

¹ Department of Conservation, Private Bag 68-908, Newton, Auckland, New Zealand.² P.O. Box 36-559, Northcote, Auckland, New Zealand.

ECOLOGY OF THE STOAT IN *NOTHOFAGUS* FOREST: HOME RANGE, HABITAT USE AND DIET AT DIFFERENT STAGES OF THE BEECH MAST CYCLE

Summary: We studied the ecology of a high-density population of stoats in Fiordland, New Zealand, in the summer and autumn of 1990-91 following a *Nothofagus* seeding in 1990. Results are compared with findings from the same area in 1991-92, a period of lower stoat density. In the high-density year, minimum home ranges (revealed by radio-tracking) of four females averaged 69 ha and those of three males 93 ha; range lengths averaged 1.3 km and 2.5 km respectively. Neither difference was statistically significant. For combined sexes, average range area in the high-density year was significantly less, and range length was significantly shorter, than in the following year.

When we compared stoat diet in the high-density year with that in the following two years, there were no significant differences in the frequencies of occurrence of birds or invertebrates in stoat guts. Overall, bird remains were found in 56% of guts, and invertebrates in 28%. Possum remains occurred in 6% of male stoats but were never found in females. Mice were only detected in stoats in the high-density year, when they occurred in 54% of guts. Lagomorphs occurred significantly more often in the guts of stoats during lower-density years (26%) than the high-density year (7%).

Seedfall in *Nothofagus* forest is synchronous and periodic. Following seedfall, mouse density rises dramatically, followed by a sharp rise in stoat numbers. It has been suggested that mice feed on the abundant seed and that stoats in turn increase because of the large numbers of mice available to them. We suggest that the situation is more complex and that increases in not only mouse, but also bird (and possibly invertebrate), densities may contribute to the high productivity of stoats in the year following a *Nothofagus* seedfall.

Keywords: stoat; *Mustela erminea*; home range; range length; habitat use; diet; radio tracking; beech forest; *Nothofagus*; beech mast.

Introduction

Introduced mammalian predators are believed to have been responsible for many extinctions and declines in New Zealand's native fauna (King, 1990). Stoats (*Mustela erminea* L.) were originally introduced from England in the 1880s to control rabbits (*Oryctolagus cuniculus* L.), and are now widely distributed in both North and South Islands. They have often been implicated in the decline of native bird species (Moors, 1983; King, 1990) but although predation by stoats on birds can be locally heavy (Fitzgerald, 1964; Moors, 1983; Beggs and Wilson, 1991; O'Donnell, Dilks and Elliott, 1992), the extent to which they threaten the survival of species is unclear.

The stoat is the most common (and sometimes the only) mammalian carnivore in South Island beech (*Nothofagus* spp.) forests, where it periodically becomes numerous (King, 1983). In these forests, huge production of seeds occurs irregularly in a phenomenon known as a mast

seeding (Wardle, 1984; Allen and Platt, 1990). Mast years have been defined as 'full', 'partial' or 'poor', depending on the quantity of seeds produced ('full' = > 4000, 'partial' = 500-4000, 'poor' = < 500 seeds m⁻²; Wardle, 1984). Mice (*Mus musculus* L.), which are normally at very low densities in beech forest, become very numerous during mast years (Fitzgerald, 1978; King, 1983; Murphy, 1992). Stoat numbers also fluctuate widely in beech forests, being particularly high in the summer following a beech seedfall. Riney *et al.* (1959) proposed a possible link between these events, suggesting that

"mouse and kiore 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."

This sequence was generally supported by King (1983). Riney *et al.* (1959) also suggested that when

mouse density fell, there might be increased predation of birds by stoats. King (1983) showed that there was little change in the number of birds eaten per stoat at a wide range of mouse densities, but noted that a greater absolute number of birds would be eaten in a season of high mouse density simply because of the greater number of stoats present. Local control of stoats may therefore be necessary after a beech seedfall to protect vulnerable endemic bird species.

In order to better understand the biological consequences of a beech mast, we compared some aspects of the ecology of high-density and lower-density stoat populations in a *Nothofagus* forest. 1989-90 was a full mast year (C. O'Donnell, P. Dilks and G. Elliott, *unpubl. data*) and the expected irruptions of house mice and stoats occurred during the 1990-91 spring and summer. We describe here home range dimensions and habitat use by stoats in the Eglinton Valley, Fiordland, in the summer and autumn of 1990-91; these are compared with data (from Murphy and Dowding, 1994) from the same area in 1991-92, a period of lower stoat density and very low mouse density. We also compared the diet of stoats in the high-density year with that in the following two years of lower density.

Methods

The study was undertaken in an area of about 150 ha at Knobs Flat on the valley floor of the Eglinton Valley (c. 380 m a.s.l.), in northern Fiordland (44°58'S, 168°01'E) (Fig. 1). Approximately 33%

was open terrain (mostly grassed but including a river) and the remainder was forest dominated by red beech (*Nothofagus fusca* Hook) and silver beech (*N. menziesii* Hook). Further details (including the mammals present) are given by Murphy and Dowding (1994).

Seasons were defined by three-month periods: spring (September-November), summer (December-February), autumn (March-May) and winter (June-August). Years are numbered relative to the beech mast of 1989-90 (year Y0); the period October 1990 - May 1991 is designated Y1 (one year after the mast), October 1991 - May 1992 is Y2, and October 1992 - May 1993 is Y3.

The number of stoats killed each year on a 50 ha grid of Mk 4 Fenn traps at Deer Flat (1 km south of the Knobs Flat study area) was used as one index of stoat density in the valley. Trapping effort was constant each year. Fifty-six wooden tunnels, with two traps per tunnel, were spaced 100 m apart. Further details of the Fenn-trapping are given by Dilks, O'Donnell and Elliott (1992). Stoats from the Deer Flat grid were autopsied, aged and sexed by E.C.M. Live-trapping (as described by Murphy and Dowding, 1994) was undertaken in each month from October 1990 to May 1991; traps were placed in lines beside the road and along a walking track in forest about 300 m from the road. The total number of stoats captured (spring, summer and autumn combined) in the Knobs Flat study area was used as a second index of stoat density. Stoats were anaesthetised with Halothane ('Fluothane', I.C.I. New Zealand Ltd., Lower Hutt, N.Z.), ear-tagged, weighed, sexed, aged as juvenile or adult, and released at the capture site.

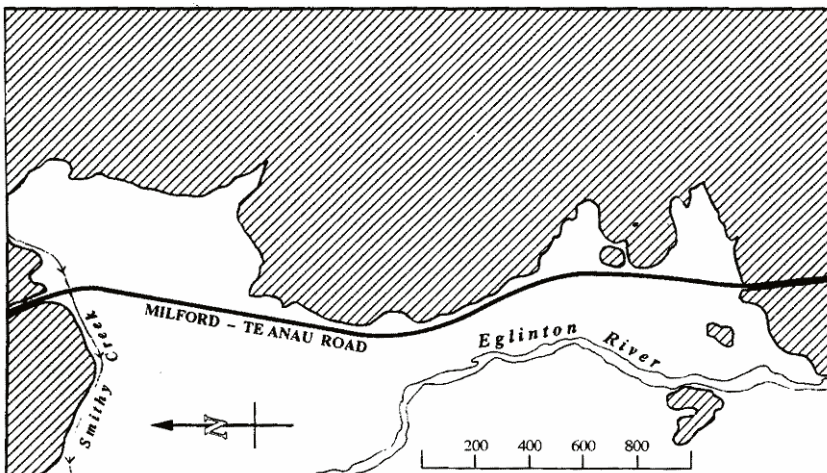


Figure 1: Map of the Knobs Flat study area, showing forested (cross-hatched) and open areas. The scale bar represents 1000 m. The same area is represented in Figures 2a-c.

Radio-tracking

Stoats were fitted with a radio-transmitter incorporated into a collar with a whip aerial (Sirtrack, Landcare Research NZ Ltd., Havelock North, New Zealand). As stoats had not previously been radio-tracked in New Zealand, this transmitter package was still under development and was modified during the study. Initially, single-stage transmitters were used but their range was found to be very limited in forest (50-150 m). After January 1991, two-stage transmitters weighing 9-12 g were used; these had a range of 150-300 m in forest and 2-5 km in open terrain. Transmitters were shed by some stoats and damaged by others. Six two-stage transmitters, all badly chewed and non-functional, were retrieved from stoats caught in live-traps. During summer-autumn 1990-91, no stoat retained a functioning transmitter for more than 9 days at a time, but some stoats were recaptured and fitted with new transmitters when collars were lost or damaged.

We recorded each animal's position and whether it was moving or stationary at intervals of three hours minimum (spot records); preliminary data showed that stoats were capable of moving to any point in their home range within this time. Spot records were obtained between 0730 hr and 0200 hr. Den sites were defined as places where stoats were stationary for two or more spot records.

Radio-tracking techniques were described by Murphy and Dowding (1994). Home range was measured by the minimum convex polygon method (Harris *et al.*, 1990). Each range was also reduced to a peeled polygon (Kenward, 1992) containing 70% of records. Means are quoted ± 1 S.E.

The study area was divided into three habitat categories: forest, forest margin (land within 20 m of a forest edge), and open ground. Habitat use by individual stoats was examined as described by Murphy and Dowding (1994) and habitat preferences were determined by the log-ratio differences method of Aebischer and Robertson (1992). A log-ratio analysis was also undertaken to determine whether the road had any effect on habitat use; home ranges of individual stoats were divided into road (which included a 20 m strip either side of the road) and non-road (everything else).

Diet

Between October 1990 and March 1993, 131 stoats were collected in the Eglinton Valley and autopsied. Of these, 105 were caught in Fenn traps at Deer Flat, nine were found dead on the road, six were accidentally killed in traps set for other reasons, three died in live-traps, two were found dead from unknown causes, one was killed by a dog and five

by people. Of the 131 guts examined, 35 were empty and were excluded from further analysis. Of the remainder, 14 were from adult females, 17 from juvenile females, 25 from adult males and 40 from juvenile males. At autopsy, the contents of the stomach and intestine were stored in 70% ethanol.

Ninety-five stoat scats were also collected, mainly from live-traps and latrines located outside known den sites, between December 1990 and May 1992. Some of this diet information (from 26 guts and 44 scats collected between October 1991 and May 1992) has already been published in less detail (Murphy and Dowding, 1994). Before analysis all material was washed in a fine sieve and then sorted under a low-power (x10) microscope. Many of the bird remains included feet and claws, which were measured and compared to reference specimens; birds were also identified by feather colour patterns and downy barbule characteristics (Day, 1966; E. Murphy, *unpubl. data*). Bird nomenclature follows Turbott (1990). Mouse remains were easily recognised, as they often contained feet and tail pieces, as well as fur. Guard hairs from other mammals were identified by scale patterns (Day, 1966). Results of the diet analysis are presented as a frequency of occurrence; i.e., the percentage of scats, or guts with food, containing each prey category. Differences in the occurrence of prey were compared between year Y1 (high mouse density) and years Y2 and Y3 (low mouse density; C. O'Donnell, P. Dilks and G. Elliott, *unpubl. data*) which were combined (Y2+3) to increase sample sizes. Means are quoted ± 1 S.E. Where sample size ≤ 5 , Yates' correction was applied to chi-squared analyses (Campbell, 1974).

Age

Stoats less than one year old are defined here as juveniles. Females were classed as adults or juveniles by the presence/absence of enlarged nipples or by measuring the post-orbital ratio (interorbital width divided by postorbital width). The presence of enlarged testes or the weight of the baculum was used to categorise males as juveniles or adults (Grue and King, 1984). Autopsied adult stoats were further aged by counting the number of incremental lines in the canine cementum (Grue and King, 1984).

Results

Stoat abundance

Live-trapping at Knobs Flat began in October 1990 but no stoats were caught until December. Between December 1990 and May 1991, 25 individual stoats (12 females, 13 males) were caught at least once in

Table 1: Numbers of stoats caught in the Eglinton Valley, Fiordland, from October 1990 – March 1993. The total numbers caught in subsequent years relative to those caught in Y1 (1990-91) are shown in brackets. A = adult; J = juvenile.

Year	No. of stoats killed on Deer Flat grid					No. of stoats caught alive at Knobs Flat				
	Female		Male		Total	Female		Male		Total
	A	J	A	J		A	J	A	J	
Y1 (1990-91)	3	12	3	44	62	1	11	4	9	25
Y2 (1991-92)	11	0	18	0	29 (0.47)	4	0	4	0	8 (0.32)
Y3 (1992-93)	0	4	7	3	14 (0.23)					

the 150 ha study area; including re-traps there was a total of 90 captures. Sixteen of these stoats (eight females, eight males) were fitted with radio-transmitters.

Table 1 shows the number, age and sex of stoats killed each year on the Deer Flat kill-trapping grid and the same data for stoats caught in live-traps in the Knobs Flat study area in years Y1 and Y2 (Murphy and Dowding, 1994; this study). Since trapping effort was the same in both years, these figures suggest that stoat density in year Y2 was one-third to one-half the level that it was in Y1. Only kill-trapping figures are available for Y3; they suggest that stoat density then had fallen to about one-quarter of the Y1 level. Kill-traps and live-traps caught similar proportions of juveniles and adults in Y1; 56 (90%) of 62 stoats kill-trapped and 20 (80%) of 25 live-trapped were juveniles. All stoats caught (both trap types) in Y2 were adults and in Y3 (kill-traps only) equal numbers of adults and juveniles were caught.

Home range and habitat use

The minimum home ranges of eight stoats (four female, four male) radio-tracked between January and May 1991 (Y1), varied from 50-105 ha in area and from 1.0-4.5 km in length (Table 2). The full extent of M65's home range may not have been revealed because only 13 records were obtained, and it is excluded from further analysis. Ranges of stoats

overlapped between and within sexes (Fig. 2). During January and February, seven female stoats (one adult, six juvenile) were live-trapped in the study area. Detailed home range information was collected for two of these (Table 2; Fig. 2A). Juvenile F58 was tracked only in January and was never detected after this. F56, an adult known to be 5 years old, was tracked in both months but was found dead from unknown causes in March. Two of the females caught (but not radio-tracked) in February were re-captured in the study area throughout autumn; both were radio-tracked in May, by which time they had occupied F56's home range between them (Fig. 2B). They both remained in the area until at least August 1991. Four other juvenile females were also caught in the study area (two of them only once) during autumn but detailed home range information was not gained on these. From February to April, five male stoats (two adults, three juveniles) were live-trapped in the same area; detailed home range information was collected on two of these (Table 2; Fig. 2C).

The 70% core ranges of six stoats radio-tracked varied little (18-25 ha) but one was much smaller (juvenile F58, 4 ha) (Table 2). With one exception, 70% core ranges did not overlap. The exception was the core range of F56 (the only adult female known to be in the study area) which overlapped with that of the juvenile F58 who may have been her offspring (Fig. 2A).

Table 2: Home range area (HR) and length (RL) of stoats at Knobs Flat, Fiordland in 1991, calculated by the minimum convex polygon method (radio-tracking and live-trapping data combined). F = female; M = male.

Sex & Stoat	Age (yr)	HR (ha)	RL (km)	Month tracked	No. of records	Days tracked	70% core ranges (ha)
F56	5	88	1.3	Jan-Feb	21	7	22
F70	<1	77	1.6	May	47	10	21
F58	<1	56	1.1	Jan	20	9	4
F67	<1	56	1.0	Mar, May	28	7	22
M69	2	105	4.5	May	34	9	25
M71	>1	95	1.8	Mar	20	7	18
M64	<1	80	1.2	Feb-Apr	34	13	25
M65	<1	50	1.2	Feb	13	9	-

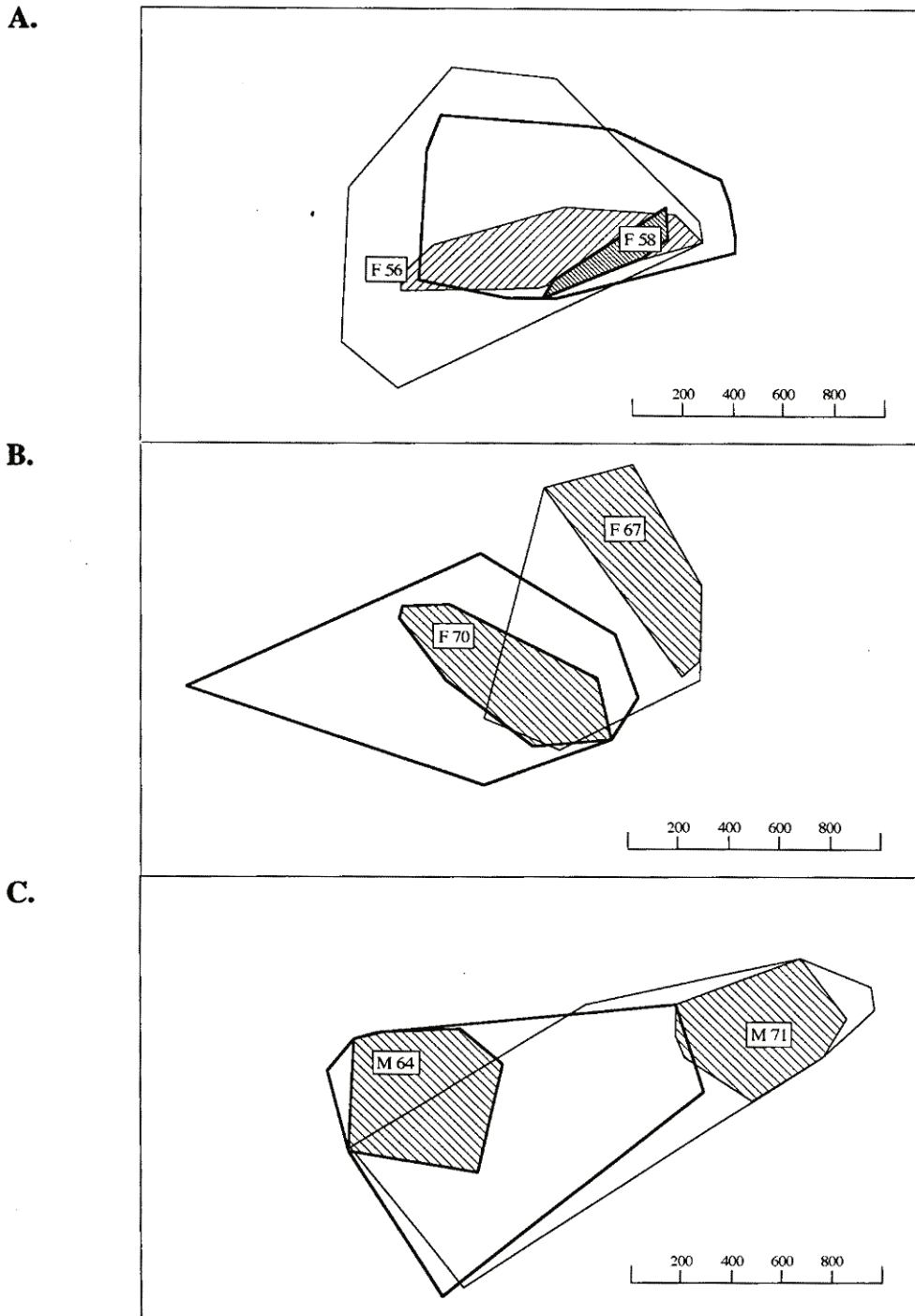


Figure 2: Home ranges (outline) and 70% core ranges (cross-hatched) of stoats at Knobs Flat, Eglinton Valley. The scale bar represents 1000 m. **A:** Females F56 (an adult; light outline) and F58 (a juvenile; heavy outline). **B:** Juvenile females F67 (light outline) and F70 (heavy outline). **C:** Males M64 (a juvenile; heavy outline) and M71 (an adult; light outline).

The average home range area of females ($n=4$) was 69 ± 8 ha and that of males ($n=3$) was 93 ± 7 ha (independent t -test on log-transformed values, $t = 2.06$, d.f. = 5, $P = 0.10$). The average range length of females was 1.3 ± 0.1 km and that of males was 2.5 ± 1.0 km (independent t -test on log transformed values, $t = 1.58$, d.f. = 5, $P = 0.18$). The mean number of fixes for male and female stoats was not significantly different ($t = 0.04$, d.f. = 5, $P = 0.97$).

Using data from Murphy and Dowding (1994), range areas and lengths during the period January-May were compared between 1991 and 1992. No significant differences were found between sexes in either year, so female and male ranges were combined. In 1991 the average home range area was significantly less than in 1992; 80 ± 7 ha ($n = 7$) and 160 ± 35 ha ($n = 9$) respectively (independent t -test on log-transformed values, $t = 2.35$, d.f. = 14, $P = 0.04$). The average range length was also significantly lower in 1991 than 1992; 1.8 ± 0.5 km and 3.1 ± 0.5 km respectively (independent t -test on log-transformed values, $t = 2.47$, d.f. = 14, $P = 0.03$). The mean number of fixes for stoats was not significantly different between 1991 and 1992 ($t = 0.64$, d.f. = 14, $P = 0.53$).

Although individuals showed different preferences for forest, forest margin, open areas and road habitat within their ranges, there were no significant preferences overall in 1991 (Table 3). Using data from Murphy and Dowding (1994), habitat use during the January to May period was compared between 1991 and 1992. There were no significant differences in the use of forest and forest margin habitats between years (forest: $t = 0.86$, d.f. = 14, $P = 0.40$; margin: $t = 0.19$, d.f. = 14, $P = 0.85$); however stoats showed a significant avoidance of

Table 3: Log-ratio differences and t -test indicating habitat utilisation within home ranges for individual stoats in 1991, Knobs Flat, Fiordland. A positive value indicates preference and a negative value avoidance. F = female; M = male.

Stoat	Habitat			
	Forest	Margin	Open	Road
F56	-0.78	0.18	0.80	-0.17
F67	-1.18	1.22	-2.83	-3.85
F58	-1.97	2.83	0.14	0.89
F70	0.79	-0.31	-0.78	-4.65
M69	0.66	0.46	-1.32	-1.21
M71	0.39	0.42	-0.56	0.04
M64	0.42	0.62	-0.66	-4.32
Mean	-0.24	0.77	-0.74	-1.90
S.E.	0.40	0.38	0.43	0.88
t value	0.59	2.02	1.72	2.16
P	0.58	0.09	0.14	0.07

open areas within their home ranges in 1992, compared to 1991 ($t = 3.01$, d.f. = 14, $P = 0.01$). There was no significant difference in use of road habitat by females in 1991 and 1992 ($t = 0.44$, d.f. = 6, $P = 0.68$) but male stoats made significantly more use of road habitat in 1992 than 1991 ($t = 3.11$, d.f. = 5, $P = 0.03$).

Dispersal

Because transmitters were usually retained for a short time, we were able to collect little information on dispersal. Of the 25 stoats ear-tagged between December 1990 and May 1991, 13 (six females, seven males) were never re-captured in the study area and may have dispersed. Three of the males were subsequently killed in traps about 2 km to the south, suggesting they may have been dispersing down the valley. The most distant recovery was of a juvenile female first caught and ear-tagged at Smithy Creek ($44^{\circ}57'S$, $168^{\circ}01'E$, see Fig. 1) on 20 December 1990, weighing 175 g. She was never recaptured in the study area but was found in a kill-trap at the Takahe Rearing Unit, Burwood Bush ($45^{\circ}33'S$, $168^{\circ}00'E$) on 13 January 1991. This means she travelled a straight-line distance of 65 km within four weeks.

Activity and den sites

Between January and May 1991, 169 spot records were obtained (88 from females, 81 from males). Stoats were moving in 64 records (38%) and were stationary in 105 (62%). During daylight hours only, stoats were recorded moving in 44 of 130 records (34%).

Most animals used many dens but had a small number (1-3) that were used regularly. Although most dens ($n=22$) were obvious holes in the ground under tree roots, dens were also found up trees ($n=3$) and in the middle of the grass plain ($n=4$). No particular areas within the forest seemed to be favoured and dens did not appear to be located near obvious features.

In December 1991, a male still dependent on its mother was caught and radio-tracked back to its den. By the next day, the mother had moved all the young to a new den site 500 m away. Although the new den was ringed with live-traps, no further stoats were caught, even though up to four young stoats were observed playing around the den entrance.

On two occasions during daytime radio-tracking, female stoats were seen stalking birds in grass; in both instances the targets were yellow-crowned parakeets (*Cyanoramphus auriceps*) and chaffinches (*Fringilla coelebs*) feeding on grass seed at ground level.

Diet

Mice were only detected in the diet of stoats in 1990-91 (Y1), when they occurred in 29 (53.7%) of the 54 guts that contained food (Table 4). There was no significant difference in the frequency of occurrence of mice in female and male guts ($\chi^2 = 0.37$, d.f.= 1, $P = 0.54$). There was also no significant difference between the occurrence of mice in stoat guts in summer and autumn ($\chi^2 = 1.16$, d.f.= 1, $P = 0.28$).

Lagomorph remains occurred in 15 (16%) of the 96 guts that contained food. There were no significant differences in the frequency of occurrence of lagomorphs in female and male diets in either year Y1 or in Y2+3 ($\chi^2 = 0.3$, d.f.= 1, $P = 0.58$; $\chi^2 = 0.46$, d.f.= 1, $P = 0.50$ respectively). Combining data from both sexes, lagomorphs occurred significantly more often as prey items in Y2+3 (26.2%) than in Y1 (7.4%) ($\chi^2 = 5.0$, d.f.= 1, $P = 0.03$). If data from all three years after the mast are combined, lagomorphs also occurred significantly more in the guts of adult stoats (28.2%) than those of juveniles (7.0%) ($\chi^2 = 7.9$, d.f.= 1, $P = 0.01$).

Australian brushtail possum (*Trichosurus vulpecula* Kerr) was never found in the guts of female stoats (Table 4). It occurred in only one (2.5%) of the 40 male guts that contained food in

year Y1, and in three (12%) of the 25 male guts that contained food in years Y2+3.

Bird remains occurred in 54 (56%) of the 96 guts that contained food. Most of the birds were passerines, which occurred in at least 39% of guts examined (Tables 4 and 5). There was no significant difference in the frequency of occurrence of birds in female and male diets in either Y1 or Y2+3 ($\chi^2 = 2.5$, d.f.= 1, $P = 0.11$; $\chi^2 = 0.19$, d.f.= 1, $P = 0.66$ respectively). Combining the data for sexes, there was also no significant difference between the frequency of occurrence of birds in Y1 and Y2+3 ($\chi^2 = 0.07$, d.f.= 1, $P = 0.80$). If data from all three years after the mast are combined, there was no significant difference in the frequency of occurrence of bird remains in adult and juvenile, female and male stoats ($\chi^2 = 6.84$, d.f.= 3, $P = 0.08$); there was also no significant difference in the seasonal occurrence of birds in spring, summer or autumn ($\chi^2 = 4.04$, d.f.= 2, $P = 0.13$).

Invertebrate remains occurred in 27 (28%) of the 96 stoat guts that contained food. There was no significant difference in the frequency of occurrence of invertebrates in female and male diets in either Y1 or Y2+3 ($\chi^2 = 0.08$, d.f.= 1, $P = 0.77$; $\chi^2 = 1.6$, d.f.= 1, $P = 0.21$ respectively). Combining the data for sexes, there was no significant difference in the frequency of occurrence of invertebrates between Y1

Table 4: Percent frequency of prey occurrence in the gut contents of stoats caught in the Eglinton Valley, Fiordland from October 1990 to May 1991 (females, $n = 14$; males, $n = 40$) and October 1991 to May 1992 and November 1992 to March 1993 combined (females, $n = 17$; males, $n = 25$).

Prey	Females		Males		Total	
	90-91	91-93	90-91	91-93	90-91	91-93
Mammal	71.4	17.7	60.0	48.0	63.0	35.7
Mouse	64.3	0.0	50.0	0.0	53.7	0.0
Lagomorph	7.1	17.7	7.5	32.0	7.4	26.2
Possum	0.0	0.0	2.5	12.0	1.9	7.1
Stoat (baby)	0.0	0.0	0.0	4.0	0.0	2.4
Bird	35.7	58.8	65.0	52.0	57.4	54.8
Passerine	21.4	47.1	47.5	28.0	40.7	38.1
Parakeet	0.0	0.0	5.0	0.0	3.7	0.0
N.Z. pigeon	0.0	0.0	2.5	0.0	1.9	0.0
Kingfisher	0.0	0.0	2.5	0.0	1.9	0.0
Long-tailed cuckoo	0.0	0.0	2.5	0.0	1.9	0.0
Unidentified bird	14.3	11.8	5.0	24.0	7.4	16.7
Invertebrate	21.4	47.1	22.5	28.0	22.2	38.1
Coleoptera	14.3	11.8	12.5	12.0	13.0	11.9
Orthoptera	7.1	35.3	7.5	20.0	7.4	26.2
Hymenoptera	0.0	0.0	2.5	0.0	1.9	0.0
Diptera	0.0	0.0	2.5	0.0	1.9	0.0
Lepidoptera	0.0	0.0	0.0	4.0	0.0	2.4
Unidentified	0.0	0.0	0.0	8.0	0.0	4.8

Table 5: Birds identified from 96 stoat guts, of which 54 contained bird remains, collected from December 1990 to March 1993 in the Eglinton Valley, Fiordland. Eleven of the bird remains could not be identified to Order.

Order	Species	Common name	Number
Columbiformes	<i>Hemiphaga novaeseelandiae</i>	N.Z. pigeon	1
Psittaciformes	<i>Cyanoramphus auriceps</i>	Yellow-crowned parakeet	2
Cuculiformes	<i>Eudynamys taitensis</i>	Long-tailed cuckoo	1
Coraciiformes	<i>Halcyon sancta vagans</i>	N.Z. kingfisher	1
Passeriformes	<i>Petroica macrocephala</i>	N.Z. tomtit	7
	<i>Acanthisitta chloris</i>	Rifleman	4
	<i>Petroica australis</i>	N.Z. robin	3
	<i>Mohoua ochrocephala</i>	Yellowhead	1
	<i>Fringilla coelebs</i>	Chaffinch	4
	<i>Turdus philomelos</i>	Song thrush	4
	<i>Turdus merula</i>	Blackbird	3
	not identified to spp.		12

Table 6: Percent frequency of prey occurrence in the scats of stoats collected between October 1990 to May 1991 and October 1991 to May 1992, in the Eglinton Valley, Fiordland.

Prey category	Females		Males		Unknown		Total	
	90-91 n=30	91-92 n=18	90-91 n=16	91-92 n=17	90-91 n=5	91-92 n=9	90-91 n=51	91-92 n=44
Mammal	70	44	81	71	100	22	77	50
Mouse	63	0	38	0	100	0	59	0
Lagomorph	7	44	13	41	0	22	8	39
Possum	0	0	13	29	0	0	4	11
Sheep	0	0	13	0	0	0	4	0
Unidentified	3	0	19	0	20	0	10	0
Bird	50	44	31	53	40	78	43	55
Passerine	27	28	25	24	40	44	28	30
Parakeet	10	11	0	6	0	0	6	7
Canada goose	0	0	0	6	0	0	0	2
Unidentified	13	6	6	18	0	33	10	16
Skink	10	0	0	0	0	0	6	0
Invertebrate	37	33	13	47	0	22	26	36
Coleoptera	10	6	6	6	0	22	8	9
Orthoptera	10	17	0	18	0	0	6	14
Diptera	0	0	0	6	0	0	0	2
Spider	0	0	6	0	0	0	2	0
Unidentified	20	11	6	18	0	0	14	11

and Y2+3 ($\chi^2 = 2.1$, d.f.= 1, $P = 0.15$). If data from all three years after the mast are combined, there was no significant difference in the frequency of occurrence of invertebrate remains in adult and juvenile, female and male stoats ($\chi^2 = 2.34$, d.f.= 3, $P = 0.51$); there was also no significant difference in the seasonal occurrence of invertebrates in spring, summer or autumn ($\chi^2 = 0.71$, d.f.= 2, $P = 0.70$).

Frequencies of occurrence of mouse, lagomorph, possum and bird remains in 95 scats (Table 6) were very similar to those from the gut

analysis. However, some further prey items were identified; skink remains were in three scats, wool from sheep (*Ovis aries* L.) in two, spider remains and Canada goose gosling (*Branta canadensis*) feathers in one each.

Prey remains found at nine stoat dens, collected from December 1990 to May 1992, were eel (*Anguilla* sp.), possum, rabbit, black-fronted tern (*Sterna albobriata*), Canada goose gosling, N.Z. pigeon, yellow-crowned parakeet, yellowhead, N.Z. robin, N.Z. tomtit, chaffinch and song thrush.

Discussion

Range and habitat use

Home range sizes of stoats world-wide vary from 2 to 368 ha (King, 1989; Alterio, 1994; Murphy and Dowding, 1994). The home ranges in our 1990-91 (Y1) study were similar to those of adult male stoats in a coastal area of New Zealand (Alterio, 1994), but significantly smaller than those found in the same area of Fiordland in 1991-92 (Y2) (Murphy and Dowding, 1994). Five of the eight stoats radio-tracked in 1990-91 were juveniles but sample sizes are too small to detect whether this age difference could explain the smaller ranges. Rodent density in the Eglinton Valley was much lower in Y2 (C. O'Donnell, P. Dilks and G. Elliott, *unpubl. data*); stoat home ranges in northern Europe may become larger when small rodents are scarce (Nyholm, 1959; Vaisfeld, 1972; Erlinge, 1977a), but circumstances probably differ considerably in *Nothofagus* forest in New Zealand (see below).

In our study, home ranges in year Y1 overlapped both between and within sexes, whereas in Y2 females had exclusive ranges (Murphy and Dowding, 1994). This may have been because most of the stoats present in Y1 were juveniles (only one of the females tracked was an adult). In Sweden, stoats established territories in autumn, excluding other members of the same sex from their territories (Erlinge, 1977b). Young females usually settled near their birth place and remained there throughout life, but juvenile males remained in their natal areas only until winter, then moved extensively in spring. In our study however, about half the stoats caught (females as well as males) appeared to be dispersing in summer and autumn. Previously, the longest dispersal recorded in New Zealand was for a juvenile male stoat, who travelled at least 23 km (King and McMillan, 1982). Our finding that a juvenile female (probably pregnant) dispersed at least 65 km within four weeks is of particular concern from a conservation perspective. Clearing stoats from sensitive areas (and even from large buffer zones around them as well) is only an effective strategy while trapping is continued; stoats may re-invade within a few weeks after trapping stops. It is worth noting that re-invasion of trapped areas is not only a problem in the year following a beech mast – stoats re-invaded the Deer Flat grid within two months after trapping ended in the autumn of Y2 (Murphy and Dowding, 1994).

In year Y1, radio-tracking showed that male stoats did not have a preference for road habitat, which they did in Y2 (Murphy and Dowding, 1994). This may have been due to the greater food supply available in the year following the seedfall, reducing

the need for males to scavenge road-kills. It is interesting to note however, that in the Deer Flat kill-trapping area (P. Dilks, C. O'Donnell and G. Elliott, *unpubl. data*) male stoats were not caught significantly more often along the road in Y2. This may have been because most stoats were caught there between October and December that year, when males would have been searching for mates; our radio-tracking data are for males from January to May (after the breeding season), when finding food may have been more important than finding females.

In Y1, open terrain within home ranges was also utilised in relation to its availability, whereas in Y2 this habitat was avoided by both males and females (Murphy and Dowding, 1994). This may also have been partly a reflection of food availability – parakeets and introduced finches (which often feed in open grassed areas) increase in abundance in the year following a seedfall (Wardle, 1984; Clout and Gaze, 1984; G. Elliott, *unpubl. data*) and we also caught mice in stoat live-traps in grassed areas (E.C. Murphy and J.E. Dowding, *unpubl. data*).

Diet

In Y1, mice were abundant in the Eglinton Valley (C. O'Donnell, P. Dilks and G. Elliott, *unpubl. data*) and were a major prey item for stoats, whereas in Y2 mice were at very low densities and were not detected in the diet of stoats (Murphy and Dowding, 1994). These results agree with the findings of King (1983). In our study, stoats appeared to respond functionally to a decrease in mice by switching to lagomorphs. In Fiordland, King (1983) found no difference in the frequency of larger mammals (possums, lagomorphs and rats pooled) eaten in Y1 years compared with other (non-seedfall) years, but did not consider lagomorphs by themselves. However, in *Nothofagus* forest at Craigieburn Forest Park (King, 1983) the number of lagomorphs eaten did not vary significantly with mouse density.

Native and introduced birds were a major prey of stoats in all three years. Stoats did not eat birds less frequently when mice were abundant, a result also found by King (1983). Passerines were the most frequently eaten order of birds and this probably reflects their availability – eight of the 10 most common forest birds recorded in the Eglinton Valley by Efford and Morrison (1991) were passerines. Yellow-crowned parakeets were the second most common bird recorded by Efford and Morrison (1991); in our study they occurred in at least 3.7% of stoat guts examined in Y1 but were not detected in Y2 or Y3. In overseas studies where bird remains have been sorted by order, passerines were also the most frequently occurring bird prey of stoats in

Ireland (Sleeman, 1992), but Galliformes occurred more frequently in the diet of stoats from Britain (Day, 1968; Pounds, 1981).

Comparisons of male and female diets in different studies have shown little consistency. There were no significant differences in male and female diet in Britain and Canada (Day, 1968; Simms, 1979), but in Switzerland males ate more birds (Debrot, 1981). We found no significant differences except for the occurrence of possum in the male diet. Comparison of stoat diets in different forest types throughout New Zealand supports our observation that male stoats ate more possums (King and Moody, 1982); however, King and Moody (1982) also found that female stoats ate significantly more mice than males, which we did not find. Male stoats in a coastal scrub area in New Zealand ate significantly more lagomorphs than female stoats (Alterio, 1994), as did stoats in Sweden (Erlinge, 1979); this was not the case in King and Moody's (1982) study or in our own. The wide range of prey and the variety of sexual dietary differences recorded in different parts of the world tend to support the suggestion that stoats are flexible and opportunistic in their diet, although males appear to eat more carrion than females (Murphy and Dowding, 1994).

Male stoats have been identified as eating significantly more 'larger mammals' than females, but this category contained possums, lagomorphs, rats (*Rattus* spp.), hedgehogs (*Erinaceus europaeus* Barrett-Hamilton), carrion and unidentified mammals combined (King and Moody, 1982). We suggest that this pooling of items obscured the fact that both sexes mostly kill and eat the same sized prey, but that males eat more carrion. In the King and Moody (1982) study, rats and lagomorphs occurred equally often in guts of both sexes, and hedgehogs and identifiable carrion were relatively unimportant items. The only items eaten significantly more often by male stoats were possum and unidentified mammal, which the authors suggest probably included much possum carrion. In fact, it is likely that most possum eaten by stoats is carrion (King and Moody, 1982; Murphy and Dowding, 1994).

A significant seasonal difference in the frequency of occurrence of birds and mice in the diet was identified by King and Moody (1982), with more mice and fewer birds eaten in autumn than in summer. We found no such seasonal differences but our sample sizes were relatively small.

The beech mast cycle and stoat productivity

At high latitudes in northern Europe, rodent numbers fluctuate greatly and there is a close relationship

between stoat density and the abundance of small rodents, their main prey (Aspimov and Popov, 1940; Vershinin, 1972; Erlinge, 1983). When rodents are scarce, stoats exploit a wide spectrum of prey, particularly birds and their eggs (Myrberget, 1972; Järvinen, 1985; Korpimäki, Norrdahl and Rinta-Jaskari, 1991), but remain at low density because these alternative prey are scarce (Henttonen *et al.*, 1987). When rodents become abundant, stoats exploit them intensively, excluding other foods (Nasimovich, 1949; Debrot, 1981; Erlinge, 1981). In contrast to the situation in the far north, alternative food is available in southern Sweden, and stoat densities can remain relatively high even when vole populations decline sharply (Korpimäki *et al.*, 1991).

When they are available, small rodents are the commonest prey item of stoats in many parts of Europe and North America (see King, 1989), a fact which may have contributed to the suggestion of a relationship between stoats and mice in *Nothofagus* forests in New Zealand (Riney *et al.*, 1959). Mouse density can rise dramatically in these forests following a seedfall, and there is a relationship between mouse and stoat densities (King, 1983). It has been generally assumed that mice feed on the abundant seed available and that stoats in turn increase because of the large numbers of mice available to them, but there is little actual evidence that the relationships are causal (King, 1983; Efford, Karl and Moller, 1988).

A number of lines of evidence suggest that the situation is more complex. First, the density of mice may be affected by factors other than a beech seedfall (Murphy, 1992); in the Orongorongo Valley, invertebrates increased following a seedfall and there was a stronger correlation between densities of the moth *Tingena epimyliella* Meyrick and mice than between seedfall and mouse density (B.M. Fitzgerald, *pers. comm.*). Second, in contrast to the situation in high northern latitudes, stoats in *Nothofagus* forest do not appear to be largely dependent on mice, either in the year following a seedfall or in subsequent years. In these forests, the number of birds eaten per stoat varies little with mouse abundance (King, 1983; this study). The fact that mice are not the only prey of stoats to increase following a seedfall is often overlooked. Introduced finches flock to *Nothofagus* forest when trees are seeding heavily (Wardle, 1984; Clout and Gaze, 1984) and yellow-crowned parakeets breed throughout winter and spring after a seedfall and their numbers increase dramatically (Rutland, 1890; G. Elliott, *unpubl. data*). Kaka (*Nestor meridionalis*) are also known to breed much more successfully in a mast year (P. Wilson, *pers. comm.*). It may be, therefore, that increases in mouse, bird and

invertebrate densities contribute to the high productivity of stoats in the year following a seedfall. This relationship between stoats and their prey in the year following a seedfall in *Nothofagus* forest is summarised in Figure 3. It should be noted that stoats are also eating lagomorphs at this time, but we know of no evidence that lagomorph density is influenced by beech seedfall.

Although stoat numbers decline following the post-seedfall peak in Y1, breeding does occur in some years before the next seedfall (King, 1983; this study); no juveniles were caught in Y2 but 7 (50%) of 14 stoats Fenn-trapped in Y3 were juveniles (Table 1). King (1989) found that although productivity fluctuated, there was a "relatively steady number of breeding adults every season". Because of the lack of a standard technique for estimating stoat density, comparisons between studies are difficult. However, Table 1 shows that almost five times more adults were caught in Y2 than in Y1; King (1990) stated that "newly-independent young ... quickly disappear over the winter" but our data suggest that high survival of the juveniles produced in Y1 over the following winter is possible.

There appears to be a general perception that only in the year following a heavy seedfall are stoats sufficiently numerous to cause significant declines in vulnerable bird species, such as the yellowhead (*Mohoua ochrocephala*). King (1990) stated that "by the following spring [after a year of high stoat density] the normal low density is restored". King (1989) noted that stoat density "declines quickly after each peak and remains low in the meantime". In our

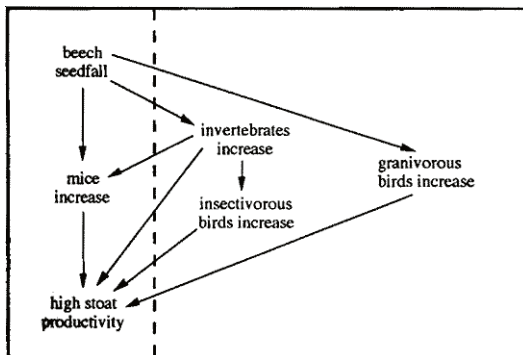


Figure 3: Impact of a *Nothofagus* mast year on stoat productivity. To the left of the dashed line is shown the sequence of events proposed by Riney et al. (1959) and generally supported by King (1983; 1989); to the right of the line are the additional elements that we believe are also important.

study, undertaken after a full mast year (Wardle, 1984), the decline between Y1 and Y2 was approximately 30-50% and by Y3 numbers had fallen to about 25% of the Y1 level. There is relatively little information on the damage that stoats can do at intermediate or lower densities, but the possibility that they can continue to have a serious impact on threatened species in *Nothofagus* forest at these levels, two (and even three) years after a full mast year, should not be discounted when conservation management operations are being planned.

In addition, stoats may pose a threat without heavy beech seedfall. Mouse and stoat numbers can rise after poor mast years (Fitzgerald, 1978; King, 1983), so assessing potential impacts on threatened species may require a better predictor than heavy beech seeding alone.

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