POPULATION STRUCTURE AND DISPERSAL OF PEAK-YEAR COHORTS OF STOATS (*MUSTELA ERMINEA*) IN TWO NEW ZEALAND FORESTS, WITH ESPECIAL REFERENCE TO CONTROL

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SUMMARY: During a peak summer for stoats in 1979/80 (density indices in two study areas 8.2 and 10.7 new captures per 100 trapnights) a total of 134 stoats were caught, marked and released (86% young of the year, 58% males). Fifty-seven of 110 stoats were recaptured at least once, of which 42 moved 0.4 - 1.6 km between first and second captures. Frequency distributions of numbers of captures and first recapture-distances up to 1.6 km were similar in males and females, adults and young, but Leslie's test showed significant ($P<0.05$) inequality of catchability of 21 stoats known to be present over seven trapping rounds. Dispersal movements recorded by young males exceeded 20 km. Nine males and five females, from a possible 107 animals, were recovered up to 18 months after the end of livetrapping. Significantly more marked adult males (45%) than young males (9%) were recovered. Two important implications of these data for conservation are (a) kill-trapping over large areas at considerable effort (400 m trap spacing) may only hasten an inevitable post-peak decline in stoat density, because the chances of capture are low and not the same for all stoats; and (b) those killed may be replaced by immigrants from over 20 km away.

INTRODUCTION

Stoats (*Mustela erminea*), active predators of small mammals and birds, are native to the Holarctic. They were introduced to New Zealand farmlands in the 1880s, to control rabbits, but subsequently colonised all types of forest. Their presence in National Parks, which are among the most extensive reserves for New Zealand's diminishing native fauna, causes concern. In Fiordland National Park, birds comprised half the food items identified in 383 stoats by King & Moody (1982), and a sudden decline in numbers of the endangered takahe (*Notornis mantelli*) in 1976/77 coincided with a temporary increase in numbers of stoats (Mills, 1978). However, formulation of effective stoat control policies has always been hampered by ignorance of the natural population dynamics of stoats in New Zealand forests, and the extent to which control operations affect them, if at all.

Populations of stoats were studied in Eglinton and Hollyford Valleys, Fiordland National Park, in 1972/78 and 1975/78 respectively (Fig. 1). These studies (King, 1980, 1981) recorded substantial variations in the numbers of stoats killed per 100 trapnights along standardised lines in summer, and found that these were related to population fluctuations of mice, (*Mus musculus*). A heavy fall of beech (*Nothofagus* sp.) seed in autumn (March to May inclusive) of 1976 was followed by increases in the numbers of mice, and also of stoats, during summer (December to February) of 1976/77.

Autumn, 1979 produced another heavy fall of beech seed. The present study was then planned, with the main objectives being (i) to establish a marked population of young stoats in the wild, which could be retrieved later to serve as known-aged standards for age-determination studies, (ii) to confirm the changes in density and population structure of stoats which had followed the 1976 seedfall, and (iii) to observe if possible the dispersal of a peak-year cohort of young stoats.

METHODS

The study areas were two, steep-sided, forested valleys on opposite sides of the Southern Alps, South Island, New Zealand, connected by a pass at 530 m (below treeline), as described by King (1980, 1981). "Edgar" live traps and Fenn kill traps were used for live capture and for retrieval respectively (King and Edgar, 1977), set as transects along the roadside in each valley. Trap-sites average 400 ± 10 m apart

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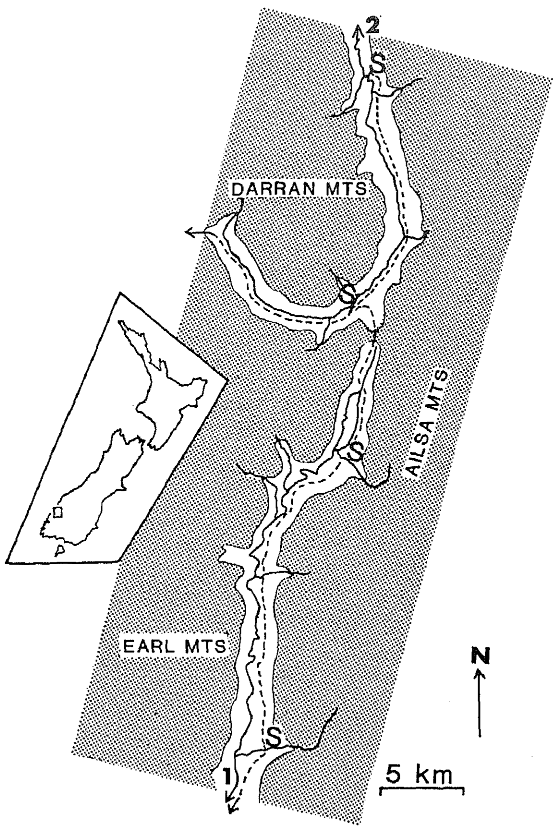

FIGURE 1. *The study areas and their position (45° S, 168° E) in New Zealand. The dotted line is the road; S - S, positions of stoat traplines; 1, Eglinton River; 2, Hollyford River.*

and the same sites were used for live-traps in summer and for kill-traps later. Previous experimental work in the same areas (King, 1980) had suggested 400 m as an optimum spacing in these habitats, allowing the maximum number of stoats to be caught per kilometre of trapline (greatest at closer spacings) for the minimum effort (time, wages etc., least at more distant spacings). Both traplines ran roughly north-south, and the last trap of the Eglinton line was 9.6 km south of the first trap of the Hollyford line.

Livetrapping was conducted between 20 November 1979 and 1 February 1980, for a total of nine weeks (35 trap rounds). Live traps were usually set on Mondays, checked once daily for four days, and closed on Fridays. Kill traps were set for one week each in April and May 1980, then irregularly from October 1980 to March 1981, being checked whenever possible, usually weekly. To assist recovery of marked animals, especially from outside the study areas, a reward of $NZ10 for the return of tagged stoats was advertised locally by posters, and by an article in the region's newspaper on 27 November 1980.

Trapping success was low from 20 November to 14 December, so additional live traps were set (see Fig. 2). These could not be maintained after the sudden increase in capture rate in early January, so after 15 January, only 35 traps were set in each valley.

On each line, the 14 km along which traps were set throughout the study is referred to as the Central Study Area. Analyses of recapture frequency and

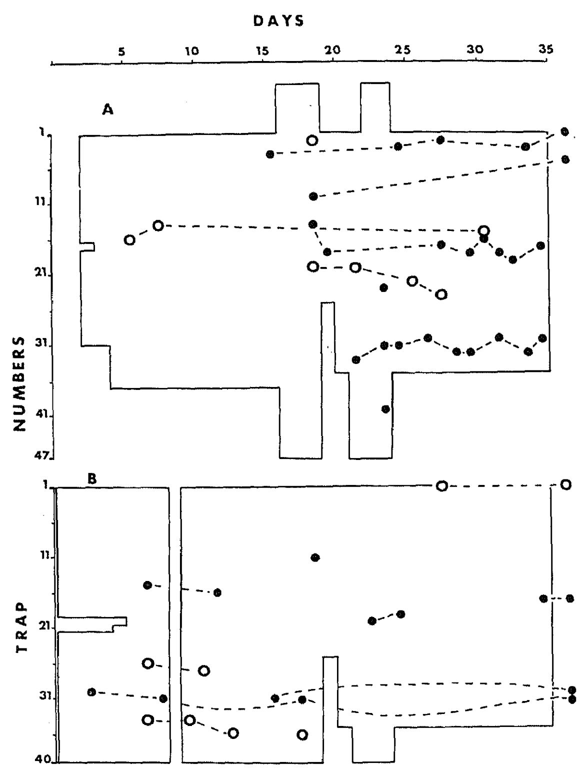

FIGURE 2. *Frequency distribution of capture records of adult stoats along the Eglinton (A) and Hollyford (B) traplines (open circles, females; dots, males). Solid outline encloses space/time co-ordinates of all possible live-capture records from 20 November 1979 (day 1) to 1 February 1980 (day 35). Capture records after day 35 refer to later recoveries in Fenn traps. Distance between traps, 400 m.*

TABLE 1. *Capture rates and proportion of unmarked stoats caught (alive or dead) per week in livetraps in Eglinton and Hollyford Valleys betwen 20 November 1979 and 1 February 1980.*

	EGLINTON					HOLLYFORD					TOTAL	
Date	TN (1)	Tagged	Not Tagged	C/100 TN(2) new	total	TN	Tagged	Not Tagged	C/100 TN new	total	captured & recaptured	% not tagged
Nov. 20-23	59	0	0	0	0	147	0	1	0.7	0.7	1	100
27-30	144	1	1	0.7	1.4	151	1	4	2.6	3.3	7	71
Dec. 4- 7	146	1	1	0.7	1.4	115	3	0	0	2.6	5	20
11-14	142	1	6	4.2	4.9	158	1	3	1.9	2.5	11	82
Jan. 1- 4	166	6	30	18.1	21.7	125	10	29	23.2	31.2	75	79
8-11	175	14	16	9.7	17.1	136	25	14	10.3	28.7	69	43
15-17	96	15	4	4.2	19.8	94	18	6	6.4	25.5	43	25
22-25	127	21	5	3.9	20.5	126	12	13	10.3	19.8	51	35
29-Feb. 1	128	22	2	1.6	18.8	127	13	3	2.4	12.6	40	13
Total	1183		65	5.5		1179		73	6,2		302	
Total January	692		57	8.2		608		65	10.7 (3)			

(1) Total number of trapnights per session corrected for unavailable (sprung) traps. (Nelson and Clark, 1973).

(2) Captures per 100 trapnights.

(3) Including 4 found dead, not tagged.

movements were confined to the 110 stoats known only from the two Central Study Areas. Stoats known to move beyond them may not have had equal opportunity of capture after 15 January. Only distances between first and second captures are used because mean or maximum recapture distances are influenced by the number of captures recorded per stoat.

Capture rate in both kinds of traps is expressed as captures per 100 trapnights (C/100TN), correcting for unavailable traps as recommended by Nelson and Clark (1973).

Live stoats were anaesthetised and marked with metal eartags (King and Edgar, 1977). Ages of live stoats were determined mainly from their genitalia: over 99% of adult males have enlarged testes in summer, but young-of-the-year do not (King and Moody, 1982); adult females have visible nipples, small if they have not borne young, large and obvious if they have, while the nipples of female young-of-the-year are invisible. Non-breeding adult females were unlikely to have been scored as young, since four captive adult females kept in isolation developed small, visible nipples in spring (King, unpubl.) and the probability is high that all wild adults produce young in a peak year (King, 1981). Wear of the canine teeth, and body weight were also noted. Teeth from 14 stoats marked during this study showed full agreement between ages designated in the field and from canine cementum layers.

RESULTS

Capture rate

The overall capture rate of new individuals in January 1980 was 8.2 and 10.7 C/100TN in Eglinton and Hollyford Valleys respectively (Table 1). Similar figures (9.0 and 7.6 C/100TN) were recorded from kill-trapping during the previous peak in January 1977, while in January 1975, 1976 and 1978, the capture rates in the two valleys ranged from 0.8 to 2.2 C/100TN (King, 1980). In this study, results from the two lines generally supported each other and although there were some differences between them (Figs. 2, 3), the data are combined to increase sample sizes.

Population structure

Altogether, 134 stoats were caught and tagged, of which 86% were young-of-the-year (2-5 months old) and 58% were males. In Hollyford Valley, a further four untagged stoats (2 male, 2 female, all young) were found dead in the traps, and one (not counted) escaped alive before marking. Total numbers caught, and the age and sex ratios, were similar in the two valleys (Table 2).

Only 16 stoats (eight adults) were caught in 16 trapping days between 20 November and 14 December. The first young-of-the-year, a male, was caught on 6 December. After two weeks' break (15-31 December) trapping resumed on 1 January, and in 19 trapping days to 1 February, 118 new individuals

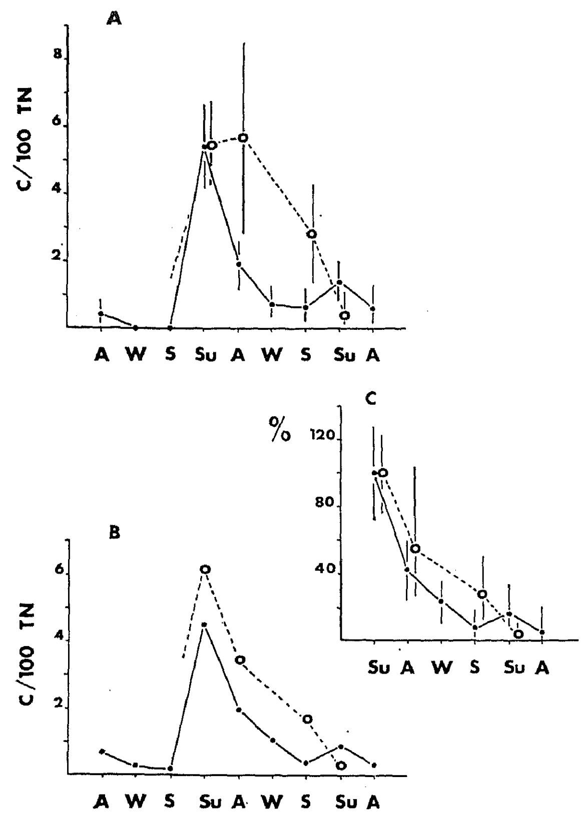

FIGURE 3. *Number of stoats caught per 100 trapnights (C/100TN) during two peak population years in Eglinton (A) and Hollyford (B) Valleys. In 1976/77 (solid line), Fenn traps were used throughout and captured individuals removed at once. In 1979/80 (dotted line) live traps were used in summer, Fenns thereafter. A, Autumn; W, Winter; S, Spring; Su, Summer. Vertical lines through each point are 95% confidence intervals. In the Hollyford valley the two peak summer density indices were different, and the samples not directly comparable. To allow direct comparison, the declining density indices (± 95% confidence intervals) for each year are standardised as percentages of the summer (peak) index for that year (C).*

were marked: 11 adults, 105 young-of-the-year, and two unclassified.

The composition of the live-trapped sample may be compared with that of one comparable high-density and three contrasting low-density summer populations, all from the same study areas. In the distribution of ages and sexes, the samples from peak populations in the summers of 1979/80 and 1976/77 were similar, despite the difference in trapping methods used (Tables 3, 4). Both had significantly more young stoats than in the low-density years, but the same sex ratio (data for both valleys combined). There was no sign of improved body condition (eg. a consistent rise in body weight) associated with increased food supplies in high-density years, in either young or adults.

Recaptures

Of the 134 stoats marked, 56 were never recaptured, and one died during tagging. The remaining 77 were all recaptured at least once, 69 before the end of summer (28 February) and eight later. Total captures and recaptures (live or dead) up to 1 February 1980 were 302 (Table 1).

There were no differences in the frequency distributions of recaptures of males and females, or adults and young that could be measured by Kolmogorov-Smirnov 2-sample tests, although the individuals recaptured most frequently were all males (Table 5).

The percentage of stoats caught each week that were unmarked dropped from 100% to 20% by early December, rose to 79-82% in late December and early January as large numbers of young began to enter the traps, and then dropped to 13% in late January (Table 1). Over the same period, the number of new captures per 100 trapnights rose to a peak in early January, then declined by c. 90% by the end of the month. We continued to release newly marked stoats in every week of livetrapping, but the number available to be caught was apparently declining: the proportion of the trappable population of stoats that was marked eventually exceeded 80%.

All capture-mark-recapture methods suitable for the analysis of these data, (eg. White, 1971), assume equal catchability of all individuals, a stringent condition that can be checked by Leslie's test (Caughley, 1977). On the two Central Study Areas, there were a total of 21 stoats, marked on or before

TABLE 2. *The age and sex of 134 stoats caught in Eglinton and Hollyford Valleys between 20 November 1979 and 1 February 1980.*

	MALES		FEMALES		TOTAL	
	Adult	Young	Adult	Young	Age/sex Unknown	
Eglinton	6	30	3	25	1	65
Hollyford	6	35	4	23	1	69
TOTAL	12	65	7	48	2	134

TABLE 3. *Ages of male and female stoats caught in summer in Eglinton and Hollyford Valleys.*

	Adults	Young	χ^2 and P[1]
MALES			
High density 1976/77	7	69	16.31, P < .001
Low density seasons pooled	16	23	
High density 1979/80	12	65	9.15, P < .02
FEMALES			
High density 1976/77	5	39	4.57, P < .05
Low density seasons pooled	17	42	
High density 1979/80	7	48	4.43, P < .05

(1) Difference between high and low density years. The differences between the two high density years were insignificant in both sexes.

TABLE 4. *Sex ratios of young and adult stoats caught in summer, in Eglinton and Hollyford Valleys.*

	Males	Females	χ^2[1]
ADULTS			
High density 1976/77	7	5	0.05
Low density seasons pooled (2)	14	11	0.29
High density 1979/80	12	7	
YOUNG			
High density 1976/77	69	39	2.91
Low density seasons pooled (2)	14	16	0.97
High density 1979/80	65	48	

(1) Difference between high and low density years P > 0.05 in all cases. The differences between the two high density years were insignificant in both age groups.
(2) Using data from stoats caught in traps set at 400 m intervals (King, 1980).

15 January, known to be still present nearby on, or after, 25 January. Between these dates, each stoat could have been recaptured a maximum of seven times (Table 6). If all 21 were equally catchable, their recapture frequencies should form a binomial distribution, which can be tested as a chi-square with (Σf)−1 degrees of freedom (Caughley, 1977). From Table 6, χ^2 = 37.4, 20df, 0.05 > P > 0.01. Nine of the 21 were not recaptured at all during this period, compared with an expected frequency of 5.6 in the zero recapture class (Orians and Leslie, 1958). Hence, the variability in the frequency of recapture of these 21 individuals was significantly greater than that expected if they had been sampled at random. This inequality in catchability may be between individuals, or between classes of stoats (age or sex groups) differing in their mean catchability. Both are likely, but cannot be tested from these data.

Movements and dispersal

Of 110 stoats on the two Central Study Areas, potentially exposed to live-traps throughout, 57 were recaptured at least once. A frequency distribution of the distance each moved between first and second captures (Table 7), shows that 13 were caught for the second time in the same trap, 42 had moved 0.4 km - 1.6 km, one had moved 3.6 km, and one 6 km. There was no difference between males and females, young or adults, in the frequency of distri-

TABLE 5. *Frequency of capture of 110 stoats caught only within the central study areas in Eglinton and Hollyford Valleys, between 20 November 1979 and 1 February 1980.*

	Number of captures (alive or dead)										
	1	2	3	4	5	6	7	8	9	10	Total
ADULTS											
Males	5	2	1	1				1	1		11
Females	2	1	1	1							5
YOUNG											
Males	26	10	7	2		5	1	1	1	1	54
Females	20	10	9	1							40
TOTALS	53	23	18	5	0	5	1	2	2	1	110

TABLE 6. *Leslie's test for equal catchability of 21 stoats known to be present on the central study areas in Eglinton and Hollyford Valleys between 15 and 25 January 1980.*

Number (n_i) of the total (N = 21) caught each day		Frequency distribution of recaptures	
	n_i	i	f
January 15	7		
16	1	0	9
17	3	1	5
22	3	2	2
23	3	3	4
24	4	4	1
25	4		
	Σn = 25		Σf = 21

χ^2 = 37.35. 20 d.f., 0.05 > P > 0.01. For method, see Caughley (1977).

TABLE 7. *Distances between first and second captures of 57 stoats confined to the two central study areas within Eglinton and Hollyford Valleys and caught at least twice between 20 November 1979 and 1 February 1980.*

	Distance between first two captures (km)						
	Same trap	0.4	0.8	1.2	1.6	2.0+	Total
ADULTS							
Males	0	4	1		1		6
Females	1	1	1				3
YOUNG							
Males	7	10	3	2	4	2	28
Females	5	5	4	5	1		20
TOTALS	13	20	9	7	6	2	57

bution of first recapture-distances up to 1.6 km, in any combination of separate Kolmogorov-Smirnov 2-sample tests. In a previous study in the same areas, King (1980) found no significant difference in the number of males and females caught in traps set up to 0.8 km apart.

All capture records of adults were mapped in two dimensions (Fig. 2). Adults were few and generally well spaced out, though some moved into boundary areas where separation may have been in time rather than in space. Three of the four recorded only once lived near the edges of the study areas, or were not exposed to traps throughout the study. Young were much more numerous, and their capture records showed a confused pattern with broad overlaps and occasional long movements. The breakup of family groups may have occurred in the last two weeks of December when no traps were set; before 14 December, very few young were caught, but by 1 January they were very numerous and already well scattered.

Long movements were more often recorded for males than for females. One young Hollyford female travelled 5.6 km northward between first and second captures, was caught twice in this trap and then returned 3.2 km south to the fourth and last capture site. Seven males, all young-of-the-year, travelled much longer distances. In Hollyford Valley, one moved 6 km, one 8 km and two 15 km. The second of these was caught three times in two adjacent traps (0.4 km apart) at the south end of the trapline, then reappeared, three weeks later, 6.8 km northwards in three traps, spanning 1.2 km, on consecutive days. The two that moved 15 km were first caught at the south end of the line, one twice in the same trap, and the other, four times in three traps less than 1.2 km apart. Both then traversed the entire length of the line and were caught by Park staff beyond the end of the trapline. The journey took one under four weeks, and the other, under two weeks.

Three young males marked in Eglinton Valley were later recaptured in Hollyford valley. All three cases were confirmed because two were re-trapped at least twice each in Hollyford Valley and the third was killed and the tags retrieved. The minimum distances travelled were 12.1 km in 27 days (plus a further 2.8 km the next day), 20.0 km in five days (plus a further 4.4 km in the next two days) and 23.3 km in 39 days.

Of 14 stoats (9 m, 5 f) recovered from 10 weeks to 18 months after the end of livetrapping, eight had never been seen since marking. All were recovered within 3.2 km of the last recorded capture site; eight were at or within, 0.4 km of, the same trapsites they visited in the summer. Six were adults when first marked, eight were young. No recoveries were reported from further afield, although the reward for the return of tags was well-known locally.

Retrieval trapping

By the end of February, 27 of the 134 stoats originally marked were known to have died (12 found dead in live-traps; 7 died under anaesthetic; 6 killed by Park staff outside the study areas; 2 found dead on the road). Hence there were, at most, 107 stoats available for recovery later in the year.

In autumn, 1980, and in spring and summer, 1980/81, kill-traps were set to recover marked stoats. Of 54 collected, 11 had been tagged. Three additional tagged stoats were handed in for reward; one was picked up dead on the Hollyford road, and two were caught in traps set casually by Park staff working in Eglinton Valley. Of the 107 marked stoats possibly available, 14 (13%) were recovered; 5 of 11 adult males, 1 of 7 adult females, 4 of 47 young males, 4 of 40 young females, and neither of the two unknowns. A much greater proportion of adult than of young males (45% to 9%) was recovered (χ^2 = 9.3, ldf., 0.0- > P > 0.001). The difference between recoveries of adult and young females (14% to 10%) was not significant (P > 0.1). Adult males were recovered more often than females of all ages (P < 0.01) but young males and females were recovered at the same rate.

In the last two days of live-trapping, 13 male and 2 female stoats were caught, of which 12 and 1 respectively were already marked. Subsequently, the proportion of marked stoats declined: in April-May 1980, 5 of 17 males and 2 of 7 females were marked; in October-November 1980, 2 of 18 males and 1 of 4 females were marked; in December-March 1980-81, four males (none marked), two females (one marked) and one unmarked, unclassifiable carcase were recovered.

In the previous peak summer, 1976/77, 122 stoats were killed in Fenn traps in the two valleys. In 1979/80, 138 stoats were caught, of which most were released alive. In Eglinton Valley (Fig. 3A), the density indices for the uncontrolled 1979/80 peak population remained considerably higher for longer than those for the controlled population of 1976/77, and slightly higher in Hollyford Valley (Fig. 3B). By summer, 1980/81 the density indices for both uncontrolled populations were extremely low.

DISCUSSION

Comparable studies

The only other live-trapping study of stoats in a New Zealand forest habitat is that of King (unpubl.) who worked in Orongorongo Valley, near Wellington, for a total of 12 months from January 1972 to January 1975. Between January and April 1972, after the heavy beech seedfall of 1971, four stoats were caught in 40 traps set in a circular trapline about 1.4 km long, and a fifth about 2.1 km away (total 30 captures and recaptures). No stoats were caught in the same traps in November and December 1972. From August 1974 to January 1975, 51 traps were set in a 5.5 km line, but only three stoats wer caught, once each. These results are consistent with our experience in Fiordland, that trapping may be very successful for a few months in summer and autumn after a seedfall, but thereafter swiftly becomes unproductive.

In the Northern Hemisphere, there have been three studies, all in habitats modified to various degrees by Man. In Switzerland, Debrot (1981) described a population of stoats in the Brévine Valley (1875 ha) which decreased from 50 in summer, 1977 to three in summer, 1979, coinciding with drastic decrease in its main prey, the watervole (*Arvicola terrestris*). By contrast, Erlinge (1977) and Simms (1979) described Swedish and Canadian study areas where conditions were more stable, and the population density of stoats varied less from year to year than did ours. However, Erlinge also reported a high rate of disappearance of marked individuals, especially of young, and movements between recaptures of up to 6 km.

The only other common mustelids in New Zealand are ferrets (*Mustela putorius furo*), whose movements, recapture frequencies and home ranges on a North Island marsh are described by Moors and Lavers (1981).

Recovery of marked young

The primary objective of this study was to retrieve marked stoats of known age from the wild. The recapture, from March 1980 to August 1981, of only 14 of a possible 107 was disappointing, especially as only eight of these were known to have been young-of-the-year when first marked. However, in the attempt, we also gathered field data which offer an explanation for this result.

Most of the stoats marked and released (86% of 134) were young of the year, whereas only 57% of the 14 recovered were young. Long distance movements were recorded only by young stoats, especially young males, and significantly more adult than young males were recaptured later in the same area where they had been marked. This pattern is consistent with the expectation that established adult males should be less inclined to emigrate, and/or should survive longer, than young males, and that established males probably deter young ones from settling (Erlinge, 1977; Simms, 1979).

Young males began to disperse almost as soon as they were independent. They first appeared in the traps only in December, but by the end of January, some had recorded very long movements. We infer continued dispersal after the end of livetrapping from the rapid decline, between February and May, in the proportion of marked males killed in Fenn traps. If the mortality of marked and unmarked males was similar, this implies continued movement by males, both to and from the study areas, resulting in the exchange of marked for unmarked males observed. Young females tend to settle near their natal ranges (Erlinge, 1977), perhaps because they need less space and/or because it is in the interests of the local adult male not to drive them out.

These data are unsuitable for cohort life-table analysis because the possible causes of disappearance of the marked young not recovered (death, emigration, trap avoidance) are inseparable. However, since the total number of stoats caught in summer declined, from 6/100TN in 1979/80 to 0.5/100TN in 1980/81, it seems that few of the marked young lived as long as one year. Once established though, individual stoats may live for several years; one marked in Orongorongo Valley must have lived at least three years, and the marked adults recovered during this study included two with three annual lines in their teeth, and one each with four and five annuli.

Implications for Conservation

This study touches on two questions relevant to the problem of control of stoats in National Parks: (a) can sufficient numbers be removed to cause a peak population to decline more quickly than by natural means alone?, and (b) how far do immigrant stoats travel to replace those removed?

In the present study, with traps set about 400 m apart, the probability of capturing a stoat was low. Over a period of ten days in mid-January, 9 of 21 marked stoats known to be present were not recaptured during a total of 490 trap-nights. Hence, kill-trapping at this intensity would not eliminate even the trappable portion of the population, itself an unknown proportion of the total. However, if carried on for long enough, kill-trapping may be able to hasten the natural disappearance of at least some peak populations. If each marked stoat is viewed as having been killed, then persistent Fenn trapping might remove about half the available trappable animals (not the 80% that were eventually live-trapped, since removal of residents encourages immigrants to settle). A similar suggestion was made previously from kill-trapping alone (King, 1980). This implies that at least as many stoats were removed from the 1976/77 populations by natural causes as were caught in traps.

Data in Figure 3 suggests that control may have brought forward the post-peak decline in stoats in Eglinton Valley. However, by the following summer, density indices in both study areas were very low, and such a reduction, after trapping in summer, is not proof of effective control.

Traps set closer than 400 m apart catch more stoats per kilometre of trap-line (King, 1980), and presumbly remove a higher proportion of the population. In theory, then, a greater effect might be had by placing traps at 100 m spacings instead of 400 m. However, closer-spaced traps take much more time per kilometre to operate, and are economic only in small or especially valuable areas (e.g. near nesting sites of endangered birds), where it is still worthwhile to trap intensively even though the number of stoats caught is small in relation to the effort expended. For a sustained, widespread trapping effort, e.g. for long-term population monitoring, 400 m is about the closest practicable.

Immigration into the trapped out area must be regarded as inevitable, and in summer, may quickly neutralise the effect of a trapping campaign. However, immigrants may arrive at any season (King, 1980) and may come from more than 20 km away.

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