

STUDIES ON THE CONTROL OF STOATS (MUSTELA ERMINEA) IN THE NATIONAL PARKS OF NEW ZEALAND

CAROLYN M. KING, 3 Waerenga Road, Eastbourne, New Zealand

ABSTRACT: Stoats were introduced to New Zealand at the end of the 19th century and have colonized the native forests, including all the National Parks. The presence of stoats in the Parks, which are important refuges for some of New Zealand's surviving endemic birds, causes concern. From 1972 - 1980, research on stoats has included: 1) a general survey of food habits, size, reproduction, moult, and some parasites in 1,599 stoats from all the Parks; 2) field experiments to improve efficiency of trapping; and 3) observations of the effect of irregular seeding of southern beech (Nothofagus spp.) on populations of rodents and stoats. I consider that general population control of stoats (permanent reduction of the breeding stock) is impossible in mainland Parks, but at least in beech forests, prevention of damage by stoats (temporary reduction of numbers in peak years only) is possible if justified by ornithological evidence. The life-history strategy of stoats is of the type that is best manipulated by reducing fertility, not increasing mortality; i.e., by methods such as chemosterilization rather than by trapping. There is also an urgent need for information on the population dynamics of the birds that these measures are intended to protect.

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The 10 National Parks of New Zealand at present cover over 2.2 million hectares, about 1/10 of the land area of the country. They protect about 1.5 million hectares of indigenous forest, just less than 1/4 of the total remaining, and less than 10 percent of the forest that stood before the arrival of man. Besides its intrinsic beauty and value in watershed protection, this remnant is of unique interest to students of ecology and evolution. New Zealand has been isolated since the Cretaceous period; that is, since before the evolution of modern flowering plants, snakes and mammals. The absence of these groups profoundly influenced the evolution of the flora and fauna of New Zealand, including the birds, most of which have colonized the islands at various times since their isolation. Other natural colonists include many flowering plants, and 2 species of bats, but no strictly terrestrial mammals. As

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a result, New Zealand now contains communities and species unique in the world, of international interest and value.

The birds of New Zealand are not especially diverse, but they include an exceptionally high proportion of endemic species. Of 65 native species of land and freshwater birds now living in New Zealand, 57 percent are endemic; if subfossil and recently extinct species are included, the figure is 70 percent (Bull and Whitaker 1975). Mills and Williams (1979) estimated the proportion of endemics as 60 percent of 77 living species. Of the endemics, the ancestors of 2 orders, the kiwis and moas (about 29 species), were probably present when New Zealand first drifted away from the rest of Gondwanaland. The ancestors of 3 families (8 spp.), 24 genera (29 spp.), 15 species and 17 subspecies, all now endemic, followed at successively later times since then (Fleming 1962). All of these long-resident native birds adapted to an island environment free of terrestrial mammals, and many of them reduced or abandoned their powers of flight.

In the last 1,000 yr, there have been rapid and radical changes in the vertebrate fauna of New Zealand, of which predation, in various forms, is certainly among the major causes. In the approximately 800 yr between the arrival of Polynesian man and the year 1800 A.D., 45 species of birds (24 of which were moas) became extinct and are known only from subfossil remains (Kinsky 1970).

This surprising toll does not imply that the Polynesian hunters and their companions (dogs Canis familiaris, and the Maori rat, Rattus exulans) were especially voracious killers, only that the island faunas were especially vulnerable to disturbance by hunting, predators, and fire (Bull and Whitaker 1975). In the 180 yr since 1800, the extent of disturbance has greatly increased and a further 14 species or subspecies have certainly or probably become extinct. The total effect has been catastrophic, largely because of New Zealand's relatively small size and long history of remote isolation. Evolution in security from the necessity to find ways of coexisting with mammals favored slow reproduction and long life at the expense of physical and demographic defenses against ground predators. When man, Maori rats, dogs, brown (R. norvegicus) and black rats (R. rattus), cats (Felis catus), ferrets,

weasels (Mustels sp.), and stoats arrived (in about that order), many ground-dwelling, slow-breeding native birds had virtually no defenses and no refuges, and certainly no time to produce enough genetic variants among which natural selection might have found some saving adaptation.

The evidence that predation (by man, rats, and carnivores, in unknown proportions) was 1 of the foremost among several causes of the historical decline in numbers of species of birds in New Zealand is substantial. The effect of predation on contemporary populations of the remaining species is much less clear. Coker and Imboden (1980) believe that most of the damage within the capacity of predators has been done, and that loss of habitat has now assumed the most significant role in further depletion of mainland native species. If "loss of habitat" includes also degradation of habitat, this is probably true. The takahe (Notornis mantelli), an endangered flightless rail, is found in the middle of 1 of the largest blocks of native forest remaining, Fiordland National Park. Despite rigorous protection, the known population of takahe has generally declined in recent years; Mills and Mark (1977) have suggested that this is due to competition with introduced red deer (Cervus elaphus) for preferred plant foods. However, very few native birds of New Zealand have been investigated as intensively as the takahe. Williams (1973) lists the reasons, peculiar to New Zealand, for the lack of comprehensive life-history studies on native birds: scarcity and secretive habits of many species; difficult access of many potential study areas; legal restrictions on the taking of adequate samples and on the keeping of native birds in captivity. Other common difficulties are lack of manpower and the time and effort demanded. It can be inferred that at least some of the historical extinctions were inevitable, because the area of forest has been reduced from about 67 - 22 percent. What we do not know is how many further extinctions are inevitable, and what controls the density of the remaining bird species that are not in danger of extinction.

The National Parks of New Zealand, therefore, contain enormously important examples of some of the results of an unrepeatable natural experiment in the evolution of, particularly, forest vegetation and birds. They should have strong protection, and the legislation controlling them naturally includes the demand that all introduced species be, so far as is possible, exterminated. In some cases, this is worth attempting; the

benefit to native forest of reducing populations of introduced red deer (New Zealand Forest Service unpubl.), probably does justify the enormous expense of control operations. However, it is not yet clear what benefits might follow from successful control of predators. We do not know if removal of predators would result in an increase in abundance and distribution of the species which are not endangered; in fact, it is even possible to argue quite seriously (Jenkins 1979) that, if surviving species have developed a behavioral response to predators, it would be unwise to aim at general predator extermination. This question must be resolved, because if the remaining nonendangered birds really are limited by factors other than predation, there is no justification for attempting general predator control. The present status of the endangered species is reviewed by Mills and Williams (1979); predation is often 1 factor restricting their numbers and distribution, but other factors are usually important too. As Halliday (1978) has emphasized, conservation of endangered birds depends on an intimate understanding of their biology, because species vary in their biological susceptibility to extinction and to the different agents that can cause it. Similarly, successful control of predators depends on an understanding of their biology and life-history strategy (King and Moors 1979). Research on both of these subjects has hardly started, and needs to make further progress before economic, effective, and necessary predator-control work can be planned. My work attempts to contribute some of the information required on stoats, whereas other workers in New Zealand are studying rodents (Dingwall et al. 1978) and feral cats (Fitzgerald and Karl 1979) and their effects on bird populations.

#### THE BIOLOGY OF STOATS IN NEW ZEALAND

From 1972 - 1976, 1,599 stoats collected from 14 study areas - including all 10 National Parks - were autopsied. A description of the variability within and between samples in food habits, size, reproduction, pelage, and certain parasites is planned for publication in a New Zealand journal (King and Moody in prep.). In 3 areas, changes in the numbers, breeding, and food habits of stoats through 3 population peaks of forest rodents were monitored between 1973 and 1980; these data will be published separately. Other studies have considered types of traps (King and Edgar 1977) and their effectiveness (King 1980).

The diet of stoats was examined from 1,514 guts; the distribution of 2,643 prey items was expressed as the percentage frequency of occurrence in the 1,250 guts which were not empty. In the total sample, the frequency of occurrence of the major prey categories was: mice (Mus musculus), 19 percent; Rattus sp. (mostly R. rattus), 6 percent; lagomorphs (Oryctolagus cuniculus and Lepus capensis), 18 percent; Australian brushtailed opossums (Trichosurus vulpecula), 10 percent; birds (native and introduced, all species pooled), 43 percent; lizards [mostly native geckos and skinks (Leiopisma sp. and Hoplodactylus sp.)], 5 percent; insects (mostly large native Orthoptera), 41 percent; freshwater crayfish (Paraneohpops sp.), 2 percent; and carrion, about 1 - 2 percent. The diet of stoats in relation to age, sex, season, and habitat was examined more closely in the subsamples from forest (n = 866, 3 classes of forest recognized) and from 1 area of native grassland (n = 146). There were no general and consistent differences in the diets of young and adult stoats. When prey were classed as large (carrion to rat size), medium (birds to lizards), or small (insects), female stoats ate more small prey ( $p < .01$ ) and males more large prey ( $0.02 < p < .05$ ). There were differences in diet between forest types and seasons, of which at least some probably reflected changes in the availability of prey. Large prey supplied most of the biomass of the stoat's diet: insects and birds, though frequently eaten, contributed only about 1/10 and 1/5, respectively, of the volume ingested. There was no evidence from these data that stoats in New Zealand forests compensate for the lack of voles (important in their diet elsewhere) by eating birds more frequently than they do on British farmland. However, this does not imply similar levels of predation, because the diversity and number of birds available in New Zealand is less than in Britain.

Young stoats are born September - October and females reach adult weight by March, though males not until after August. There was pronounced geographic variation in body size; males from lowland podocarp/broad-leaved forests averaged 3 percent smaller than males from upland beech forest in condylobasal length, 4 percent in head-and-body length. The pattern was repeated, less clearly, in females and young of 2 - 5-month-old. Sexual dimorphism averaged 9.6 percent of condylobasal length, ranging from 6.5 - 12.0 percent. Compared with stoats from Britain, assumed to be still the same size as the colonizing stock introduced in

1882 - c. 1900, New Zealand males from lowland podocarp forests were unchanged, or possibly smaller, and those from upland beech forests were larger. New Zealand females were larger in both habitat types. In males, the extent of geographic variation in New Zealand was almost as great as in the whole of continental Europe, but average body size was not significantly larger than in Britain; in females the range was less and average size was significantly larger than in Britain. The extent and sexual differentiation of adaptation in body size by New Zealand stoats must have evolved in less than 100 yr.

There was a pronounced seasonal variation in sex ratio of stoats collected, from 43 percent males in March - 77 percent males in October. The critical months for studies of reproduction are August - November inclusive and in all these months the proportion of females among the adults caught was 30 percent or less. Hence, although the reproductive condition of 528 females was established, only 77 were from August - November and only 13 of these were pregnant. This makes studies of reproduction in stoats more difficult and certain classes of information (e.g., variation in litter size) virtually unavailable.

The annual cycle of gonad weights in 528 females and 821 males showed a simultaneous peak in October, the season of births and of postpartum estrus. The mean number of embryos in 13 pregnancies was 8.8, range 6 - 13; 8 females contained fewer embryos than corpora lutea and there was evidence of transuterine migration of blastocysts in 6. Of 451 females caught during the period of delayed implantation (December - July inclusive), all but 2 carried the small corpora lutea of delay. Few adult and no young females were in estrus, though adult males were fertile from August - February. No young males were fertile. There was some evidence of a slight shift in breeding season with latitude in both males and females. The mean number of corpora lutea per female was 9.7 ( $n = 439$ ) and there was a significant inverse correlation between counts for the 2 ovaries of 1 individual. There was no significant variation in fecundity of females with age, body weight, or year, although in years when mice were particularly abundant some exceptionally high counts of corpora lutea (up to 19 per female) were observed. By contrast, in years when mice were particularly scarce, some females probably failed to produce a litter at all.

Moult and color change were recorded independently from flat skins of 1,298 stoats. A moult cycle begins when hair follicles enter the anagen phase and begin to accumulate melanin (visible on the skin side as black patches) and ends when the old hair is shed. Growth of the hair was inferred from the disappearance of the anagen follicles and shedding from color change. The spring cycle in New Zealand usually begins in August and ends in December; the autumn cycle begins in November and ends in July. These periods will be shorter in any given district. The spring moult is later in the south (44 - 45° S) than in the north (39 - 40° S) and is synchronized with the breeding season, but is not later at higher altitude. The autumn moult is earlier in the south. The proportion of stoats turning white is inversely related to minimum temperatures and to numbers of days with ground frosts, but not to mean temperature, number of days with snowfall, or snow-lie. Both altitude and latitude influenced whitening. These data are consistent with hypotheses developed from experimental work on animals in captivity, that moult (and breeding) is controlled by day length (i.e., latitude, not altitude), but winter whitening by temperature (i.e., latitude and altitude). Three anomalous specimens were possibly examples of pituitary malfunction.

The natural distribution of the destructive cranial parasite, Skrjabiningylus nasicola, was surveyed in 1,492 stoats. Infestation was rare in the young, so distribution was expressed as the frequency of occurrence of skulls containing nematodes in stoats over 6-mo-old. Subadult males (6 - 10-mo-old) were infested as frequently as adult males (> 10 mo) and adult males as often as adult females. Conservative estimates of incidence ranged from 0 - 37 percent in 27 local subsamples with  $n > 6$  (mean 10 percent,  $n = 1,005$ ), sometimes varying substantially across short distances. Up to 73 worms were recovered from each of 97 infested individuals, averaging 12.9 in females, 14.2 in males, and the difference was not significant. Incidence was highest in beech forest/grassland habitats with rainfall less than 1,600 mm per yr. There was no evidence that infested stoats were smaller or lighter than uninfested ones. Among 680 fleas found on 1,501 stoats, there were 662 Nosopsyllus fasciatus, 8 Leptopsylla segnis, 1 Ceratophyllus gallinae, 1 Parapsyllus n. nestoris, and 8 unidentified. Stoats caught in leghold traps had more fleas than those caught in humane Fenn traps because the former lived

longer after capture. The incidence of fleas on stoats found alive in the trap was higher in beech forest than in podocarp and mixed forest ( $p = .008$ ), but not significantly different between sexes and seasons.

#### PROSPECTS FOR CONTROL OF STOATS IN NATIONAL PARKS

In discussing the possibility of "control", distinction should be made between: a) control of the overall population density of stoats, and b) prevention of potential damage done by them. In this context, population control means the permanent reduction by artificial means of the average breeding stock of stoats in a given area; prevention of damage means the temporary reduction in numbers of stoats only when and where they could be a particular threat, whether or not the breeding stock is affected. In my opinion, population control is at present virtually impossible on the mainland; damage prevention is possible, if ornithological evidence can justify the expense.

The only means of reducing a local population of stoats now practicable is by imposing additional mortality by trapping. Other means of increasing mortality, or of achieving the same ends by the converse means, reducing fertility, are not yet practical alternatives. But population control of stoats over any substantial mainland area by trapping alone is impossible, because certain features of the breeding cycle of stoats make them very resistant to artificially augmented mortality.

Young female stoats are extremely precocious and can be mated before leaving the nest. On the assumption that ovulation is induced by copulation (Rowlands 1972) 99 percent of the young females leaving the family in summer are already pregnant, with 9 - 10 blastocysts in delay. This means that even if every male is killed during the summer and autumn when trapping is most productive, the next generation is already assured. Early maturity, large potential litter size, and prior mating of dispersing females are typical of opportunist, "r-strategist" species (King and Moors 1979) and make them very difficult to control. In the 19th century, English gamekeepers undertook the most intensive and sustained attempt at predator control ever made; "K-strategist" species such as the pine marten (Martes martes) and wildcat (Felis silvestris) were exterminated, but "r-strategist" stoats and weasels (Mustela

nivalis) were not permanently affected in numbers or distribution (Langley and Yalden 1977).

Experiments attempting to define the most efficient means of using traps to catch stoats in New Zealand have reinforced this conclusion (King 1980). In most New Zealand National Parks, access is so difficult that the only practical plan is to set a single line of traps up the center of a valley. On 2 such lines using traps spaced at 100-m, 200-m, 400-m, and 800-m intervals, freshly baited and checked daily, an apparent reduction averaging 60 percent in capture rate was achieved between the beginning and end of each 14-day session, but immigration between sessions occurred virtually all the year round. Between immigration and trap-shyness, it appeared that probably not more than 1/2 of the total stoats available were removed. Whether or not this benefited the birds of the area is unknown. However, trapping at this intensity is very expensive in labor and unlikely to become general policy. If the trap spacing is increased, to say 2 km, the catch will probably comprise mostly males which may be quickly replaced; many females will escape and, being already pregnant, will produce their young in any case. Another possible way of saving time, and therefore cost, is to omit baiting, but this results in a significantly lower capture rate (King and Edgar 1977).

Even if some advance in control techniques made it possible to substantially reduce the numbers of stoats present at a given time, effective control of the populations of stoats in the mainland areas of the National Parks is unlikely to last long, because it would soon be counteracted by immigration from surrounding uncontrolled areas.

On the other hand, prevention of potential damage by a local population of stoats may be possible, if required. Damage is most likely to occur in spring and summer when young stoats are demanding food and birds are breeding. It could still be worthwhile to reduce the possibility of damage at this crucial time, even if the breeding stock of stoats is not permanently affected. For example, in Fiordland, the area most intensively studied so far, the density of stoats in summer varies from year-to-year, largely in response to variations in the numbers of forest rodents, which in turn tend to follow variations in the production of

beechmast (King 1978). In summers when stoats are particularly numerous, birds may be especially at risk: there are many more stoats looking for meals and they apparently do not eat proportionately fewer birds even when rodents are abundant (unpubl. data). In a particularly important area such as the Murchison Mountains (the area of Fiordland National Park set aside for takahe) it could be considered worth a special effort to reduce the numbers of stoats in high-risk seasons (King 1978), provided there was definite evidence from population studies of the birds that such action was needed. At present there is none for this or any other mainland species, but it is not impossible that future research might identify a situation where a carefully planned and well-timed control operation for damage prevention could be profitable. If that happens, work conducted on stoats so far suggests that: 1) if an effective means of sterilizing females in spring could be devised, it would more efficiently reduce damage in a given season than trapping; and 2) if trapping is the only possible means available, it should be short-term and intensive (traps set November - March, kept freshly baited, not > 500 m apart, and frequently checked). However, I would point out that we do not yet understand the food web in the forest well enough to predict the possible side effects of such a policy. For example, would birds suffer more interference from rodents if stoats were removed, even temporarily?

By contrast, there are some areas where predator-control is at least theoretically possible and in certain cases could be more than justified. Many of the small offshore islands around the coast of New Zealand are the last refuges of several species now extinct on the mainland, including the famous tuatara (Sphenodon punctatus). There are 234 islands of 8 ha or more within 50 km of the coast; the list of our extinct species would be longer but for them (Atkinson and Bell 1973) and they are obviously of great importance in any management strategy for the protection of our rare native vertebrates (Crook 1979). Some are relatively untouched and must remain so. Most of the rest are at present unsuitable as reserves for 1 reason or another, but occasions could arise in the future when rehabilitation of a few carefully chosen islands (Taylor 1968) might be worth the effort.

## CONCLUSIONS

The presence of stoats in the National Parks of New Zealand poses conflicting managerial and scientific problems. On the one hand, there is a general official and public awareness of the unique nature of New Zealand's fauna and flora and of the history of devastation caused partly by introduced predators; therefore, there is an expectation that predators, especially stoats, should be controlled in major reserves such as the Parks.

On the other hand, it seems clear that any large-scale, effective, and permanent stoat control in the mainland Parks is probably impossible by means available at present. The attempt would be prohibitively expensive and inadequately justified by present ornithological evidence. My research on stoats is intended to provide information on 3 main subjects which may contribute to the resolving of this dilemma.

- 1) I have described the general biology of stoats in the habitats preserved in the National Parks, especially the ecology of their reproduction and feeding and their probable response to various control measures.
- 2) I consider that general, low-intensity attempts to control stoats are unlikely to have any effect, and if so, Parks authorities can at least avoid wasting resources on them. Public criticism so provoked could be answered by: a) public education, emphasizing that the historical and contemporary situations are different, for example; and/or b) a policy of maintaining some trapping effort in frequently visited areas, primarily for purposes of public relations.
- 3) There are the possibilities that further research on birds may lead to requests for means of localized damage control on the mainland and/or rehabilitation of further islands. In case either happens, I have tried to define the most efficient use of traps and would like to investigate the potential uses of chemosterilants. More work is required to establish the costs and benefits of a policy of temporary damage prevention compared with alternative policies.

Halliday (1978) pointed out that there are 2 different approaches to the conservation of endangered birds: a passive one, involving only the establishment and protection of reserves; and the active one, involving a direct intervention by biologists attempting to prevent, by various means including control of introduced predators, an otherwise probable extinction.

In New Zealand, both approaches are important. Protection of the remaining forest is currently the subject of heated public debate and active research, and the Wildlife Service has a respectable record of active management of endangered fauna on islands. The control of stoats has some prospect of making a significant contribution to this combined effort provided we can improve our knowledge of stoat biology, develop new control techniques, and use them with discrimination.

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THE REPRODUCTIVE TACTICS OF THE STOAT (MUSTELA ERMINEA) IN NEW ZEALAND FORESTS

CAROLYN M. KING, 3 Waerenga Road, Eastbourne, New Zealand

ABSTRACT: The reproductive performance of stoats (Mustela erminea) was observed in 3 areas between 1972 - 1973 and 1979 - 1980, giving a total of 17 area/season records. Variations in the population density of mice and rats were observed through 14 of the same seasons. The number of stoats caught per 100 trapnights was highest in summer. The summer peak was 2 - 5 times higher in some years than in others. Most of the stoats caught during the occasional large peaks were juveniles (2 - 5 months old); hence, most of the variation in total catch in summer is explained by variations in the number of juveniles caught. In 2 forests in Fiordland, the number of juveniles caught in summer was significantly correlated with the density index of mice in spring and with the frequency of occurrence of mice in the guts of stoats in the same summer. At Craigieburn Forest Park, Canterbury, where lagomorphs were important prey of unknown density, there were no such correlations with the mice. The mean fecundity of female stoats ranged from 8.3 to 10.6 corpora lutea per female per season, with little local or seasonal variation. Ovulation rates increased slightly when mice were numerous in November, but there was no relationship between the fecundity and the productivity of a given mating season. Productivity must be controlled by variation in fertility, not in fecundity. In Fiordland, the number of breeding adults caught in spring was always less by about 90 percent than the number of juveniles caught the previous summer, regardless of mouse density. At Craigieburn, a relatively small forest without natural boundaries, this effect could be overruled by immigration.

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The biology of stoats in New Zealand forests was surveyed from 1972 to 1976. The report of this work (King and Moody, in prep.) includes a general account of the annual reproductive cycle and feeding habits of stoats. In 3 of the 14 areas sampled for that survey, where population fluctuations of Mus musculus were also monitored, sampling was extended for several further years. Mus musculus is the principal small rodent,

and the only mouse-sized prey available. This paper describes the breeding performance of stoats in relation to these fluctuations.

New Zealand is a good place to study the ecology of reproduction in stoats. There are still large blocks of native forest in which stoats are the most common, often the only carnivore, and where the variety of prey is limited. The effects of variation in food supplies on stoat populations are therefore easier to trace than in more complex communities. Simplified habitats are also found in boreal forests, but the climate and working conditions in New Zealand are much easier than in the far north.

#### STUDY AREAS

##### 1. Eglinton Valley, Fiordland National Park (44°50'S; 168°05'E)

Length approximately 40 km; aspect NNE-SSW; altitude of floor 270 - 550 m; rainfall in center section 2,300 mm/yr; range of monthly mean temperatures about 0 - 8° C; years sampled 1973 - 1980. A glaciated valley with steep sides and flat floor about 0.5 - 1.0 km wide; continuous evergreen forest of Nothofagus sp. (in the area sampled, mostly N. fusca, up to 30 m tall) up to treeline at average 1,070 m (Figure 1).

##### 2. Lower Hollyford Valley, Fiordland National Park (44°45'S; 168°10'E)

Length approximately 35 km; aspect mostly N-S; altitude of floor 90 - 370 m; rainfall at least 4,250 mm/yr; range of monthly mean temperatures about 1 - 10° C; years sampled 1975 - 1980. Steep sided but narrower than Eglinton; continuous diverse evergreen forest of mixed podocarps and Nothofagus menziesii (up to 20 m); separated from the Eglinton by a low pass across the Main Divide of the Southern Alps (Figure 1).

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

Area approximately 4,500 ha; aspect SE; altitude 790 - 1,340 m; rainfall at field station 1,450 mm/yr; range of monthly mean temperatures 1 - 13° C; years sampled 1973 - 1978. A remnant of high altitude evergreen forest, virtually pure Nothopagus solandri var. cliffortioides (up to

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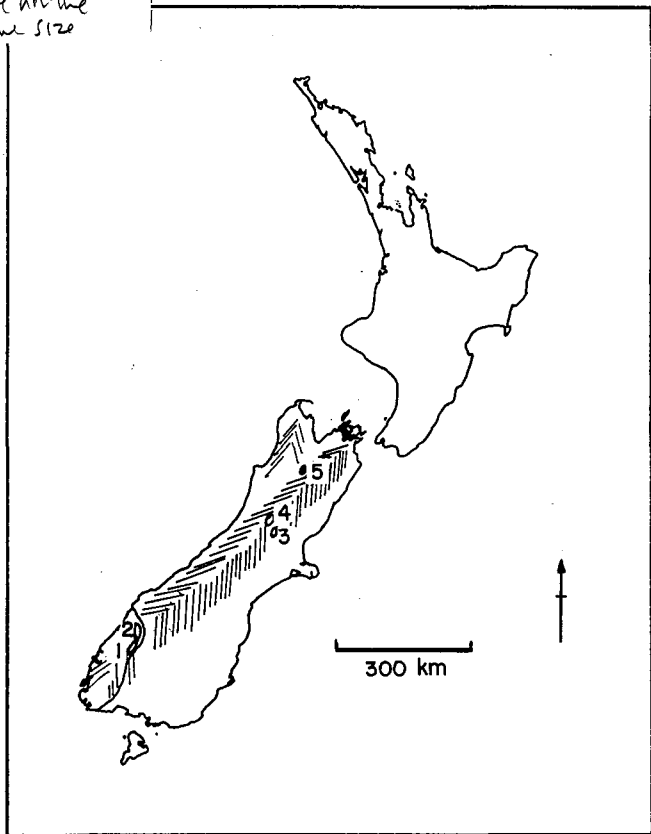


Figure 1. Study areas. (1 = Eglinton Valley, Fiordland National Park; 2 = Hollyford Valley, Fiordland National Park; 3 = Craigieburn Forest Park; ~~Fiordland National Park~~; 4 = Arthur's Pass National Park; and 5 = Nelson Lakes National Park.)

15 - 20 m), perched on the flank of a range of foothills of the Southern Alps, adjacent to very large areas of cleared pastoral country and semi-natural alpine grasslands (Figure 1).

Subsidiary samples referred to in the text came from Arthur's Pass and Nelson Lakes National Parks (Figure 1).

#### MATERIALS AND METHODS

The numbers of stoats and of rodents caught per 100 trapnights in standardized traplines were taken to indicate their densities. In Fiordland (in the Eglinton and Hollyford Valleys), baited Fenn traps (King and Edgar 1977) for stoats were operated 14 days a month from June 1974 - March 1976, and 10 days a month from then until April 1978. They were checked daily and rebaited often. Between 20 November 1979 and 1 February 1980, Edgar livetraps were set for 4 nights a week, for a total of 9 weeks. Recaptures of marked stoats were omitted in estimating stoat density from livetrapping. At Craigieburn, Fenn traps were left permanently set, unbaited, and checked most days. Guts of dead stoats, and scats collected from live ones, were examined; age was determined from the skull and baculum; ovaries were sectioned and corpora lutea counted, all by methods described by King and Moody (in prep.). There were very few data on litter size and lactation rate, since pregnant and lactating females are very difficult to catch and samples of females in spring were small. Snaptraps for rodents were set according to the standardized procedure developed by Fitzgerald and Karl (1979). One mousetrap and 1 rattrap were set at each of 36 stations, at 50 m intervals, baited with rolled oats and peanut butter, for 3 consecutive nights in the last week each of February, May, August, and November.

The use of the frequency of captures as an index of density can be criticized, but frequency and density are linearly related at least until captures reach 20 per 100 trapnights (Caughley 1977). All the stoat density figures, and all but 3 of the mouse density figures, were below that limit. Teplov (1962) stated that the number of ermine caught in traps with edible bait depends less on their numbers than on their hunger; in years when voles are scarce, the population of ermine (indexed from

tracks) falls but the pelt harvest increases. However, stoats enter tunnels containing traps out of curiosity as well as in response to the bait and similar seasonal variations in capture rate may be observed in baited and unbaited traps. Brand and Keith (1979) showed that lynx fur returns accurately reflected the timing of known density changes of lynx in Alberta. In the present study autopsy data for both mice and stoats, caught on the density assessment lines, were invariably consistent with the density trend.

Unbaited stoat traps catch at a significantly lower rate than baited ones (King and Edgar 1977); so the stoat traps in Fiordland (baited) and Craigieburn (not baited) probably did not sample the populations at the same level and their results cannot be plotted together on the same scale.

## RESULTS

### Density Index for Stoats

In all 3 areas the density index showed a regular annual cycle, despite variation in the trapping regimes employed. Most stoats were caught in summer (Figure 2). Superimposed on this regular cycle was an irregular variation in the size of the summer peak. In Fiordland, the highest peaks in the summers of 1976 - 1977 and 1979 - 1980 were 4 - 5 times higher than in other years. This variation is well known among local residents who have trapped regularly in the past (R.W. Willett, pers. comm.). The density index figures for the unbaited Craigieburn traps are lower but showed, in 3 of the 5 yrs, a similar variation between seasons in relative capture rate.

The summer peak coincides with the period of dispersal of the single annual crop of young. Plotting the capture rates of adults and juveniles (young of the year caught up to the end of February) separately shows that the occasional large peaks are composed almost entirely of young stoats (Figure 3). The capture rate of adults varied much less. Hence, there is a close correlation between the total number caught and the number of juveniles per 100 trapnights each summer ( $r_s = .91$ ,  $p < .01$ ):

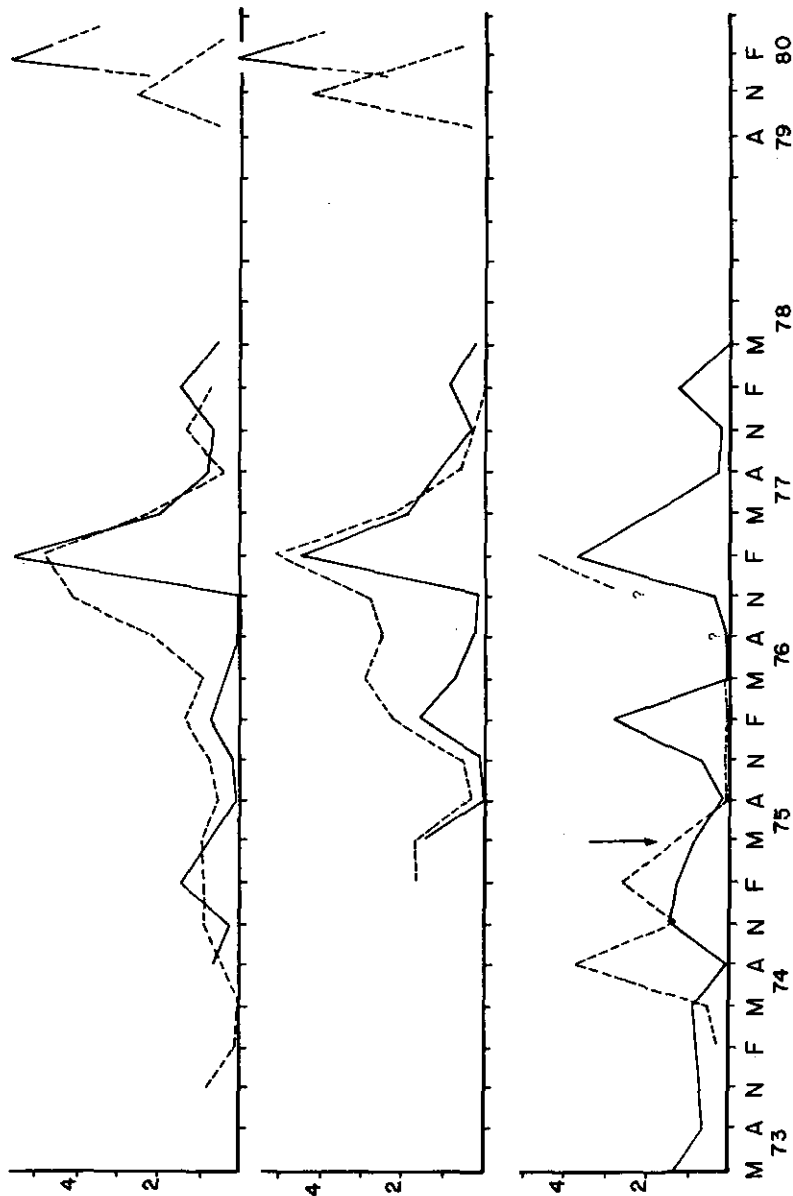


Figure 2. Numbers of stoats and of mice caught per 100 trapnights each season. F=February (summer); M=May (autumn); A=August (winter); N=November (spring). Solid line and vertical axis numbered as shown, stoats. Dashed line and vertical axis times 5, mice. Arrow: point at which trapping routine was changed at Craigeiburn. August and November 1976 mouse density index for Craigeiburn missing; February 1977 index by courtesy of Eric Spurr, N. Z. Forest Service. Upper: Eglinton Valley. Middle: Hollyford Valley. Lower: Craigeiburn.

REPRODUCTION OF NEW ZEALAND STOATS

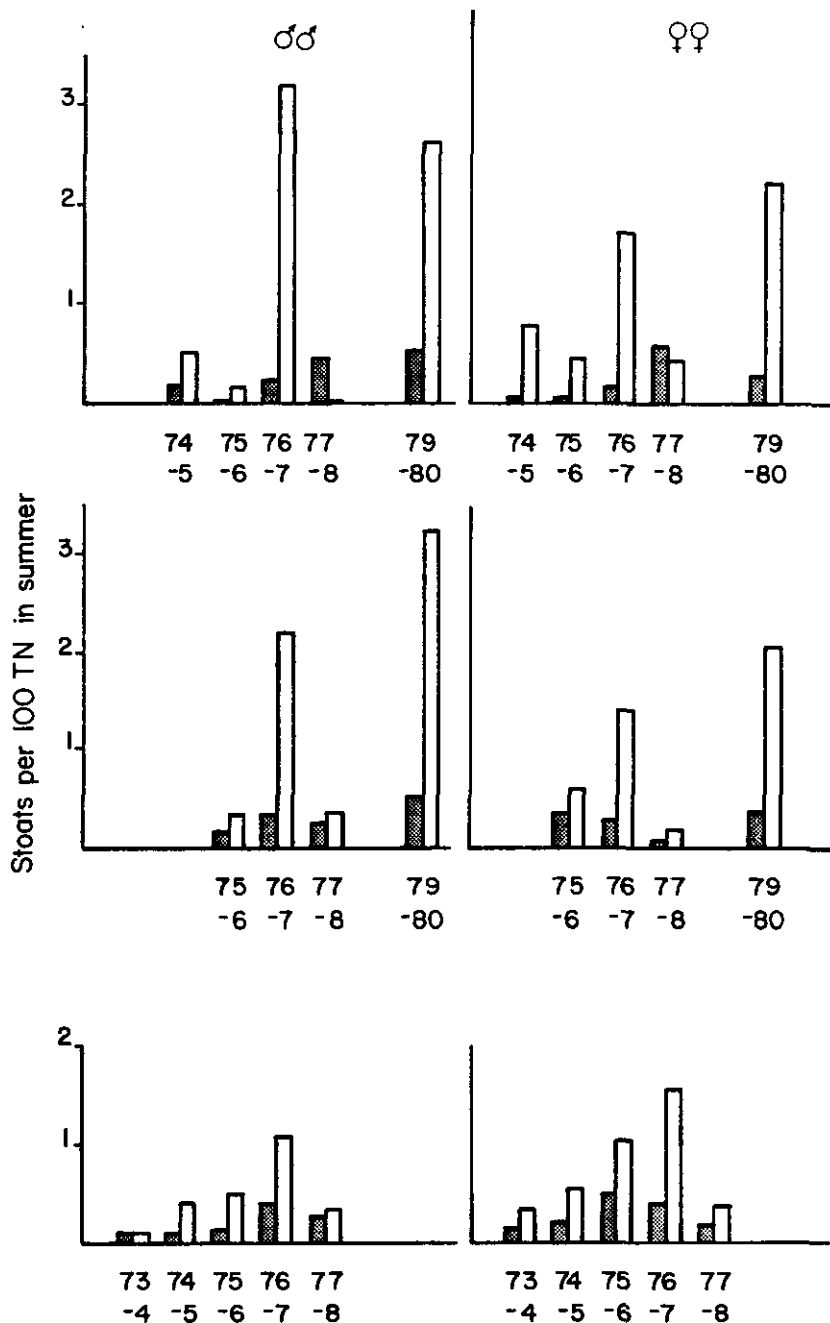


Figure 3. Numbers of adult and juvenile stoats caught in summer 1973-74 to 1979-80 (December-February incl.). Stippled columns = adults; plain = juveniles. Vertical axis = number of captures per 100 trapnights. Upper = Eglinton Valley; Middle = Hollyford Valley; Lower = Craigieburn.

variation in the number of juveniles caught explains most of the variation in the total catch. Clearly, in order to understand what controls the population density of stoats in these forests, it is important to determine what factors control the annual production of young.

#### Food of Stoats

Figure 4 compares the food habits of stoats in the 3 areas in summer only (December - February inclusive; the period when young disperse), ages and sexes pooled. The principal food items are mice (the single species Mus musculus); birds (perhaps 10 - 20 species); larger mammals (rats, mainly Rattus rattus; lagomorphs, Oryctolagus cuniculus or Lepus capensis; opossums, Trichosurus vulpecula in various proportions) and insects (mostly large, native, flightless Orthoptera). Of these potential prey, only mice and rats were monitored. They were not the most frequently occurring prey, but they were the only small rodents available; the mice showed substantial annual fluctuations in numbers, the rats less so. Variation in populations of the other prey was unknown, but was certainly less than in the mice. Further details of the seasonal and annual variation in diet of stoats in these 3 areas in relation to rodent density will be presented elsewhere.

#### Effect of Variation in Numbers of Mice on Stoat Breeding Success

The study detected population peaks of mice in Fiordland in 1976 - 1977 and 1979 - 1980 and at Craigieburn in 1974 - 1975 and 1976 - 1977. The density index for mice varied from 0 to 25 captures per 100 trapnights (Figure 2).

Previous observations (Riney et al. 1959, Marshall 1963) suggested that summers of high production of young stoats will coincide with high densities of mice, and in Fiordland, this expectation was confirmed. However, at Craigieburn there is clearly some other factor involved, since in 1975 - 1976 fewer stoats were caught than would be expected from the peak in mice and in 1975 - 1976 many stoats were caught in a season when mice were virtually absent.

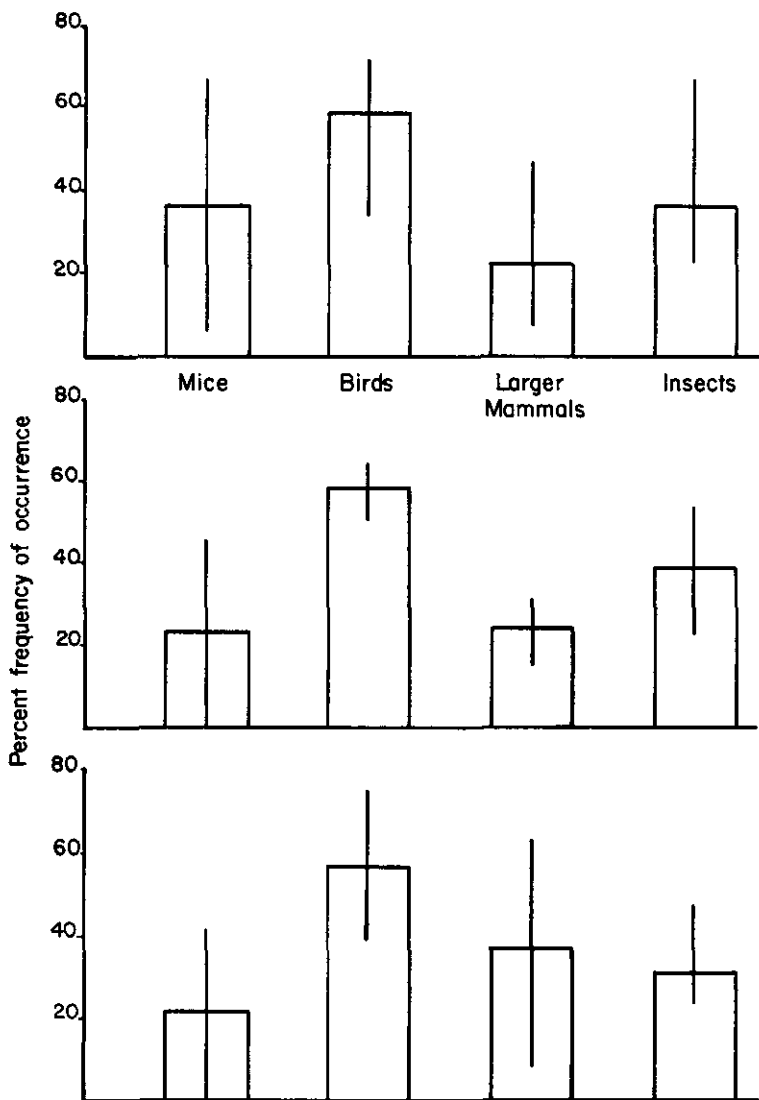


Figure 4. Food habits of stoats in the 3 study areas in summer. Columns show frequency of occurrence averaged over all summers observed; bars show range in means for individual summers. Mice: *Mus musculus* only. Larger mammals: *Rattus* (mostly *R. rattus*) + European rabbit and hare + Australian brush-tailed opossum. Upper = Eglinton Valley (7 summers, n = 6, 17, 27, 11, 63, 17, 88). Middle = Hollyford Valley (5 summers, n = 57, 21, 44, 8, 74). Lower = Craigieburn (5 summers, n = 8, 17, 39, 40, 13).

The crucial period in the annual reproduction cycle of the stoat is in October - November, when adult females are producing, suckling and hunting for young, and both adult and juvenile females are fertilized. In Fiordland, there was a significant correlation ( $r_s = 0.72$ ,  $p < .05$ ) between the density index of mice in November and the number of juvenile stoats caught per 100 trapnights in the following 3 months (the southern hemisphere summer, December - February inclusive) (Figure 5). This implies that there should also be a correlation between the number of juvenile stoats caught per 100 trapnights and the number of mice found per 100 stoat guts examined in summer. This was so ( $r_s = 0.70$ ,  $p < .05$ ; Figure 6). At Craigieburn, the production of young is probably influenced also by the availability of lagomorphs, the most important mammalian prey in that area in most years, but the sample of 5 summers from this area showed no correlation between production of young and incidence of lagomorphs alone.

For the analysis of food data, ages and sexes of stoats were pooled. The earlier work (King and Moody, in prep.) showed that female stoats ate significantly more mice than did males. The correlation between production of juveniles and number of mice eaten by females alone was also significant, but less so ( $r_s = 0.62$ ,  $p < .05$ ), perhaps because of increased random error introduced by using smaller samples.

#### Annual and Local Variation in Fecundity of Stoats

Fecundity of female stoats may be estimated from counts of corpora lutea in ovaries of animals of all ages collected from December to July inclusive, the main period of delayed implantation. All but 3 of the 300 females examined carried corpora lutea of delay. Ovulation is apparently induced (Rowlands 1972); if so, all these females had been mated. The counts were conservative, i.e., they could be higher, but not lower. Only females with valid counts for both ovaries were included. No examples of polyovuly were observed.

Figures 7 and 8 show the frequency distribution of total numbers of corpora lutea per female between years for each area, and between areas controlling for density of mice. Juvenile stoats tended to be slightly

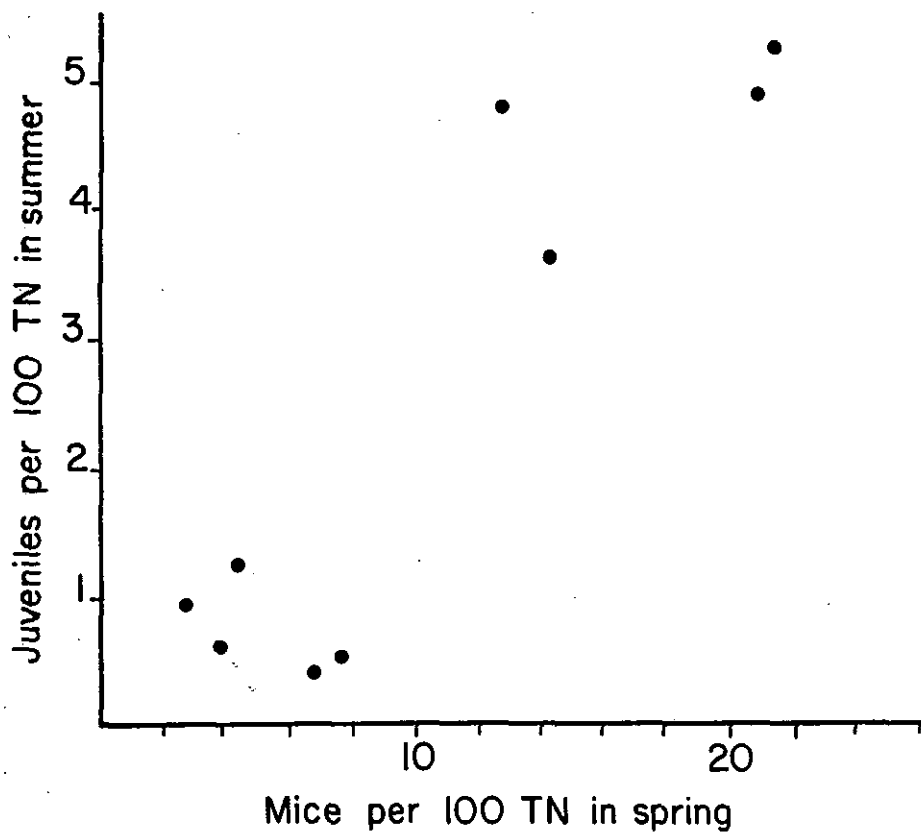


Figure 5. Relationship between the number of juvenile stoats caught per 100 trapnights in summer (December-January) and the number of mice caught per 100 trapnights in spring (November).  $r_s = 0.72$ ,  $p < 0.05$  Fiordland data only.

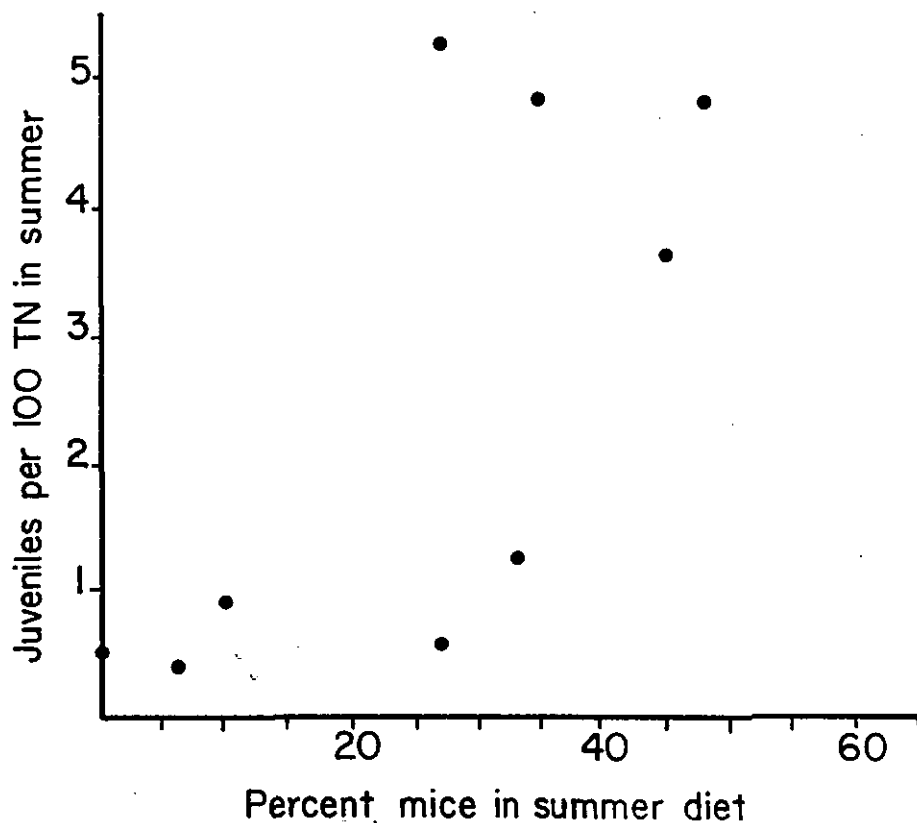


Figure 6. Relationship between the number of juvenile stoats caught per 100 trapnights in summer (December-January) and the percentage frequency of occurrence of mice in the guts of stoats of all ages during the same period.  $r_s = 0.70$ ,  $p < 0.05$ . Fiordland data only.

REPRODUCTION OF NEW ZEALAND STOATS

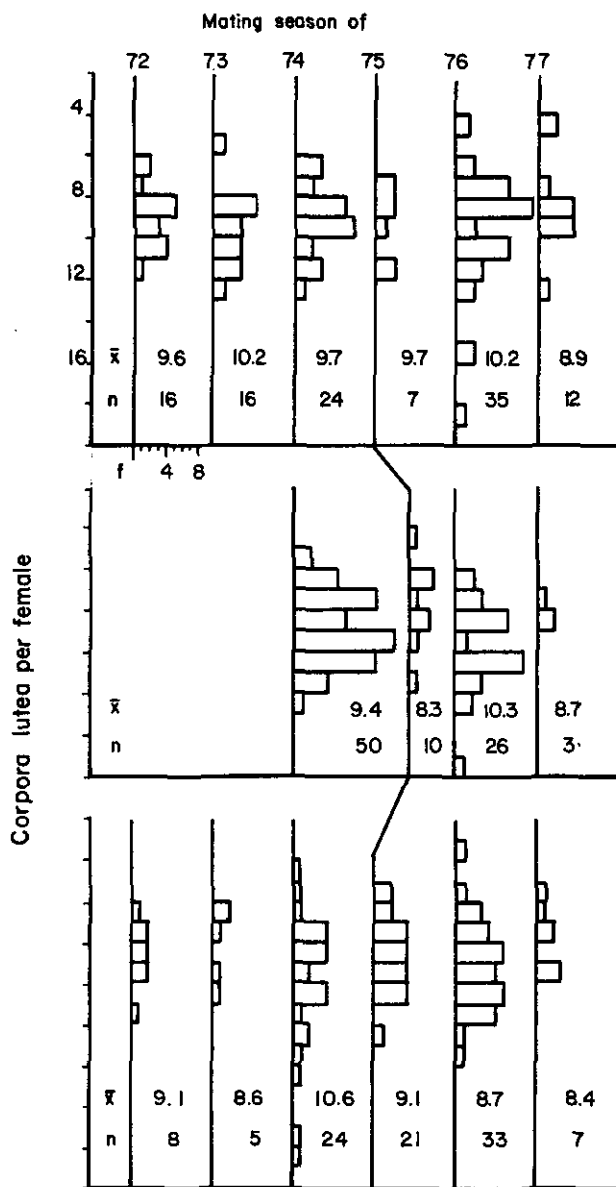


Figure 7. Annual variation in fecundity of females, all ages pooled. Upper = Eglinton Valley. Middle = Hollyford Valley. Lower = Craigieburn. Kruskal Wallis analyses of variance gave values for H of 2.86 (NS), 8.10 (.05 > p > .025), and 5.76 (NS), respectively.

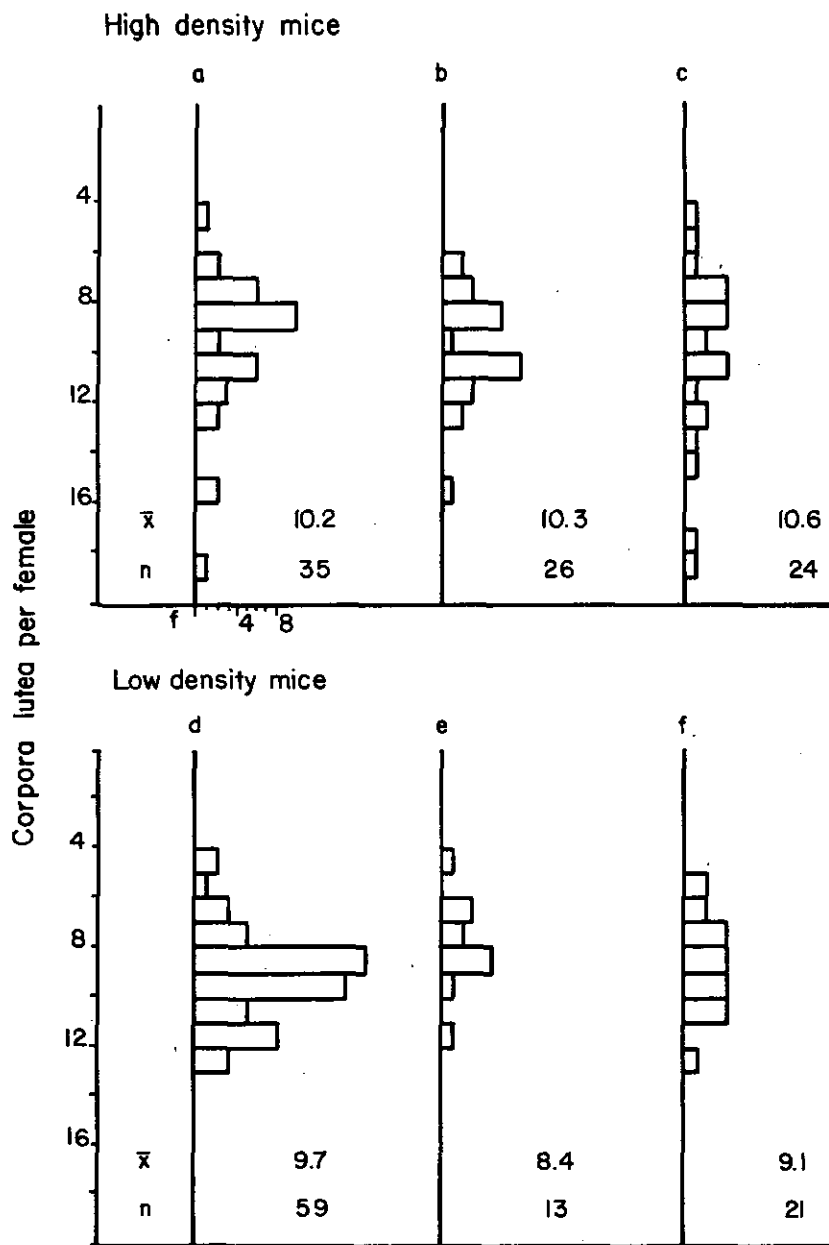


Figure 8. Local variation in fecundity of females, all ages pooled, controlling for density of mice. (a) Eglinton Valley 1976; (b) Hollyford Valley 1975, 77; (f) Craigieburn 1975. Kruskal Wallis analysis of variance gave values for H of 0.39 (NS) for the upper set, and 6.64 ( $0.05 > p > 0.25$ ) for the lower set.

more fecund than adults, but not significantly (in 5 of 7 year/area comparisons with  $n > 3$ , juveniles had more corpora lutea;  $p = .227$ , one-tailed signs test). Ages were therefore pooled in Figures 7 and 8.

The mean fecundity varied relatively little between years and areas. The mean in 16 annual samples ranged only from 8.3 to 10.6 corpora lutea per female. There was no significant variation between years in the Eglinton Valley and at Craigieburn, each with 6 yr samples. There was significant variation between the 4 yr in the Hollyford Valley, although in 1977, only 3 sets of corpora lutea were counted, and the result was not significant if this year was omitted. When mice were numerous in November, the mean in all areas was over 10 corpora lutea per female (due mainly to a few outlying individuals with exceptionally high counts) and not significantly different between areas. When mice were not numerous in November, means were lower and significantly more so in the Hollyford Valley (8.4 corpora lutea per female) than in the other 2 areas (9.1, 9.7 corpora lutea per female).

Deanesly (1935) also reported a general mean of 9.8 corpora lutea per female in delay. Considering the extent of variation between sample areas and conditions in Britain and New Zealand, this consistency is remarkable. The inverse relationship between counts of corpora lutea in the 2 ovaries of 1 individual, shown by King and Moody (in prep.), suggests a physiological mechanism for regulating the number of ova produced which is a fairly constant characteristic of stoats in the temperate habitats of Britain and New Zealand.

The mean number of corpora lutea released per female in October - November each year is significantly correlated with the density index of mice in the same November ( $r_s = 0.64$ ,  $p < .05$ ; Figure 9). (The implied associate correlation between fecundity and consumption of mice in spring could not be tested, because few gut samples of stoats could be collected in spring.) However, there was no correlation between the number of corpora lutea shed and the number of juveniles per 100 trapnights caught 13 - 16 months later ( $r_s = -0.21$ ,  $p > .05$ ). Annual variations in fecundity do not therefore explain the peaks in production of juveniles shown in Figure 3.

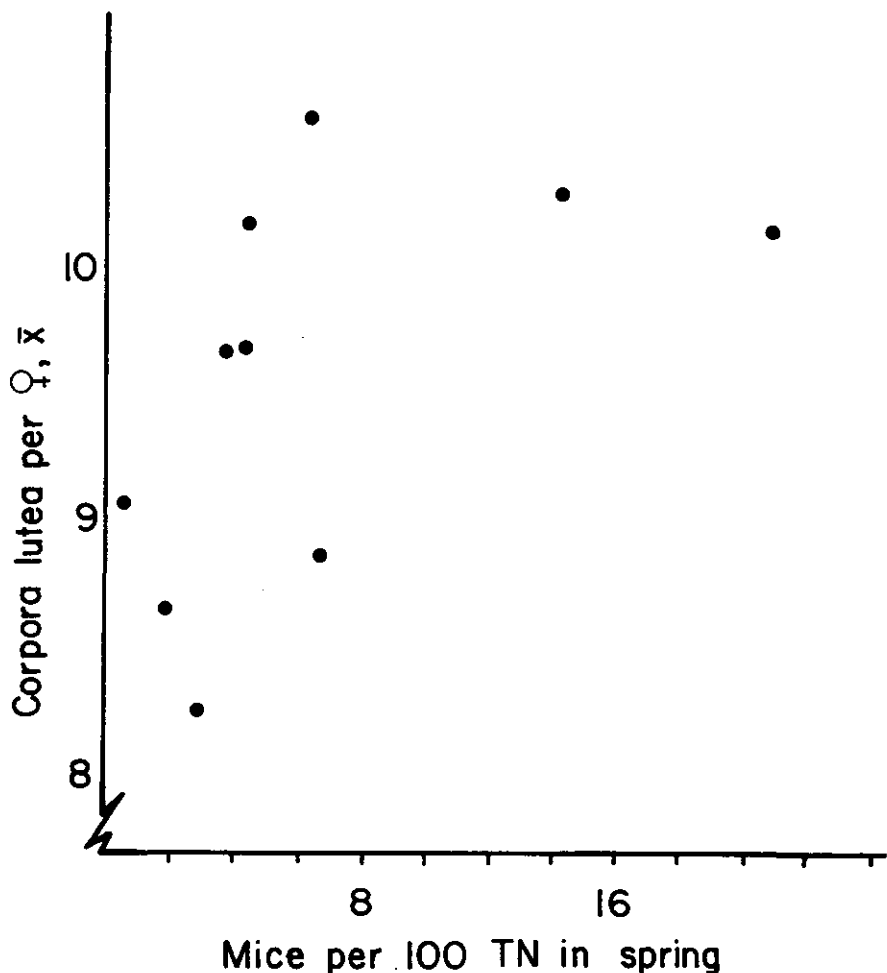


Figure 9. Relationship between the mean fecundity of females (mean number of corpora lutea, released in October or November) and the number of mice caught per 100 trapnights in November (spring).  $r_s = 0.64$ ,  $p < .05$ . Means are for 5 seasons in the Eglinton (1972-77), 3<sup>s</sup> in Hollyford (1975-77) and 2 at Craighieburn (1974-75). Note added in proof: Means of 10.6 and 13.6 corpora lutea per female for the 1979 mating season in the Eglinton and Hollyford, respectively ( $n = 8$  and 5), raise this correlation to  $r_s = 0.75$ ,  $p < .01$ ,  $n = 12$ ).

## Annual Variation in Fertility of Stoats

Since the maximum potential number of young that can be produced each year is set in the previous year, fertility can be adjusted only by reduction. Even in optimum years, larger and/or additional litters are ruled out. Some reduction probably occurs in most years. King and Moody (in prep.) report 13 pregnancies among 528 female stoats examined in 1972 - 1976. In 11 of these (including 4 from Fiordland and Craigieburn), there was a total of 113 corpora lutea, but only 98 embryos, of which 12 were resorbing. At least 1 resorption was observed in 42 percent of litters. Hence, there was an average 13 percent loss from ovulation to implantation and 12 percent from implantation to parturition. Deanesly (1935) gives data for British stoats from which equivalent figures of 20 percent and 5 percent can be derived. There were too few pregnancies to compare with mouse densities, but the data suggest that partial intrauterine loss is a common occurrence in stoats.

The most drastic reduction of all is total failure of implantation or total resorption, but this probably happens only in seasons when food is exceptionally scarce. There was some evidence of total failure of reproduction in the "crash" years which follow peak years for mice. Definite "crash" years were 1975 at Craigieburn and 1977 in Fiordland (Figure 2). Also, over most of New Zealand, 1971 was a peak year for mice; collecting for stoats began in 1972 in 2 beech forests north of Craigieburn, Nelson Lakes, and Arthur's Pass National Parks, continuing to 1976. There are therefore samples of stoats available from "crash" years in 4 areas, all in beech forests in the South Island.

The reproductive cycle of female stoats is quite well synchronized (King and Moody in prep.). Females collected in September, October, and November which are about to produce or have already successfully produced a litter can be classified as pregnant or lactating. Females which have failed to produce a litter this season are those which are not pregnant in September or October, or not lactating in November, when other females from the same areas and months are so classified. The reproductive success of females collected in September which are still in late delay or at the preimplantation stage cannot be assessed.

A total of 34 female stoats was collected in September, October, and November in the 4 South Island beech forests. Of 15 collected in average or good years (Fiordland 1973 - 1976, 1978; Craigieburn 1973, 1976; Nelson Lakes 1973 - 1976; Arthur's Pass 1973 - 1976), 7 successfully produced litters, 8 could not be assessed, and none failed. Of 19 collected in the same areas in "crash" years (Fiordland 1977; Craigieburn 1975; Nelson Lakes and Arthur's Pass both 1972), 2 successfully produced litters, 6 could not be assessed, and 11 failed. Hence, total failure of implantation or total resorption is possible in some individuals and could explain why, in some seasons, exceptionally low numbers of juveniles were caught (Figure 3).

#### Effect of Variation in Productivity on Breeding Density in the Following Year

Figure 10 plots the number of juveniles caught per 100 trapnights in summer (December - February) against the number of adults caught in the following spring (September - November) in the 2 Fiordland areas. The 1st season of trapping, when capture rate may be higher than average, was omitted; hence, the figure refers to regularly exploited population only. Although there are only 5 points, the correlation is quite close ( $r_s = 0.90$ ,  $p = 0.05$ ). The number of breeding adults caught in spring averaged 89.6 percent (range 82 - 91 percent) fewer than the number of juveniles caught per 100 trapnights in the previous summer. This does not imply that as many as 90 percent of young in the real population always die before spring. The density index of adults in spring will be an underestimate, since females are very difficult to catch at that season (King and Moody in prep.). However, if the figures are representative, they do imply that the survival of the young after independence is about the same regardless of the density of mice, perhaps by that age they are able to survive on other prey. The difference between a "good" and a "bad" production season would then be in the total number of young born, not the proportion of them surviving from independence to breeding.

At Craigieburn, the capture rate of adults in spring 1974 was exceptionally high (1.5 per 100 trapnights,  $n = 19$ , all males), whereas the production of juveniles in the previous summer, 1973 - 1974 had been low

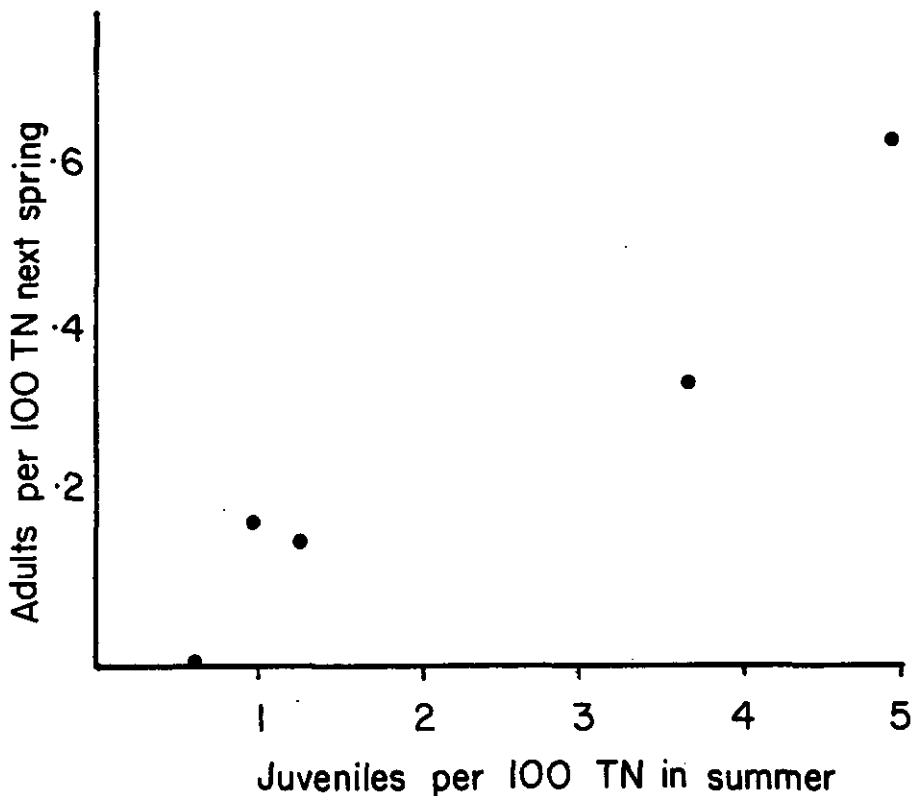


Figure 10. Relationship between the number of juveniles caught per 100 trapnights in summer (an index of the breeding success of the season) and the number of adults caught per 100 trapnights next spring (an index of the density of the breeding stock).  $r_s = 0.90$ ,  $p = 0.05$ , Fiordland data only.

(0.45 per 100 trapnights: Figure 3). The forest at Craigieburn is relatively small, without natural boundaries, and open to immigration from surrounding open country. Young breeding males tend to travel more widely in spring and in the spring of 1974, when mice were still numerous at Craigieburn (Figure 2), many male stoats were caught there which had almost certainly arrived since the breeding season of 1973 - 1974. The young stoats born in 2 later summers at Craigieburn (1975 - 1976, 1976 - 1977) disappeared at about the same rate (86 percent, 93 percent) as those in Fiordland. Data for 1974 - 1975 cannot be used because a change in trapping routine invalidated comparisons between December - February 1974 - 1975 and November 1975.

#### Variation in Other Breeding Characters

The age at maturity of both male and female stoats, and the timing and duration of the breeding season in a given district, vary rather little (King and Moody in prep). They appear to be virtually fixed characters scarcely affected by normal variation in food resources. The effect of good conditions on the survival of adults is unknown, since adult stoats cannot as yet be divided into year classes. There was some suggestion that relatively more females were caught in summers of low density (sex ratio  $49.3 \pm 5.9$  percent males,  $n = 71$ ) compared with high ( $60.6 \pm 3.7$  percent,  $n = 170$ ), but the difference was not significant ( $X^2 = 2.61$ , 1 df,  $p > 0.05$ : King 1980a).

## DISCUSSION

### The Reproductive Tactics of the Stoat

The optimum reproductive strategy of an animal is to assemble that combination of inherited reproductive traits, which together result in the greatest possible number of descendants to the individual possessing them. Strategies develop over the long term and the assembly of characters favored by selection can change only in evolutionary time. By contrast, the adjustment of reproductive effort to the probability of success is the business of short-term tactics, which change from year to year, within the range permitted by long term strategy, in response to

environmental conditions. Physiologists would use the terms ultimate and proximate factors to make the same distinction. By these definitions, this paper concerns only tactics. Questions of strategy such as the origin and adaptive value of delayed implantation must be discussed elsewhere.

The prolonged delayed implantation in stoats means that mating takes place about 9 - 10 months before the young are born: in fact, ovulation and parturition occur in different years. The maximum number of young that can be born this year is therefore set by the number of ova shed last year: what controls the actual number of young born this year? From the data presented in this paper, I propose the hypothesis that the productivity of stoats is controlled mainly by variation in the extent of intrauterine and/or nestling mortality. The initial fecundity (number of ova shed) is fairly constant, and high enough to provide the most young that could be reared in the best conditions likely to occur. In all other years, the number of young can be reduced at successive stages in the cycle as conditions dictate. By the time of implantation, 28 days before birth (Rowlands 1972), some environmental cue(s) will indicate to the female her chances of rearing the full potential number of young. If the chances are poor, the size of the litter can be reduced over the next few weeks, by failure of implantation or resorption. If conditions are very bad, the whole litter may be resorbed and some females may appear in spring with no sign of recent or impending pregnancy: in New Zealand beech forests, this was observed mainly in "crash" years after peaks of forest rodents. In non-forest or forest-edge habitats, variations in other prey, such as lagomorphs, may have the same effect. However, because of the difficulty of obtaining data on litter size, either before or after birth, there is as yet no way of determining whether intrauterine or nestling mortality has the greater effect on productivity.

This method of controlling productivity in stoats is made both necessary and possible by delayed implantation. Necessary, because even in optimum conditions, no additional reproductive effort can be made until next year; possible, because very little energy is invested in the blastocysts for 9 - 10 months, so very little is lost if few or none mature. It also means that the question of how stoats maximize their reproductive success

has to be reversed. The natural response to Figure 5 is "How do stoats increase productivity in good mouse years?" But fecundity is constantly high; the question should be "How and why do stoats produce so few young in poor mouse years?" As in studies of vole cycles, it is the declines that need explaining, not the increases.

Reproductive success for a female stoat consists of producing each year the greatest number of young that she can feed and educate at the least cost to her own prospects of surviving to the next breeding season. The slightly higher fecundity of females in good mouse years (Figure 9) is probably a simple physiological response to good nutritional condition; it is not adaptive, since it occurs a year too early to help the females to adjust their reproductive effort to the probability of success. The important cue must be presented in spring, during active gestation and lactation. It could be related to the overall nutritional condition of the female, or perhaps a more specific cue picked up during hunting.

If failure to breed is associated with very poor food supplies, the mean weights of stoats in "crash" years should be lower than in average or good years. This suggestion could not be tested from these data, because samples for the relevant period, late winter and spring, were usually very small (Figure 2) and the normal variance in body weight is very high (King and Moody in prep.). In coyotes (Canis latrans), depressed reproduction in a year of food scarcity was not reflected in reduced body weight of adults in winter and Clark (1972) concluded that the effect of poor condition on reproduction was likely to be more subtle than that.

Stoats eat a variety of prey (Figure 4); and in Fiordland, mice comprised, on average, only 25 percent in frequency and 14 percent in biomass (data for 1972 - 1976, in King and Moody in prep.). In seasons when mice were abundant, the frequency of occurrence of mice could reach over 70 percent. Much of the annual variation in productivity of stoats in Fiordland could be related to variation in the numbers of mice available in November. Similar disproportionate effects of small rodents on productivity are known in other predators with catholic tastes, e.g., foxes (Englund 1970) and harriers (Hamerstrom 1979), among others. Juvenile stoats require meat in small packages presented frequently, which their

parents can provide most easily when rodents are abundant. Larger prey, such as adult lagomorphs, may sustain the adult stoats, but are less easily carried to and cut up for the young. Hamerstrom (1979) suggested that, in good vole years, female harriers are more readily stimulated to breed by the frequent receipt of voles presented by their mates. Perhaps female stoats in spring are inhibited from resorbing embryos in proportion to the number of times a day they are stimulated by making a successful kill; or perhaps a female living mostly on mice in spring receives some nutritional or hormonal stimulus not received by a female eating the same biomass of meat from larger prey. The survival of nestling stoats could easily be more influenced by the density of mice than of any other prey, since mice are ideal food for young stoats: they are caught quickly and without risk by the hunting female, and are easily carried to and into the nest. In areas such as Craighieburn, where lagomorphs are a more important component of the diet of stoats than they are in Fiordland (found in 39 percent of guts, compared with 6 percent on average in all seasons pooled), the role of abundant, easily caught and carried prey is probably taken by nestling and juvenile rabbits and hares.

Goodman (1979) has shown, by a theoretical model, that if a change in environment affects the survival rate of adults less than that of dependent young, then reproductive effort should increase in good years and decrease in bad years. In other words, in a bad year, if the female herself has a higher chance of surviving to the next season than would any young she might produce now, her best plan would be to wait: in a good year, she should seize the chance to produce as many young as she can feed. This is what stoats appear to do, though we do not have the information on the relative survival rates of juveniles and adults needed to test Goodman's model.

Readshaw (1973) pointed out that the numerical response of predators to increased prey density has 2 components, reproductive and aggregative. The Fiordland stoats, collected from large, enclosed valleys, showed a reproductive response in 1976 - 1977 and 1979 - 1980. The Craighieburn stoats, collected from a relatively small remnant of forest, open to immigration on all sides, showed an aggregative response, at least in the

spring of 1974. However, we do not know if either was proportionate to the increase in mice.

Few previous studies are available with which the present data can be compared. Vershinin (1972) found that the fecundity of winter-caught stoats in Kamchatka decreased with the capture rate of voles in the previous summer; however, the figures he gives for the number of corpora lutea per female examined range from 2.6 to 5.0. Either Kamchatkan stoats are only half as fertile as New Zealand and British ones, or else Vershinin was quoting the number of corpora lutea per ovary, not per female. Aspisov and Popov (1940) found a significant positive correlation ( $r = 0.71 \pm 0.09$ ) between the harvests of skins of stoats and of water voles (Arvicola amphibius) in 34 year/area comparisons in various parts of Central Russia: Vershinin (1972) reported a 3 - 4 year fluctuation in the yield of stoat skins from Kamchatka, adding that the size of the catch is determined by the number of voles, and usually coincides with similar variations in the yield of sable.

#### Comparison with the Reproductive Tactics of Other Predators

The weasel (Mustela nivalis), like the stoat, is a specialized predator of small mammals, and the reproductive efforts of both are known to vary with the population fluctuations of their prey. However, the means by which they do so are quite different, as summarized below:

	<u>M. nivalis</u>	<u>M. erminea</u>
Fecundity	Lower (4-8)	Higher (6-13)
Earliest age at possible 1st littering	c. 3mn	12 mn
Delayed implantation	No	Yes
In good years	Extra summer litters produced by adults and precocious juveniles; +? increase in fecundity	Much of fixed high potential fecundity realized single large litter (ads only)

REPRODUCTION OF NEW ZEALAND STOATS

M. nivalis

M. erminea

In poor years	<u>Decrease</u> in fecundity and fertility of adults; no breeding by juveniles	<u>Increase</u> in intrauterine and nest mortality
Reference	Tapper 1979 King 1980b	King and Moody in prep. and this study

Most adults of other carnivores which, like the stoat, depend on unstable prey but are limited to 1 litter per year, also ovulate every season and then adjust productivity largely by mortality, e.g., Arctic fox (MacPherson 1969) and lynx (Brand et al. 1976). However, these species may also reduce the proportion of young females fecund in bad years, as the weasel does; but the stoat, at least in temperate climates, cannot do this since virtually all young females are fecund in every year.

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