

## Field experiments on the trapping of stoats (*Mustela erminea*)

C. M. KING

Ecology Division, Department of Scientific and Industrial Research,  
Private Bag, Lower Hutt, New Zealand

Steel Fenn traps spaced at 100 m, 200 m, 400 m, and 800 m intervals (total 88 traps) were set in the Eglinton and Hollyford valleys, Fiordland, New Zealand, for 14 days a month from November 1974 to March 1976. A total of 173 stoats were caught, mostly in the two summers. The number of stoats caught and the proportion of females did not change with trap spacing, but both were higher than in an earlier, informal trapping campaign in the same area (20 traps at 2.1 km average interval; 124 stoats caught). The capture rate on the experimental lines declined from 1.07 stoats per 100 trap-nights at the beginning of the average 14-day session to 0.42 at the end, a reduction of 60%. Immigration between trapping sessions probably occurred in all months, but was most marked in summer. The usefulness of the data for the formulation of management policies concerning stoats in the National Parks of New Zealand will be discussed, along with other relevant information, elsewhere.

**Keywords:** *Mustela erminea*; trapping; trap spacing; sex ratio; population trends; Fiordland.

### INTRODUCTION

The aim of this study was to define the most effective way to operate traps to kill stoats in the National Parks of New Zealand. Consideration of techniques for control is a part—though not the first or most important part—of the process of formulating a policy for the management of these introduced predators in fauna reserves. Some of the results, describing the general techniques of setting traps and experiments on the use of bait, have already been published (King & Edgar 1977). The present and previous results together could be of interest to workers in other fields, such as the practice of population sampling or the conservation of game birds in Europe.

The spacing of the traps may affect the proportion of the total stoat population caught, probably differentially for the sexes, and hence it is important to consider this when laying out traps, whether for control or for sampling a population. This analysis, therefore, examines the effect of trap spacing on the number of stoats caught, and their sex ratio.

### METHODS AND STUDY AREAS

Humane steel 'Fenn' traps were set in tunnels and baited with a strong-smelling fish-based cat food, as described by King & Edgar (1977). The study areas were two large glaciated valleys in Fiordland National Park, on opposite sides of the Main Divide of the Southern Alps. The Eglinton Valley, on the east side, rises gently from 300 m to the Divide at 550 m, and has a moderate annual rainfall (2300 mm at 360 m a.s.l.); the vegetation in the area of the

trapline is mainly mature forest of southern beech (*Nothofagus* spp.) with intermittent wide, grassy flats along the river. The lower part of the Hollyford Valley, on the west side, falls from 344 m at Marian Camp to sea level, has a heavy annual rainfall (4250 mm at Marian Camp), and contains a richer mixed forest of beech and podocarps, with few grassy flats. (Rainfall data: N.Z. Meteorological Service 1973.)

In late October 1974 I set up the first experimental line of 48 traps along 18 km of the middle part of the Eglinton Valley, in 4 sections with 12 traps each at 100 m, 200 m, 400 m, and 800 m intervals (occupying 1.2 km, 2.4 km, 4.8 km, and 9.6 km respectively). The traps were set and inspected daily for 14 days per month by field staff of the Fiordland National Park Board. Detailed field data sheets were returned each month, recording stoats and other species caught and traps sprung but empty, with dates and trap numbers. Fresh bait was laid whenever necessary. In February 1975 a replicate experimental line was established in the lower Hollyford Valley, with 10 traps at each spacing (i.e., occupying 1, 2, 4, and 8 km) and operated in the same way as the first.

The experiments ended in March 1976, but trapping for other purposes continued in both valleys for a further 2 years, though reduced to 10 days per month (King 1978).

A common measure of the effectiveness of trapping is the number of animals caught per unit of effort. A series of such figures, if carefully standardised, gives a useful (but uncalibrated) index of changes in

population density. It does not indicate the effectiveness of control, since the captures may represent too small a proportion of the number of stoats present or (as is usual in collections of small mustelids: the average for stoats (Corbet & Southern 1977) is 60–65% males) too few of one sex. Measures depending on a change in age-ratios are not useful either, if the target species is short-lived or if all ages are about equally liable to be caught (Caughley 1974). In this paper, experimental results are expressed as numbers of stoats caught per kilometre of trapline and, for changes in capture rate, as numbers caught per 100 trap-nights.

### RESULTS

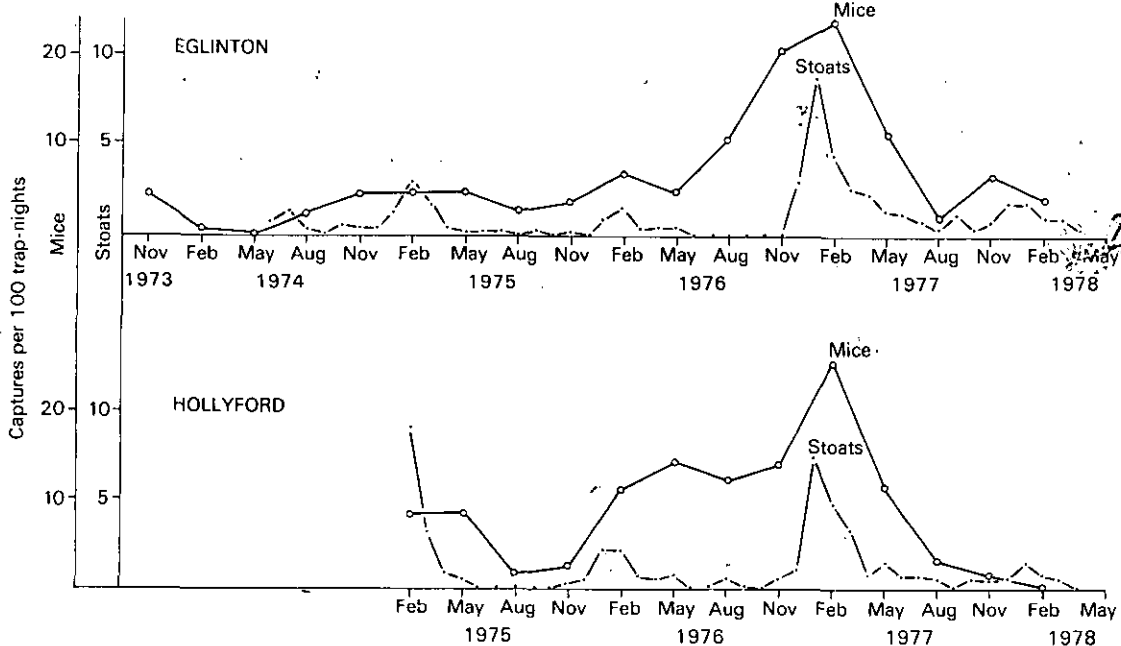
#### TOTAL NUMBER OF STOATS CAUGHT

Table 1 shows the number of stoats caught on the experimental traplines in both valleys. A few stoats were also caught in traps other than those on the experimental lines. In the upper and lower parts of the Eglinton Valley 10 stoats (8 of them males) were trapped between June 1974 and April 1975. In the lower Hollyford Valley in 1975, 15 stoats (8 males) were trapped in various places near to but not in the experimental traps (e.g., at the airstrip, after stoats had been observed feeding on deer offal). The removal of these animals may or may not have affected the results of the experimental lines, in that they were no longer available to be caught.

**Table 1.** Stoat trapping returns, November 1974 to March 1976, Eglinton and lower Hollyford valleys.

	Stoats caught in								Grand total
	Eglinton (48 traps over 18 km)				Hollyford (40 traps over 15 km)				
	♂	♀	?	Total	♂	♀	?	Total	
1974									
Nov	0	2		2					2
Dec	1	1		2					2
1975									
Jan	4	4		8					8
Feb	7	11	1	19	17	31	1	49	68
Mar	7	4		11	5	12		17	28
Apr	1	1		2	3	2		5	7
May	0	1		1	1	2		3	4
Jun	0	1		1	0	0		0	1
Jul	0	1		1	0	0		0	1
Aug	0	0		0	0	0		0	0
Sep	0	1		1	0	0		0	1
Oct	0	0		0	0	0		0	0
Nov	2	0		2	2	0		2	4
Dec	0	0		0	2	1		3	3
1976									
Jan	1	4		5	2	3	7	12	17
Feb	2	5	2	9	3	6	3	12	21
Mar	0	2		2	2	2		4	6
Totals									
All:	25	38	3	66	37	59	11	107	173
Sexed:*	25	38		63	37	59		96	159

\*The sex of 14 stoats was not determined; 2 were eaten, probably by other stoats, while in the trap, and the other 12 were in a box which was lost in transit to the laboratory.



**Fig. 1.** Seasonal and annual changes in the capture rate of stoats in the Eglinton and Hollyford experimental areas, in relation to population changes in mice. Data from King (unpubl.).

## SEASONAL CHANGES IN NUMBER OF STOATS CAUGHT

Most stoats were caught in the summer months (Table 1). This pattern continued each season until trapping ended (Fig. 1), and correlates well with the recruitment of the single annual crop of young into the trappable population. The 6 stoats caught in November and the 5 in December were all adults, but 16 of 18 examined in January and 29 of 34 in February (excluding February 1975, Hollyford; see below) were young of the year. The peak of captures each January or February is therefore probably related to an increased density of stoats available to be trapped as families disperse in summer, perhaps augmented by the inexperience of the young animals.

An exceptionally large number of stoats were caught in the first month's trapping in the Hollyford, in February 1975, compared with February 1976. In the Eglinton, the February catch was only marginally higher in 1975 than in 1976. High densities of stoats may be correlated with local fluctuations in populations of mice (Fig. 1), but mice were not particularly abundant in either valley in February 1975. The simplest explanation is that the February catch in the Hollyford included animals which would have been caught in the preceding November, December, and January if the traps had been set then. This suggestion is supported by the rather large proportion of adults in the first Hollyford sample ( $39 \pm 7\%$ ;  $n = 49$ ) compared with the average in the other three February samples of  $15 \pm 6\%$  ( $n = 34$ ). The average for these three samples over the period November-February inclusive was  $28 \pm 6\%$  ( $n = 63$ ).

## EFFECT OF TRAP SPACING ON NUMBER AND SEX RATIO OF STOATS CAUGHT ON EXPERIMENTAL LINES

Table 2 shows the number of stoats caught at each trap spacing. Kolmogorov-Smirnov two-sample tests showed no significant difference in the relative numbers of male and female stoats caught at the different trap spacings in the two valleys, separately or combined ( $P > 0.1$ ). Neither was there any significant

difference between the two valleys in the total number of stoats caught at each spacing ( $P > 0.1$ ).

## ESTIMATES OF EFFECTIVENESS OF TRAPPING

In each fortnightly period of trapping, the number of stoats caught declined with time elapsed since the first day of setting. This was so both in most months of the year calculated separately and on average (Fig. 2). If all stoats are equally trappable, extrapolation to zero of the regression of captures on time in a given month would give an estimate of the total number of stoats present and the time it would take to catch them all. However, in most months more animals were caught than the downward trend in the previous month's trap returns indicated were still free. Many of these additional animals must be immigrants. Indeed, inspection of Table 1 suggests that more stoats were removed from the traplines each year than could live there together.

A high rate of immigration into a long, narrow sampling area is to be expected, but makes estimation

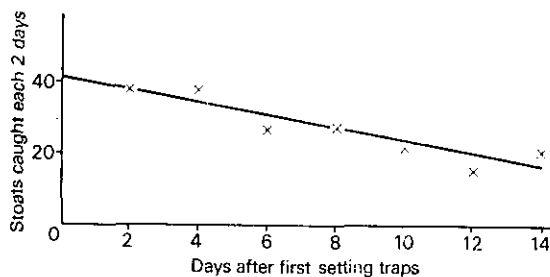


Fig. 2. The average decline in stoat capture rate through a trapping session. The regression slope is significantly different from zero ( $P < 0.01$ ). The number caught in a given 2-day period =  $41.4 - 1.79 \times$  the number of days since first setting. On average, the number of captures is reduced by 60% by day 14, with 95% confidence limits of 43% to 74%.

Table 2. Numbers of traps and of ♂ and ♀ stoats caught at 4 trap spacings on experimental lines, Eglinton and lower Hollyford valleys.

	End traps	At 100 m interval	Border traps	At 200 m interval	Border traps	At 400 m interval	Border traps	At 800 m interval	End traps	Totals	Kolmogorov-Smirnov 2-sample tests
EGLINTON											
Traps	1	10	1	11	1	11	1	11	1	48	} n.s. ( $P > 0.1$ )
♂ ♂	0	2	2	3	0	6	0	12	0	25	
♀ ♀	2	6	0	8	0	8	0	14	0	38	
HOLLYFORD											
Traps	1	8	1	9	1	9	1	9	1	40	} n.s. ( $P > 0.1$ )
♂ ♂	2	2	0	5	1	10	0	15	2	37	
♀ ♀	2	4	0	9	2	12	5	24	1	59	

of the effect of trapping on stoat density very difficult. However, during an average trapping session the number of stoats caught declined from 1.07 per 100 trap-nights by day 2 to 0.42 per 100 trap-nights by day 14, an apparent reduction (each 14 days) averaging 60% of the number originally present (Fig. 2). There was no difference between ages or sexes in this pattern ( $P > 0.5$  in separate  $\chi^2$  tests), nor did it differ between the experimental spacings. However, it does not follow that 60% of the total

population present over a year would be removed by a trapping regime such as this. More than 60% of the population present would disappear if some of the stoats missed in one month were caught the next month, or died from natural causes, but less than 60% if the trapped animals were continuously replaced by immigrants, or if the removal of some animals improved the life-expectancy of the survivors. I suggest that it is not reasonable to expect a single line of traps to remove much more than about half the total number of stoats living in or visiting an area sampled over a given year, unless the area is small and isolated.

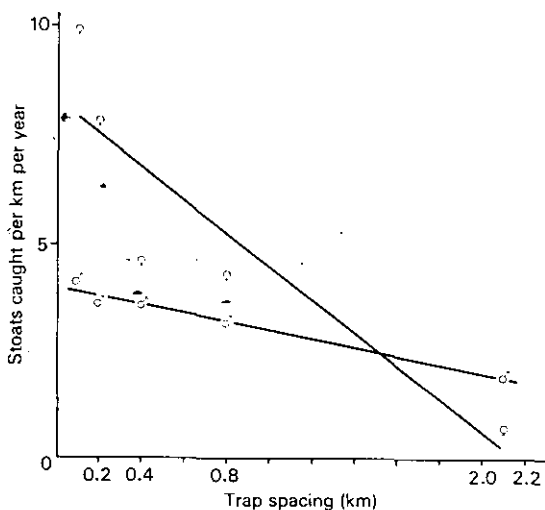


Fig. 3. The effect of trap spacing on the number and sex ratio of stoats caught per km per year, calculated omitting end and border traps but including Mr Slater's material (Table 3). The lines are fitted least-squares regressions. The line for ♀♀ appears ill-fitting, but on present data a curve cannot be shown to be better than a straight line. Kolmogorov-Smirnov 1-sample tests showed that the number of ♀♀ caught declined significantly with increasing trap spacing ( $P < 0.01$ ), and nearly so for ♂♂ ( $0.05 < P < 0.1$ ). The difference between the sexes was also significant ( $P < 0.001$  in a Kolmogorov-Smirnov 2-sample test), i.e., relatively more ♀♀ were caught at the closest spacings.

#### RESULTS OF TRAPPING AT VERY WIDE SPACINGS

The Eglinton and upper Hollyford valleys carry the only road from the Fiordland National Park headquarters, in Te Anau, to Milford Sound, an important tourist centre on the west coast. Between November 1972 and June 1974 the National Park Ranger in charge of the area, Mr R. Slater, set out 20 Fenn traps at 19 roadside sites along the whole length of the Eglinton (40 km), and inspected them at irregular intervals (usually weekly) in the course of his routine travels. The average distance between trap sites was 2.1 km; traps were left permanently set, and the bait was renewed each visit. Of the 123 sexed stoats collected during this period 76% were males, compared with an average of 40% males in the experimental traps (Table 3). The very large difference between these figures invites closer examination.

Only four experimental spacings (100, 200, 400, 800 m) were used, because in order to include an equal number of traps at the next spacing (1600 m) the total length of trapline required would have exceeded the length of the road along the replicate trapline, and would also have greatly increased the cost of the fieldwork. However, if Mr Slater's data are regarded as providing almost the equivalent of the missing fifth spacing, the results fall out quite differently. The number of female stoats killed per kilometre decreases sharply with increasing trap spacing, whereas the decrease in males is significantly less; i.e., relatively more female stoats appear to be

Table 3. Numbers of ♂ and ♀ stoats caught at each trap spacing on experimental lines and Slater's line combined.

	EXPERIMENTAL TRAPS (both valleys pooled)							SLATER'S TRAPS		Totals	Kolmogorov-Smirnov 1-sample test
	2 end traps	18 at border 100 m traps	20 at border 200 m traps	20 at border 400 m traps	20 at border 800 m traps	20 at 2.1 km	(20 at 2.1 km average)				
♂♂	2	4	2	8	1	16	0	27	2	93	} highly significant ( $P < 0.001$ )
♀♀	4	10	0	17	2	20	5	38	1	30	
Totals	6	14	2	25	3	36	5	65	3	123	
% ♂♂		29		32		44		42		76	
S.E. (p)		12.1		9.3		8.3		6.1		3.9	
$\Sigma$ St/km		18		4.0		8.0		16.0		42	
		7.8		6.3		4.5		4.1		2.9	

caught at the closer spacings ( $P < 0.001$ ; Fig. 3). This result suggests that it would be unwise to conclude, from the controlled experimental data alone, that spacing has no effect on the number and sex ratio of stoats caught.

The inclusion of Mr Slater's results in the regressions could be judged invalid on the grounds that they are mostly derived from traps set at a different time (November 1972 to June 1974) and operated according to a different schedule. However, between June 1974 and April 1975 in the Eglinton Valley Mr Slater continued to operate 8 traps set at either end of the experimental line, and he caught 10 stoats. Their sex ratio (80% males), when compared with that of the 58 stoats caught at the 4 experimental spacings during this period of overlap (47% males), was significantly different ( $P < 0.05$  in a one-tailed  $\chi^2$  test). The number caught by Mr Slater is more difficult to compare, because his traps were set continuously but checked and rebaited only weekly, not daily. A higher capture rate per kilometre could be expected in traps available 4 weeks a month instead of 2; on the other hand they were checked less often, and the bait in them became stale. Both these factors could decrease the chances of catching a stoat (King & Edgar 1977). If Mr Slater's effort per month is reckoned as being roughly equivalent to the 2 weeks' effort of the experimental traps, a  $\chi^2$  test still shows that significantly fewer stoats were caught per kilometre on Mr Slater's line ( $P < 0.005$ ).

Mr Slater's traps were not set out with technical experiments in mind, and their spacing varied from 0.6 km to 3.5 km. However, the median spacing (2.2 km) was very similar to the mean, and there was no significant relationship between variation in spacing and sex ratio or number caught per kilometre ( $P > 0.05$ , both tests).

The need to consider Mr Slater's figures is debatable. On the one hand it may be argued that the range of experimental spacings was inadequate, that Mr Slater's work provides relevant missing information, and that it should not be ignored. This argument is difficult to dismiss. On the other hand it may be pointed out with equal force that Mr Slater's figures are derived from uncontrolled trapping done at a different time, and therefore should not be included. This argument is weakened to some extent by the consistency of his results despite that disadvantage (see above). Therefore, I incline to the conclusion that it would be a greater source of error to omit than to include Mr Slater's data, and that there is, more probably than not, a general decline in the ratio of females caught with increasing trap spacing (Fig. 3). King (1975) offers a possible biological explanation for the same effect in weasels (*Mustela nivalis*).

## DISCUSSION

The present results are primarily from the summer and autumn (December–May), when 150 of the 159 sexed stoats from the experimental traps were collected (Table 1). If there is any seasonal variation in the way in which stoats encounter or respond to traps, these results may not be valid for the months of winter and spring (June–November). Such a variation is quite possible, because in a large collection of stoats from all over New Zealand (King, in prep.) females are better represented during December–May than over the rest of the year (51% of 936 stoats, compared with 31% of 525 stoats caught from June to November:  $P < 0.005$ ). Though there was no significant seasonal variation in sex ratio in this sample, only 9 stoats were caught in winter and spring with which to compare the large summer and autumn collection.

Trapping in the Eglinton Valley had been carried on continuously, if not very intensively, for over 18 months before the experimental line was set up, and 76% of the 123 sexed stoats caught by Mr Slater were males. This might have reduced the number of adult males available to the traps in the first summer of experimental trapping, but only six adult stoats (three of each sex) were caught on this line from November 1974 to February 1975—insufficient to test for any difference.

Kukarcev (1978) reported that in the population of stoats he examined the proportion of females increased at low density. In the valley of the Ob River (Tumen, U.S.S.R.) the sex ratio of stoats killed by fur trappers in 1972–73, a season of low density, was 39% males, compared with 63% during 1968–69, a season of high density (total 13 500 stoats examined over 8 seasons). The controlled trapping in the Eglinton and Hollyford valleys spanned 4 years, and in 1976–77 the summer peak was about three times higher than in the two previous years and the one following (Fig. 1). From April 1976 all the traps were set at 400 m intervals, so it is possible to compare the sex ratio of stoats caught in summer and autumn at this spacing in years when the summer peak was low (1974–75, 1975–76, 1977–78) and when it was high (1976–77). The difference was not significant ( $\chi^2 = 2.61$ , 1 d.f.,  $P > 0.05$ ), though it did tend in the direction suggested by Kukarcev (low peaks  $49.3 \pm 5.9\%$  males,  $n = 71$ ; high peak  $60.6 \pm 3.7\%$  males,  $n = 170$ ).

It is difficult to derive a firm conclusion from these data, partly because of the relatively small samples inevitable in field experiments with carnivores, and partly because of doubts as to the importance of including consideration of Mr Slater's results. Ideally the experiments should be repeated, preferably during a period of high population density

and including measured spacings between 0.8 km and 2.0 km. However, the effort and expenditure necessary to obtain improved data are large, and some time may elapse before they become available. Since information on this subject has been almost totally lacking, the present results may have some value in the meantime.

Stoat trapping is most often undertaken in the hope of controlling the numbers of stoats, and thereby protecting birds (native species in New Zealand; game species in Europe) from predation. The two most important of the unstated assumptions behind such a policy are that it is possible to reduce a local population of stoats by trapping, and that predation by stoats controls the population densities of the birds in question. There is some reason to doubt the first assumption, at least over the long term (King & Moors 1979), and data concerning the second are inadequate. Formulation of a rational management policy requires information on many aspects of the biology of the protected species besides the possible value of various forms of predator control. Proper treatment of this large subject requires fuller discussion elsewhere.

#### ACKNOWLEDGMENTS

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## The life-history tactics of mustelids, and their significance for predator control and conservation in New Zealand

CAROLYN M. KING

3 Waerenga Road, Eastbourne, New Zealand

and

PHILIP J. MOORS

Wildlife Service, Department of Internal Affairs,  
Private Bag, Wellington, New Zealand

Intensive predator control on game estates in 19th-century England is believed to be largely responsible for the decline of two large native mustelids, the pine marten and polecat. Two small, related, species, the stoat and weasel, were also killed in large numbers but are still common in England, and have been introduced into New Zealand. The theory of life-history tactics offers an explanation for the different effects of persecution on large and small mustelids. It also suggests that stoats in New Zealand national parks cannot be exterminated by trapping, and that the first priority for the conservation of rare native birds such as the takahē is active management to stimulate breeding.

### INTRODUCTION

During the nineteenth century in England, two species of native mustelid—the polecat (*Mustela putorius*) and the pine marten (*Martes martes*)—became extinct, largely because of persecution by gamekeepers (Corbet 1974, Langley & Yalden 1977). In contrast, the stoat and the weasel (*Mustela erminea* and *M. nivalis*), which were killed in even greater numbers, are still common and widespread (Corbet & Southern 1977). We suggest that the theory of life-history tactics offers an explanation for this differential effect, and has implications for contemporary programmes for predator control and for the conservation of declining species in New Zealand.

### LIFE-HISTORY THEORY

Stearns (1977) reviews ideas and data on the evolution of life-history traits. There are two contrasting models, one deterministic ( $r$ - and  $K$ -selection) and one stochastic, which approach from different angles the general problem of predicting the association of key life-history traits in specified circumstances. Both models can also be applied simply as systems of classification; for example, the familiar terminology of the  $r$ - $K$  dichotomy can be used as a convenient shorthand denoting the two contrasting suites of reproductive traits, without implying anything about their evolutionary origin. Species showing the combination of early maturity, large litters, large reproductive effort, small young, and a short life

may be called ' $r$ -selected', and species with the opposite syndrome, ' $K$ -selected'. Both theoretical models predict these same associations of reproductive traits, but for different reasons. Since we are concerned here only with the different consequences of the actions of man for species with contrasting reproductive strategies, it is not relevant to our argument which of the two models, if either (Stearns 1977), is correct on theoretical grounds.

### LIFE-HISTORY TACTICS IN THE NATIVE BRITISH MUSTELIDS

Related species may be ranged along a spectrum, from the most  $r$ -selected types through intermediates to the most  $K$ -selected types. The series is relative only within the group being compared. For example, all mustelids are vertebrates, and vertebrates as a whole are  $K$ -strategists compared with invertebrates; however, within the mustelids, some species show more of the characters of  $K$ -strategists than others.

The native British mustelid fauna comprises six sympatric species (Table 1). They may be ranked in order of declining importance of the reproductive traits which most tend to increase  $r$ , which are early maturity, more than one litter per year, large litter size, and more than one litter per adult female's life-time (Slobodkin 1961). These characters are maximised in  $r$ -strategists. Associated characters, summarised by Southwood (1976), include small body size, a short period of parental care, short generation time, unstable populations in which food

supplies are the main arbiter of a high and variable annual mortality, great resistance to total (though not local) extinction, and the ability to persist in diverse and changeable habitats. In all these characters the weasel and stoat are the most *r*-selected species of the group. Both are specialised predators of small mammals, and in both the production and survival of young is influenced mainly by the availability of prey (King & Moors 1979 and unpubl. data). In both species mean survival after attaining independence is only a year or so, and the chances of a given female breeding more than once are not good. Hence, the populations of both these small carnivores (females are under 250 g) tend to fluctuate markedly from year to year (King 1978 and in press).

The characters of *K*-strategists are generally the opposite. So far as is known, female martens, otters (*Lutra lutra*), and badgers (*Meles meles*) all mature in their second year or later, produce small litters, care for them for many months, and, once mature, have a good chance of surviving to breed several years in succession. They are all large species (females are over 1 kg) with fairly general (or even, in the badger, omnivorous) food habits, and when undisturbed have relatively stable populations in which density- and age-dependent mortality are probably important. They tend to become closely adapted to particular habitats, and to lose the ability to live elsewhere if their requirements are not met (Southwood 1976). When their populations are depressed too far below equilibrium level they are slow to recover, and are particularly susceptible to both local and species extinction.

The European polecat has some of the characters of both groups: it is larger than the *r*-strategists, but matures earlier and has larger litters than the *K*-strategists. Very little is known about the population dynamics of wild polecats, but the available information indicates that it occupies a central position in the *r*-*K* series (see Table 1).

Both models of life-history theory predict that reproductive effort should be smaller and more constant in the more *K*-selected species. Reproductive effort—the mean proportion of its total metabolic resources which a species puts into reproduction—may be roughly estimated from the average annual ratio of reproductive to somatic tissue (Gadgil & Solbrig 1972). This is only an index, because the biomass of something as highly differentiated as a flower or an embryo may not fairly reflect the cost of producing it (McNaughton 1975), and because the calculation does not take account of energy spent in parental care. Even so, as a first approximation, reproductive effort estimated in this way does vary among the mustelids as both models predict (Table 1).

The ranking in Table 1 also agrees with the rank order of reproductive abilities in mustelids inferred by Stubbe (1969) from his estimates of the annual mortality rates of young, which ranged from 75% in weasels to 32% in badgers.

#### EFFECTS OF CONTROL ON SPECIES WITH CONTRASTING LIFE-HISTORY TACTICS

The additional mortality imposed by nineteenth-century English gamekeepers on the native mustelids

Table 1. Relative positions of native British mustelids on the *r*-*K* spectrum. Source mainly Corbet & Southern (1977) and Neal (1977). Parenthetic figures following a mean give the range; bracketed figures are rough estimates.

Ranking: Species:	<i>r</i> ←	1 <i>Mustela nivalis</i>	2 <i>Mustela erminea</i>	3 <i>Mustela putorius</i>	4 <i>Martes martes</i>	5 <i>Lutra lutra</i>	6 → <i>Meles meles</i>	<i>K</i>
Earliest possible age at first littering (not conception), in years		0.25	1	1	[2]	1.5-2	2	
Mean litter size		6.2(4-8)	9*(6-13)	[5-?10]	3	[2-3]	2.9(1-4)	
No. of litters per year		1 or 2	1	1	1	1 [? or 1 per 2 y]	1 [? or 1 per 2 y]	
Approximate mean life-span (♀), years		<1	?1	[?1-2]	[?1-3]	[?2-5]	[?2-5]	
Delayed implantation?		No	Yes	No	Yes	No	Yes	
Mean body weight (♀), kg		0.062	0.213	0.620	[1.3]	7.4	10.1	
Weight of newborn (g)		1.5	c.3	9-10	28	[130]	104	
Reproductive biomass produced per year (g)†		9-18	27	45-100	84	130-390	151-302	
Ratio of reproductive to somatic biomass (♀), %		15-29	13	7-16	6	2-5	1-3	

\*From embryo counts, including some resorption; no litter counts available.

†Total birthweight of young produced per year. Some allowance should be made for maternal genitalia, placenta, and mammary glands, but data are not available.

had different consequences for each species, corresponding to the differences in their life-history tactics. The weasel and stoat already had the low adult survival and short life-span typical of relatively *r*-selected types. Only about one-quarter of the animals taken in any sample of either species are likely to be over a year old (Corbet & Southern 1977). Gamekeepers had little chance of even substituting for this normally high mortality, still less of exceeding it by artificial means. Moreover, in years of abundant food, if not every year (King 1978 and in press), the high annual productivity of both species would certainly be more than enough to replace individuals removed by gamekeepers. On the other hand, for the *K*-strategist marten, the increased mortality from keeping could easily have exceeded the level that could be countered by any possible increase in productivity, and in lowland England, where the most intensively protected sporting estates were, martens had disappeared well before 1900 (Langley & Yalden 1977). That the other two *K*-selected species, the otter and the badger, survived through the nineteenth century is largely because both were able to escape some of the persecution. Otters were conserved for the chase (Corbet 1974), i.e., they were "protected from gamekeepers so that they could be hunted with hounds" (Langley & Yalden 1977); and badgers were able to dig deep, secure setts where at least some were able to resist eradication (Neal 1977).

Of course, there were also other factors operating before and during the nineteenth century which could have had differential effects on the populations of the six species. The most important, large-scale deforestation, merely reinforced the effects of persecution, and for the same reasons. In contrast to stoats and weasels, martens are particularly sensitive to destruction or dissection of their habitat, because inability to adapt rapidly to changes in habitat and food supply is also a consequence of the *K*-type life-history strategy (Southwood 1976). Badgers were much less affected by deforestation (Corbet 1974), and otters less still. The spread of rabbits and brown rats during the nineteenth century (Corbet 1974) might be expected to have arrested the decline of polecats, but apparently it did not. Either the keeping pressure was great enough to overcome this potential advantage, or some other, unknown, factor was involved.

#### IMPLICATIONS FOR PREDATOR CONTROL AND CONSERVATION IN NEW ZEALAND

This story has more than just theoretical or historical importance for New Zealand. The two species which most successfully resisted the attentions of the

English gamekeepers have both been introduced here, and the stoat is now very common in all forests, including all National Parks. The Parks are among the most important reserves for the conservation of our remaining native birds, and the reduction (or, if possible, extermination) of stoats in them is considered a highly desirable aim by the National Parks Authority. What can we learn from England's experience when we are considering what, if anything, can be done to achieve this aim?

First, it is clear that control of stoats or weasels by trapping is unlikely to be successful except locally and temporarily. The trapping done by nineteenth-century keepers in England, over huge areas of easily accessible country, must be one of the most intensive and sustained attempts at predator control ever made, yet it had no long-term effects on stoats. It seems obvious that such an effort could not be repeated or bettered in twentieth-century New Zealand, and field experiments on trapping of stoats confirm that trapping is relatively inefficient and very labour-intensive (King, in prep.), and therefore prohibitively expensive. This does not, of course, exclude the possibility that short-term, local campaigns may sometimes be justifiable or desirable - for example, in certain seasons in the Takahe Area (King 1978), or to clear an island for rehabilitation. But, except within such limits of time or space, trapping is not a satisfactory control strategy. Increasing the mortality of a relatively *r*-selected species is rarely effective in controlling its numbers (French *et al.* 1975), certainly not without massive expenditure. The vulnerable point in this type of life cycle is the production of young: because of the short life span of adults, a series of years of low recruitment and/or immigration must be followed by lowered population density. Hence, our best hope of achieving a measure of control over stoats lies in some means of reducing productivity, and future research along these lines may find ways of doing this at reasonable cost.

In contrast, many of the birds most needing protection in National Parks are extreme *K*-strategists. For example, the takahe (*Notornis mantelli*) has a long adult life-expectancy and low annual productivity of chicks (Mills 1978). Its survival in the wild has depended on the low mortality rate of adults; if this is suddenly increased, the production of chicks cannot compensate (at present about 74% of them die within 3 months of hatching). Conservation of such a species must depend on encouraging production of chicks while taking precautions to prevent unusual losses of adults, as advocated by Mills *et al.* (1978). In practical terms this means that, though predator control may be important in some seasons, protection and improvement of the habitat (including

removal of introduced competitors) is important in all seasons.

Stoats are not the only introduced predators in New Zealand, and in certain habitats are not the most important. On pastoral land another mustelid, the feral ferret (*Mustela putorius furo*), is more common, and on offshore islands the worst pests are undoubtedly rats. The ferret is a domesticated strain of the polecat, and the two forms may well have similar life-history tactics. There are few data on the trapping of ferrets other than the figures given by Wodzicki (1950) for sales of ferret pelts bought from rabbit trappers during the 1940s. There is no way of estimating the ecological effect of this harvest, which has anyway greatly decreased since the regional Rabbit Boards have managed to control most rabbit populations. However, ferrets remain locally common and a potential nuisance, for instance at the albatross breeding colony at Tajaroa Head, near Dunedin. The decline in Britain of polecats, at least partly as a result of keeping, suggests that ferrets might be easier than stoats to control by trapping. However, the surest way to reduce the numbers of ferrets is to control their staple food, rabbits (Gibb & Flux 1973). The control of rats is a specialised subject, recently reviewed by Dingwall *et al.* (1978).

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