HOLARCTIC ECOLOGY 14: 173–185. Copenhagen 1991

Body size – prey size relationships in European stoats Mustela erminea: a test case

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King, C. M. 1991. Body size – prey size relationships in European stoats *Mustela erminea:* a test case. – Holarct. Ecol. 14: 173–185.

From the close correlation between the body size of European stoats and the mean size of their vertebrate prey it ought to be possible to predict the body size of European stoats living on a prey fauna of a given size distribution. In New Zealand, stoats of European stock have lived for >100 yr on a prey fauna containing fewer small and more large vertebrate prey than in Europe. They have become generally larger than their ancestors, as expected – especially the females. The vertebrate prey size index for New Zealand stoats extends the correlation predicted from European data. New Zealand stoats also eat large numbers of native insects. If these are included the local prey size indices are lower but still tend to vary with the substantial local variation in body size of stoats within New Zealand. Recent results from southern Ireland also fit the European correlation, but the few data so far available from Northern Ireland do not.

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Introduction

Erlinge (1987) presented data on the variation in body size of stoats from five locations in Europe. Stoats from northern Sweden (adult males 184 g, females 98 g) average roughly half the size of those from Britain (321 g, 213 g), while stoats from southern Sweden, Switzerland and France are intermediate (males 230–243 g; females 137–157 g). Erlinge calculated a prey size index, from the frequency distribution of sizes of vertebrate prey eaten by stoats in the five areas, and showed that stoats generally ate smaller prey in the north. There was a significant correlation between prey size index and stoat body weight ($r_s = 0.74$, $p < 0.05$). Even though these data were calculated from gross averages (material from both sexes pooled despite significant sexual dimorphism in size and food habits; prey data not controlled for season, habitat etc.), nevertheless this correlation provides the best clue available from present data for the observation (documented by King 1989) that the latitudinal variation in body size of European stoats runs in the opposite direction to that predicted by Bergmann's rule (i.e., they are smaller in the north). In Switzerland, stoats are smaller at high altitude (>2000 m a.s.l.) than in the valleys, where water voles *Arvicola terrestris* are an important prey ($p < 0.001$ for body weight and length, both sexes: Güttinger and Müller 1989). Other possible explanations for geographic variation in body size of *Mustela* species in general were examined by Erlinge and by Harvey and Ralls (1985), and were all rejected. Erlinge concluded that "size variation in the stoat is caused primarily by regional differences in the size frequency distribution of their available prey".

If this correlation is valid and general, it should be possible to predict the body size of European stoats living on a prey fauna of a given size distribution. The more such a fauna is unlike the faunas included in Erlinge's correlation, the more interesting the test should be. The key requirements are for adequate data on the prey fauna, and on the size and diet of the stoats. All this information is available from New Zealand, where the contrast with Britain and mainland Europe in species composition and size distribution of the fauna of small mammals, the main prey of stoats, could hardly be more pronounced.

Accepted 25 May 1990

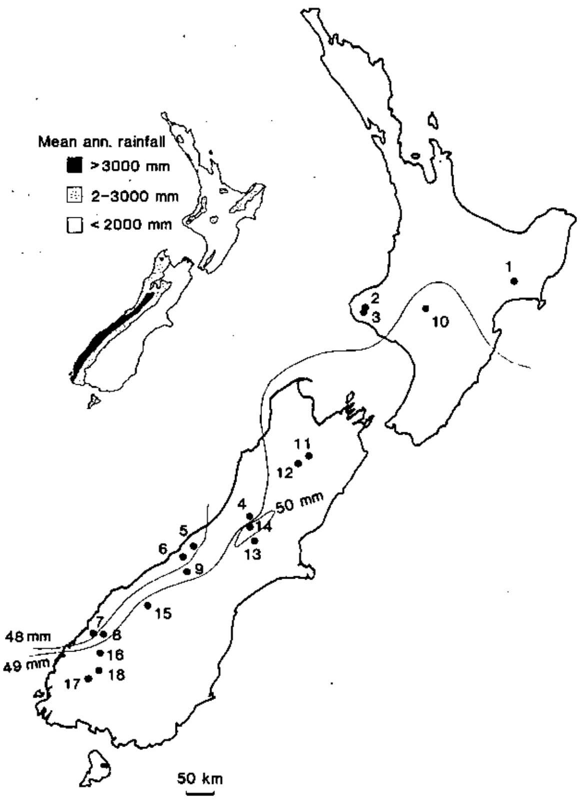

Fig. 1. Locations of study areas from which stoats were collected, numbered as in Tab. 3. The contour lines show the approximate distribution of size classes of condylobasal length in males. Inset: distribution of mean annual rainfall in New Zealand. For statistical analyses and further information, see King and Moody 1982.

Stoats of British stock were imported into New Zealand in substantial numbers during the twenty or so years after 1884 (King and Moors 1979, King 1984). By that time, European rabbits *Oryctolagus cuniculus* (introduced in the 1860s) were causing massive damage to sheep pastures. The first stoats were liberated on the worst-infested farms, but they very soon spread into the then still extensive native forests. They found a prey fauna radically different from that of Britain, but they thrived on it, and are now among the most widely distributed of all the introduced mammals in New Zealand (King 1990).

This paper has two purposes. First, I point out that the extensive data available on the size and food habits of New Zealand stoats, if handled in the same way as those quoted by Erlinge for Europe, offer a test of Erlinge's hypothesis. If the hypothesis is correct, a point for New Zealand should fit into or continue the trend shown on Erlinge's graph. This is a matter of simple observation of contemporary populations. Second, if such a correlation between body size and prey size exists in New Zealand stoats, I ask how has it arisen. This question entails the much more difficult matter of distinguishing cause from effect, and of inferring historical processes from contemporary data. The two questions are related, but separate, and the problems inherent in discussing the second question do not invalidate documentation of a simple answer to the first.

Study areas and methods

Stoats are regarded as pests in New Zealand, especially in nature reserves such as National Parks. The duties of park rangers include destruction of introduced animals whenever possible. From 1972 to 1976, over 1600 dead stoats were collected and sent to our laboratory for analysis from all the ten national parks then gazetted, plus a forest park, a wildlife reserve, a seabird nesting colony and a private hunting reserve. The 14 areas, subdivided into 30 distinct locations, were fully described by King and Moody (1982), and 18 of them are mapped in Fig. 1.

All but two of the 14 areas were covered with or close to evergreen native forest of two main types. Most of the southern beech (*Nothofagus* spp.) forests were in mountain country, and often had more or less extensive open grasslands nearby. The mixed podocarp – hardwood forests were usually adjacent to pastoral farms. The extensive lowland agricultural lands that dominate the landscape of New Zealand support mainly introduced flora and fauna, which are not protected by any wildlife legislation, so few samples could be obtained from them under the collection system we operated. Nevertheless, the study areas represented a wide range of altitudes, latitudes, climates and broad types of the native vegetation.

Carcases were measured and dissected by standard procedures, fully described by King and Moody (1982). The measures of body size employed were whole body weight, length of the head and body, and condylobasal length of the skull. We did not measure the teeth, although future students might do so since Dayan et al. (1989) have suggested that canine diameter might be a more sensitive indicator of predator-prey size relationships in North American weasels than is condylobasal length. Empty guts or those containing trap bait only were discarded. All guts from traps baited with possum or lagomorph meat were omitted from the analyses for possums and lagomorphs, whether or not they contained those remains, although other items they contained were counted. Mammals were identified from hairs, using a local version of Day's (1966) key. Few birds could be identified to species, but we considered that most were probably small passerines.

For mammals and birds, only one individual was assumed to have been eaten at one time, unless there was clear evidence to the contrary. Smaller items (lizards, crustaceans and arthropods, bird's eggs) were identified from skins, feet or hard parts, and, except eggs, could often be counted, so were recorded as the minimum number of specimens identified.

Most of the analyses presented by King and Moody (1982) were based on the frequency of occurrence of positive records (presence or absence) of a given prey type calculated as a percentage of the total number of guts with food in a given sample. This method allows the distribution of each prey type identified to be compared between samples without reference to the rest of the diet. We assumed that the time during which different prey items remained in the gut, and the probability of correct identification, were constant across all samples, but not that these factors were equal for all types of prey. In order to maximise homogeneity of samples, the statistical comparisons were limited to the nine most important prey categories found in the 866 guts collected in forest. This large sample could be broken down into subsamples according to forest type, age, sex, season etc., and these subsamples were still large enough to test. The local samples were not analysed separately because we had reservations about presenting data not controlled for variables which we knew would affect the results.

The contribution to the total diet of items of different sizes was also estimated, by summing the frequency counts for each item, loading them according to prey size, and expressing the result as a percentage of all items identified in forest stoats of each sex. There are serious problems with this approach. First, the values for each category are by definition relative to the total, so differences between samples cannot be related to different rates of consumption of a given prey. Second, one must necessarily assume that all prey items remain in the gut for equal lengths of time, and all are equally easily identified. Third, and worse, too little is known of the feeding behaviour and digestive processes of stoats in the wild to determine sensible loading factors for large prey species. The live body weight of adult prey is not an appropriate factor, since it is impossible to estimate how often stoats take juveniles and subadults, and how much of each carcase is eaten. We had reason to believe that New Zealand stoats usually take only a few meals from a single large carcase. In the mild climate of most of the sample areas, decay of carrion, and invasion by carrion-inhabiting insects, is seldom much delayed by cold. If carrion is an important resource for the local stoats, we would expect to find carrion insects well represented among the very large number (1127) of insects identified in our material. In fact, such insects were scarce. New Zealand stoats may well eat carrion whenever the opportunity offers, but probably take only a few meals from each carcase during the short time it remains fresh.

We therefore estimated the contribution of items of different sizes with reference to how much a stoat is likely to eat at one time. Captive stoats normally eat only c. 10 g at a time (Day 1968) so we took that figure as the average stomach capacity. Therefore, small items under 10 g comprise less than one meal, so we multiplied the minimum number found by their approximate mean weight (lizards 7 g, Orthoptera 3 g, other arthropods 1 g). Medium-sized items (birds, mice, freshwater crayfish) were weighted as one 10 g meal each. For large items, we assumed that if a stoat takes several meals from a single large carcase, the appropriate weight is the average amount of food in the gut (stomach plus intestines) at one time, c. 20 g (Day 1968); therefore large items were weighted as two meals each. These loadings were used to calculate the data reproduced from our original paper in Fig. 3. Elsewhere in this paper, for the purpose of comparison with Erlinge (1987), I have used the same loadings for mammals and birds as used by Erlinge, as defined on Tab. 2.

Size distribution and species composition of potential prey for stoats in New Zealand compared with those of Europe

The frequency distribution of body sizes in the fauna of small mammals (< 5 kg) in New Zealand is, compared with that of Europe, strongly skewed toward the larger species (King 1990). All land mammals in New Zealand except bats are introduced. There are no shrews or voles, and feral house mice *Mus musculus* are the only rodents with < 50 g mean weight. They are widespread but not common except locally and temporarily. At the other end of the scale of body size, rats (mostly *Rattus rattus*), rabbits *Oryctolagus cuniculus* and Australian brush-tail possums *Trichosurus vulpecula* are widespread and locally abundant. *Lepus europaeus* and *Rattus norvegicus* are also present in lower numbers. There is a pronounced reciprocal distribution between lagomorphs and possums in the two main types of forest. Lagomorphs are more common in the grasslands and adjacent beech forests, and possums in the podocarp – mixed forests. Both are often made available to stoats as carrion (e.g. road-kills and carcasses left by furtrappers and poisoning operations).

Native prey include insects, lizards and birds. The contemporary mainland faunas of insects and lizards are far less diverse and abundant than formerly, although still common by European standards. The large, terrestrial native Orthopterans, known collectively by their Maori name "weta", once included species that grew to 5–10 g, which were widespread on the New Zealand archipelago before human colonisation. Wetas have been called "invertebrate mice" or "insect rodents" (Stevens 1980), because they to some extent occupied the niche held by small rodents elsewhere in the world. The native fauna has been devastated by the consequences of human settlement, and now few wetas exceed about 3 g. Birds are still very abundant on certain predator-free offshore islands, but on the contemporary

Tab. 1. Body and skull size in adult stoats from New Zealand and Britain compared, and t-test on the geographical difference in mean condylobasal lengths in the two sexes. For comments on origin of data, see text.

Body weight, g	Males			Females			Ref.
	n	x̄	SE	n	x̄	SE	
New Zealand	395	324	2.63	398	207	1.51	1
England and Wales	204	321	–	99	213	–	2
Scotland	28	295	9.6	23	187	5.6	3
Condylobasal length, mm							
New Zealand	350	50.1	0.09	378	45.7	0.06	1
Britain	45	49.6	0.24	23	44.8	0.28	4
t-test	$t = 1.87$ $0.1 > p > 0.05$			$t = 3.34$ $p < 0.01$			

References: 1. King and Moody 1982; 2. Deanesly 1935; 3. Pounds 1981; 4. P. J. Moors, in King and Moody 1982 and unpubl. data.

mainland they are now scarce compared with Europe (Brockie and Moeed 1986).

This description of the prey resources of New Zealand is necessarily very general. We made no detailed surveys of the distribution of all potential prey in a given locality, although we did document the important relationship between the population dynamics of stoats and of rodents in three areas (King 1983). The data presented in this study are derived from gut analyses, and therefore deal with what the stoats actually ate, not with what was available for them to choose from. The frequency distributions of actual and of potential prey at any given place or time are not necessarily the same. This problem was not addressed by Erlinge and does not arise in the first part of this paper, which aims only to extend the comparison he made and by the method he used. But it hampers interpretation of the origins of evolutionary adaptation in New Zealand stoats within historic time, as discussed below.

Frequency distributions of the number of prey eaten, calculated as percentages of all items identified in guts or scats, produce relative values for each item that are not independent of each other. Stoats in Europe eat few insects, and none was listed in the analyses quoted by Erlinge; but the high frequencies for insects in the New Zealand data distort the relative values for vertebrate prey. Therefore, any valid comparison between European and New Zealand data must be confined to vertebrates. However, for comparisons of body size, diet and prey size index among local samples within New Zealand, the insects must be included, since they are important prey in all areas and cause no statistical problems in comparisons confined to subsets of New Zealand data.

Results

Relationship between body size, diet, and prey size index of stoats in New Zealand generally

The mean body weight and condylobasal length of the total sample of stoats collected from throughout New Zealand are shown in Tab. 1.

Tab. 2 lists the total number of items recovered from the 1250 stoat's guts analysed, in descending order of size. Fig. 2 shows the most important foods of stoats (ages and sexes pooled) in three types of forest by season. Significant variations with season and habitat were demonstrated. The most frequently eaten prey are, as in Europe, mammals and birds. Invertebrate prey, especially wetas and other insects, are far more often eaten by stoats in New Zealand than in Europe. Nevertheless, in terms of biomass, the large items as defined in Tab. 2 make by far the greatest contribution to the diet of all stoats living in forest, especially the males (Fig. 3). Insects, though eaten frequently, contribute a relatively small proportion of a stoat's energy needs.

The vertebrate prey size index for New Zealand in general is 132.8, that is, somewhat higher than for the large stoats from Britain (Tab. 2). This figure fits the correlation predicted by Erlinge (Fig. 4).

Variation in body size, diet and prey size index within New Zealand

There is pronounced local variation in body size of New Zealand stoats (Tab. 3). The variation is visible in all body measurements; we applied significance tests to head-and-body length, a measurement with a low coefficient of variation, large sample sizes and relative immunity to short-term variations such as whether the stomach was full or empty. Kruskal-Wallis one-way

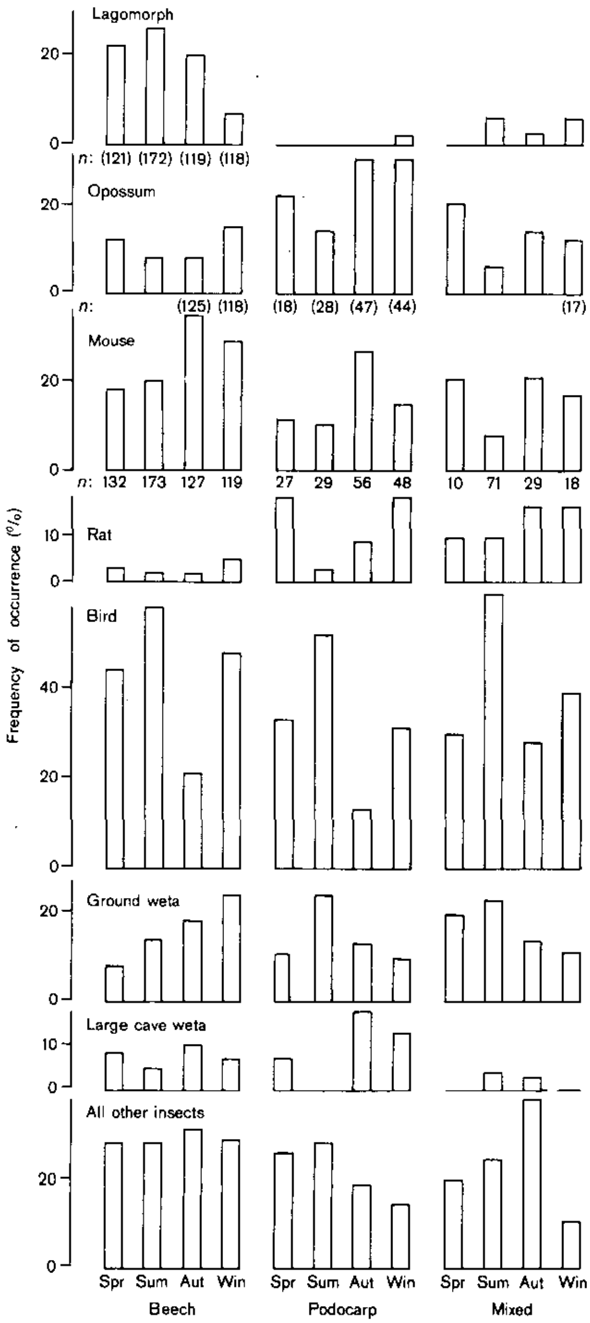

Fig. 2. Frequency distributions of the nine principal prey of New Zealand stoats (ages and sexes pooled), in the three main types of forest by season. Sample sizes (number of guts containing food) all as for mice except those in parentheses (all guts from traps baited with lagomorph or possum were discarded, reducing the sample size for these prey). Data presented as the frequency of occurrence of positive records (maximum one per gut) as a percentage of the number of non-empty guts examined. Since this figure was published in King and Moody (1982), the common name of *Trichosurus vulpecula* has been shortened, by common consent, from "opossum" to "possum".

analyses of variance of data grouped by collection area (i.e., pooling local subsamples taken from within one park) were done separately for each sex. For adult males, $H = 27.30$ ($df = 12$), $p < 0.01$, and for adult females, $H = 26.81$ ($df = 10$), $p < 0.01$.

Local variation is consistently related to habitat. In condylobasal length, adult males from the podocarp-mixed forests are clearly smaller than those from beech forests and adjacent grasslands (Fig. 5). The same pattern reappears in adult females and in young, and even in samples taken a short distance (20–40 km) apart. Mann-Whitney U-tests show that these differences are highly significant in both sexes (adult males, $z = -5.692$, $p < 0.001$; adult females, $z = -3.719$, $p < 0.001$).

There is an apparent positive correlation between local variation in body size and altitude (King and Moody 1982, King 1989) but it cannot be explained by Bergmann's rule. The relationship between length and weight does not change in the direction expected. The higher-altitude animals, though distinctly heavier than the lowland ones, are relatively longer and slimmer than the shorter, stockier lowlanders, i.e., they have a less favourable ratio of surface to mass (Tab. 3).

The link with altitude is probably a consequence of other correlations between habitat, body size and climate. In every one of the 8 local populations from podocarp-broadleaf forests, the mean condylobasal length in males was <49.99 mm (Tab. 3), and the local mean annual rainfall was >2500 mm. In every one of the 9 local populations from beech forests, the mean condylobasal length in males was >50.00 mm and in all but one the local mean annual rainfall was <2500 mm. The correlations between mean condylobasal length and annual rainfall (Fig. 5) were significant in both sexes (males: $r_s = -0.609$, $p < 0.05$; females: $r_s = -0.782$, $p < 0.01$).

The diets of stoats in beech forest, podocarp-broadleaf forest and in mixed forest are compared in Fig. 2. There are substantial differences, which mostly reflect the variation in distribution of prey species. For example, the beech forest-grassland stoats ate relatively more lagomorphs than those living in podocarp-hardwood and mixed forests. But in the podocarp-hardwood and mixed forests, stoats ate more possums and rats. Because of the reciprocal distribution of lagomorphs vs possums and rats in relation to forest type, large mammalian prey are available to all forest stoats in New Zealand. Overall, large-sized prey are the staple diet of stoats living in all forests, so there is no obvious relationship between size and diet (King 1989). When, however, the data are broken down by sex and habitat, a different conclusion emerges.

Female stoats are always substantially smaller than males (Tabs 1, 3), and they generally take smaller-sized prey. When the prey categories were grouped and classified as small, medium or large, as defined in Tab. 2, males ate more large, and females more small prey (differences significant in Wilcoxon matched pairs, signed

Tab. 2. Prey of New Zealand stoats: species and number identified, body weight, frequency of occurrence (% of items), and the correction factors (CF) based on the loadings ("weight, g") used by Erlinge (1987) for calculating the mean prey size index (PSI). Items recorded <25 times are excluded (freshwater crayfish 25, carrion 17, bird's egg 16, unidentified food 13, rubbish 12, stoat 4, hedgehog 2, fish 2); also the 29 cases in which a trapped stoat had chewed off and eaten part of its own foot. Only guts with food analysed (sexes pooled); total guts examined 1514, of which 1250 contained food.

Species		Mean wt (g)[1]	Min. no. items	CF	All items		Vertebrates only	
					f	PSI	f	PSI
Large	*Trichosurus vulpecula*	2500	121	300	0.05	14.4	0.09	26.0
	Oryctolagus cuniculus / *Lepus europaeus*	1500 / 3500	213[4]	300	0.08	25.3	0.15	45.8
	Unidentified large mammal	1500[2]	128	300	0.05	15.2	0.09	27.5
	Rattus rattus / *R. norvegicus* / *R. exulans*	140 / 220 / 90	80[3]	250	0.03	7.9	0.06	14.3
Medium	birds[4]	?	535	40	0.21	8.5	0.38	15.2
	Mus musculus	20	241	20	0.09	1.9	0.17	3.5
	Skinks	7	42	7	0.02	0.12	0.03	0.21
	Geckos	7	35	7	0.01	0.10	0.02	0.18
Small	Weta (Orthoptera)	3	625	3	0.25	0.74		
	Lepidoptera	1	156	1	0.06	0.06		
	Carabidae	1	68	1	0.03	0.03		
	Other arthropods	1	278	1	0.11	0.11		
Items		All	2522					
		Vertebrates only	1420					
Mean prey size index					All 74.4		Vertebrates only 132.8	

[1] Approximate.
[2] Indistinguishable but mostly possums and rats.
[3] Indistinguishable but almost all *R. rattus*.
[4] Indistinguishable.

ranks tests: for large prey, $T = 39.5$, $0.02 < p < 0.05$, $N = 19$; medium prey, $T = 53$, $p > 0.05$, $N = 18$; small prey, $T = 59.5$, $p < 0.01$, $N = 25$). Small and medium prey made a greater contribution to the biomass of foods eaten by females than of males (Fig. 3). Females still take what small rodents there are more often than do males, and also more insects, but they take birds, rats and lagomorphs as often as do males.

In the largest of the local samples, each representing a relatively homogeneous habitat, the prey size indices (including insects) could be calculated for the two sexes separately (Appendix 1, Fig. 6). The general correlation between prey size index and body weight was significant overall ($r_s = 0.775$, $p < 0.01$, $N = 11$). Within each sex the trend clearly runs in the same direction, but there were too few samples to test them separately.

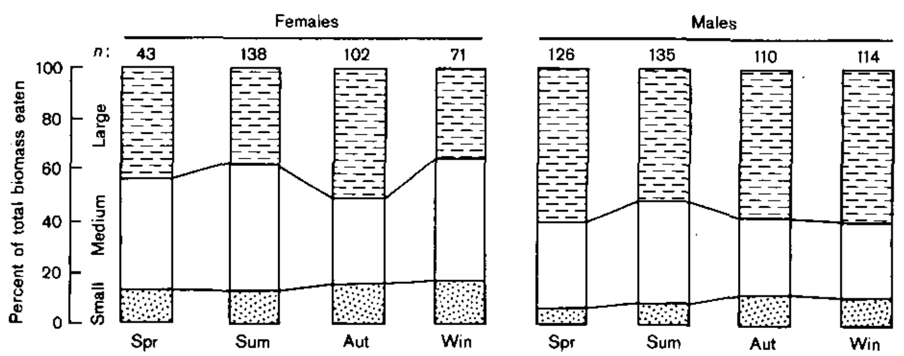

Fig. 3. The relative importance of small, medium and large prey to male and female stoats living in New Zealand forests. For species included in each category, see Tab. 2; for method of calculation and loadings used (not the same as used to calculate Erlinge's prey size index), see text. Data presented as numerical counts of each prey item, weighted for size, as a percentage of the total number of prey items identified. From King and Moody 1982.

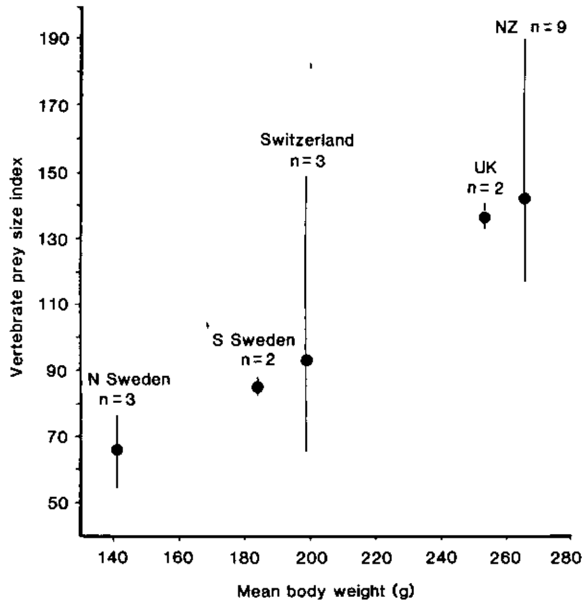

Fig. 4. Erlinge's prey size index (vertebrates only) plotted against mean body weight (sexes pooled) of stoats in Europe and New Zealand. The circle marks the grand mean prey size index for each country, the bars show the extent of the range of local means within that country, and n = the number of local means included. The European food data are recalculated from Appendix 3 of Erlinge (1987). The point for Britain is the mean of the data provided by Day (1963) and Pounds (1981) (*see Appendix 2 for data and reasoning*). The New Zealand mean is from Tab. 2 and the range from King unpubl. data.

Adaptation in historic time

If British stoats are still about the same size as they were a hundred years ago – or at least, if they have not become smaller in that time – then the present British average can be taken as representing the general body size of the colonising stock. Unfortunately, there are surprisingly few data available on the body size of British stoats, then or now. Deanesly (1935) gave monthly mean body weights for adults and young of each sex, calculated from a collection of 662 stoats from 30 counties of England and Wales, of which 306 came from Caernarvon. She did not give an overall mean with SE for adult males and females, but stated that the adult weight of males was "about 325 g", and of females, "about 190 g" (p. 490). The most widely quoted figures (mean 321 g and range 200–445 g for males; mean 213 g and range 140–280 g for females; Southern 1964), were apparently derived by averaging Deanesly's January to July means for adults. These figures probably somewhat overestimate the body size of British stoats in general, because they exclude all animals caught in the second half of the year (August to December), of which many would be young adults (16–20 months old) just completing their first breeding season, plus the generally smaller Scottish stoats. No data on the body weights of the stoats of England and Wales have appeared since, but Pounds (1981) recently documented the body measurements of stoats from Aberdeenshire (Tab. 1).

The condylobasal lengths of the stoat skulls, collected from all over Britain and held by the British Museum (Natural History), were measured by P. J. Moors (King and Moody 1982). The mean for adult males was 49.6 mm, range 45.2–52.3 mm; for adult females, 44.8 mm, range 41.7–47.7 mm (Tab. 1). These figures are somewhat more reliable, since measurements from skulls can be made accurately and controlled for age. Nevertheless, it is clear that, by comparison with the New Zealand data, the information available from Britain is sparser (smaller samples, local variability poorly known).

The mean of Pounds' and Deanesly's figures gives the nearest we can get at present to an overall mean body weight for British stoats, 308 g for males and 200 g for females. The mean body weight of New Zealand stoats of both sexes (324 g, 207 g) is therefore slightly higher than that of their ancestors, and the maximum weights attained (ranges 160–475 g for males, 102–314 g for females) are greater. In condylobasal length, the New Zealand adults are distinctly larger (males $\bar{x} = 50.1$ mm, range 43.0–54.0 mm; females $\bar{x} = 45.7$ mm, range 41.7–48.6 mm), much more so in females ($T = 3.34$, $p < 0.01$) than in males ($T = 1.87$, $0.1 > p > 0.05$).

The variability in size and the exact provenance within Britain of the stoats imported to New Zealand are unknown. Even if variability among local forms in Britain were substantial, consignments of animals from different sources would certainly have become confused during transit in any case. Yet the adjustment in the body size of the descendants of the colonising stock to the range of local conditions in New Zealand is distinctly non-random, has developed in <100 yr, and is remarkably extensive. The range of local mean condylobasal lengths in adult male stoats in New Zealand is almost as great as in continental Europe. The range for New Zealand (Tab. 3) is 48.9–51.5 mm (18 locations: difference 2.6 ± 0.45 mm) and that for western Europe is 46.8–49.6 mm (2.8 ± 0.33 mm) (Stubbe 1978); the ranges of sizes in the two areas are not significantly different ($F = 1.31$, $p > 0.1$).

Discussion

Because conditions in New Zealand are radically different from those anywhere else in the world, observation of animals acclimatised here should be useful in testing theoretical ideas developed in the northern hemisphere. Many of the mammals introduced to New Zealand have developed pronounced differences in morphological, ecological or behavioural characters compared with their parent stocks (King 1990). Stoats are among the most interesting, because they represent a test case for

Tab. 3. Geographical variation in body and skull size of stoats in New Zealand. The larger samples are graphed in King and Moody 1982; the rest are from King, unpubl. data. For statistical test, see text. Capital letters stand for one of 14 main collection areas; lower case suffixes indicate separate localities within the main area. Localities 1–8 = podocarp hardwood forest; 9 = tussock grassland without forest; 10–18 = beech forest/grassland.

Locality code	Number on Fig. 1	Head and body length (mm)			Tail length (mm)			Body weight (g)			Condylobasal length (mm)		
		mean	SE	n	mean	SE	n	mean	SE	n	mean	SE	n
Males													
UW	1	278	5.1	10	104	1.8	9	313	14.3	9	49.4	0.86	6
EGs	2	280	2.1	23	104	1.8	23	338	11.6	19	49.0	0.34	12
EGd	3	281	2.5	17	105	1.4	17	341	11.94	17	49.6	0.52	11
APw	4	284	3.1	7	106	2.2	7	306	10.0	5	49.7	0.51	5
WLm	5	276	3.1	10	101	2.1	10	288	11.6	10	49.1	0.22	8
WLx	6	278	5.2	5	106	1.9	5	327	17.0	4	48.3	0.85	4
FLm	7	275	4.7	9	102	1.7	9	291	16.1	7	48.5	0.43	7
FLh	8	278	2.8	36	103	1.8	36	303	10.1	34	49.1	0.39	30
MCb	9	289	1.7	34	103	0.8	34	336	10.4	25	49.7	0.35	26
TG	10	288	2.6	22	102	1.8	22	355	12.5	18	50.5	0.41	17
NLb	11	285	1.9	26	109	1.4	26	306	9.9	21	50.6	0.26	18
NLm	12	287	6.4	5	102	6.9	5	315	25.2	5	50.7	0.79	5
CB	13	290	1.4	50	107	1.9	50	356	7.0	47	50.4	0.25	39
APe	14	290	3.3	17	114	1.7	18	345	9.3	14	51.5	0.42	14
MA	15	284	3.0	11	110	1.7	11	294	16.6	9	50.4	0.40	9
FLe	16	286	1.1	74	109	0.8	77	331	6.5	62	50.5	0.16	70
FLt	17	287	2.2	14	107	1.9	14	314	12.8	14	50.2	0.38	12
TK	18	286	2.5	23	108	2.1	23	311	10.2	18	50.7	0.35	14
Females													
UW	1	259	4.9	8	89	3.2	8	224	13.0	7	45.8	0.58	8
EGs	2	258	1.5	17	90	1.1	17	219	7.0	16	46.0	0.31	12
WLm	5	248	1.4	10	82	2.0	10	179	3.6	9	45.2	0.18	32
Flm	7	247	1.1	7	88	1.5	7	204	13.7	6	45.8	0.58	6
FLh	8	250	2.6	46	87	0.9	47	200	3.3	43	45.0	0.17	41
MCb	9	261	2.1	38	91	1.0	38	228	4.9	35	45.9	0.18	37
TG	10	255	2.3	12	87	1.6	12	219	7.8	18	45.4	0.34	12
NLb	11	258	2.5	12	94	1.3	12	195	5.9	10	46.7	0.28	11
CB	13	261	1.0	51	93	0.8	51	222	3.4	49	46.1	0.14	49
APe	14	257	2.1	19	95	1.0	19	204	5.2	16	45.9	0.33	15
FLe	16	256	1.4	57	93	0.9	57	206	4.2	52	45.6	0.19	51
FLt	17	258	2.4	6	92	1.4	6	174	10.2	6	45.7	0.52	6
TK	18	255	1.4	24	91	1.3	24	190	6.1	20	45.8	0.20	22

two variations on the well-known prey size – predator size hypothesis. Any general theory attempting to explain either geographical variation or sexual dimorphism in body size of stoats must take account of the New Zealand data.

Body size and prey size of New Zealand stoats

The first question I asked in this paper was, does the prey size index for New Zealand taken as a whole continue the correlation with body weight that Erlinge (1987) showed in Europe? Fig. 4 shows that it does. Small mammals are by far the most important prey for stoats throughout their range. The size distribution of the fauna of small mammals in New Zealand is, by comparison with Europe, skewed towards the larger species. The mean body size of stoats in New Zealand is slightly larger than that of their contemporaries in Britain. If the comparison is confined to the vertebrate prey identified in all samples, the New Zealand data fit perfectly into the predicted trend (PSI = 132.8; Fig. 4). I conclude that the New Zealand data support Erlinge's hypothesis.

There is a possible objection to this conclusion. If invertebrate prey items, mainly insects, are included in the calculations, the prey size index for New Zealand (74.4) falls well outside the expected correlation. Whether or not the insects should be included raises some interesting questions concerning the foraging

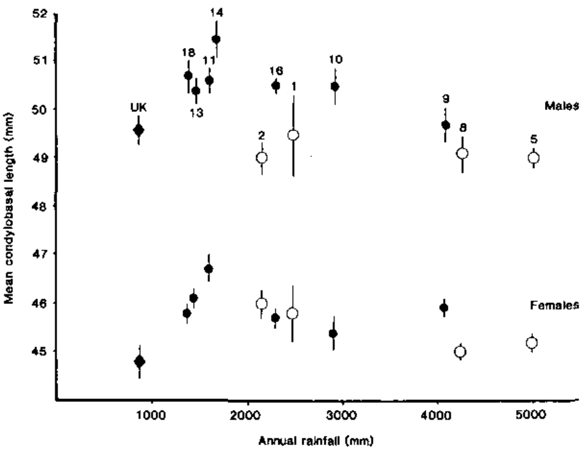

Fig. 5. Local variation in mean condylobasal length of stoats (± 1 SE) within New Zealand, plotted against mean annual rainfall in the collection area. Samples numbered as in Tab. 3. ●: beech forests and grasslands. ○: podocarp-hardwood and mixed forests. ◆: means for Britain (condylobasal lengths from Tab. 2; mean rainfall of the areas sampled for gut analysis by Day (1968) estimated by comparing Day's map of localities with a detailed rainfall map). Correlations between skull length and mean rainfall in New Zealand: males, $r_s = -0.609$, $p<0.05$; females $r_s = -0.782$, $p<0.01$. For t-tests comparing New Zealand and British means, see Tab. 1.

strategy of stoats in New Zealand. We have already shown (Fig. 3) that insects contribute only a small proportion of the biomass of their food, so we might expect that a foraging stoat would not actively seek out insects, but merely snatch them up in passing. However, that depends on the probability that the stoat has the choice between insects and more favoured prey. If the probability of encountering something better than an insect is low, and especially if that probability is even lower for smaller stoats, then insects may be regarded as significant prey, not to be ignored in our comparisons. If, on the other hand, insects are always taken only incidentally and are equally available to stoats of any size, then their incidence in the diet can be neglected on the grounds that they are unlikely to have any influence on the body size of stoats. Nothing is known about the hunting behaviour of New Zealand stoats, so these questions remain unanswered at present. Future studies might produce more information on their foraging strategy, which may have implications for the theory of foraging in small carnivores generally.

The correlations between body size and climate in the New Zealand material (Fig. 5) are strong, but the explanations for them are obscure. One possibility is suggested by James' (1970) "expansion" of Bergmann's rule. He proposed that optimum body mass might be adapted to a combination of climatic variables, including both temperature and humidity. He predicted that small size should be associated with mild humid conditions (at lower altitude in the New Zealand samples) and large size with cool or dry conditions. But this interpretation fails as a general explanation, since the correlation between stoat body size and altitude in Switzerland runs in the opposite direction (Güttunger and Müller 1989).

Prey size and sexual dimorphism in stoats

These data also provide a test for theories developed in the northern hemisphere to explain the very marked sexual dimorphism among small mustelids. Erlinge (1979) assumed that males tend to become larger as a result of sexual selection and competition for mates, whereas females remain small so as to maximise their efficiency as hunters of small rodents. Females concentrate on small rodents because they bring up their young alone, and throughout their native range small rodents are the most abundant, most rapidly replaced, most easy to carry and least risky to kill of all potential prey available to a small predator hunting solo (King 1989). Sandell (1989) proposed a complex energetic model allowing for the different energy budgets of breeding and non-breeding individuals and the different forms of sexual selection operating on males and females. He concluded that there is substantial selection pressure favouring smaller females.

To maximise foraging efficiency and reproductive success, females in the northern hemisphere therefore remain small. In New Zealand, it is no longer profitable for a female to remain small so as to specialise on small rodents. Perhaps this explains why females have responded to the change in hunting conditions in New Zealand (by becoming larger than their British ancestors in all

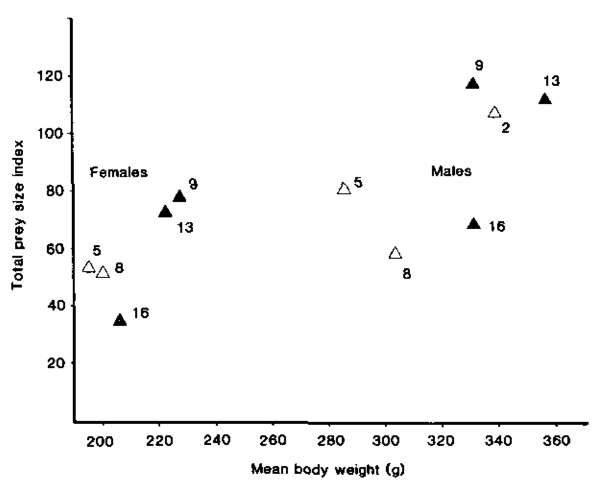

Fig. 6. Local variation in mean prey size index (including insects) within New Zealand, in relation to body weight, sex and habitat. Samples with <40 non-empty guts of one sex or representing heterogenous conditions were omitted. For details, see Appendix 1. Data presented as numerical counts of each prey item, weighted for size as in Tab. 2, as a percentage of all prey items identified. $R_s = 0.775$ ($p<0.01$). ▲: beech forest and grasslands. △: podocarp and hardwood forests.

habitats) to a greater degree than have males (Tab. 1, Fig. 5).

Some other hypotheses developed in Europe are not confirmed as generally valid by the New Zealand data. For example, Moors (1980) suggested that the most important advantage of small size to northern hemisphere females is not the ability to hunt in rodent burrows, but the lower absolute energy demands of a small body. He pointed out that a normal female requires less energy for maintenance than a hypothetical male-sized female, and is therefore able to channel more of the energy acquired from hunting into reproduction than could a larger female. If energy conservation alone were the most important consideration, then the New Zealand females, almost always short of food of the preferred size range, should have remained small. Korpimäki and Norrdahl (1989) pointed out that larger body size may decrease the vulnerability of small mustelids to predation by larger carnivores and raptors. They linked the southward increase in body size of European stoats with the southward increase in risk of predation posed by the much greater diversity and abundance of vertebrate predators in the south. In New Zealand, larger carnivores and raptors are much scarcer than in southern Europe.

Evolution of predator size – prey size relationships

Stoats have clearly been remarkably successful in adjusting to the totally different prey fauna in New Zealand. So the second question I asked in this paper was, how has that adjustment been achieved? Lack of the critical data makes it more difficult to give a definite answer here, since any statement must rest on the rather inadequate measurements available on UK animals and on the assumption that their mean size has not decreased during the last hundred years. Clearly there is an urgent need for a comprehensive morphometric study of the stoat in UK, both of the contemporary population and also, if possible, a survey of old museum records to see if any historical data exist. That may take some time; meanwhile, I present the above data and infer from them that there have been parallel upward shifts in both prey size index and in body size of New Zealand stoats.

This interpretation is weaker than the conclusion that the New Zealand data on prey size index fit the trend on Erlinge's graph. But the correlation between prey size index and body size appears not only in the gross comparison between New Zealand and Europe (sexes pooled), but also within the sexes and in the local variation within New Zealand when controlled for habitat and sex (Figs 4, 6). Neither is this apparently remarkable shift in body size unique. A comparable evolution of a consistent north–south variation in body size has also been observed among the brushtail possums introduced to New Zealand; in their case it apparently took only about 50 yr (30–35 generations) (Yom-Tov et al. 1986).

The implication is that there is some causal relationship between the change in diet and the change in body size of stoats in New Zealand. If two factors A and B are functionally related, a change in A should lead to a change in B. But on the other hand, it is also possible that both are unrelated consequences of a third factor C, in which case a change in C would be followed by parallel and independent changes in A and B.

There is therefore a logical difficulty in concluding, with Erlinge, that the size distribution of prey is the primary consideration determining the body size of stoats. The correlations that he and I have presented are between stoat size and diet. The frequency distributions of prey available and prey eaten are not necessarily equivalent. It is possible, even likely, that stoats of differing body size or in different habitats exploit the available large prey to different extents. If the prey eaten is a skewed sample of the prey available, the correlations merely show that larger stoats select larger prey if they can, without proving that the prey size distribution has any direct influence on stoat size. For example, the males and females of a given population hunt prey of the same size distribution, but are themselves very different in body size. It is clear that other considerations besides the mean body size of the prey need to be taken into account in explaining general patterns in body size-prey size relationships.

Sandell (1985, 1989) argues persuasively that the key factors determining optimal body size in stoats are ecological energetics and sexual selection. His model was adapted and extended by King (1989) to explain the general southward increase in body size among the Holarctic weasels as a group. At low temperatures, both sexes must minimise daily energy expenditure by maximising foraging efficiency; in the prolonged winters of the far north, this means remaining small enough to live and hunt under the snow. There are no other predators, and no prey larger than small rodents, in this subnivean habitat. Sexual selection favouring larger males is probably always present, but in a cold climate it is overridden by the prime necessity of retaining access to the tunnels and well-insulated nests of rodents. By contrast, in the milder climates further south, the lesser need to avoid exposure to the air relaxes the constraints on sexual selection in males. In addition, there are larger prey such as lagomorphs and sciurids, more easily tackled by larger than smaller weasels, and other predators both to prey on weasels and to compete with them for small rodents. These conditions would make small size and extreme specialisation on small prey less viable strategies in warmer climates, and reinforce sexual selection in favouring larger size in the south. King (1989) concluded that "this combination of energetics, size of available prey and sexual selection (in unknown proportions) explains why the niche for a weasel-shaped carnivore allows only smaller individuals in severe climates, but larger ones in mild climates".

The increase in size of New Zealand stoats is consistent with both Erlinge's (1987) and King's (1989) hypotheses. Erlinge's single-factor model is not falsified by the New Zealand data, but neither does it show whether the correlation with prey size index is a cause or a consequence of the larger size of the New Zealand stoats. It does not account for the different response of males and females to New Zealand conditions, nor for the consistent correlations between body size and environment (forest type, rainfall) in both sexes.

A possible alternative interpretation is that the availability of large-sized prey is a necessary, but not a sufficient condition allowing natural selection to favour larger body size in stoats in certain environments. If the size distribution of prey shifts upwards, the body size of stoats will increase provided it is permitted by the energy economy of individual stoats. This in turn depends on their sex, on the local climate, and also on other important but so far unknown attributes of the prey fauna which determine the foraging rate of stoats (one of the main variables in Sandell's (1989) model) and so modify the effects of size distribution. For example, if a larger stoat can more easily catch important large prey without reducing its ability to catch important small prey, then if all other things are equal, selection should favour large size; but if a larger stoat is less efficient at catching important small prey than a smaller stoat, the outcome will depend on whether large or small prey are the key resource. Moreover, the key resource need not be the same everywhere, nor prominent in the diet at all times. In New Zealand, feral house mice form a relatively minor component of the biomass eaten by stoats living in all types of forests, but in beech forest they are liable to occasional short-lived population irruptions, during which they have a disproportionate effect on the breeding success of female stoats (King 1983). The scarcity of raptors and larger carnivores in New Zealand may also be a relevant consideration. With so many unknown factors potentially involved, it is hardly surprising that prey size distribution alone does not account for all the observed variation in body size of New Zealand stoats.

Ireland

The stoats of Ireland, like those of New Zealand, live on a prey fauna which lacks *Microtus*, and which is nearly as different in prey size distribution from that of mainland Europe as is that of New Zealand. Ireland could therefore be regarded as a parallel test case. Stoats in southern Ireland average about the same size as in Britain and New Zealand (males 328 g, females 163 g; Sleeman 1987). Collection of samples in Eire is hampered because stoats are protected there; however, Sleeman (1987) managed to acquire a total of 196 road casualties, nearly all from the south especially around Cork, and the prey size index calculated from the 89 that had guts containing food (PSI = 139.3) is remarkably close to those for Britain and New Zealand (Appendix 2). This figure, when plotted against mean body weight, would fit comfortably on to the trend shown in Fig. 4. The stoats of southern Ireland therefore fit the correlation as well as do those of New Zealand.

However, stoats in northern Ireland are much smaller than those in the south (males 233 g, females 120 g; Fairley 1971). The only sample of gut contents from the north is far smaller than any accepted here as representative of other areas, and, as stoats in Ulster are not protected under British law, collected largely from gamekeepers. The prey size index calculated from this inadequate and possibly not strictly comparable sample (PSI = 140.2) is, nevertheless, practically the same as that from the southern sample, which puts it well outside the correlation between body size and prey size index found elsewhere (Appendix 2).

This observation adds a new twist to the well-known conumdrum of why the Irish stoat is different from the British (Sleeman 1987, King 1989). If confirmed, it would suggest that the question to concentrate on is why the northern Irish individuals, and only they, are so much smaller than expected. The single significant difference in prey resources with latitude in Ireland is provided by the bank vole *Clethrionomys glareolus*, which was discovered in County Kerry in 1964. But it is confined to the southwest, and Sleeman found that the body size of the southern stoats is the same whether they come from the area occupied by voles or not. Outside the range of the voles, the prey size distributions in the north and south appear to be the same. The puzzle is inexplicable from present information. A new, substantial ecological study of stoats in northern Ireland would be very interesting.

Summary

The scarcity of small rodents and the greater frequency of large (to 3 kg) mammalian prey for stoats in New Zealand compared with Britain has been matched by an increase in body size among New Zealand stoats compared with their British ancestors. This increase is especially pronounced in the females. The vertebrate prey size index for New Zealand stoats fits the correlation with body size proposed by Erlinge (1987). The pronounced local variation in body size within New Zealand is correlated with prey size index in 11 local subsamples controlled for sex and habitat. These data support two hypotheses developed from observations on stoats in the northern hemisphere; (1) on the correlation between prey size and predator size, and (2) on the adaptive advantage of small size to female stoats. Prey size and body size of stoats in the south of Ireland fit the same correlation, but not (on present data) in the north.

Acknowledgements – The original analysis of the New Zealand data was done with skill and care by M. G. Efford. I thank the publishers of the New Zealand Journal of Zoology for permission to reproduce Figs 2–3 from King and Moody (1982), and M. G. Day, C. J. Pounds and D. P. Sleeman for permission to quote from their theses. Drafts of this ms have been improved by the constructive criticisms of S. Erlinge, M. Sandell, R. Powell, D. P. Sleeman and M. G. Efford.

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Appendix 1. Geographical variation in body size of stoats and in prey index. Large, homogeneous samples or subsamples only: diets of males and females estimated separately.

Males	Number of items identified per collection area					
	EGs	MC	CB	WL	FLe	FLh
Possum	15	0	5	12	19	6
Lagomorph	1	41	32	0	10	1
Unidentified mammal	14	2	9	9	11	1
Rat	3	0	0	10	4	6
Bird	16	23	25	26	47	19
Mouse	5	4	7	8	26	3
Skink/Gecko	9	13	0	0	1	0
Wetas	17	27	12	36	59	31
Other insects	18	9	13	23	49	14
Total items	98	119	133	124	226	81
non-empty guts	49	68	67	67	103	40
Prey size index	108.6	118.2	113.0	81.7	69.1	59.6
Body weight, g	339	331	356	285	331	303

Females	MC	CB	WL	FLe	FLh
Possum	0	5	7	6	1
Lagomorph	35	23	0	1	6
Unidentified mammal	2	4	6	6	1
Rat	1	0	6	3	10
Bird	25	31	20	42	30
Mouse	5	17	20	26	11
Skink/Gecko	30	3	0	1	0
Wetas	52	46	52	85	35
Other insects	11	24	14	29	28
Total items	161	153	125	199	122
non-empty guts	78	70	60	72	62
Prey size index	79.7	74.2	54.1	35.9	52.9
Body weight, g	227	222	195	206	200

Appendix 2. Data on prey of stoats in Britain.

	Number of items identified			
	Day (1963)[1] General	Pounds (1981) Scotland	Sleeman (1987) S. Ireland	Fairley (1971) N. Ireland
Microtus spp.	11	26	–	–
Clethrionomys spp.	6	2	3	–
Apodemus spp.	4	5	5	5[2]
Unidentified small rodents	6	11	0	0
Squirrel	2	0	0	0
Rat	3	0	13	1
Insectivore	1	0	24[3]	0
Lagomorph	30	38	29	10
Bird	36	17	17	11
Total items	99	99	91	27
non-empty guts	87	97	89	29
Prey size index	123.0	130.9	139.3	140.2
Mean body weight, g	267	242	245	176

[1] These data are compiled from the original appendix table in Day's thesis, because in the published version Day (1968) counted remains found in the stomach and intestine as separate records, and included vegetation as prey.
[2] Two *Apodemus* plus three *Mus*.
[3] All pygmy shrews, weighted at 5 g.