) and after seedfalls. Daniel also suggested that predation by stoats may

be one explanation for the much lower densities of rats observed in mainland forests, compared with predator-free offshore islands. This unproven idea is apparently supported by our observation that ship rats, like mice, did not increase as much in the Hollyford after the 1979 seedfall, when stoats were live-trapped and released, as they had after the 1976 one, when stoats were removed. However, against this there is some doubt as to how much effect the summer kill-trapping actually had in hastening the overwinter decline in the Hollyford stoats in early 1977 (p. 150 and King & McMillan 1982). A second problem incidentally raised by the present data is that of the factors controlling the distribution of *R. exulans* (Atkinson 1973; cf. Taylor 1975, 1978). The present data can only point out that closer studies of ecology of rats in the Hollyford and Eglinton Valleys might be profitable.

Implications for the conservation of birds

The results of this study also support the second part of the Riney *et al.* (1959) hypothesis, but not in its original form. Their suggestion that 'when the mice declined to normal densities there might be increased predation on birds' was not confirmed during the mouse declines of the autumns of 1977 or 1980; in fact, the opposite was observed. The previous general survey noted a regular seasonal switch to mice in autumn, in all forest types (King & Moody 1982), and after a mouse peak this was especially pronounced (Fig. 7(b)). In other words, there were still more stoats present than after a non-peak summer, but they were eating more mice and fewer birds. By winter and spring of 1977, 15 months after the 1976 seedfall, mice were at low density; if there was any switching by stoats to birds, it might have been then. This study provides no data on this, but even if more birds per stoat were eaten then, the total impact would be low, probably lower than in the previous summer, because few stoats were left.

However, the suggestion that birds might be especially at risk in mouse peak summers is probably still correct, for another reason. Although there was little change in the number of birds eaten per stoat, there were so many more stoats present, compared with a non-peak summer, that the total number of birds eaten must have been higher. Some idea of the total effect can be gained by calculating a 'bird predation index' from the product of two other indices, the number of stoats caught per 100 trap-nights and the number of birds eaten per 100 stoats. In summer the 'bird predation index' is strongly correlated with the summer density of mice ($r_s = 0.85$, $P < 0.01$, $n = 9$, Fig. 8(a)), largely because of the great increase in number of stoats present in mouse peak years. The effect was observed in both 1976/77 and 1979/80, but the total impact must have been much greater in 1979/80, when about the same number of individual stoats counted as in 1976/77 were released after capture instead of being removed. By autumn 1977, the number of stoats had declined, and those that were left ate few birds, so the 'bird predation index' for the autumn of 1977 was not higher than in the autumns of non-peak years in either valley (Fig. 8(b)). The autumn of 1980 in the Eglinton was different, because the stoat density index was still high (Fig. 2) which made the 'bird predation index' much higher than in autumn 1977.

These data suggest the following hypotheses:

(i) More birds are eaten in the summer of a mouse peak year, because stoats are more numerous and the large numbers of mice available apparently provide no protective buffering effect (cf. Dunn 1977; Tapper 1979). This effect is greater if stoats are not controlled, but may still be real even if they are.

(ii) If sufficient effort is made to control stoats during a peak summer, then by autumn the few left, switching as usual to mice, kill no more birds in total than after non-peak summers. If stoats are not controlled in the summer, there may be enough still present in

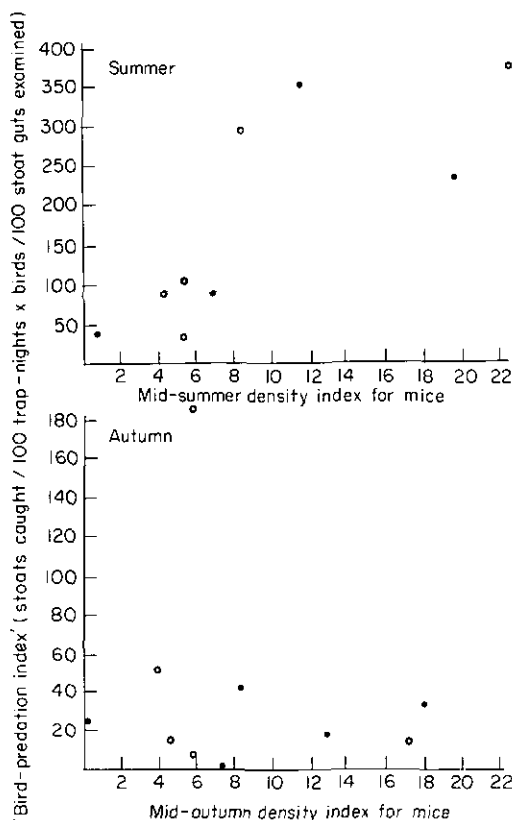


FIG. 8. Effect of the combined numerical and functional responses of stoats to mouse density on the total number of birds eaten in summer ($r_s = 0.85^{**}$, $n = 9$); and of the autumn switch to mice in reducing the number of birds eaten in autumn ($r_s = 0.021$, NS, $n = 10$). Fiordland data only: ○ Eglinton; ● Hollyford.

autumn so that, even though they eat fewer birds each, the total number of birds killed may still be higher than after non-peak summers.

There is nothing in these data to suggest what effect these changes might be having on bird populations. The number of birds available from year to year, the proportion of total mortality due to predation compared with other causes, the replacement capacity, even the species, of the birds eaten, were all unknown. Kikkawa (1966) believes that the general scarcity of passerines in Fiordland predates the arrival of introduced mammals, and that it is related to the cool, very wet climate. On the other hand, if the uncontrolled irruption of stoats in 1979/80 had such an effect on a peak population of mice, one wonders what effect (even temporary) it might have had on the birds. The only local data are very sparse. Flack & Lloyd (1978) attributed a virtually constant 30–40% of nest failures of South Island robin (*Petroica a. australis*) over 5.5 breeding seasons to predation by mustelids. A further 2–18% of failures were attributed to rodents, and 2–11% to unidentified predators. Since the number of mustelids present in any year was unknown, the effect of variations in their density and the total effect of predation on the productivity and population density of the robins has still to be worked out. But there is evidence from overseas studies that temporary changes in numbers of rodents, by affecting the functional or numerical response of predators, may cause increased predation on birds and

sometimes reduce the density or productivity of their populations (e.g. Myrberget 1972; Ryabitsev, Ryzhanovskii & Shutov 1976; Keith *et al.* 1977; Dunn 1977).

Of the vast literature on predator-prey interactions the only directly comparable study is that of Tapper (1979). His results have three similar features, and two especially interesting differences, to these. He showed that weasels (*Mustela nivalis*) on English farmland responded rapidly both functionally and numerically to changes in numbers of voles (*Microtus agrestis*); that when vole numbers were low the reproductive output of the female weasels was greatly reduced; and that predation by weasels may have affected the numbers of voles, so that the two populations were interacting, much as did the stoats and mice. However, increases in numbers of weasels lagged behind increases in voles by about 9 months, whereas the New Zealand stoats reached peak numbers at the same time as the mice and dropped as quickly; and the weasels ate significantly fewer birds when voles were abundant, whereas stoats' guts contained about the same proportion of birds at all densities of mice. These differences are probably related to the differences in reproductive biology of stoats and weasels, and to the relative lack of alternative prey for stoats in New Zealand. Clearly, the indirect consequences of rodent irruptions for birds in New Zealand should be examined further.

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