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Variation in body size, sexual dimorphism and age-specific survival in stoats, *Mustela erminea* (Mammalia: Carnivora), with fluctuating food supplies

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Most hypotheses attempting to explain the evolution of pronounced sexual dimorphism in body size in the three species of weasels (*Mustela erminea*, *M. frenata*, *M. nivalis*) assume that sexual dimorphism is a long-term adaptation, associated with the different reproductive strategies of the two sexes. We here examine an auxiliary hypothesis which predicts that the degree of sexual dimorphism may also vary over the short-term, because when food is temporarily abundant, sexual selection should favour a greater growth rate of males than of females. This hypothesis concerns a phenotypic response which could introduce temporarily increased variation into an existing genotypic trait. We document the present size and sexual dimorphism of stoats introduced last century to New Zealand from Britain in relation to between-year variation in food supply in a single habitat (forests of southern beech, *Nothofagus* sp.). Southern beech trees produce heavy crops of flowers and seed at 3–5 year intervals, which are associated with very variable supplies of important prey of stoats, including several species of seed-eating birds, litter-feeding insects, and feral house mice (*Mus musculus*). Alternative prey are scarce. Regressions of condylobasal length and head-body length on mouse population indices were significant in both sexes. Mean condylobasal length was larger in both male and female stoats born after a heavy seedfall compared with those born in non-seedfall years. However, the largest males born in years of heavy seedfall were removed by selective mortality before the age of 3 years, so the condylobasal lengths for old (≥ 3.0 yr) males converged on a common mean regardless of food supply in their birth year. Sexual dimorphism did not vary with food supplies (as reflected in seedfall records or mouse population indices) at any age. First-year survivorship, at least from the age of independence, was significantly negatively correlated with density of stoats in the summer of their birth year.

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ADDITIONAL KEY WORDS:—nutrition – ‘silver spoon’ effect – growth rate – age-specific mortality, fecundity – *Mus musculus* – New Zealand – density-dependent survival.

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INTRODUCTION

In their native ranges in the Holarctic, the three species of weasels (*Mustela erminea* L., *M. nivalis* L., *M. fennata* Lichtenstein, defined in King [1989b] and their close relatives vary extensively in body size and degree of sexual dimorphism. Many authors have attempted to find patterns in this variation, most recently Ralls & Harvey (1985), Holmes (1987), Eger (1990), Meia (1990), van Zyll de Jong (1992) and Dayan & Simberloff (1994). The general pattern suggests that where the local prey are large, weasels tend to be large, especially the males (Erlinge, 1987; King, 1991a). In northern climates with cold air temperatures and severe windchill in winter, however, small weasels are better able to hunt and to nest under the shelter of the snow, and this appears to limit the sizes of males in such environments (Kopein, 1969; King, 1989a, 1991a). On the other hand, general hypotheses do not explain all the observed variation, not least because the diversity of local conditions could not be accommodated appropriately in the large-scale analyses performed so far.

After an extensive review and investigation, Ralls & Harvey (1985) concluded that "geographic variation in size [and dimorphism] probably results from the interaction of local environment conditions and genetic differences among populations. . . . Female size may be correlated with an appropriate measure of prey size. Male size covaries with female size and, therefore, may be partly related to prey size. However . . . the extent to which males are larger than females may depend on the environmental potential for polygyny . . . and on the amount of food available during the period of rapid growth of young males." This flexibility probably explains

why recent analyses suggest that neither prey size nor ecological energetics alone can explain variations in weasel body size (Sandell, 1989; King, 1991a, cf. Erlinge, 1987).

Sexual dimorphism in weasels is usually attributed at least in part to different strategies of growth and reproduction in the two sexes. The full potential size of males is presumably set by long-term sexual selection; but field data collected by Powell (1979), and the conclusions of Ralls & Harvey (1985), suggest that the capacity of individual young males to grow to their full size may be affected by short-term variations in prey abundance. Maximum size for females, in contrast, appears to be set by the energy requirements of reproduction (Moors, 1974, 1980) or by the sizes of the burrows used by prey (Simms, 1979), rather than by food supplies during growth. Consequently, variation in nutritional status during the period of growth is predicted to have different consequences for males and females (Clutton-Brock, 1991). The logical consequence is that the mean body size of adult males, and the extent of sexual dimorphism, should vary positively, both among populations and among cohorts within a single population, with the abundance of prey during the period of growth. This is the hypothesis we have tested.

Limited observations conform to this prediction. In laboratory-reared litters of common weasels (*M. nivalis*), young males fed *ad libitum* grow larger than their wild counterparts to a much greater degree than do females (East & Lockie, 1964; Hayward, 1983). Conversely, Erlinge (1983) reported a significantly lower average weight for juvenile male stoats (*M. erminea*) born in 1976, a year of poor food supplies for rodent predators in his study area. Arctic foxes (*Alopex lagopus*), which are even more dependent on fluctuating supplies of rodents than are any temperate predators, show variation in juvenile body size correlated with fox numbers, breeding success and rodent populations (Ramesky, 1983). Artificial feeding at dens significantly increased the body weight and short-term survival of arctic fox pups, but not their long-term survival (Tannenfeldt, Angerbjörn & Arvidson, 1994). To our knowledge, ours is the first ontogenetic study of these effects on wild stoats (S. Erlinge, pers. comm.).

Southern beech (*Nothofagus* spp.) forests in New Zealand are subject to occasional population irruptions of feral house mice (*Mus musculus*) following periodic heavy seedfalls and the associated flush of forest insects and birds (King, 1983; Murphy & Dowding, 1995; Fitzgerald *et al.*, 1996). Irruption years offer a temporary bonanza of food for stoats living in beech forests, which stimulates strong functional and numerical responses (King, 1983; Murphy & Dowding, 1995). These irruptions offer the opportunity to test the clear prediction of our hypothesis: male stoats born in beech forests during years of beech seedfall when food is abundant should grow larger than males born in the same forests during non-seedfall years. The same variation in food supply during growth should have less effect on females (1) because they are much smaller than males, so they need less food to reach full size and (2) because their maximum size may be genetically determined by, or at least more clearly linked to, their energy output as breeding adults rather than their energy intake during growth. We predict that, in southern beech forests the body sizes of male stoats (but not females), and sexual dimorphism, will show short-term variations linked with variation in food supplies as a result of a sex-specific phenotypic response to the nutritional status of each cohort during the period of juvenile dependency. This is the only hypothesis on sexual dimorphism we know of that can be tested directly from ecological data.

Kozłowski (1989) noted that questions about sexual dimorphism cannot be considered properly without reference to the whole life history of the species concerned. King (1989b) summarized the life history characteristics of stoats, of which three are pertinent here. (1) Unequal parental investment in the two sexes of young: males grow faster than females and are already larger than females by the end of the period of parental care at age 2–3 months, so males should be more expensive to raise than females. (2) Bimaturism: females are reproductively mature a year earlier than are males. (3) Heterochrony: skulls of males continue to grow and to develop through ages beyond the cessation of growth in females. Consequently, skulls of mature males are not merely large versions of skulls of females the same age (Petrov, 1956; King & Moody, 1982). Mean expected lifetime reproductive success for newborns of each sex should also influence the development of dimorphism (Kozłowski, 1989), but reproductive success has never been measured in any species of *Mustela*. The large annual variation in numbers of young females available for mating (i.e. the operational sex ratio: Madsen & Shine, 1993) should also affect sexual dimorphism. The significance of these potentially important life history characteristics of stoats is unknown.

Our prediction that sexual dimorphism changes in response to changes in food abundance during the period of growth assumes sexual selection for large size in male stoats and associated reproductive advantages for large males. Male stoats born during food abundance are assumed to be more likely to grow to the full potential size set by their genotype, and they should experience a lifetime advantage over males born during food scarcity. Grafen (1988) has labelled this the 'silver spoon effect'. Unfortunately, the literature offers no information on whether such advantages or disadvantages exist in *Mustela* spp, largely because weasels present several serious obstacles to field investigators (King, 1989b). Our data allow testing for indirect evidence of a 'silver spoon' effect from calculations of survivorship of stoats born during poor and good food regimes. We also documented the fecundity of females in relation to food availability during growth.

THE STOAT IN NEW ZEALAND

In the 1880s, stoats were introduced to New Zealand in an unsuccessful effort to control excessive populations of European rabbits (*Oryctolagus cuniculus*; King, 1989b, 1990). The environment for stoats in New Zealand differs from any in the northern hemisphere. The only small vertebrate prey (<50 g) available are feral house mice, and when they are abundant, female stoats kill mice more often than do males (King & Moody, 1982; King, 1989b; 1991a). Most of the time, however, female stoats in New Zealand must kill large prey (rabbits and ship rats [*Rattus rattus*]) as often as do males.

Mice become very abundant in southern beech forests from the winter after a heavy seedfall to the following autumn. The most important alternative prey of stoats in beech forests, birds and insects, also increase in abundance after seedfalls (Murphy & Dowding, 1995; Elliott, Dilks & O'Donnell, 1996; Fitzgerald *et al.*, 1996). Post-seedfall population irruptions of mice are an easily-monitored indicator of these linked changes in food supply of stoats, which collectively have disproportionate effects on stoat productivity and population dynamics (King, 1983) and the probability

of their infestation with *skrjabingylosis*, a nematode disease (King, 1991b). During the summer after a seedfall, stoat populations in beech forests may increase by a factor of 3–5.

After a hundred generations, stoats in New Zealand have become slightly larger on average than their British ancestors, but not equally so in both sexes or in all habitats (King & Moody, 1982; King, 1991a). Hence, our study was confined to one habitat, southern beech forest. Condylbasal lengths of skulls of stoats also vary extensively and geographically in New Zealand, closely linked to variation in habitat and prey size (King, 1989a, 1991a; King & Moody, 1982) and almost matching the variation found across continental Europe (Stubbe, 1978). We do not know whether this variation has a genetic basis or is environmental in origin; we know only that it is very consistent, appearing in both adults and young and even across short geographic distances.

In different parts of the Holarctic, sexual dimorphism in body size of stoats (male-female/female $\times 100$) reaches 65% or more in weight and 15% or more in linear measures (Erlinge, 1979; Holmes, 1987; King, 1989b; Moors, 1974, 1980; Powell, 1979; Ralls & Harvey, 1985). Current data suggest that average dimorphism in body weight is presently about 54% in Britain and 57% in New Zealand, implying a possible slight increase in dimorphism among the New Zealand descendants of the British colonizers (King, 1991a). By contrast, sexual dimorphism in condylbasal lengths of skulls averages slightly less in New Zealand than in Britain (mean 9.6% cf 10.7%) but ranges from 6.5% to 12.0% in local New Zealand populations. As in Holarctic populations of common weasels (van Zyll de Jong, 1992), the New Zealand populations of stoats with the largest males tend to show the largest dimorphism, but the local and temporal variation is enormous and not necessarily the same in all measures of body size.

STUDY AREAS

We collected samples of stoats and mice from three relatively undisturbed forests in the *Eglinton and Hollyford Valleys*, both in *Fiordland National Park*, and in *Craigieburn Forest Park* in Canterbury. All are in the South Island of New Zealand (Fig. 1) and all contain or are dominated by southern beech. The trapping area on the Hollyford Valley floor has only scattered beech trees, so this area was classified among the podocarp forests by King & Moody (1982) and King (1991a), but the solid beech forests on the valley sides and in adjacent valleys strongly influenced the biology of the stoats and mice we sampled. Full descriptions of the study areas were presented by King (1983).

Records of annual beech seedfall in the vicinity of our rodent traps at Craigieburn for the years 1965–88 were published by Allen & Platt (1990), and for the Eglinton and Hollyford Valleys for 1974–7 and 1979 by King (1983, see also Burrows & Allen 1991). The year 1971 was one of huge seedfall throughout the country; 1970, 1972 and 1973 were poor in Fiordland. Hence, the seedfall status of the birth year is known for all stoats except those born before 1964 at Craigieburn and before 1969 in Fiordland, which were deleted from all analyses of seedfall effects.

Some local inconsistencies have been noted in the recorded associations between counts of seedfall and mice and the responses of the stoats, but the general correlation

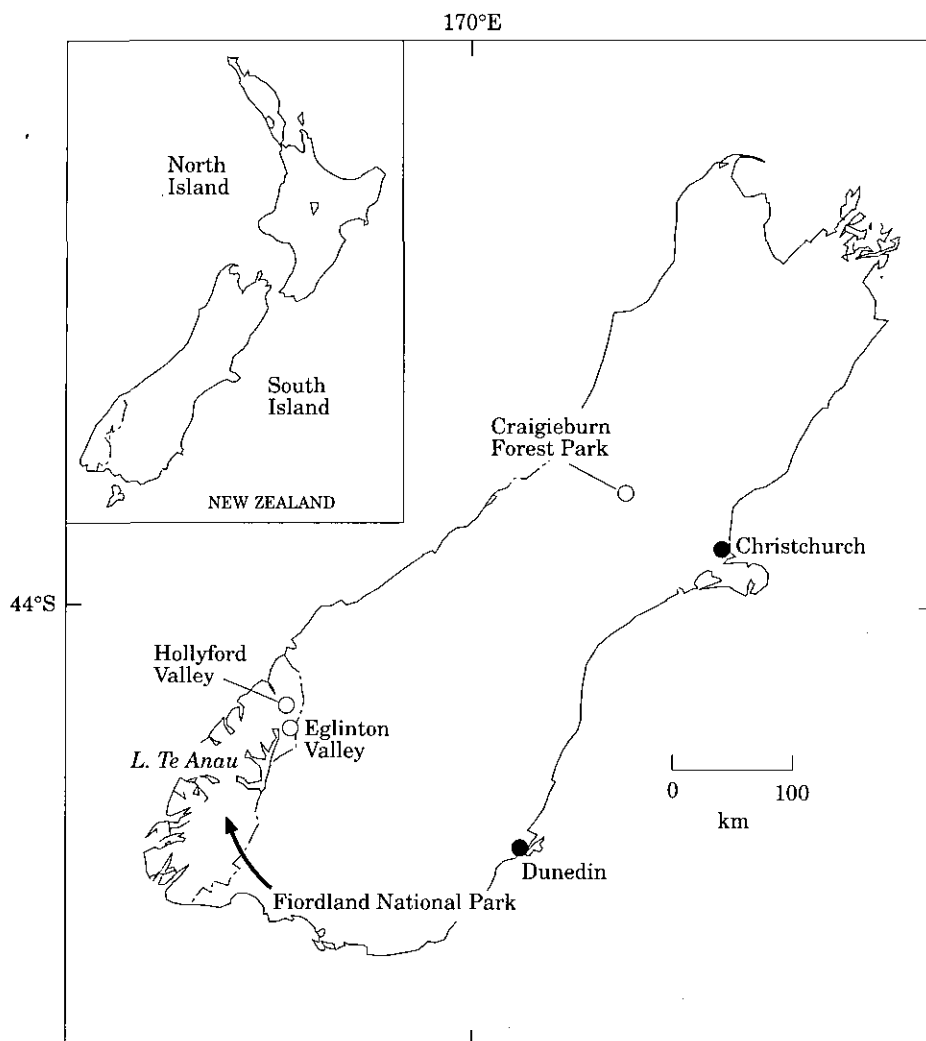


Figure 1. Map of the study areas. The Eglinton and Hollyford valleys (referred to together as the Fiordland study areas) are connected by a pass at 549m (below tree line) across the main divide of the Southern Alps.

is very reliable. A heavy seedfall is now always taken by the New Zealand Department of Conservation as a dependable warning of an irruption of stoats in the following summer, and, where necessary, as a cue to implement expensive predator control measures for the protection of threatened species in beech forests (O'Donnell & Phillipson, 1996). In our study, we used this correlation to reconstruct from seedfall records the history of variation in food supplies for stoats, since past years of heavy seedfall can be assumed with confidence to have been years of high densities of mice.

MATERIAL AND METHODS

Field observations

Mouse population data are available for all or part of four summer seasons (1974–7) at Craigieburn, six (1973–7, 1979) in the Eglinton Valley and four (1975–7, 1979) in the Hollyford Valley (King, 1982). Full details of the methods used to catch and to measure both stoats and mice, and to calculate their population indices and reproduction rates, were presented by King (1982, 1983).

From 1972 through 1978, stoats were collected only in humane Fenn traps, set in transects 7–20 km long and averaging 400 m apart (King & Edgar, 1977; King, 1980, 1983). Unbaited stoat traps catch at a significantly lower rate than do baited ones (King & Edgar, 1977), so the populations at Craigieburn (unbaited) and in Fiordland (baited with fish-based catfood) were probably sampled at different levels. We, therefore, controlled for site in all analyses for which site differences existed.

From 20 November 1979 to 1 February 1980 (excluding December 15–31), baited live traps were set for 4 days a week at the established Fenn trap sites in Fiordland, averaging 48 sites in the Eglinton Valley and 40 in the Hollyford. Until the end of January, live-trapped stoats can be separated into two classes: young of the year and adults (criteria described by King & McMillan, 1982). The ages of the live-trapped adults could not be estimated. Altogether, 134 stoats were caught and tagged, of which 86% were young of the year (King & McMillan, 1982). The first field record of body weight for each live-trapped individual was added to the carcass data as the equivalent of a Fenn-trap record. In addition, the weight records of all recaptured young of the year were analysed separately to document possible weight changes through the month of January 1980. No live-trapping was done at Craigieburn.

Laboratory

All animals collected were processed as described by King & Moody (1982). The serial sectioning of ovaries had to be discontinued after April 1976, so only 289 of the 364 female carcasses included in this study provided age-specific data on both fecundity and longevity. The final sample sizes were 665 carcasses plus 211 capture-recapture records from live-trapped stoats. We could not use data from all individuals in all analyses, however.

Using a collection of canine cementum sections of wild Fiordland stoats of known ages (Grue & King, 1984), Helen Grue estimated the ages of all Fenn-trapped males over 10 months of age and all females over 6 months. To check that the cementum readings were correct, Grue read the slides 'blind' a second time a year later. Since accurate estimation of age was crucial to our study, King (1991c) made exhaustive checks of the ages assigned, by extensive comparisons with other methods including data on reproductive condition, and eliminated any doubtful individuals (10% of 136 adults from Craigieburn and 1% of the 287 adults from Fiordland) from analysis.

In southern New Zealand, most young stoats are born in October (King & Moody, 1982) and first venture out of the nest in family parties in late November. We calculated the ages of all stoats in months assuming a mean birth date of 1 October. Few young are caught before mid-December, so age structures derived

from our material exclude all individuals that died before the age of independent dispersal (2–3 months).

Young female stoats reach puberty at under 2 months and males at about 10 months (King & Moody, 1982). Since both sexes reach full size about 3–4 months after puberty, stoats of opposite sex complete their growth at different ages and have very different reproductive strategies (King, 1989b). For this study, we defined three growth classes. (1) Growing stoats: individuals that had not yet completed physical growth, i.e. females collected within 6 months of birth, and males collected within 15 months. We avoided the term 'young' for these animals because that term was defined differently by King & Moody (1982). (2) Fullgrown stoats: females 7–35 months old and males 16–35 months old. (3) Old stoats: males and females 36 months or older.

We recorded whole body weights, head-and-body lengths (body length) and condylobasal lengths of skulls (skull length) from carcasses, and body weights from live-trapped stoats. We used the data from Fenn-trapped carcasses from all three study areas to investigate between-year variation in body sizes among cohorts in relation to the abundances of mice in the seasons of birth, either known (from mouse density estimates) or inferred (from the correlation with beech seedfall records). We also used body weights recorded from live-trapped stoats to investigate within-year variation in body sizes of one cohort born in spring 1979 and observed during the summer of 1979–80, when mice were exceptionally abundant in Fiordland.

For some analyses, we allocated individuals to one of two categories of skull size, defined from the long-term mean skull length for each sex and study site. The category 'Large males' included males from Craigieburn measuring >50.9 mm plus those from the Eglinton >50.5 mm plus those from the Hollyford >49.4 mm, and the category 'Small males' included all those with skull lengths less than or equal to each local threshold. The thresholds defining 'Large females' were >46.4 mm, >46.7 mm and >45.4 mm, respectively.

We did not use canine width as a measure of body size, as suggested by Dayan *et al.* (1989) and Dayan & Simberloff (1994), because it was not relevant for our study. Dayan's team investigated niche divergence and community structure, and used canine width as a measure of long-term character displacement within a multispecies carnivore guild. By contrast, we investigated the contrasting growth and survivorship of the two sexes of one species, and we used body and skull sizes as measures of the short-term morphological consequences of temporary variations in resources for that species. Dayan *et al.* needed to measure a fixed character, and assumed that canine width was fixed. We needed variable characters, which body measurements certainly are.

Statistical treatments

Our analyses are based on the proposition that high beech seedfall counts and high mouse population indices are both effective indicators of favorable food conditions for young stoats. We deduced the birth years of stoats from cementum annuli and capture dates, and analysed body sizes and survival of stoats with respect to each of the two indices of food supply in the year of birth. First, we analysed stoat sizes with respect to mouse density indices during growth. Second, we compared the sizes and survival of stoats born after a heavy seedfall (associated with high

mouse densities) and in non-seedfall years. Using seedfall data allowed us to increase our sample size to include the years before the mouse population records began.

For those cohorts born in years for which we had mouse population indices (expressed as captures per 100 trapnights, C/100TN, corrected for unavailable traps [King, 1982 plus errata, 1983]) we regressed (SAS, 1985) body size measures for stoats of each sex, and indices for sexual dimorphism, against the mean mouse population index taken during the first two trapping periods of a young stoat's life (trapping done in November and February). For those cohorts born in years for which we had records of beech seedfall, we used SAS (1985) GLM (General Linear Model, equivalent to ANOVA but able to accommodate unbalanced sample sizes) to test whether body size measures and sexual dimorphism indices varied with seedfall in the year of birth. We used a 4-way GLM to test whether each measure of body size varied with beech seedfall blocked by site, growth class and sex. The advantage of this procedure is that it had the power to test each variable independently of all the others, thus minimizing the risk of finding spurious significance in many small tests. Site, growth class and sex each contributed significantly to the overall variation. We therefore used further, smaller tests to investigate how size varied among the sites, growth classes and sexes.

For all three measures of body size and all three growth classes of stoats born from 1966 through 1977, and for live bodyweights of growing stoats born in 1979, we explored the variation in sexual dimorphism using both ratios and residuals. Ratios between male and female means have been used widely to index sexual dimorphism in body size, but Ranta, Laurila & Elmberg (1994) showed that ratios are appropriate only if the size measures for the two sexes are isometric, i.e. if a linear regression of either one against the other passes through the origin. For each measure of size, we regressed the mean for males of each growth class for each year and site on the corresponding mean for females. We then tested (GLM) whether the residuals differed between years of high and low beech seedfall and also whether the residuals varied among growth classes (Ranta *et al.*, 1994). Regressions of the female size data on the male data gave appropriately identical results.

Mean body weights and lengths were isometric in the two sexes, so both regression analyses and proportional ratio indices of sexual dimorphism were appropriate. We calculated proportional ratios, from the local means for (male-female)/female, because they are intuitive, directional and properly scaled for species in which the male is always the larger sex (Lovich & Gibbons, 1992). The simple ratio, used by many previous authors (the mean measure for males divided by that for females), behaved in the same manner.

The skull length data were not isometric, so only the regression analyses were appropriate to investigate sexual dimorphism of skull length. To allow comparisons with other studies, however, we calculated (but did not use in analyses) ratio indices for condylobasal length.

The frequency distributions of the three measures of body size, partitioned by sex, growth class, site and seedfall (high or low) did not differ from normal; nor did the frequency distributions of the indices of sexual dimorphism. Sample sizes are given in Tables 2-4.

Using the regression and GLM procedures described for analyses of stoat sizes, we also investigated the relationships between indices of sexual dimorphism for a given cohort and (1) estimated mouse density during the 6 months following birth and (2) beech seedfall (high or low).

For analyses of survivorship, we used only the Fenn-trapped stoats collected in 1972–8. We first tested (Chi-square) whether the age structure of the raw data for males and females captured were the same at each study site. We then tested (GLM) for differences among study areas and for differences between stoats born in years of high or low beech seedfall in the mean age (in months) of members of each sex (mean ages transformed to meet assumption of normality). Most beech seeds fall in March–June, so, for example, stoats of the seedfall year cohort of 1976 were born in October 1976 following the seedfall of March–June 1976, and entered the traps in large numbers over the summer of 1976–77 (King, 1983).

We assumed that the distribution of ages among the animals trapped was the same as that in the living population (Caughley, 1977: 93; King, 1989b: 173). Our observations showed (King, 1980; King & McMillan, 1982) that trapping became selective when the spacing between traps exceeded 800 m. Hence, we excluded from the analyses of survivorship the earliest samples from the Eglinton Valley, dated from November 1972 to June 1974, when trap spacing averaged 2.1 km. Age-specific fecundity data from females caught then are included.

For each cohort of stoats at each study site, we estimated p_x , the proportion of animals known to have been alive at age x and that survived to age $x+1$, using Caughley's (1977) Method 4, which does not require that $r=0$. Caughley cautioned that use of this method for cohorts not sampled with equal intensity each year can introduce errors in estimates of p_x . We estimated p_x separately for each cohort, thereby deriving a mean and variance for each estimated p_x . Our analyses therefore incorporated sampling error for p_x . G.C. Caughley (pers. comm.) concurred with our approach.

We calculated p_x separately for each sex, site and seedfall class (high or low), and tested (GLM) for differences in p_x due to seedfall, blocked by sex and site. Finally, we averaged p_x over all cohorts to develop l_x and q_x tables. This method avoided the two worst problems of analysis of fluctuating populations having great variation in cohort size: (1) that the rate of increase is never 0, and (2) that life tables calculated on the basis of individuals give undue influence to the members of large cohorts at the expense of those of small cohorts. Both corrections are particularly important in any analysis of our data.

We entered the live-capture data into the program CR (Cezilly *et al.*, 1993) to make independent estimates of survival and recapture probabilities of the cohort of young stoats born in 1979. By dividing the records into subcategories, we compensated for the significant inequality in the willingness to enter traps of individuals of different ages and sexes noted by King & McMillan (1982).

RESULTS

Body size in relation to mouse population indices

Body size in both sexes consistently increased with increasing values of the mouse population index. Linear regressions of each size measure on mouse index were all positive, and were significant for body length and skull length of both sexes (Table 1). Confirmation was provided by linear multiple regressions for the two significant size measures on the mouse index, site (ranked by mean adult stoat sizes at each site) and age in months. The same comparisons for body weight were not significant,

with or without the additional data from live-trapped stoats weighed in summer 1979–80. Figure 2 shows the variation in the mouse density index in the three study areas, and its effect on skull lengths of growing males; Figure 3 compares the data for growing males and females by study area.

Body size in relation to beech seedfall records

Tables 2–4 provide the mean measurements (\pm SE) of stoats of each sex and growth class at each site according to seedfall class. Skull lengths of stoats varied significantly with beech seedfall ($P < 0.0001$, GLM blocked by site, sex and growth class; Table 5). Blocking contributed significantly to the test for all three blocked variables: site ($P < 0.0001$), sex ($P < 0.0001$), growth class ($P < 0.03$). No significant relationships existed between beech seedfall and either body weight or length, but both varied significantly with site, sex and growth class (all $P < 0.0001$, overall $P < 0.0001$). No interactions were significant.

For each size measure, growing females were significantly smaller ($P < 0.05$ LSD test blocked for seedfall) than fullgrown and old females; old females were somewhat smaller than fullgrown females but not significantly so. The same pattern held for body weights and lengths of males; but in skull length, growing and old males were both significantly smaller than fullgrown males ($P < 0.05$, LSD), though not significantly different from each other.

Separate analyses of males and females confirmed that both sexes born in seedfall years grew significantly larger in skull length whilst still in the first growth class than did those born in non-seedfall years ($P < 0.0001$, GLM). Fullgrown males born in seedfall years were still significantly larger in skull length than males of the same ages born in non-seedfall years, but old males born in seedfall and non-seedfall years did not differ in skull length (Fig. 4). Mean skull size for males declined between fullgrown and old ageclasses ($P < 0.01$, LSD). In females, the effects of birth in a seedfall year were no longer detectable in the mean skull length of either the fullgrown or old age classes.

Many more large males were caught in seedfall years than in non-seedfall years, but they disappeared far more rapidly. The distributions of ages at death for large and small males differed significantly both for those born in years of beech seedfall ($\chi^2 = 21.84$, $df = 3$, $P < 0.001$) and for those born in non-seedfall years ($\chi^2 = 20.02$, $df = 3$, $P < 0.001$). The same comparisons for females were not significant ($\chi^2 = 0.68$, 4.48 respectively, both $df = 3$ and $P > 0.05$).

Years of heavy seedfall, such as 1976 (and even more so, 1979: King 1983) are usually synchronized over very wide areas, but moderate seedfalls are more localized (e.g. 1974 was a seedyear in one area but not in the other two; Fig. 2). The variation in stoat body size therefore cannot be analysed merely with reference to a simple external factor such as climate.

Coefficients of variation

To learn whether there were patterns of variation in sizes of stoats differing between the sexes, between seedfall and non-seedfall years, among sites and among growth classes, that might affect our analyses, we calculated coefficients of variation (CV) for all three size measures. The CVs for skull length did not vary significantly in any comparison ($P > 0.05$, GLM). The CVs for body length differed between the

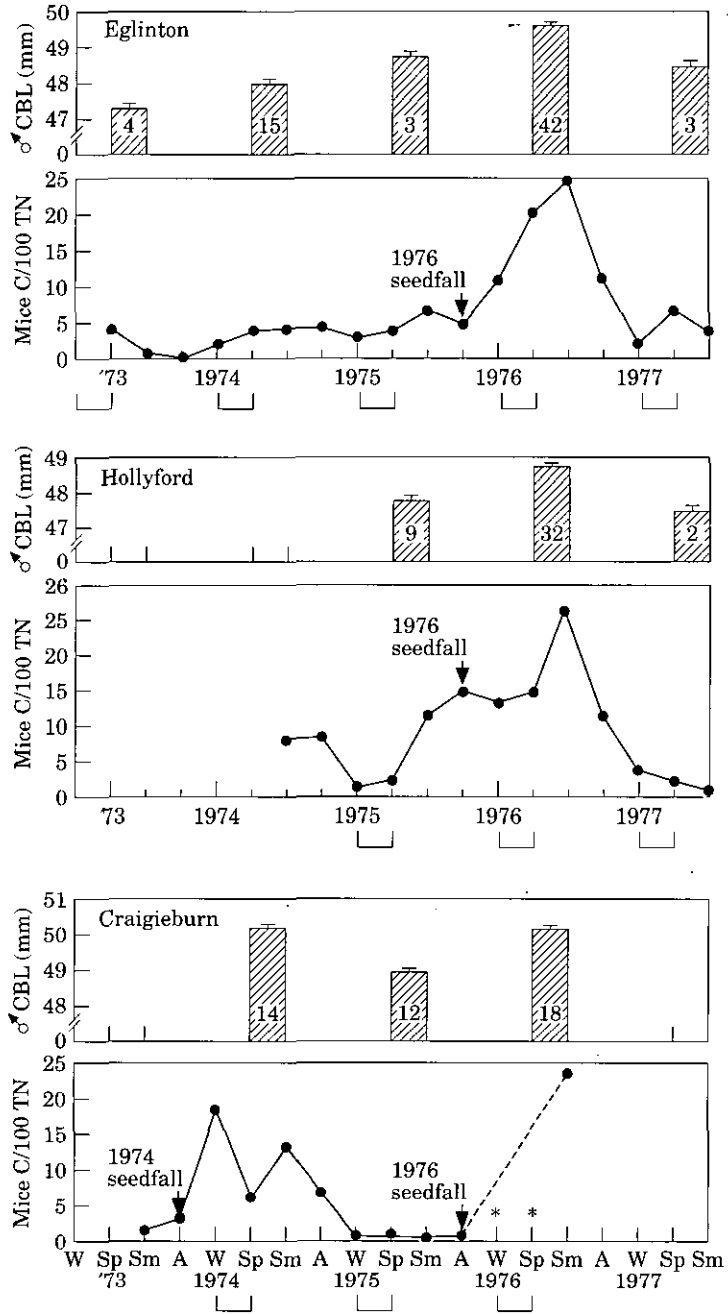


Figure 2. Condylobasal lengths of skulls of growing male stoats (\pm SE, with sample sizes) in relation to mouse density indices in the three study areas. Bars distinguish the winter-spring season, when mouse density strongly influences the mortality rate of implanted embryos and early nestlings (King, 1981, 1983). The data for females show similar patterns of variation in condylobasal length. Young stoats of both sexes born when mouse densities were high in winter-spring had grown larger than average in mean condylobasal length when collected in summer three months later. *Mouse trapping omitted. C/100TN: Captures per hundred trapnights.

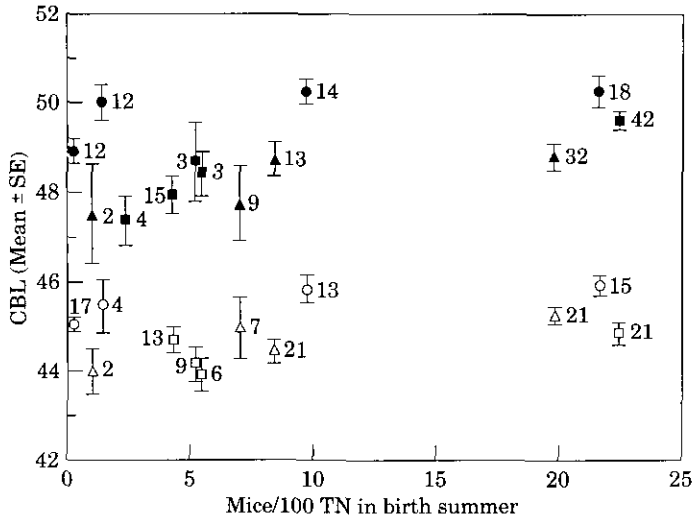


Figure 3. Mean condylobasal length of skull in mm (\pm SE, with sample sizes) of growing male (filled symbols) and female (open symbols) stoats plotted by cohort against the mouse density index taken in the summer of their birth. (○, ●), Craigieburn; (□, ■), Eglinton Valley; (△, ▲), Hollyford Valley. For statistics, see Table 1.

TABLE 1. Regression coefficients for three measures of size of stoats against mouse population density indices. The 3-way partial regression included terms for study site and age in months.

	Linear regressions		Partial regressions	
	r^2	P	r^2	P
Males				
Condylobasal length	0.202	0.0001	0.438	<0.0001
Body length	0.228	0.002	0.486	<0.01
Body weight	0.086	>0.05	0.537	>0.005
Females				
Condylobasal length	0.122	0.067	0.377	<0.03
Body length	0.301	0.0001	0.462	<0.0001
Body weight	0.058	>0.05	0.437	>0.05

sexes (CV males = 0.042, females 0.035, $P=0.05$) but not in any other comparison. Hence, the proportional variation in body length was greater in males than in females. The CVs for weight varied among the growth classes: CV (growing) (0.170) was not different from CV (old) (0.153), but both were different from CV (fullgrown) (0.099, $P<0.001$). Hence, proportionately less variation in weight existed among fullgrown stoats than among growing and old stoats. These patterns of variation in CVs did not affect our analyses.

Sexual dimorphism and food abundance during growth

Sexual dimorphism did not vary significantly with the mouse population indices recorded during the stoats' first six months of life for any size measure (regression of skull length residuals on mouse index, and GLM and partial regressions of

TABLE 2. Condylbasal length of skulls (CBL) (mean mm \pm SE with sample size in parentheses) for growing (females ≤ 6 months old, males ≤ 15 months), fullgrown (females 7–35 months, males 16–35 months) and old (≥ 36 months) stoats captured at the three study sites. In the column headed 'Beech seedfall', stoats in the category 'Yes' were born in a year of heavy beech seedfall, and hence abundant feral house mice; those in the category 'No' were born in a year of poor or no seedfall. CBL in male stoats is always significantly longer than in female stoats at all age classes ($P < 0.001$, GLM), and in fullgrown stoats of both sexes it also varied significantly among sites, controlled for beech seedfall ($P < 0.0001$, GLM). For statistics, see Table 5

Sex	Beech seedfall	Growing	Fullgrown	Old
Craigieburn Forest				
F	No	44.9 \pm 0.22 (27)	46.3 \pm 0.27 (18)	46.7 (1)
F	Yes	45.9 \pm 0.21 (29)	46.4 \pm 0.26 (20)	45.8 \pm 0.66 (3)
M	No	49.4 \pm 0.27 (32)	50.7 \pm 0.62 (6)	49.4 \pm 0.54 (8)
M	Yes	50.2 \pm 0.27 (32)	51.0 \pm 0.67 (5)	49.0 \pm 0.88 (3)
Eglinton Valley				
F	No	44.4 \pm 0.21 (30)	45.6 \pm 0.24 (22)	45.1 \pm 0.38 (9)
F	Yes	44.7 \pm 0.25 (21)	45.7 \pm 0.24 (22)	46.1 \pm 0.81 (2)
M	No	49.0 \pm 0.23 (42)	49.9 \pm 0.57 (7)	49.9 \pm 0.38 (16)
M	Yes	49.5 \pm 0.23 (42)	50.9 \pm 0.28 (29)	50.0 \pm 1.1 (2)
Hollyford Valley				
F	No	44.5 \pm 0.21 (30)	45.3 \pm 0.36 (10)	45.1 \pm 0.43 (7)
F	Yes	45.2 \pm 0.25 (21)	45.4 \pm 0.66 (3)	45.5 \pm 0.47 (6)
M	No	48.2 \pm 0.31 (24)	49.4 \pm 0.57 (7)	49.3 \pm 0.57 (7)
M	Yes	48.7 \pm 0.26 (32)	49.2 (1)	48.6 (1)

TABLE 3. Head-and-body length (mean mm \pm SE with sample size in parentheses) for growing (females ≤ 6 months old, males ≤ 15 months), fullgrown (females 7–35 months, males 16–35 months) and old (≥ 36 months) stoats captured at the three study sites. In the column headed 'Beech seedfall', stoats in the category 'Yes' were born in a year of heavy beech seedfall, and hence abundant feral house mice; those in the category 'No' were born in a year of poor or no seedfall. Head-and-body length in male stoats is always significantly longer than in female stoats at all age classes ($P < 0.001$, GLM) and in fullgrown stoats of both sexes it also varied significantly among sites, controlled for beech seedfall ($P < 0.0001$, GLM)

Sex	Beech seedfall	Growing	Fullgrown	Old
Craigieburn Forest				
F	No	251 \pm 1.9 (30)	258 \pm 2.3 (20)	249 (1)
F	Yes	252 \pm 1.6 (42)	258 \pm 2.2 (21)	256 \pm 6.0 (3)
M	No	279 \pm 2.2 (41)	290 \pm 4.8 (8)	284 \pm 4.9 (8)
M	Yes	278 \pm 2.1 (44)	300 \pm 6.3 (5)	283 \pm 7.0 (4)
Eglinton Valley				
F	No	246 \pm 1.7 (37)	254 \pm 2.0 (27)	250 \pm 3.3 (10)
F	Yes	238 \pm 2.1 (25)	251 \pm 2.1 (25)	261 \pm 5.2 (4)
M	No	270 \pm 1.9 (52)	283 \pm 5.3 (7)	281 \pm 3.4 (17)
M	Yes	267 \pm 1.7 (65)	286 \pm 2.5 (31)	282 \pm 9.9 (2)
Hollyford Valley				
F	No	245 \pm 1.5 (47)	248 \pm 3.3 (10)	254 \pm 3.9 (7)
F	Yes	243 \pm 2.2 (21)	244 \pm 4.6 (5)	252 \pm 4.0 (7)
M	No	261 \pm 2.2 (38)	271 \pm 4.9 (8)	273 \pm 5.3 (7)
M	Yes	264 \pm 2.2 (41)	271 (1)	281 (1)

bodyweights and lengths on mouse index, all $P > 0.3$). Nor did sexual dimorphism in any size measure differ significantly between stoats born in years of high or low beech seedfall (GLM for differences between residuals and between sexual di-

TABLE 4. Weight (mean \pm SE with sample size in parentheses) for growing (females ≤ 6 months old, males ≤ 15 months), fullgrown (females 7–35 months, males 16–35 months) and old (≥ 36 months) stoats captured at the three study sites. In the column headed 'Beech seedfall', stoats in the category 'Yes' were born in a year of heavy beech seedfall, and hence abundant feral house mice; those in the category 'No' were born in a year of poor or no seedfall. Body weight in male stoats is always significantly longer than in female stoats at all age classes ($P < 0.001$, GLM) and in fullgrown stoats of both sexes it also varied significantly among sites, controlled for beech seedfall ($P < 0.0001$, GLM)

Sex	Beech seedfall	Growing	Fullgrown	Old
Craigieburn Forest				
F	No	201 \pm 5.2 (31)	223 \pm 6.7 (18)	225 (1)
F	Yes	215 \pm 4.4 (41)	221 \pm 6.4 (20)	220 \pm 16.6 (3)
M	No	299 \pm 8.4 (38)	363 \pm 18.4 (8)	344 \pm 18.4 (8)
M	Yes	319 \pm 7.9 (43)	356 \pm 26.0 (4)	325 \pm 26.0 (4)
Eginton Valley				
F	No	180 \pm 4.9 (35)	204 \pm 5.8 (24)	200 \pm 9.5 (9)
F	Yes	173 \pm 4.1 (50)	210 \pm 5.9 (24)	206 \pm 14.3 (4)
M	No	258 \pm 7.5 (48)	321 \pm 19.6 (7)	335 \pm 14.4 (13)
M	Yes	256 \pm 5.5 (88)	331 \pm 10.0 (27)	328 \pm 36.7 (2)
Hollyford Valley				
F	No	181 \pm 4.2 (45)	200 \pm 10.1 (8)	206 \pm 11.7 (6)
F	Yes	168 \pm 4.1 (48)	208 \pm 12.8 (5)	203 \pm 11.7 (6)
M	No	236 \pm 8.7 (35)	317 \pm 18.3 (8)	282 \pm 21.2 (6)
M	Yes	227 \pm 6.3 (67)	349 (1)	252 (1)

TABLE 5. Results of GLM tests on the sources of variance in condylobasal length (CBL) of the skull shown in Table 2. Beech seedfall, site, growth class and sex were each significant independently of all the other effects, but no interactions between them were significant

Sources of variance in CBL	df	F-ratio	P
Both sexes			
Total	6	260.05	<0.0001
Seedfall	1	42.42	0.0001
Site	2	92.80	0.0001
Growth class	2	6.14	0.0023
Sex	1	1455.52	<0.0001
Males			
Total	5	15.08	0.0001
Seedfall	1	13.20	0.0003
Site	2	14.04	0.0001
Growth class	2	17.08	0.0001
Females			
Total	5	14.89	0.0001
Seedfall	1	15.79	0.0001
Site	2	11.48	0.0001
Growth class	2	17.85	0.0001

morphism indices, $P > 0.4$, Table 6, Figs 5 and 6). No significant relationships existed between sexual dimorphism in any size measure and beech seedfall, mouse population index, growth classes or study sites.

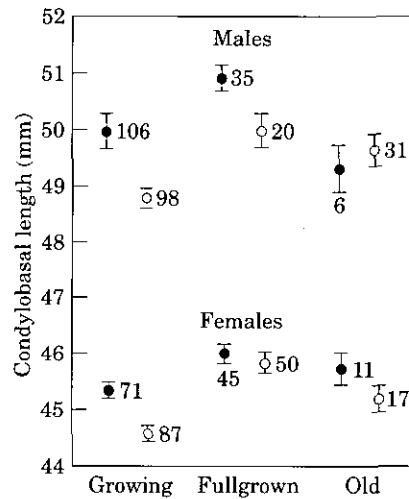


Figure 4. Condylbasal lengths of skull of males and females (\pm SE, with sample sizes) in relation to seedfall in year of birth, by growth class, all study areas pooled. Stoats born in seedfall (●) and non-seedfall (○) years. Local variation in site means introduced wide scatter (Fig. 3), but regressions of these data controlled for site, age and year were significant in both sexes (Table 5). Years of high seedfall can be presumed to be correlated with years of high density of mice (Fig. 2).

TABLE 6. Mean sexual dimorphism indices (with SE and sample size in site-years) for cohorts of stoats born in New Zealand during years of high beech seedfall (= abundant mice) or low/no seedfall. No measure of sexual dimorphism, at any age, differed significantly between stoats born in seedfall and non-seedfall years. See Fig. 6

Age	Seedfall	Mean		CBI. n	Head-body length			Body weight		
		Mean	SE		Mean	SE	n	Mean	SE	n
Growing	High	.093	.006	4	.102	.008	4	.428	.032	6
	Low	.081	.009	11	.088	.011	11	.408	.063	11
Fullgrown	High	.092	.009	4	.092	.026	4	.624	.032	4
	Low	.103	.010	11	.107	.009	10	.616	.049	10
Old	High	.083	.008	3	.113	.021	3	.528	.151	3
	Low	.101	.022	6	.119	.022	6	.532	.112	5

Sexual dimorphism in skull length and body weight did vary among growth classes (skull length: GLM for residuals varying among growth classes, $P=0.05$; body weight: GLM for index varying among growth classes, $P<0.05$). Sexual dimorphism was generally smallest in the growing stoats, regardless of beech seedfall (Fig. 6, Table 6), and significantly smaller in body weight (LSD test on both residuals and sexual dimorphism indices, $P<0.05$), and in skull length in growing stoats born in non-seedfall years (LSD on residuals, $P<0.05$). Dimorphism was generally smaller in the old than in fullgrown stoats, but not significantly so.

Size, dimorphism and survival among live-trapped growing stoats of the 1979 cohort

We examined the field records of body weights of growing stoats of both sexes live-trapped in January 1980 to detect the effects of post-seedfall conditions on body

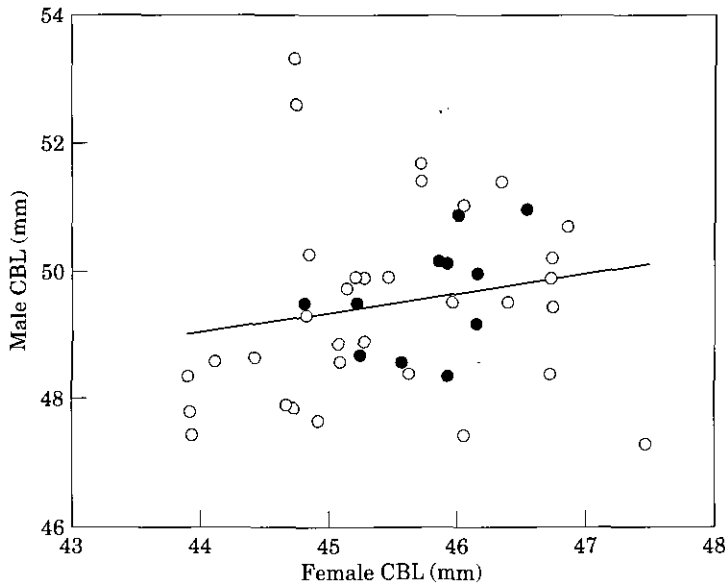


Figure 5. Regression of male condylobasal length on female condylobasal length ($Y = 34.83 + 0.324X$, $r^2 = 0.04$, $P = 0.01$). (●) years of high beech seedfall and associated high numbers of mice; (○) years of low beech seedfall. Each point represents one growth class at one site in one year.

weights of growing young stoats. A smaller than expected weight gain through the month for individual young stoats would indicate poor hunting ability or food shortage. Body weights recorded for both sexes increased unevenly but much as expected for growing stoats, especially in those most likely to reach large size (i.e. greater weight gains were recorded for males than females, and greater weight gains for stoats from the Eglinton than from the Hollyford). Many individual young stoats of both sexes, however, showed significantly less weight gain through successive captures than expected from their ages (shown by a steady decrease in weight adjusted for age [Table 7]). These declines were significant for stoats of both sexes in the Eglinton, and for males from the Hollyford. Adult weights for both sexes, however, did not vary with capture week or with capture number.

Variation in age structure and survivorship with food abundance during growth

At all three study sites, stoats born in non-seedfall years lived longer (mean age at death of males 16.1 months, females 11.5 months) than those born in seedfall years (males 11.0 months, females 10.9 months; $P < 0.0001$, GLM). Mean ages of males and females did not differ, however, in comparisons controlled for whether individuals were born in years of beech seedfall or not, so we pooled data for the two sexes in analyses that controlled for seedfall.

Age specific survivorships (p_x) calculated for stoats at the three study sites did not differ significantly, so analyses of p_x s were not blocked by study site. The mean survivorships for first-year stoats in the three forests ranged from 0.22 to 0.36. In most year classes after the first, estimated survivorship ranged from 0.40 to 0.70, but the small samples of older animals introduced high between-year variability.

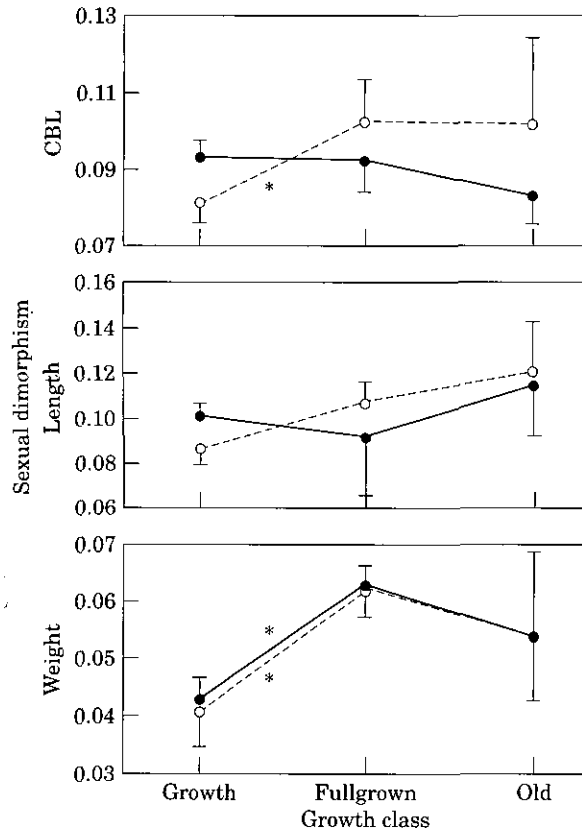


Figure 6. Proportional indices of sexual dimorphism (\pm SE) for all size measures and growth classes in years of low (○) and high (●) beech seedfall. The indices for condylbasal length are presented for comparison only; significance tests on condylbasal length were confined to regression analyses. In three of six comparisons between growing and full-grown stoats (marked with an asterisk), sexual dimorphism significantly increased with age (for details see text). Abundance of mice (as indexed by beech seedfall) had no significant effect on sexual dimorphism in any measure of size.

At each study site and for all sites together, p_x s were significantly lower for the large cohorts born in years of good beech seedfall than for the small cohorts born in poor years ($P < 0.05$, GLM; Table 8, Fig. 7). The difference was especially pronounced for p_0 : first-year survivorship among the numerous young of the 1976 seedfall-year cohort was reduced to under 0.10 in all study areas. Consequently, first-year survivorship, at least from the age of independence, was significantly negatively correlated with the density of stoats in the summer of their birth year ($r^2 = -0.55$, $P = 0.0225$; Fig. 8).

Proportionately more stoats from cohorts born in non-seedfall years lived long lives, especially males regardless of size. Of the 40 old males in the sample (≥ 3 years old), 33 (82%) had been born in non-seedfall years and only 7 in seedfall years ($P < 0.01$). The skew was less extreme for old females (57% of 30 born in non-seedfall years; Table 9). Only a few individuals of each sex lived to be very old (8–10 years old).

Old male, but not old female, stoats born in years of abundant food had

TABLE 7. Changes in body weight (g) ± SE with time of newly dispersing young stoats live-captured during January of the post-seedfall summer of 1979-80. No comparisons of live body weights measured in non-seedfall years are available. The few captures recorded before January 1 or after February 2 are omitted. The first capture of a given individual was often early in January but not necessarily so, since some individuals were caught for the first time in the last week of trapping. Fully factorial ANOVAs calculated *F*-ratios and adjusted least squares means for capture number and week independently. Sample sizes in parentheses give the number of independent measures of weight of different animals taken at a first, second etc. capture, and by week of capture, respectively

Eglington Valley		Capture 1	Capture 2	Capture 3	Capture 4	Capture 5	Capture 6	<i>F</i> -ratio	df	<i>P</i>
Sex										
M		256 ± 7.7 (28)	248 ± 7.9 (18)	242 ± 9.8 (12)	228 ± 15.6 (5)	215 ± 16.1 (5)	194 ± 17.5 (4)	2.44	5	0.044
F		183 ± 5.7 (22)	167 ± 7.6 (11)	135 ± 11.7 (6)	130 ± 26.4 (1)			4.54	3	0.008
Sex		Jan 1-4	Jan 8-11	Jan 15-18	Jan 22-25	Jan 29-Feb 1		<i>F</i> -ratio	df	<i>P</i>
M		216 ± 9.1 (16)	247 ± 10.3 (11)	237 ± 11.7 (8)	262 ± 8.2 (16)	261 ± 9.6 (17)		3.69	4	0.010
F		159 ± 7.3 (15)	166 ± 7.0 (13)	189 ± 11.4 (5)	181 ± 13.4 (5)	206 ± 18.1 (2)		2.29	4	0.080
Hollyford Valley										
Sex										
M		213 ± 6.0 (37)	211 ± 8.2 (19)	206 ± 11.3 (10)	199 ± 12.8 (8)	176 ± 14.8 (6)	182 ± 16.4 (5)	1.48	5	0.207
F		152 ± 4.6 (22)	149 ± 6.5 (11)	150 ± 9.8 (9)	165 ± 21.7 (1)			0.21	3	0.886
Sex		Jan 1-4	Jan 8-11	Jan 15-18	Jan 22-25	Jan 29-Feb 1		<i>F</i> -ratio	df	<i>P</i>
M		192 ± 7.8 (25)	197 ± 7.2 (25)	204 ± 11.3 (11)	224 ± 9.3 (15)	240 ± 12.5 (9)		4.08	4	0.005
F		148 ± 6.7 (11)	154 ± 5.9 (14)	151 ± 7.6 (9)	149 ± 13.1 (3)	156 ± 16.1 (2)		0.13	4	0.970

TABLE 8. Age specific survivorship (p_x) and mortality for stoats captured in Eglinton Valley, Hollyford Valley and Craigieburn Forest Park, calculated as means for cohorts born in seedfall years and non-seedfall years. The last p_x for each site represents p_x for that age on. Age specific survivorships differed significantly between cohorts born in seedfall years and non-seedfall years (GLM $P < 0.05$). The significant difference was caused by low survivorship of stoats born in seedfall years (disproportionately low numbers of stoats captured after age 1 in seedfall years, χ^2 test $P < 0.01$). n = the number of cohorts used to estimate p_x . The totals for the two categories were comparable mainly because the non-seedfall year cohorts, although comprising fewer stoats each, represented more years surveyed

Eglinton Valley								
Age	seed years (159 stoats)				non-seed years (147 stoats)			
	l_x	q_x	$p_x \pm SD$	n	l_x	q_x	$p_x \pm SD$	n
0.2-1	1.00	0.92	0.09	1	1.00	0.73	0.27 ± 0.14	3
1-2	0.09	0.62	0.38 ± 0.42	5	0.23	0.40	0.60 ± 0.45	4
2-3	0.03				0.14	0.31	0.69 ± 0.03	2
3-4					0.10	0.71	0.29 ± 0.41	2
4+					0.07			
Hollyford Valley								
Age	seed years (79 stoats)				non-seed years (118 stoats)			
	l_x	q_x	$p_x \pm SD$	n	l_x	q_x	$p_x \pm SD$	n
0.2-1	1.00	0.91	0.09	1	1.00	0.55	0.45 ± 0.48	3
1-2	0.09	0.63	0.37 ± 0.48	5	0.55	0.40	0.60 ± 0.28	4
2-3	0.06				0.22	0.47	0.53 ± 0.50	3
3-4					0.10	0.63	0.37 ± 0.39	3
4+					0.08	0.43	0.57 ± 0.61	2
					0.05	1.00	0.00	1
					0.00			
Craigieburn								
Age	seed years (126 stoats)				non-seed years (98 stoats)			
	l_x	q_x	$p_x \pm SD$	n	l_x	q_x	$p_x \pm SD$	n
0.2-1	1.00	0.92	0.08 ± 0.08	2	1.00	0.60	0.40 ± 0.28	3
1-2	0.08	0.75	0.25 ± 0.35	2	0.41	0.62	0.38 ± 0.07	3
2-3	0.02	0.43	0.57	1	0.25	0.52	0.48 ± 0.50	3
3-4	0.01	0.30	0.70 ± 0.05	3	0.13	0.42	0.58 ± 0.42	8
4+	0.00	0.66	0.34 ± 0.15	3	0.06			
	0.00	1.00	0.00 ± 0.00	3				

significantly smaller skulls than fullgrown animals of the same cohorts (Table 2, Fig. 4). Individuals are unlikely to shrink in size, so this implies that mortality is selective against the largest males of the seedyear cohorts during their first 3 years of life. Large males born in seedfall years did, in fact, disappear significantly faster than did the small males born in seedfall years ($\chi^2 = 21.84$, $df = 3$, $P < 0.001$).

It could be argued that sampling by removal trapping created a sink effect exaggerating the representation of young stoats in our samples, because the young are presumed to be the most likely to be drawn to a sink. Such sampling error would depress our estimates of survivorship for the first year class relative to older, more sedentary animals. If such a sampling error existed, it would have been most pronounced for cohorts born in years of beech seedfall, when the largest cohorts of young stoats were produced. We were able to check for this sampling error, because in Fiordland the effects of the seedfall year of 1976 were monitored with Fenn traps,

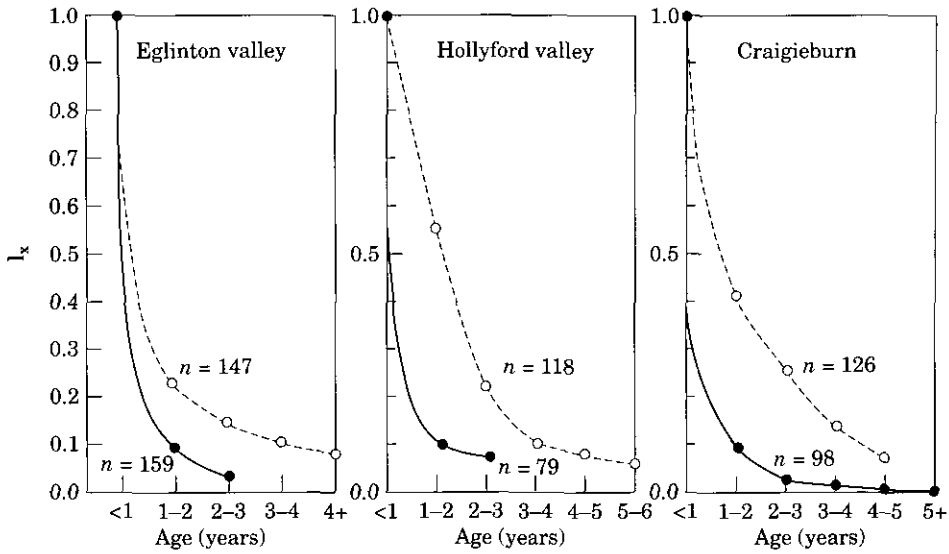


Figure 7. The probability of surviving from independence (at 2-3 mn) to a given age in years (l_x), calculated as means for cohorts born in seedfall (●) and non-seedfall (○) years. For associated $p_x \pm SD$, see Table 8.

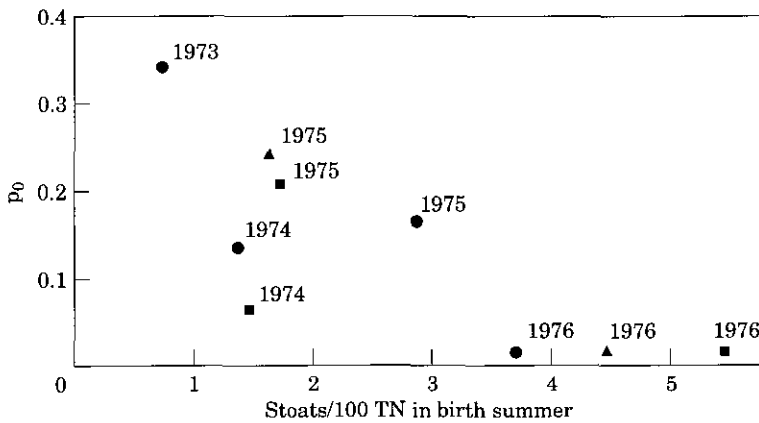


Figure 8. Density-dependent survivorship of first-year stoats from independence to 1 year old (p_0), omitting the first year of trapping in any study area. There was a heavy beech seedfall in 1976 in all study areas, and a moderate one at Craigeburn in 1974 (Fig. 2). Craigeburn (●); Eglinton Valley (■); Hollyford Valley (▲). $r^2 = 0.55$, $P = 0.0225$.

whereas those of the seedfall year of 1979 were monitored with livetraps set in the same positions. The density indices for the two summers were similar in both valleys (King, 1983), and the proportion of first-year stoats of the 1976 cohort, collected at the time that Fenn-trapping could have created a sink (69 young to 7 old males and 39 to 5 females) did not differ significantly from the proportion (65 to 12 males and 48 to 7 females) in the 1979 live-trapped cohort ($P < 0.05$, $\chi^2 = 1.43$). The full data underlying this comparison were presented by King & McMillan (1982).

We also used the live-trapping data to test independently the evidence from the

TABLE 9. Numbers of stoats born in seedfall years and in non-seedfall years that died young (up to 35 mn) and old (36 mn +). Significantly more stoats born in non-seedfall years reached 3 years old (χ^2 test, $P < 0.01$ sexes pooled, $P < 0.01$, males only)

Age at death	All stoats		Males		Females	
	seed	non-seed	seed	non-seed	seed	non-seed
Young	345	342	192	161	53	181
Old	20	50	7	33	13	17

carcasses that newly independent young born in years of beech seedfall disappeared very rapidly. The live-trapping data for the month of January 1980 were divided into five weekly blocks (corresponding to the Monday-to-Friday trapping regime of King & McMillan, 1982). These yielded the following weekly survival estimates: young males 0.80 ± 0.51 SE (95% CI = 0.69–0.89); young females 0.61 ± 0.72 (95% CI = 0.46–0.74; A. Kielland, pers. comm.). The estimated survivorship for the whole of January was 0.41 for males and 0.13 for females. The recapture probability per week for both sexes pooled was 0.38 ± 0.54 SE. These survivorship estimates are not strictly comparable with those from the carcass data, cannot be extrapolated to cover an entire year, and cannot be distinguished from dispersal, but they are consistent with our previous result in showing that p_0 is very small for cohorts born in years of heavy beech seedfall.

Variation in fecundity with age

Table 10 shows the mean number of corpora lutea per female by age and site, separately for seedfall and non-seedfall years. Fecundity did not vary with increasing age in females mated either in seedfall or non-seedfall years. First-year females mated during a seedfall year were consistently but not significantly more fecund on average than those mated during a non-seedfall year. Few older females were collected after mating in a seedfall year.

DISCUSSION

Variation in size

The clearest effect of food supply on size during growth was on skull length (Figs 2 and 3, Tables 2, 5). The effect on body length was much weaker, and on body weight it was scarcely detectable. We suggest that the three body measurements were affected differently because, as previous studies on this material showed, the processes of physical growth differ between the sexes and between the skull and the body within each sex (King & Moody, 1982). When young stoats of both sexes reach 2–3 months of age, their skulls have reached 97% of the mean lengths for adults. Growth of bodies takes longer, especially in males. By 5 months of age, females have reached 99% of adult body length and 97% of adult weight, but males of the same age have reached 98% of adult length and only 80% of adult weight.

TABLE 10. Variation in fecundity (mean number of corpora lutea per female \pm SD, sample size in parentheses) with age for beech forest stoats according to the level of beech seedfall in the year of mating. Fecundity was significantly higher in females of all ages mated in seedfall years compared with nonseedfall years (King, 1981). Among females mated in nonseedfall years, there was no significant variation with age ($P > 0.05$, Student's *t*-tests¹). Total sample size was 289. Virtually all females mated and ovulated every year, though not all produced young

Site	Age	Corpora lutea per female	
		Seedfall years	Non-seedfall years
Eglinton	0.2-1	10.4 \pm 0.51 (31)	9.6 \pm .27 (42)
	1-2	(2)	9.5 \pm .43 (11)
	2-3	(2)	10.6 \pm .60 (8)
	3+	(0)	9.6 \pm .60 (10)
Hollyford	0.2-1	10.4 \pm 0.50 (19)	9.4 \pm .25 (38)
	1-2	10.0 \pm 0.63 (5)	8.6 \pm .53 (7)
	2-3	(0)	(1)
	3+	(0)	9.2 \pm .51 (15)
Craigieburn	0.2-1	9.5 \pm 0.43 (51)	8.4 \pm .54 (28)
	1-2	(2)	7.4 \pm 1.15 (8)
	2-3	(3)	8.3 \pm .61 (6)

¹ The apparent higher mean fecundity in young females noted by King and Moody (1982) was due to pooling data from seedfall and non-seedfall years. The years in which young females appeared in greatest numbers were invariably seedfall years, so the total sample of young females contains many individuals mated in seedfall years, when fecundity was slightly higher than usual in females of all ages. Conversely, most adults were collected in non-seedfall years, when fecundity was relatively low in females of all ages. By controlling for the effect of seedfall, these data now show that fecundity did not vary with age.

Males complete their growth to adult size after they pass puberty at 10 months of age (King & Moody, 1982).

Growth in bone length is a finite process in mammals, influenced by nutrition. Bone sizes are fixed at physical maturity, and changes in conditions after that time have little effect on bone size. The linear measurements of an adult stoat, therefore, reflect environmental conditions during the year it was born, not the year it died. By contrast, body mass can be added or lost at any age, so body weight is more likely than length to reflect conditions during the year a stoat died. If such additions or losses to weight are extensive, the influence of environmental conditions at the time of death will exceed the influence of conditions at birth, and body weight becomes a poor indicator of conditions during growth.

The early completion of growth of the skull of both sexes makes skull length the most sensitive indicator available for the nutritional status of young stoats—much as mandible length is for deer (Hewison *et al.*, 1996). Body length is strongly correlated with skull length, and yielded similar significant relationships with the mouse population index (Table 1), though not with seedfall (Table 3). As Johnson (1991) noted, it is difficult to measure body length with the same accuracy as skull length.

It could be argued that the smaller mean skull size in non-seed year cohorts was an artefact of trappability, since the trapped samples might be dominated by hungry, weak or otherwise atypical individuals when food was scarce. There is an important distinction to be drawn here between (1) a general year-round shortage of all prey, correlated with the reduced productivity of the non-seed year cohorts (King, 1981),

and (2) a sudden shortage of a key resource, liable to increase trappability over the short-term. The first certainly affects the non-seed year cohorts, by acting early in the reproductive cycle (in winter and spring) to reduce the number of stoats available to be trapped, while the second could affect only the seed-year cohorts, by acting later (in summer) to induce stress and hunger in the numerous and previously well fed young. Hence, the only serious period of food scarcity liable to affect trappability was met by the young of the seedyear cohorts beginning their independent life just as the mice were already beginning to decline. The live-trapping data from 1979 suggest that it was the seed-year cohorts, which were on average *larger* in skull size, that were more likely to be misrepresented by differential trappability due to hunger. Furthermore, the size differential in males was still significant in the second (fullgrown) growth class (Fig. 4), yet no such drastic effect could last so long, and indeed the starving young disappeared very quickly.

The three-fold link between nutritional status, density and body size is well known in other mammals, but has an interesting twist related to trophic level. In herbivores such as the roe deer (*Capreolus capreolus*), increased body size is associated with low density and reduced competition for normally stable supplies of forage (Hewison *et al.*, 1996). By contrast, in mustelids, increased body size is associated with the high density which is stimulated by a temporary peak in normally unstable supplies of small rodent prey.

Variation in sexual dimorphism

Our original hypothesis was that variations in food supply during growth should induce short-term phenotypic variation in sexual dimorphism through effects on adult male size. It assumed that: (a) food supply during growth is an important factor determining the adult body size of male mustelids (Powell, 1979; Ralls & Harvey, 1985), but that (b) female mustelids are constrained in size as adults by the need to retain access to rodent burrows or to minimize maintenance energy requirements or both (Moors, 1974, 1980; Simms, 1979; Gliwicz, 1988; King, 1991a), so should be less responsive to variation in food supplies during growth than males.

Our data confirmed the prediction that male stoats should grow larger when born in years of abundant mice. Unexpectedly, our data also show that body sizes of females vary in the same manner. Sexual dimorphism therefore did not vary with food supply during growth as measured by skull length, body length or weight of growing or fullgrown stoats; it did not vary among the study sites, either. The only such effect we could find was among the oldest stoats: those born during years of food abundance showed smaller dimorphism in skull length than those born during food shortage (Fig. 6). This was because the oldest males born in seedfall years had shorter skull lengths than the fullgrown and growing males of the same cohorts ($P=0.01$), but this effect was not seen in the oldest females, hence there was a drop in sexual dimorphism among old stoats born during food abundance. This extensive variation of male size and mortality with age and birth year introduces a new complication into general statements such as "... dimorphism in mammals is associated with a viability cost to the larger of the two sexes among adults" (Promislow, 1992).

Why do our data appear to confirm the hypothesis that male weasels grow large

if born when food is abundant without confirming the obvious consequence that sexual dimorphism should vary with food supplies? This apparent logical impossibility has two potential explanations. (1) Whereas female stoats in the northern hemisphere are so closely adapted to hunting in burrows that they forego a temporary advantage in size while growing in order to retain a long-term advantage in hunting and energy economy when reproducing, female stoats in New Zealand are not so constrained because they do not hunt prey that live in burrows. (2) Northern weasels of both sexes born during high food abundance also respond by growing large, but no one has yet collected the pertinent data.

The sizes of male and female weasels in different places are strongly correlated (Ralls & Harvey, 1985; van Zyll de Jong, 1992), consistent with the prediction of Lande (1980), that selection acting on one sex should produce corresponding responses in the other sex. This correlation does not preclude phenotypic variation in sexual dimorphism, however, because members of one sex may be more variable in their abilities to reach optimal adult size than those of the other sex.

The variations in body sizes of males that we found are consistent with a trade-off between, on the one hand, large size with high reproductive success during one or two breeding seasons, and, on the other hand, small size but a longer life and more opportunities to breed. We do not know whether any such trade-off is balanced, or under what conditions it could exist, but the possibility of it deserves future attention, as does the variation in body sizes of females.

Effects of early nutrition on mortality rate

In New Zealand beech forests, the increase in abundance of feral house mice and insects in the late winter and spring after a heavy seedfall permits temporary relief from the normally high mortality of pre-independent young stoats. This mechanism allows, for that season only, better survival to dispersal than is possible in other habitats, but which is quite unsustainable even in beech forests. The density of house mice declines rapidly over the summer and autumn, especially if stoats are not removed by regular kill-trapping (King, 1985), immediately precipitating high mortality among the extra large cohorts of young stoats born in years of beech seedfall from as soon as they are independent (Table 8). Hence, the age-specific mortality in the first year of life, q_0 , was higher at all three study sites for cohorts born in seedfall years than for cohorts born in non-seedfall years ($q_0 = 0.92, 0.91, 0.92$ vs $0.73, 0.55, 0.60$). These data are the first to document a density-dependent variation in survival of young stoats directly linked with food supplies (Fig. 8).

Fenn traps and live traps caught similar proportions of first-year and older stoats (a result also reported by Murphy & Dowding, 1995), so we do not think removal sampling had any substantial influence on our survivorship estimates. This suggests that the proportion of a given summer sample comprising first-year stoats depends more on the breeding success of the previous season than on the trapping regime.

The 'silver spoon' effect

The 'silver spoon' effect (Grafen, 1988) predicts that individuals born during periods of exceptionally favourable conditions should gain advantages not shared by individuals born in less favourable years. Such advantages might include high

rates of growth or survival as juveniles, or high reproductive success as adults, or all of these effects. Our data provide information, not on fitness or reproductive success per se, but on three variables that usually correlate with fitness.

Comparisons between fecundity (counts of corpora lutea) and productivity (independent young produced) showed that the normally high intra-uterine mortality of stoat embryos was drastically reduced by the favorable food supplies available to pregnant females after a heavy beech seedfall (King, 1981, 1983). Consequently, stoat embryos developing in years with abundant food experienced high intra-uterine survivorship. In addition, our data show that stoats of both sexes born in years of high mouse populations grew larger than stoats born in other years. Improved survival and large size both qualify as 'silver-spoon' effects, since they are probably both correlated with high reproductive success (Sandell, 1986).

On the other hand, these advantages in survival and size gained by stoats born during food abundance were short-lived. Their survivorship following independence was extremely low. Conditions faced by cohorts born in years of beech seedfall began to deteriorate as soon as they became independent. The live-trapping data, collected during January while the young stoats of the 1979 cohort were still growing, showed that recaptured stoats grew less rapidly than expected (shown by the decreasing body weights adjusted for age [Table 7]), and that the effect was greater on males than on females. Individuals under greatest stress, the ones likely to be recaptured most often, were not growing well and were presumably the ones most willing to enter traps to reach food. This observation helps to account for the higher mortality of the seed-year cohorts, but not their larger average skull size.

If small male stoats live longer than large males, large body size may not be of any selective advantage in the long term (Hedrick & Temeles, 1989). The relative importance of size (reproductive success during a single breeding season) vs longevity (number of breeding seasons) depends on which most influences lifetime reproductive success, a topic that has never been investigated in stoats. In Tengmalm's owls (*Aegolius funereus*), no one phenotype has the advantage at all densities of their small rodent prey (Hakkarainen & Korpimäki, 1995). Long-lived predators may be able to compensate for a bad season in the next good one, but very few stoats survive for as long as 3-4 years, the mean interval between good seed years (Table 8). Moreover, we should not expect the 'silver spoon' effect to have any influence on the genome in the long term, for reasons outlined by Williams (1992:70-71):

Size is perhaps the most generally valid example of an expensive character . . . it may be that most adults have far smaller sizes than those that would maximise adaptive performance. When this is true the measurement in question is not of a character optimised for its role in maximising fitness, but rather an index of current fitness attainment. A size ranking among similar age halibut or white pines must be very nearly a ranking according to phenotypic fitness. The same may be true of many other characters closely associated with viability or reproductive performance [such as fat reserves, antler size] . . . Such characters are neither tactics nor strategies but rather measures of current winnings in reproductive competition. Heritabilities of such characters closely predictive of fitness . . . must be low. Otherwise they would increase rapidly with the passage of generations.

To our knowledge, ours is the largest collection of reliably age-classified *Mustela* carcasses ever assembled under controlled conditions spanning a range of food abundance. Such data are required to investigate the effects of fluctuating prey populations on cohort-based differences in body size, age-specific survivorship and

fecundity. In principle, survival estimates calculated from marked, live animals may be more precise (Lebreton, Pradel & Clobert, 1993), but large enough samples of live stoats are impossible to obtain with present field technology. Stoats are small and very active animals; they have very large home ranges (up to 200 ha) and live in unstable populations dependent on widely fluctuating prey populations. At present, intensive live-trapping and radio-telemetry can not provide reliable estimates of differential survival of cohorts for any live *Mustela* species. Removal sampling also has another important advantage over live-trapping: carcasses provide vital data unobtainable from live animals. Large samples can be collected from extensive study areas, and past reproductive history and age can be estimated. Body size can be measured more accurately from carcasses than from live animals, and skull length—which turned out to be the key data for our study—can be measured only from dead animals. Problems of unequal catchability of individuals apply to both kill-trapping and live-trapping (King & McMillan, 1982). We are confident that our analyses provide a reasonably accurate first estimate of the dynamics of replicate stoat cohorts responding to variation in food supplies during the year of growth (Caughley, 1977 and pers. com.).

Our results are consistent with those of previous, less extensive studies, obtained both by live-trapping in Sweden and from analyses of fur harvests in Russia. The overall average first-year mortality rates in our three forests ($q_0 = 0.78, 0.64, 0.73$) were similar to those calculated by Sandell (1989) in Sweden ($q_0 = 0.61$ for males, 0.70 for females, from Erlinge's [1983] live-trapping data). In Sweden, as in our study (when analyses were controlled for effects of birth year and study site), the sexes did not differ in age-specific survivorship. In Russia in years of high stoat density (presumably years when vole populations were high), Kopein (1969) observed that young stoats were on average significantly larger than adults in body length and in condylobasal length. Although he presented no data on the relative longevity of stoats of different sizes or from different birth years, Kopein concluded that smaller stoats had a selective advantage over large stoats, implying that large stoats died younger than did small ones. Shiljaeva (1971) showed that arctic foxes born when lemmings are abundant live shorter lives (mean 0.77 yr) than those born when lemmings are scarce (1.6 yr).

CONCLUSIONS

1. Our analyses did not confirm the prediction that sexual dimorphism in the cohorts of stoats born in New Zealand in years of abundant food would be larger than normal (Fig. 6) because: (a) stoats of both sexes grew large in years of food abundance and (b) this effect was later negated by selection against the large males born in those years. Consequently, the oldest (3 yr) surviving males of cohorts born during high food abundance were about the same size as males of the same age born in food-poor years (Tables 2–4).
2. First-year survivorship, at least from the age of independence, was significantly negatively correlated with density of stoats in the summer of their birth year.
3. Female stoats in New Zealand are not restricted in size by access to rodent burrows. If a trade-off exists between being small enough to minimize reproductive costs and being large enough to handle the available prey, New Zealand females have found (or are finding) a new set-point appropriate to the different distribution of prey sizes in New Zealand. Our data do not demonstrate whether access to

burrows or reproductive costs actually limit the sizes of female weasels in the northern hemisphere.

4. We suggest that the general increase in body size of stoats of both sexes in New Zealand has been permitted by a combination (in unknown proportions) of sexual selection, mild climate, large mean prey size, and shortage of important burrowing prey.
5. Stoats are not native to New Zealand, and some of our results may be peculiar to the special conditions in that country. On the other hand, our data show significant phenotypic variation in an evolutionarily significant parameter. This result should be of interest to other researchers on sexual dimorphism, especially in mustelids, because evolution does not use different rules for exotic species. We hope to see comparable morphometric data collected from populations of northern stoats that depend on fluctuating populations of microtine rodents and that are subject to environmental constraints absent in New Zealand, such as severe winters and a full complement of predators, competitors and burrowing prey.

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REFERENCES

- Allen RB, Platt KH. 1990.** Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. *Oikos* 57: 199–206.
- Burrows LE, Allen RB. 1991.** Silver beech (*Nothofagus menziesii* (Hook.f.Oerst.) seedfall patterns in the Takitimu Range, South Island, New Zealand. *New Zealand Journal of Botany* 29: 361–65.
- Caughley GC. 1977.** *Analysis of Vertebrate Populations*. London: John Wiley.
- Cezilly F, Pradel R, Viallefont A, Lebreton, J-D. 1996.** *Working with CR: a guide with examples*. Centre d'écologie fonctionnelle et évolutive, C.N.R.S., bp 5051, 34033, Montpellier Cedex, France.
- Clutton-Brock TH. 1991.** *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press, Monographs in Behaviour and Ecology.
- Dayan T, Simberloff D, Tchernov W, Yom-Tov Y. 1989.** Inter-and intra-specific character displacement in mustelids. *Ecology* 70: 1526–1539.

- Dayan T, Simberloff D. 1994. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. *Ecology* 75: 1063–1073.
- East K, Lockie JD. 1964. Observations on a family of weasels (*Mustela nivalis*) bred in captivity. *Proceedings of the Zoological Society of London* 143: 359–363.
- Eger JL. 1990. Patterns of geographic variation in the skull of Nearctic Ermine (*Mustela erminea*). *Canadian Journal of Zoology* 68: 1241–1249.
- Elliott GP, Dilks PJ, O'Donnell CFJ. 1996. The ecology of yellow-crowned parakeets (*Cyanoramphus auriceps*) in *Nothofagus* forest in Fiordland, New Zealand. *New Zealand Journal of Zoology* 23: 249–265.
- Erlinge S. 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos* 33: 233–245.
- Erlinge S. 1983. Demography and dynamics of a stoat *Mustela erminea* population in a diverse community of vertebrates. *Journal of Animal Ecology* 52: 705–726.
- Erlinge S. 1987. Why do European stoats *Mustela erminea* not follow Bergmann's Rule? *Holarctic Ecology* 10: 33–39.
- Fitzgerald BM, Daniel MJ, Fitzgerald AE, Karl BJ, Meads MJ, Notman PR. 1996. Factors contributing to fluctuations in house mouse (*Mus musculus*) populations in hard beech (*Nothofagus truncata*) forest. *Journal of the Royal Society of New Zealand* 26: 237–249.
- Gliwicz J. 1988. Sexual dimorphism in small mustelids: body diameter limitation. *Oikos* 53: 411–414.
- Grafen A. 1988. On the uses of data on lifetime reproductive success. In: Clutton-Brock TH, ed. *Reproductive Success*. Chicago: University of Chicago Press, 454–471.
- Grue HE, King CM. 1984. Evaluation of age criteria in New Zealand stoats (*Mustela erminea*) of known age. *New Zealand Journal of Zoology* 11: 437–443.
- Hakkarainen H, Korpimäki E. 1995. Contrasting phenotype correlations in food provision of male Tengmalm's owls (*Aegolius funereus*) in a temporarily heterogeneous environment. *Evolutionary Ecology* 9: 30–37.
- Hayward GF. 1983. The bioenergetics of the weasel, *Mustela nivalis*. Unpublished D.Phil thesis, Oxford University.
- Hedrick AV, Temeles EJ. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution* 4: 136–138.
- Hewison AJM, Vincent JP, Bideau E, Angibault JM, Putman RJ. 1996. Variation in cohort mandible size as an index of roe deer (*Capreolus capreolus*) densities and population trends. *Journal of Zoology, London* 239: 573–581.
- Holmes T. 1987. Sexual dimorphism in North American weasels, with a phylogeny of the Mustelidae. Unpublished PhD Dissertation, University of Kansas, Lawrence.
- Johnson DR. 1991. Measurement of weasel body size. *Canadian Journal of Zoology* 69: 2277–2279.
- King CM. 1980. Field experiments on the trapping of stoats (*Mustela erminea*). *New Zealand Journal of Zoology* 7: 261–266.
- King CM. 1981. The reproductive tactics of the stoat, *Mustela erminea*, in New Zealand forests. In: Chapman JA, Pursley D, eds. *Worldwide Furbearer Conference*. Frostburg MD: Worldwide Furbearer Inc, 443–468.
- King CM. 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*), in relation to seedfall of southern beech. *New Zealand Journal of Zoology* 9: 467–480, and errata in 10: 130a–130c (1983)
- King CM. 1983. The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52: 141–166.
- King CM. 1985. Interactions between woodland rodents and their predators. *Symposia of the Zoological Society of London* 55: 219–247.
- King CM. 1989a. The advantages and disadvantages of small size to weasels, *Mustela* species. In: Gittleman JL, ed. *Carnivore Behavior, Ecology and Evolution*. Ithaca, New York: Cornell University Press, 302–334.
- King CM. 1989b. *The Natural History of Weasels and Stoats*. London: Christopher Helm, and Ithaca, New York: Cornell University Press.
- King CM. 1990 (ed). *The Handbook of New Zealand Mammals*. Auckland: Oxford University Press.
- King CM. 1991a. Body size – prey size relationships in European stoats *Mustela erminea*: a test case. *Holarctic Ecology* 14: 173–185.
- King CM. 1991b. Age-specific prevalence and a possible transmission route for skrjabiniosis in New Zealand stoats, *Mustela erminea*. *New Zealand Journal of Ecology* 15: 23–30.
- King CM. 1991c. A review of age determination methods for the Stoat *Mustela erminea*. *Mammal Review* 21: 31–49.

- King CM Edgar RL.** 1977. Techniques for trapping and tracking stoats (*Mustela erminea*): a review, and a new system. *New Zealand Journal of Zoology* **4**: 193–212.
- King CM, McMillan CD.** 1982. Population structure and dispersal of peak-year cohorts of stoats (*Mustela erminea*) in two New Zealand forests, with especial reference to control. *New Zealand Journal of Ecology* **5**: 59–66.
- King CM, Moody JE.** 1982. The biology of the stoat (*Mustela erminea*) in the National Parks of New Zealand. *New Zealand Journal of Zoology* **9**: 49–144.
- Kopein KI.** 1969. [The relationship between age and individual variation in the ermine.] In: King CM, ed. *Biology of Mustelids: Some Soviet Research*, vol. 2, (1975). Wellington, New Zealand: Science Information Division, New Zealand Department of Scientific and Industrial Research, 132–138.
- Kozlowski J.** 1989. Sexual size dimorphism: a life-history perspective. *Oikos* **54**: 253–255.
- Lande R.** 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**: 292–305.
- Lebreton J-D, Pradel R, Clobert J.** 1993. The statistical analysis of survival in animal populations. *Trends in Ecology and Evolution* **8**: 91–95.
- Lovich JE, Gibbons JW.** 1992. A review of techniques for quantifying sexual size dimorphism. *Growth, Development and Ageing* **56**: 269–281.
- Madsen T, Shine R.** 1993. Temporal variability in sexual selection acting on reproductive tactics and body size in male snakes. *American Naturalist* **141**: 167–171.
- Meia J-S.** 1990. Etude de la variation de taille de l'hermine (*Mustela erminea* L.) et de la belette (*Mustela nivalis* L.) en Europe. *Bulletin Société neuchâtoise des Sciences naturelles* **113**: 307–318.
- Moors PJ.** 1974. The annual energy budget of a weasel (*Mustela nivalis* L.) population in farmland. Unpublished PhD thesis, University of Aberdeen.
- Moors PJ.** 1980. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. *Oikos* **34**: 147–158.
- Murphy EC, Dowding JE.** 1995. Ecology of the stoat in *Nothofagus* forest: home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology* **19**: 97–109.
- O'Donnell CFJ, Phillipson S.** 1996. Predicting the occurrence of mohua predation from the seedfall, mouse and predator fluctuations in beech forest. *New Zealand Journal of Zoology* **23**: 287–293.
- Petrov OV.** 1956. [Sexual dimorphism in the skull of *Mustela erminea*]. In: King CM, ed. *Biology of mustelids: some Soviet research*, vol 1 (1975). Boston Spa, Yorks.: British Library (Lending Division), 50–58.
- Powell RA.** 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Zeitschrift für Tierpsychologie* **50**: 153–165.
- Promislow DEL.** 1992. Costs of sexual selection in natural populations of mammals. *Proceedings of the Royal Society of London Series B* **247**: 203–210.
- Ralls K, Harvey PH.** 1985. Geographic variation in size and sexual dimorphism of North American weasels. *Biological Journal of the Linnean Society* **25**: 119–167.
- Ramesky S.** 1983. [Correlation between the phase of the population cycle and the dimensions of juveniles, using the example of the arctic fox]. In: Pokrovsky AV, ed. *Quantitative methods in the Ecology of Vertebrates*. Sverdlovsk Urals Scientific Centre of the Soviet Academy of Sciences, 112–125 (in Russian).
- Ranta E, Laurila A, Elmberg J.** 1994. Reinventing the wheel: analyses of sexual dimorphism in body size. *Oikos* **70**: 313–321.
- Sandell M.** 1986. Movement patterns of male stoats *Mustela erminea* during the mating season: differences in relation to social status. *Oikos* **47**: 63–70.
- Sandell M.** 1989. Ecological energetics, optimal body size and sexual size dimorphism: A model applied to the stoat, *Mustela erminea*. *Functional Ecology* **3**: 315–324.
- SAS** 1985. *SAS User's Guide: Statistics*. Cary, North Carolina: SAS Institute.
- Shiljaeva LM.** 1971. [The structure of the Arctic fox (*Alopex lagopus*) population and the role of different generations in the control of the animal's population density]. *Zoologicheskii Zhurnal* **50**: 1843–51. Translated by Department of Internal Affairs, Wellington, New Zealand.
- Simms DA.** 1979. North American weasels: resource utilization and distribution. *Canadian Journal of Zoology* **57**: 504–520.
- Stubbe M.** 1978. Zur taxonomie und Morphologie des mitteleuropäischen Hermelins *Mustela erminea* L. 1758. *Säugetierkunde Information* **2**: 22–32.
- Tannenfeldt M, Angerbjörn A, Arvidson B.** 1994. The effect of summer feeding on juvenile arctic fox survival—a field experiment. *Ecography* **17**: 88–96.
- Williams GC.** 1992. *Natural Selection: Domains, Levels and Challenges*. New York: Oxford University Press.
- van Zyll de Jong CG.** 1992. Morphometric analysis of cranial variation in Holarctic weasels. *Zeitschrift für Säugetierkunde* **52**: 77–93.