

# The biology of the stoat (*Mustela erminea*) in the National Parks of New Zealand

## II. Food habits

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**Abstract** The gut contents of 1514 stoats from 14 collection areas (mostly forest or forest edge) were analysed. The distribution of 2643 prey items is expressed as percentage frequency of occurrence in 1250 guts containing food. In the total collection, the frequency of occurrence of the major categories of prey was: mice 19%; rats 6%; lagomorphs 18%; opossums 10%; birds 43%; lizards 5%; insects 41%; freshwater crayfish 2%; carrion about 1-2%. The diet of stoats in relation to age, sex, season, and habitat was examined more closely in the subsamples from forest ( $n = 866$ ; three classes of forest recognised) and from Mount Cook ( $n = 146$ , the only large non-forest sample). There were no general and consistent differences with age. In all seasons female stoats ate more mice and ground wetas, and males more opossums and 'unidentified mammals' (mostly opossums and rats). Grouping the prey as large, small, or medium showed that females ate more small prey ( $P < 0.01$ ) and males more large prey ( $0.02 < P < 0.05$ ), but this may reflect the greater food requirements of males rather than their ability to kill larger prey; lagomorphs and rats were eaten as often by females as by males, and opossums, the only other large prey, were probably often eaten as carrion. There were differences in diet between forest types and seasons, of which at least some must have reflected real changes in availability of prey. Stoats caught at rubbish tips or around settlements had not eaten more rats and mice than stoats caught in adjacent forest. Large prey items supply most of the biomass of the stoat's diet; insects, though frequently taken, contributed only about 10% of the volume eaten. The guts of 30 weasels sympatric with the stoats in several areas contained mostly mice, birds, lizards, and insects. There is no evidence that stoats in the

New Zealand National Parks compensate for the lack of voles by eating more birds than they do in British farmland, but they do eat more insects.

**Keywords** *Mustela erminea*; New Zealand National Parks; trapping; gut contents; prey spectrum; food habits; *Mustela nivalis*.

### INTRODUCTION

The food habits of the stoat in New Zealand are of particular interest, for two reasons. First, the stoat is a predator which has been introduced to, and has thrived in, a quite different environment from that of its native range. Second, if attempts to control stoats in the National Parks are ever to be effective, a precise description is required of the food habits of stoats in each Park and each habitat type. For reasons already explained (King & Moody 1977) this is not a study of predation, and no estimates can be made of the impact of predation by stoats on any species of bird. Such estimates would require much more intensive and localised studies of the birds and stoats simultaneously. This paper describes the variation within and between National Parks, information which is needed to interpret such local results.

### METHODS

#### Identification of prey

The contents of the stomach and intestine of each gut were stored together in 75% ethanol. Before analysis the material was washed in a fine (250  $\mu\text{m}$ ) sieve and then sorted under a low-power ( $\times 8$ ) microscope into groups as follows.

(a) *Feathers*, sometimes with avian bones, claws, gizzard, or stomach. The colours and sizes of feathers, feet, and legs were recorded. Occasionally a species could be recognised, e.g., from the red underwing feathers of a kea (*Nestor notabilis*) or the crown feathers of a yellow-crowned parakeet (*Cyanoramphus auriceps*), but for most specimens identification went no further than 'Bird'.

(b) *Eggshells*, with or without feathers alongside.

(c) *Hairs*. Guard hairs were picked out singly from all parts of the sample, washed in carbon tetrachloride, blotted dry, laid individually on a

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slide coated with warm 5% gelatin, and examined under a microscope. Identity was ascertained by comparing the medulla pattern and the scale pattern (made visible by stripping the hair away from the dried gelatin bed) with those of reference hairs. Sectioning of hairs is not necessary to distinguish between the small number of mammalian prey species present in New Zealand. Unrecognised hairs, often in small quantities, were recorded as 'Unidentified Mammal' and described; most of these probably belonged to opossums or rats, because lagomorph hairs have a distinctive medulla pattern, and the fur of mice is often recognisable by texture and length. This suggestion is supported by plots of the frequency of occurrence of 'Unidentified Mammals' against that of lagomorphs (strongly negative correlation), mice (weakly negative), opossums, and rats (both generally positive correlation); and by the associated distributions of 'Unidentified Mammals' and opossums in the results (see below, pp. 63 and 74).

Rats and lagomorphs cannot be identified to species from hair characteristics; teeth or recognisable fragments of bone were rarely found.

Stoat hairs have an easily recognisable scale pattern and often a distinct ginger tinge. When present in small quantities or as a disorganised ball they were considered to be moultings, and were ignored. If the foot of a stoat was found in the gut of an animal with a foot missing, this stoat was considered to have chewed off its own foot in the trap (29 instances). Four other stoats containing large quantities of stoat fur lying in tufts of parallel hairs, but with no injuries to their own bodies, could have eaten the remains of another stoat, probably one held in a trap.

(d) *Fragments of exoskeleton* of insects, spiders, or freshwater crayfish.

(e) *Fragments of lizard skin* were assigned to geckos if knobby and to skinks if smooth-scaled. There were rarely enough remains—such as feet or tails—to allow identification to species or counts of individuals.

(f) *Other items found* included fish, if not explicable as the fish-based proprietary catfood used as bait; unidentified meat; internal parasites or fleas; and pieces of vegetation, dirt, or grit, perhaps ingested with prey, and of rubbish, e.g., tinfoil or paper. No earthworm chaetae were found, perhaps because the gut contents were washed before examination. We may therefore have missed a possibly important prey category (cf. Osgood 1936); on the other hand, no earthworm chaetae were found in 146 scats of stoats (unwashed before examination) collected in Fiordland in the summer of 1979–80 (King, unpubl. obs.).

The prey categories recognised are listed in Table 2. Note that they are not of equal taxonomic rank;

some contain only a single species (mouse, opossum) and others more than one (lagomorph, rat) or many (birds, other arthropods). The choice of categories reflected the process of identification rather than the ecological significance of the prey.

### Presentation of results

(a) *Methods of expressing the composition of the diet.* The results of the gut analyses were recorded as the minimum number of identifiable specimens in the gut of each stoat. For most categories (mammals, birds, and carrion) only one prey item was assumed to have been eaten at one time, unless there was clear evidence to the contrary. Smaller items, except eggs, could often be counted. These raw data are presented in two ways, for different purposes and reasons.

(i) For the main analysis, each prey category was recorded as present or absent, and the frequency of occurrence of positive scores was calculated as a percentage of the total number of guts with food. Empty guts are defined as those containing no identifiable food, or only bait or the stoat's own foot. This method allows the occurrence of a particular prey category to be compared between samples without reference to the rest of the diet. It assumes that the time during which different prey items remain in the gut, and the probability of correct identification, are constant across all samples, but not that these factors are equal for all categories of prey. This section therefore describes local and seasonal differences in the extent to which stoats of a given age or sex eat any particular prey, which generally reflect differences in prey availability. However, since a change in the availability of one species is likely to affect the rate of predation on others (see, for sample, Korschgen & Stuart (1972)), the samples of different prey are not as independent in the biological sense as in the statistical sense.

(ii) The composition of the diet by weight was estimated separately by expressing the numerical occurrence of each prey category as a proportion of the total diet, estimated from the sum of all occurrences. The counts of specimens in each category were weighted to correct for gross differences in the size of different prey species (see Appendix 1). This approach has been used only for a limited series of estimates, for three reasons. (1) Although the composition of the diet by weight is of interest, its usefulness is limited. By definition, the values for each category are relative to the total, and so differences between samples cannot be related to different rates of consumption of a given prey. (2) It assumes that all prey items remain in the gut for equal lengths of time, and are equally easily identified. (3) Too little is known of the feeding behaviour and digestive processes of stoats in the

Table 1 Distribution of stoat gut samples.

Collection area (N→S)	Area code	Empty n	%	Not empty <sup>(1)</sup>	Total analysed <sup>(2)</sup>	Not analysed <sup>(3)</sup>	
Urewera National Park	UW	6	26	17	23	1	24
Tongariro National Park	TG	5	11	39	44	1	45
Egmont National Park	EG	15	16	78	93	—	93
Mount Bruce	MB	12	24	39	51	13	64
Abel Tasman National Park	AT	1	11	8	9	—	9
Nelson Lakes National Park	NL	27	26	75	102	1	103
Kaikoura	KK	1	4	23	24	6	30
Arthurs Pass National Park	AP	18	19	79	97	10	107
Craigieburn Forest Park	CB	12	7	154	166	—	166
Mount Cook National Park	MC	35	19	146	181	6	187
Westland National Park	WL	35	21	129	164	1	165
Mount Aspiring National Park	MA	11	37	19	30	—	30
Takaro Lodge	TK	18	23	61	79	4	83
Fiordland National Park	FL	68	15	383	451	42	493
		264	17.4	1250	1514	85	1599

(1) For distribution of guts with food by season, sex, and age, see Appendix 2.

(2) for distribution of total guts analysed by habitat, see Appendix 2.

(3) Carcasses damaged or decayed.

wild to determine appropriate weighting and correction factors. However, it is worth calculating at least the gross pattern of biomass composition, as it describes the prey identified in terms of their relative importance to the nutrition of the stoat, rather than simply the number of items of various sizes eaten.

(b) *Bias arising from differences between sampling areas in trapping method.* Altogether 264 of the 1514 guts analysed (17.4%) were empty, or contained only bait or the stoat's own foot. The proportion ranged from 4% to 37% in different samples (Table 1), depending on the type of trap in which the stoat was caught. Stoats caught in gin traps, a typical leg-hold type, lived longer in the traps and were more than twice as likely to have had empty guts as those caught in Fenn traps, a humane break-back type ( $P < 0.001$ ; King 1981). To avoid geographic bias due to the uneven distribution of the two trap types between localities (details in King & Moody 1982a), all empty guts were excluded.

The baits used in the traps appeared in 194 guts (13% of 1514 examined). In the forest samples they occurred slightly more often in Fenn-trapped stoats (17% of 666) than in gin-trapped ones (12% of 243), also presumably because stoats died more quickly in Fenn traps.

(c) *Adjustment for use of natural baits.* In the early stages in some study areas, traps were baited with natural foods readily obtainable locally, usually opossums at Egmont, Arthur's Pass, Westland, and Takaro and lagomorphs at Mount Cook and Nelson Lakes. After we had explained the difficulties this

causes, most of the trappers later used a strong-smelling fish-based catfood as bait. This was recognised in stoat guts from the undigested remains of wheat husks and grains included in it. Use of natural prey as bait introduces a bias which cannot be removed merely by excluding from the analysis any record of, for example, opossum remains found in a stoat caught in a trap baited with opossum. Unbiased estimates can be obtained only by excluding from the analysis of opossum occurrence all stoats caught in traps baited with opossum, whether or not opossum remains were found. This means that the size of the samples for estimating the frequency of occurrence of opossums have to be adjusted appropriately, as indicated below. The same argument applies to lagomorphs.

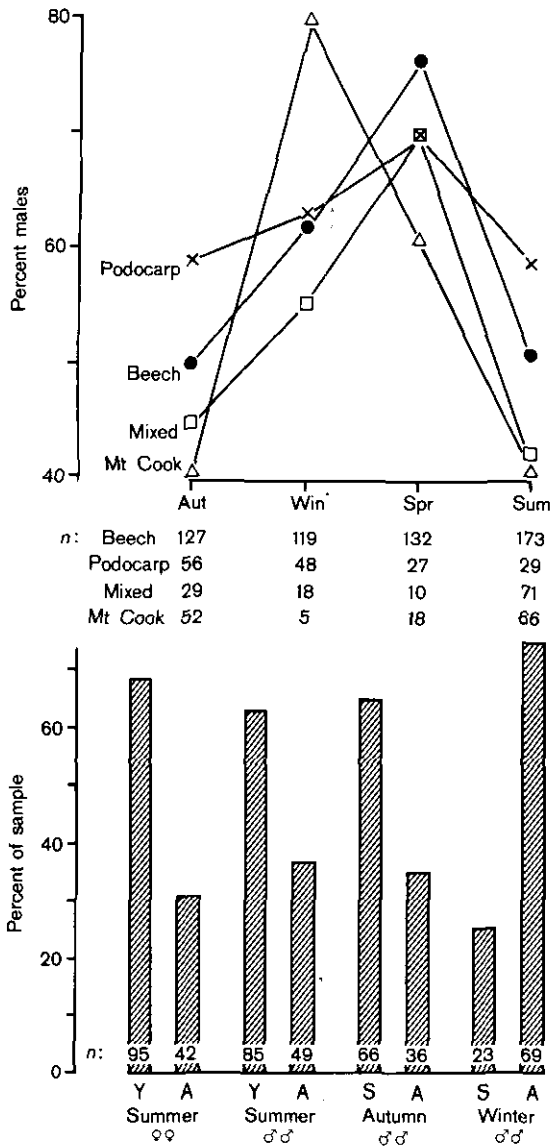
## RESULTS

### Distribution of all prey identified

Of 1599 stoats received, the guts of 1514 were analysed (Table 1). They contained 2643 identified prey items, distributed as shown in Tables 2 and 3. The composition of the samples with respect to age, sex, habitat, and season is shown in Fig. 1 and in King & Moody (1982a).

Almost all the prey species identified were wild. There were several records of stoats being killed in hen-houses (with or without hen-like feathers in their guts), and 2 stoats were sent in which had broken into a guinea-pig run and eaten at least part of one of the occupants.

Prey items recorded include species active mainly at night (rats, mice, opossums, geckos, crayfish) and species active mainly by day (skinks, birds), though



**Fig. 1** Variation in the composition of the sample of guts analysed for food content. *Above*: sex ratio and *n* by habitat and season. *Below*: age ratio and *n* by sex and season. For definitions of habitats, age, and season see King & Moody (1982a).

of course prey of either type could have been caught when at rest. Several records suggest that nests, breeding dens, or hibernacula had been raided; for example, 53 wasps in one gut, at least 2 sets of unidentified infant mammals, a group of 6 skinks together, and 14 tree wetas (*Hemideina* sp.) together.

A complete list of all insects identified is given in Appendix 3, Table 1. Of the 1127 insects and spiders

**Table 2** List of foods identified (categories in descending order of body size) in 1250 stoat guts containing food; all samples pooled.

Prey category	No. of occurrences	Minimum total no. of items	% freq. of occurrence <sup>(1)</sup>
Carriion	17	18	1.4
Opossum			
( <i>Trichosurus vulpecula</i> )	121	121	10.0
Lagomorph	213	213	17.5
Unidentified mammal	125	128	10.0
Hedgehog			
( <i>Erinaceus europaeus</i> )	2	2	0.2
Rat ( <i>Rattus</i> )	80	80	6.4
Birds	533	535	42.6
Mouse ( <i>Mus musculus</i> )	241	241	19.3
Fish	2	2	0.2
Freshwater			
crayfish ( <i>Paranephrops</i> )	25	25	2.0
Skink ( <i>Leiopisma</i> )	27	42	2.2
Gecko ( <i>Hoplodactylus</i> )	32	35	2.6
Bird's egg	16	16	1.3
Tree weta ( <i>Hemideina</i> )	64	122	5.1
Ground weta			
( <i>Hemidrus</i> )	174	277	13.9
Large cave weta	80	104	6.4
Small cave weta	55	100	4.4
Unidentified weta	22	22	1.8
Lepidoptera	95	156	7.6
Carabid beetle	39	68	3.1
Other arthropods	116	278	9.3
Own foot <sup>(2)</sup>	29	29	—
Stoat	4	4	0.3
Unidentified food	13	13	1.0
Rubbish	12	12	1.0
		<b>2643</b>	

(1) Sample sizes adjusted to correct for natural baits in 'opossum' (*n* = 1216) and 'lagomorph' (*n* = 1214).

(2) Some 'empty' guts contained 'own feet'; therefore, the incidence of 'own feet' should probably be expressed as a proportion of the total number of guts analysed (29/1514, i.e., 1.9%) rather than of the number of guts with food.

counted, only 1% could not be identified at least to ordinal level; 63% were identified to genus. Some, especially the smaller species, could have been ingested with insectivorous prey, but these could not be distinguished and discounted. As expected, the great majority of insects identified were wetas, but there were a few surprises (e.g., wasps) and a few notable absentees (e.g., large alpine grasshoppers, which were very common within the ranges of stoats collected at Craigieburn).

Recognition of 'carriion' was difficult. Deer and sheep were obviously scavenged, and many of the opossums and some lagomorphs may have been as well, so the figure of 1% for carriion probably underestimates the scavenging activities of stoats. Marshall (1963) reported 106 observations of stoats feeding, of which 24 were at carriion. However, the

**Table 3** Percentage frequency of occurrence of prey in stoat guts with food from each study area

	UW	TG	EG	MB	AT	NL	KK	AP	CB	MC	WL	MA	TK	FL e+t	FL h+m	Total FL
Carrion	—	3	—	—	—	3	—	1	—	—	—	—	—	2	5	3
Opossum	12	5	30†	—	25	3	—	7†	7	—	18†	11	5	14	9	14
Lagomorph	—	21	1	5	13	18†	—	22	39	56†	—	11	25	7	5	6
Unidentified mammal	24	3	24	18	—	12	—	18	9	3	13	21	13	8	4	6
Hedgehog	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—
Rat	29	5	12	13	25	5	—	3	—	1	12	11	—	5	12	8
Birds	6	59	27	49	50	44	91	38	42	34	36	53	34	53	49	50
Mouse	24	18	13	15	13	21	4	20	18	6	22	5	33	35	14	25
Fish	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—
Freshwater crayfish	—	10	15	3	—	7	—	—	—	—	—	—	—	—	—	1
Skink	—	—	—	—	—	7	4	3	1	8	—	—	7	1	—	1
Gecko	—	—	—	3	—	—	—	3	1	19	—	—	—	—	—	—
Bird's egg	—	3	3	5	—	—	3	1	—	1	1	—	2	1	1	1
Tree weta	12	21	3	—	25	3	—	1	3	26	2	—	—	—	10	4
Ground weta	24	3	4	5	13	3	—	4	8	1	22	16	13	31	16	23
Large cave weta	12	21	17	10	13	12	—	5	8	3	7	—	—	5	2	3
Small cave weta	—	5	4	3	13	7	—	8	6	—	5	5	7	6	3	4
Unidentified weta	—	3	1	3	—	3	—	3	1	—	3	—	2	2	3	2
Lepidoptera	12	31	9	8	—	1	—	9	3	1	7	—	10	6	3	5
Carabid beetle	—	—	1	—	—	1	—	8	2	—	1	16	5	5	9	6
Other arthropods	6	5	3	15	13	13	4	9	14	9	17	5	12	13	10	11
Unidentified food	—	—	4	3	—	1	—	3	—	—	1	—	—	1	—	1
Total guts with food	17	39	78	39	8	75	23	79	154	146	129	19	61	212	147	383

† Percentages based on sample sizes adjusted for use of natural baits, as follows:  
 opossum - EG,  $n = 66$ ; AP,  $n = 75$ ; WL,  $n = 113$   
 lagomorph - NL,  $n = 49$ ; MC,  $n = 136$

scarcity of carrion-inhabiting insects found in our samples (Appendix 3) suggests that scavenging is confined to fresh carcasses.

One certain record of scavenging concerns one of the only 2 hedgehogs found. In March 1975 at Mount Cook a hedgehog was accidentally trapped, and the body was removed and left lying on the ground 2 m away. A few days later, a female stoat was found which had dragged the dead hedgehog under the trap cover and eaten some before itself getting caught.

#### Diet in relation to age, sex, season, and habitat

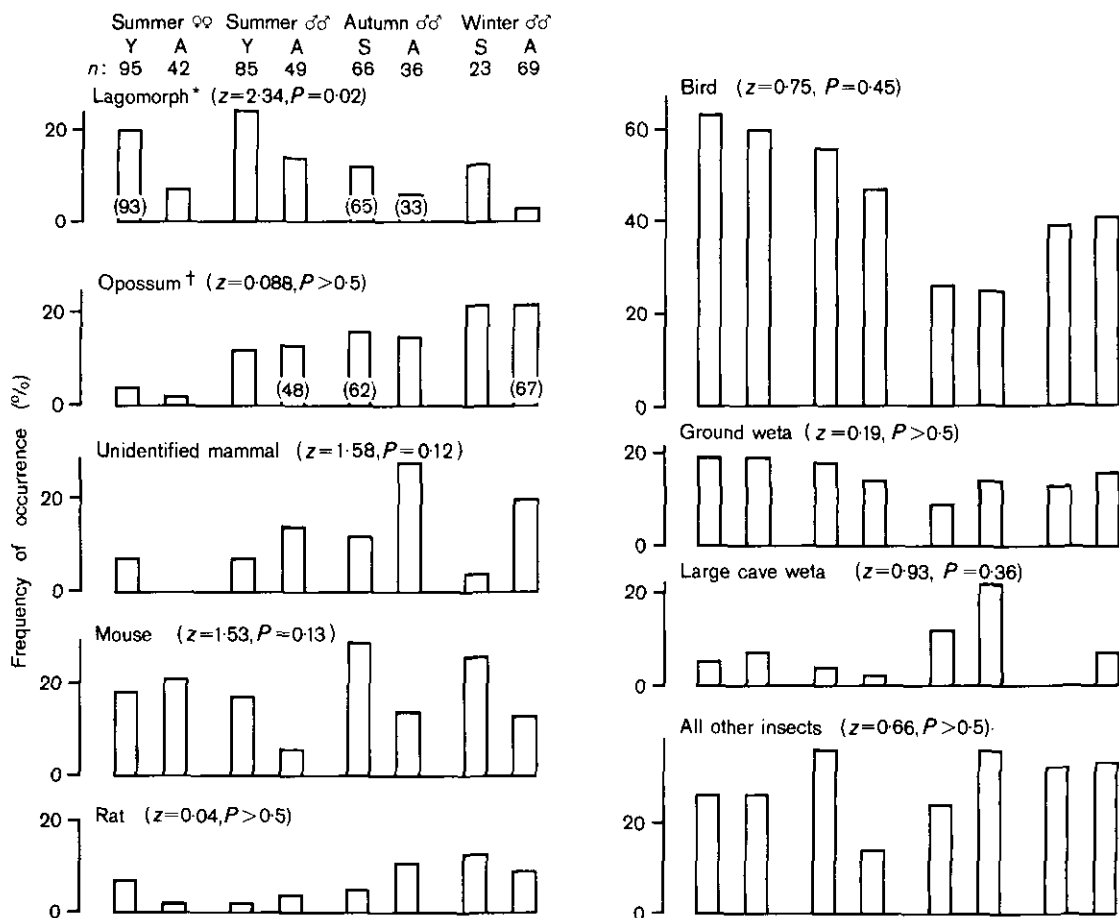
This analysis is largely restricted to samples of stoats caught in forest, though we have included a comparison with the data from Mount Cook, the only large non-forest area sampled. Further, the statistical comparisons are limited to the 9 categories of prey that appeared most frequently in the diet of forest stoats—opossum, lagomorph, rat, mouse, bird, large cave wetas (*Gymnoplectron* spp.) and ground wetas (*Hemiandrus* spp.), plus 'unidentified mammal' and 'all other insects'. The 2 artificial categories are included for testing because they occur too frequently to be ignored. The complete list of occurrences in forest stoats is shown in Table 4. The 3 major types of forest represented, and their distribution by collection area, are summarised in

King & Moody (1982a). The distribution of prey in relation to age, sex, season, and forest type was examined by tabulating one variable while controlling for the others. Significant differences found were then checked to ensure that they did not arise from geographic or other bias. Variations with age and sex, which are both attributes of individual stoats, are considered separately; season and habitat both influence the availability of prey, and are considered together.

#### Variation with age

Definitions of the age classes used are given in King & Moody (1982a). In the summer samples (December–February inclusive) young stoats about 2–5 months old can be distinguished from adults in both sexes; in autumn and winter (March–May, June–August) subadult males can be distinguished from adult males. Analysis by age class is therefore possible over 3 seasons for males, but only 1 for females. Fig. 2 shows the percentage frequency of occurrence for the 9 major prey categories in each age/sex/season sample from forest habitats.

The only age difference that is consistent across all 4 sex/season samples is also the only statistically significant difference: in comparison with adults, young and subadult stoats appeared to eat more lagomorphs, in the total forest sample and in 12 of



**Fig. 2** Comparison of food habits of stoats in forest by age. The differences in frequency of occurrence of prey between ages, controlling for season and sex, were tested by a modified  $\chi^2$  test (Simpson et al. 1960, p. 326–338); the z scores and their corresponding probabilities are given here. \*†Adjusted sample sizes given (in parenthesis) if different.

17 sex/age/area comparisons (1-tailed signs test,  $P=0.07$ ). This finding is unexpected and puzzling, so we have examined it further. A large proportion (52%) of the 64 forest stoats which had eaten lagomorphs came from Craigieburn Forest Park. Fig. 3 shows that the young and subadult stoats from Craigieburn had definitely eaten more lagomorphs than the adults; this cannot be explained as annual, seasonal, or sexual sampling bias within the sample. However, for forests other than Craigieburn the difference is less convincing. At Mount Cook, a non-forest area with the highest frequency of occurrence of lagomorph prey of all study areas (Table 3), the young and subadult stoats had eaten marginally fewer lagomorphs than adults (altogether 56%, cf. 61%) (Fig. 4). Hence, only at Craigieburn is the tendency for young and subadult stoats to have eaten more lagomorphs than had adults consistent in either sex and in every season, and we therefore

suspect that this is due to some specific character of the Craigieburn sample. The Craigieburn forest is on the edge of a very large area of pastoral country, and may be a refuge for stoats from miles in all directions except westwards. The 2 most successful traps, which caught one-third of the total sample, were placed at the forest margin. Perhaps the forest was particularly attractive to young and subadult stoats dispersing from breeding dens in adjacent open country, whereas resident adults with home ranges in the forest ventured outside less often.

At Mount Cook the relative occurrences of the 4 main prey categories (lagomorph, bird, gecko, and tree weta; see Table 3) in relation to age were tested separately. The only significant difference is that more young and subadult stoats (35%) ate tree wetas than did adults (5%) collected in the same months (Fig. 4).

**Table 4** Prey identified in 866 stoat guts containing food, collected from forests.

Prey	Number of occurrences	% frequency of occurrence
Carrion	12	1.4
Opossum	107	12.8 (of 837)†
Lagomorph	113	13.4 (of 845)†
Unidentified mammal	94	10.9
Hedgehog	1	0.1
Rat	60	6.9
Bird	364	42.0
Mouse	190	21.9
Fish	2	0.2
Freshwater crayfish	23	2.7
Skink	9	1.0
Gecko	2	0.2
Bird's egg	7	0.8
Tree weta	31	3.6
Ground weta	138	15.9
Large cave weta	66	7.6
Small cave weta	49	5.7
Unidentified weta	16	1.8
Lepidoptera	55	6.4
Carabid beetle	36	4.2
Other arthropods	98	11.3
Unidentified food	11	1.3

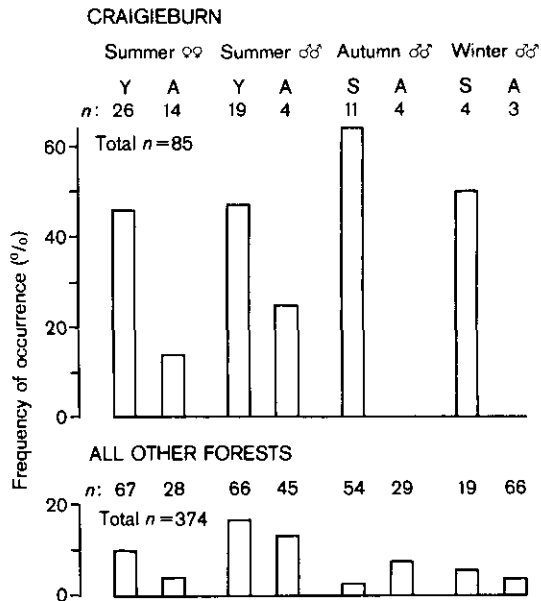
† Sample sizes adjusted for natural baits.

#### Variation with sex

As there seem to be no general and substantial differences in food habits with age, the age classes were not separated in this section. As before, patterns found in the analysis of all forested study areas pooled were then checked in greater geographic detail.

The complete distribution of prey by sex and season for the total forest sample is shown in Table 5, and the frequency of occurrence of the 9 major prey categories in Fig. 5. Four of these 9 show a consistent difference in distribution between the sexes in all seasons: females always ate more mice and ground wetas, and males ate more opossums and unidentified mammals. In each instance the total percentage occurrences differ by a factor of about 2, and a  $\chi^2$  test controlling for season shows that all 4 are significant. There is no significant difference between sexes in consumption of lagomorphs, birds, rats, large cave wetas, and all other insects.

These differences were re-examined using the Craigieburn, Eglinton, and Hollyford samples alone. These 3 were chosen because they are all large, well localised samples with background data from mouse trapping and vegetation surveys, and for none of them was natural bait used in the traps. When the data are broken down by locality and year as well as season, 1-tailed signs tests confirm that



**Fig. 3** Percentage frequency of occurrence of lagomorphs in stoat guts by age class at Craigieburn Forest Park, compared with all other forests. Sample sizes adjusted for natural baits.

males ate more opossums ( $P = 0.029$ ) and unidentified mammals ( $P = 0.046$ ), and females more mice ( $P = 0.006$ ) and ground wetas ( $P = 0.084$ ). The latter is not strictly significant, but is too nearly so to discount the difference, significant at  $P = 0.01$ , shown by the general analysis (Table 5).

Because of the pronounced sexual dimorphism in body size of stoats (King & Moody 1982b), the general hypothesis that the body size of a predator influences the size of the prey it takes can be tested by comparing conspecifics of different sizes. With prey items classified as large, medium, or small, as listed in the 3 horizontal sections of Table 5, the seasonal distribution of each class found in male and female stoats was tested by a Wilcoxon matched pairs, signed ranks test. As expected, male stoats ate significantly more large prey ( $0.02 < P < 0.05$ ), and females ate significantly more small prey ( $P < 0.01$ ); males and females ate medium-sized prey in the same proportion. Grouping the prey categories by size obscures the previously demonstrated tendency for females to eat more mice (mice were classed as medium-sized prey), but makes clearer than can comparison of individual categories of insects the general tendency of females to eat more invertebrates.

Samples from Mount Cook are of adequate size only for summer and autumn, and these show

(Table 6) that the only significant difference in diet between the sexes, at least in the 4 major prey categories in that habitat, is that females ate more geckos than did males ( $P = 0.04$ ). This cannot be explained by bias in the samples with respect to age or year. It is particularly interesting that, as for the forest stoats, there is no significant difference between males and females in the occurrence of lagomorph remains.

#### Variation with season and habitat

The gross differences between sample areas were examined for seasonal differences common to all habitats and for habitat differences common to all seasons.

For the pooled forest samples, the seasonal variation in the occurrence of prey found in stoats of both sexes is illustrated in Fig. 5. A series of  $2 \times 4 \chi^2$  tests confirms the apparent seasonal variation in occurrence of 5 main prey categories—lagomorphs, birds, and mice in both sexes, opossums in females, and large cave wetas in males (Table 5).

Most prey categories are represented in or near all the sampling areas, but their relative abundance

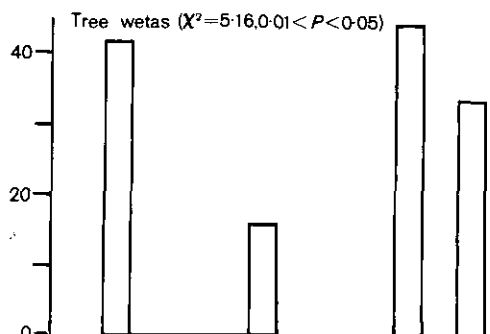
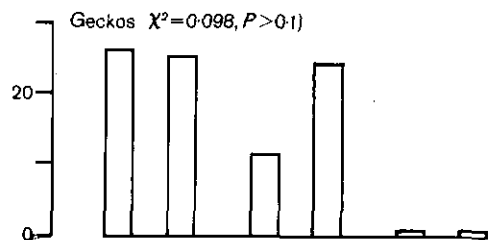
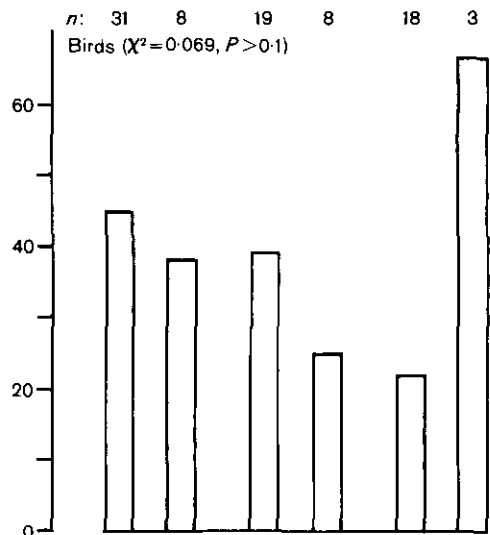
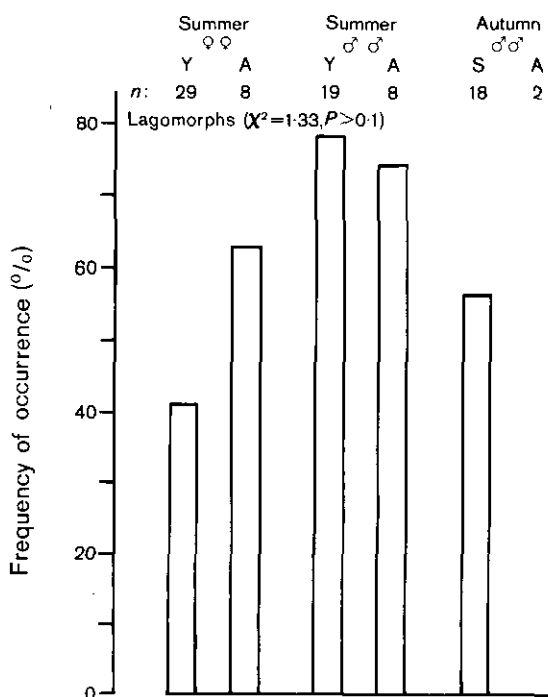


Fig. 4 Percentage frequency of occurrence of 4 principal prey categories in stoat guts by age class at Mount Cook. Differences tested by simple  $\chi^2$ , pooling seasons and sexes. Sample sizes for lagomorphs shown separately, otherwise all as for birds.

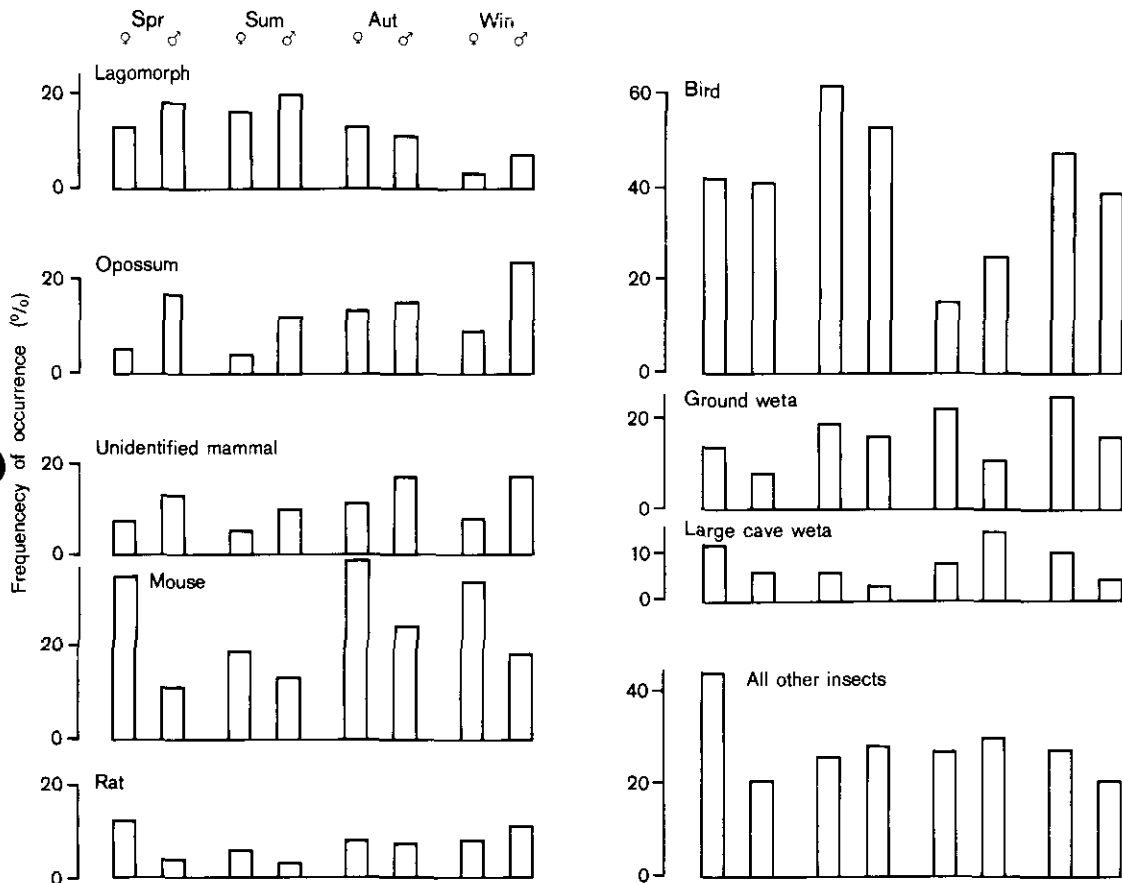


Fig. 5 Comparison of food habits of male and female stoats (all ages) in forest. For sample sizes and statistical tests see Table 5.

differs between the 3 major forest types recognised, as summarised in King & Moody (1982a). Hence, one would expect differences between forest types in the representation of prey, which do in fact appear (Fig. 6). In these comparisons the sexes were pooled in order to obtain adequate sample sizes for forests other than beech; for prey known to be eaten differentially by males and females (mice, opossums, unidentified mammals, and ground wetas) the seasonal variation in sex ratio (Fig. 1) can be a complication (see below).

The distribution of the major prey categories with season and habitat, shown in Fig. 6, can be summarised as follows.

(a) As expected, generally more opossums were eaten in podocarp forest than in mixed or pure beech forest, but the seasonal variation is difficult to interpret. Fewer opossums were eaten in summer, which suggests that stoats might obtain much of their opossum prey as fur-trapper's carrion,

especially as in podocarp forests generally the same summer drop is apparent for rats, which are also often caught by opossum trappers. However, another possible reason is the summer drop in the proportion of males in the sample (Fig. 1), since males took significantly more opossums than females (Table 5). We can discriminate between these 2 explanations by looking more closely at the seasonal distribution of opossum remains in male stoats collected in those podocarp forests in which opossum trappers are particularly active in winter and early spring (Egmont, Westland, and the Hollyford Valley). For these 3 areas pooled, opossums occurred in 24% of 21 non-empty guts in spring, 9% of 88 in summer, 17% of 63 in autumn, and 26% of 39 in winter ( $\chi^2 = 6.83, 3 \text{ df}, 0.10 > P > 0.05$ ). The additional carrion may be presumed to have been supplied by trappers rather than road kills, since road traffic in these places is heavier in summer than in winter. For the pooled forest

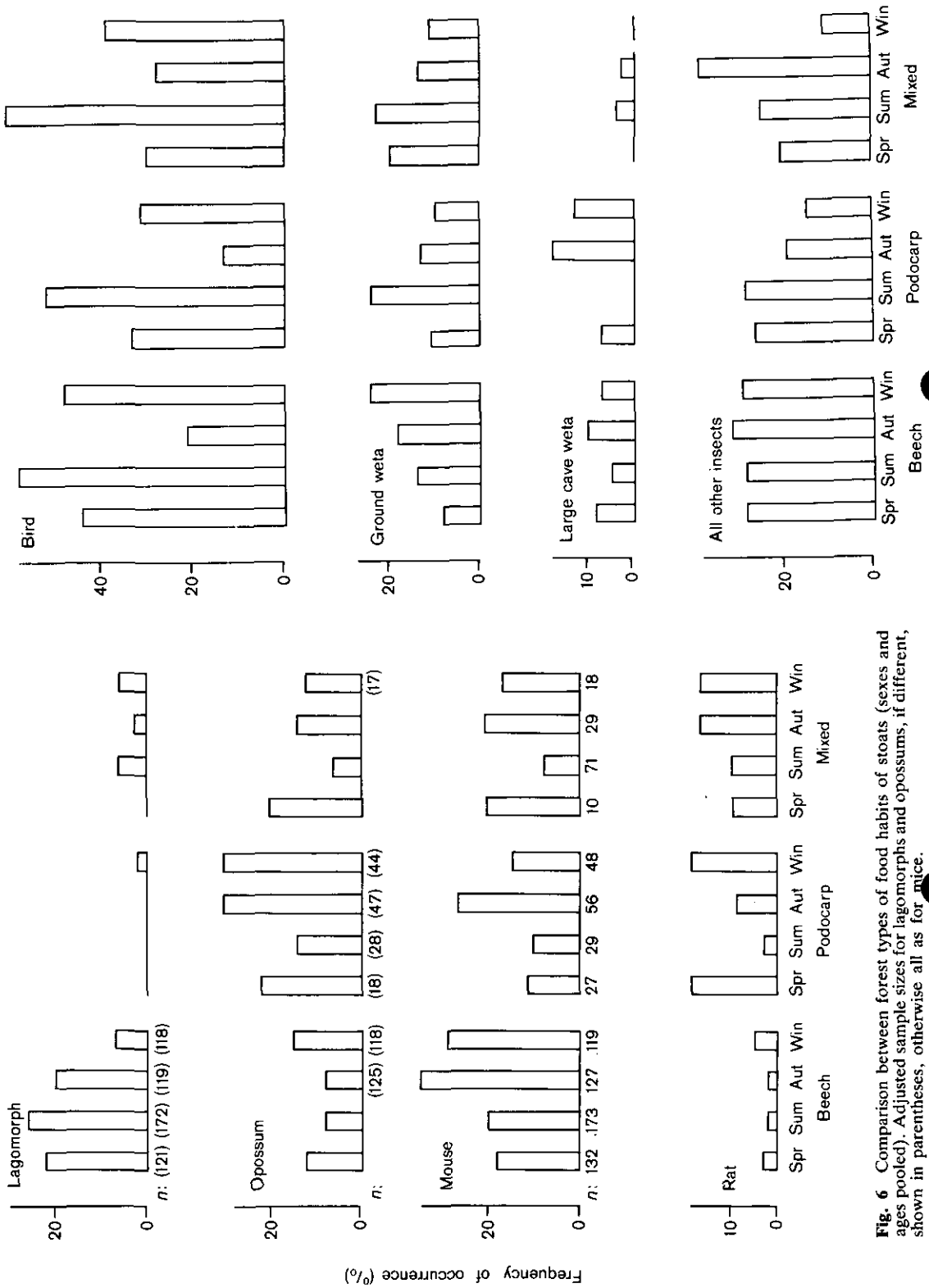


Fig. 6 Comparison between forest types of food habits of stoats (sexes and ages pooled). Adjusted sample sizes for lagomorphs and opossums, if different, shown in parentheses, otherwise all as for mice.

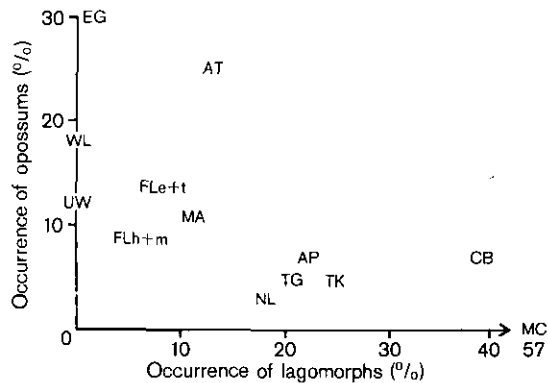


Fig. 7 Inverse correlation between the occurrence of opossums and that of lagomorphs as prey of stoats.

sample, the increase in occurrence of opossum remains in females in autumn (Fig. 5), which is significant (Table 5), is associated with an increase in the representation of podocarp forest in autumn (Fig. 1).

(b) Lagomorphs generally avoid thick forest of any kind, and one might expect few in the guts of forest stoats. However, many stoats caught near forest margins may have recently hunted on adjacent open ground. Several of the beech forests sampled have extensive grassland nearby. The high incidence of lagomorph prey in stoats 'in' beech forest is therefore more correctly interpreted as a high incidence in stoats caught at the forest/grassland boundary.

Lagomorphs and opossums, the 2 mammalian prey categories of comparable body size, have opposite habitat preferences. Stoats living in podocarp/broadleaved forest are more likely to encounter an opossum than a lagomorph, and stoats living between beech forest and grassland vice versa. The frequencies of occurrence of lagomorphs and opossums show a fairly strong negative correlation (Fig. 7).

Substantially fewer lagomorphs were found in stoats taken in winter at Craigieburn, Takaro, and eastern Fiordland, the 3 beech forest areas which yielded the largest samples. Lagomorphs were clearly the most important prey at Mount Cook, but the winter sample is unfortunately too small ( $n = 7$ ) for comparison.

(c) Again as expected, more rats were eaten in podocarp and mixed forest than in beech forest, in all seasons. The drop in summer in podocarp forest (Fig. 6) is due largely to the Westland sample, where rats occurred in 15–38% of guts in other seasons but nil in summer ( $n > 10$  for all samples). It could be

suggested that rats are less available to the Westland stoats during the opossum hunters' off-season (see above), but there was no summer drop in rats at Egmont, where opossum hunters are also very active. The seasonal variation in sex ratio of stoats caught need not be considered, since rats were eaten by both sexes about equally (Table 5).

(d) Birds were the most frequently occurring single type of prey, but this is partly because birds could not be further identified, and all species had to be grouped into the one category. There was a strong seasonal variation in occurrence: for all forests, bird remains were found most often in summer samples and least often in autumn ones (Fig. 2, 6, and 8). Differences between habitats are small in comparison. Plots of the correlation of bird and large mammal prey, controlled for season and sex, do not support the idea that stoats eat fewer birds where there is plenty of alternative food. Since the data for birds are of special interest, they are given in full in Appendix 4.

(e) In general, fewer mice were found in podocarp or mixed forest samples than in beech forest samples, and fewer again in the non-forest areas of Mount Cook and Kaikoura (Table 3). However, the average occurrence of mice in stoats collected from beech forests may be slightly overestimated, because more stoats were caught there during or immediately after population increases of mice (Fitzgerald 1978) than at other times. More mice were found in autumn samples from all forest types (Fig. 6). Given that male stoats ate fewer mice (Table 5), the smaller number of mice found in winter and spring could be due to the preponderance of males in these seasons (Fig. 1); the difference between summer and autumn requires another explanation, perhaps related to seasonal variations in the population density of mice.

(f) There was no particular seasonal pattern in the occurrence of wetas, except that no tree wetas were found in spring samples, either from forests (occurrence in other seasons 4–7%) or from Mount Cook (other seasons 11–40%). For insects other than wetas the samples are generally too heterogeneous or too small to analyse with respect to season or habitat, and some may have been ingested with insectivorous birds or lizards. The full list of species identified is given in Appendix 3.

In contrast to cats (Fitzgerald & Karl 1979), stoats generally did not eat more insects in summer. This may be because so few of the insects identified are species with a strong seasonal distribution. *Wiseana* (porina moth) was found most often in Tongariro samples (Appendix 3, Table 2)—in 1 of 12 guts in spring, 5 of 11 in summer, 1 of 12 in autumn, and 1 of 4 in winter (total 25 individual moths or larvae also recorded). However, some of the guts also contained unidentified hepialid larvae, some of



	2	28	3	27	17	44	9	33	6	19	6	27	—	4	67	0.167	>0.5
Bird	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mouse	—	—	1	—	2	5	—	—	3	10	3	14	—	—	—	—	—
Fish	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Freshwater crayfish	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Skink	2	—	1	—	3	7	1	4	2	7	2	9	—	—	—	—	—
Gecko	3	42	1	9	10	26	4	15	8	26	—	—	—	—	—	2.086	0.04.
Bird's egg	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tree weta	—	—	—	—	13	33	3	11	11	35	9	40	—	2	—	1.177	0.25
Ground weta	1	—	—	—	—	—	—	—	1	3	—	—	—	—	—	—	—
Large cave weta	—	—	—	—	1	3	1	4	2	7	—	—	—	—	—	—	—
All other insects <sup>(1)</sup>	—	—	1	—	5	4	4	—	2	—	3	—	—	—	—	—	—
Total guts with food	7	11	8	39	37	27	27	31	22	22	21	6	1	6	6	sex or season unknown	2
n for lagomorphs	5	—	—	—	—	—	—	29	21	—	—	—	—	—	—	—	—

<sup>(1)</sup> See Footnote, Table 5. For Mount Cook samples tree wetas are also treated separately, whereas for forest areas they are included with 'All other insects'.

Table 7 Percentage composition by weight of the diet of stoats for each area, for all forests, and for all areas pooled.

Prey category	UW	TG	EG	MB	AT	NL	AP	CB	MC	WL	MA	TK	FL	KK	All forests	Total
Carion	—	2.7	—	—	—	4.3	1.4	—	—	—	—	—	3.9	—	1.7	1.6
Opossum <sup>(1)</sup>	31.2	2.7	23.8	23.3	—	14.4	20.1	9.9	2.8	15.6	22.8	14.9	7.2	—	12.2	11.4
Lagomorph <sup>(1)</sup>	—	21.3	1.3	6.6	11.8	19.9	24.4	39.6	56.3	—	11.4	27.9	6.6	—	14.7	19.5
Unidentified mammal	12.5	5.3	29.6	—	23.7	2.9	7.6	7.3	—	20.9	11.4	5.8	15.7	—	14.1	11.1
Hedgehog	—	—	—	—	—	—	—	0.7	0.7	—	—	—	—	—	—	0.2
Rat	31.2	5.3	11.3	16.6	23.7	5.8	2.9	—	0.7	14.7	11.4	—	9.6	—	7.6	7.1
Bird	3.1	32.0	13.2	31.6	23.7	23.8	21.6	21.1	16.9	21.6	28.5	19.5	28.7	84.3 <sup>(2)</sup>	23.2	23.8
Mouse	12.5	9.3	6.3	10.0	5.9	11.5	11.5	9.2	3.1	12.8	2.8	18.6	14.1	4.0	12.1	10.7
Fish	—	—	—	—	—	0.7	—	0.3	—	—	—	—	—	—	0.1	0.1
Crayfish	—	6.7	7.5	1.7	—	3.6	—	—	—	—	—	—	0.3	—	1.5	1.1
Lizard	—	—	—	1.2	—	5.0	2.5	0.7	10.6	—	—	6.5	0.3	2.8	0.8	2.4
Bird's egg	—	0.9	0.9	2.3	—	—	0.5	—	0.2	0.3	—	0.7	0.4	8.4	0.3	0.5
Wetas	8.4	8.0	4.9	4.5	10.7	5.6	5.2	7.0	8.1	12.4	9.4	3.6	11.0	—	9.1	8.3
Other insects	1.2	5.7	1.3	2.3	0.6	2.4	2.3	4.1	0.7	1.7	2.3	2.6	2.0	0.4	2.6	2.2
SUBTOTALS																
Large prey	74.9	37.3	66.0	46.5	59.2	47.3	56.4	57.5	60.5	51.2	57.0	48.6	43.0	—	50.4	50.9
Medium prey	15.6	48.9	27.9	46.8	29.6	44.6	36.1	31.3	30.8	34.7	31.3	45.2	43.8	99.5	38.0	38.5
Small prey	9.6	13.7	6.2	6.8	11.3	8.0	7.5	11.1	8.8	14.1	11.7	6.2	13.0	0.4	11.7	10.5
Total guts with food	17	39	78	39	8	75	79	154	146	129	19	61	383	23	866	1250

<sup>(1)</sup> Sample sizes for 'opossum' and 'lagomorph' are smaller in some instances—see Table 3.

<sup>(2)</sup> Probably all red-billed gulls, larger than the average for forest birds.

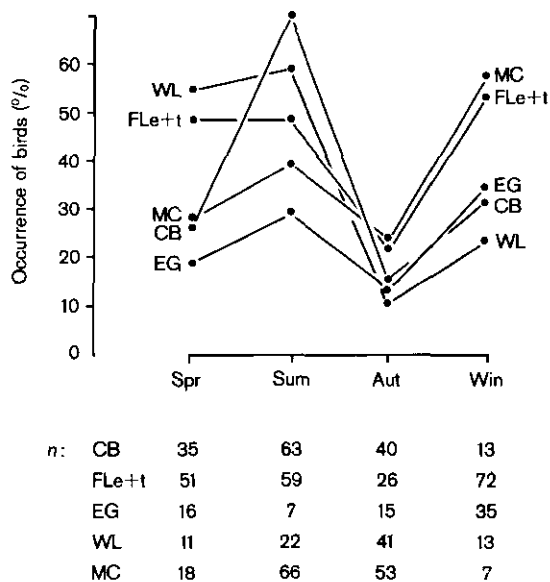


Fig. 8 Seasonal variation in occurrence of birds in stoat gut samples where  $n > 5$  for each season.

which could have been *Aenetus* (puriri moth), also known to be present, so the slight apparent preponderance of *Wiseana* in summer is not definite. The strongly seasonal cicadas (*Melampsalta* spp.) were only rarely found (15 individuals, no more than 5 in one place - Appendix 3, Table 2). Two stoats which had apparently raided a wasp's nest were both caught in the cool season; one, at Craigieburn in June, had its gut crammed with 53 wasps in all stages of development, and the other, from Nelson Lakes in May, contained 19.

(g) The small number of lizards eaten could not be analysed by season, though there was a suggestion that stoats might be able to catch skinks more easily in winter, or to find their nests: a group of 6 skinks was found in a stoat from Nelson Lakes in August, and a group of 4 in another from Takaro in June.

Stoats caught at rubbish tips or near domestic premises (including farm buildings and campsites) were excluded from these analyses, because they might catch more rats and mice there than stoats collected from forests nearby. This possibility has been examined for the 84 stoats collected from near the aviaries at Mount Bruce and from villages and rubbish tips in Westland and the Hollyford and Milford catchments in Fiordland. There is no evidence that rubbish tips or domestic premises provided especially many rodents for stoats relative to adjacent undisturbed podocarp forest, nor, indeed, even any evidence that stoats had been

Table 8 (A) Prey of weasels sympatric with stoats collected for this study (all areas pooled).

Prey	No. of occurrences		% frequency, sexes pooled
	Males	Females	
Lagomorph	3	—	10
Unidentified mammal	1	—	3
Bird	9	—	30
Mouse	7	4	37
Skink	1	—	3
Gecko	6	1	23
Bird's egg	1	—	3
Tree weta	4	—	13
Large cave weta	2	—	7
Small cave weta	1	—	3
Lepidoptera	2	—	7
Carabid beetle	1	—	3
Other arthropods	3	—	10
Total guts with food	26	4	30

(B) Comparison between male stoats and weasels in size of food items (as % frequency of occurrence); from forests and Mount Cook, all seasons pooled.

	Stoats	Weasels
Large prey	53	15
Medium prey	58	92
Small prey	48	50
n	551	26

$\chi^2 = 11.60, 2 \text{ df}, P < 0.005$

hunting there. Of the 12 stoats (Table 2) whose guts contained 'rubbish' (newspaper in 3, tinfoil in 4, paper or plastic in 5), none was caught at rubbish tips and only 1 near a village; these from a total of 212 stoats taken in the 2 'disturbed' habitats. Stoats are sometimes seen hunting in rubbish bins at rural car parks and roadsides, and of course rubbish may be found in places other than bins or tips.

#### Geographic variation

Table 3 shows large geographic variations in the occurrence of some prey species, the significance of which is generally unknown. Large cave wetas were eaten more often in northern sampling areas, and ground wetas and carabid beetles in southern areas. Tree wetas were eaten most at Mount Cook, where a small form of *Hemideina* (distinct from *H. maori*, the mountain stone weta, which does not occur down to 900 m) is common on the ground. Perhaps in forested areas the arboreal species of *Hemideina* are more difficult to catch. Freshwater crayfish (*Paraneohrops* spp.) occurred only in stoats from the north (Tongariro, Egmont, Mount Bruce, Nelson Lakes), apart from 2 isolated records from

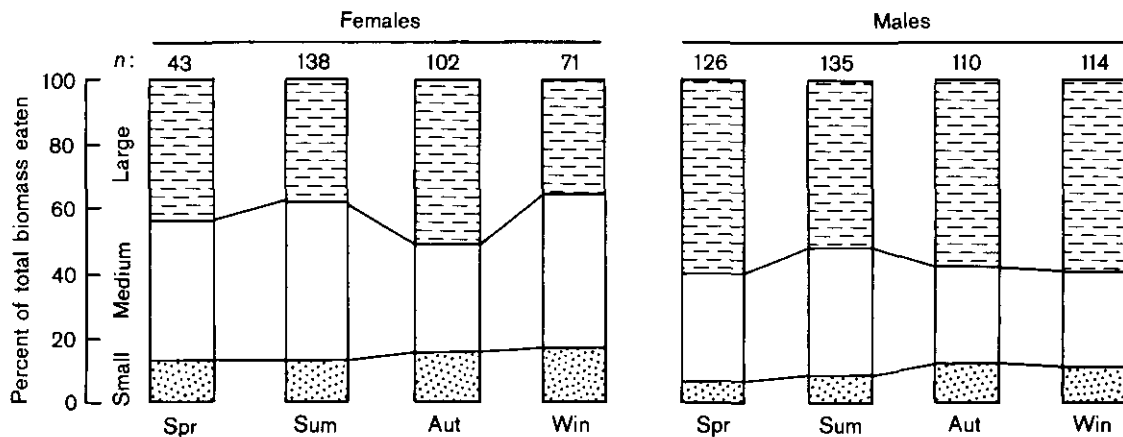


Fig. 9 Seasonal variation in the relative importance of small, medium, and large prey to male and female stoats in forest. Large prey - opossum, lagomorph, rat, etc. (> 20 g); medium prey - bird, mouse, etc. (about 7-20 g); small prey - insects (< 3 g).

Fiordland, both in adult male stoats caught in September at Lake Hauoko. This distribution identifies the species as 23 *P. planifrons* and 2 *P. zealandicus* (Waugh 1973). One of the crayfish from Tongariro had apparently just moulted.

Most of the samples from separate localities within one area are too small to break down further to check for seasonal and sexual bias, and the gross figures can be misleading. This point is well illustrated by the Eglinton and Hollyford valley samples, the only pair of large samples backed up with data on at least some of the prey. From quarterly rodent traplines we knew that rats were less common in the Eglinton than in the Hollyford during the years surveyed, and rats were found less often in the Eglinton guts (5%, cf. 13%). However, from Fig. 6 one would not have expected the stoats collected in the Eglinton (beech forest) to have eaten more opossums (14%) than those in the Hollyford (mixed forest; 10%), nor lagomorphs to occur equally in the 2 valleys (both 6%). These anomalies are probably sampling errors; the Eglinton sample contains more males (62%, cf. 47%) and more of both sexes collected in winter (32%, cf. 3%) than that from the Hollyford.

#### Biomass composition of diet

Table 7 gives an estimate of the composition by weight of the diet for each of the 14 study areas. Each estimate is perhaps accurate to within about 10% of the total, because the results are greatly influenced by the weights assigned to meals from large prey (see Appendix 1). However, they form an instructive contrast with the frequency data. Large prey—principally opossums, rats, unidentified mammals, and lagomorphs—contributed half or

more of the weight of food eaten. Their contribution to the total energy requirement of stoats must be still greater; large prey species contain less indigestible fur and bones per gram than small ones, so a stoat would get far more value from 50 g of rabbit meat than from 50 g of mice, as do weasels (Moors 1977). Insects, though occurring frequently (in 41% of all guts with food), probably contributed less than 10% of the total biomass ingested.

Because the values for each prey category given in Table 7 are, by definition, relative to the total, their distributions cannot be described and tested separately, i.e., no statements of the form 'stoats from A eat more large prey than stoats from B' are possible. However, as might be expected, the differences between forest types and between seasons in the absolute frequency of occurrence of various kinds of prey affect their relative importance in the diet. So does the interaction between sex and the size of prey; in all seasons, female stoats ate more insects and fewer large mammals than did the males (Fig. 9).

#### Food of sympatric weasels (*M. nivalis*)

Forty weasels were collected, mostly from grassland or the edge of beech forests (13 from Mount Cook, 11 from Craigieburn, 6 from Tongariro, 3 from Nelson Lakes, and 7 from various other places). This small sample is included only because the diets of sympatric predators are of considerable interest (Table 8A). Small and medium-sized prey—birds, mice, lizards, and insects—were the main foods of weasels. The distribution of large, medium, and small prey species eaten by male stoats and weasels in the same habitats is significantly different (Table 8B).

## DISCUSSION

Previous studies of the food habits of stoats in New Zealand include 1 general survey and 4 localised surveys. Fitzgerald (1964) made the first real contribution, with a wide-ranging study in which stoats were collected from all over the country, including habitats we have not sampled, e.g., farmland. Of 257 carcasses, 187 contained food; this was distributed very similarly to that in our combined sample (Table 2). Fitzgerald found almost exactly the same proportion of birds, though somewhat more eggs; the same proportions of opossums and mice, though more rats and fewer lagomorphs; and the same infrequent occurrence of lizards, hedgehogs, and rubbish, though a few more crayfish and fish. Considering the large differences between the studies, in time and in the composition of the samples, the correspondence is remarkable.

Localised studies, focused more sharply on particular areas, are difficult to compare. On Birdlings Flat, Canterbury, Fitzgerald (1964) collected scats and food remains from 10 stoat dens, and counted 16 lagomorphs, 82 mice, 227 birds (including 161 adult and 10 young skylarks), at least 58 eggs of the banded dotterel, and many skinks. In Takahe Valley, Fiordland, Lavers & Mills (1978) collected 97 stoat scats, and found in them 44 mice, 4 rats, 53 insects, and 32 birds. In the Orongorongo Valley, near Wellington, King (unpubl. data) collected 46 scats from live-trapped stoats, of which 33 contained a total of 8 mice, 4 rats, 4 lagomorphs, 7 birds, 4 lizards, and 23 insects; 13 had bait only. In several valleys in the Milford catchment searched by Wildlife Service officers for kakapo (*Strigops habroptilus*), 22 stoat scats were found; they contained 4 rats, 6 mice, 15 birds, 1 egg, 12 insects, and 2 opossums (D. A. Merton, pers. comm.). The general picture which all these studies convey is that the most frequently eaten prey of New Zealand stoats are birds, feral house mice, lagomorphs, rats, opossums, and insects.

In general the prey species identified in this study seem to correspond fairly well with those available. For example, the contrasting habitat preferences of opossums and lagomorphs are clearly reflected in the gut content analyses (Fig. 7). The only common mammal within the acceptable range of sizes which was not regularly eaten is the hedgehog. However, the small number of birds' egg-shells identified is surprising, and may underestimate stoats' visits to birds' nests. Stoats are good climbers, and are sometimes observed stealing eggs. Some may be capable of sucking out the contents of an egg without ingesting shell fragments (Fig. 10). Teer

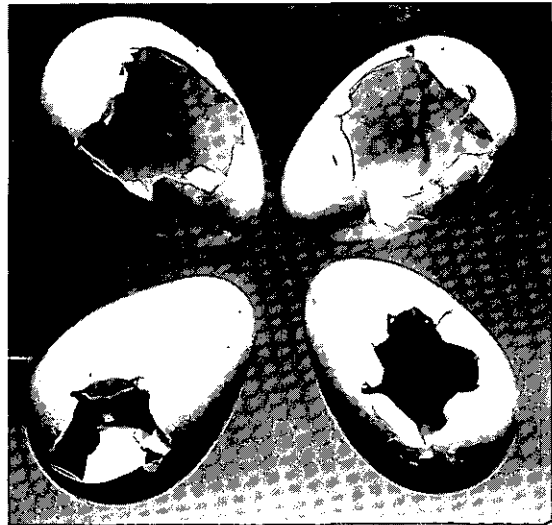
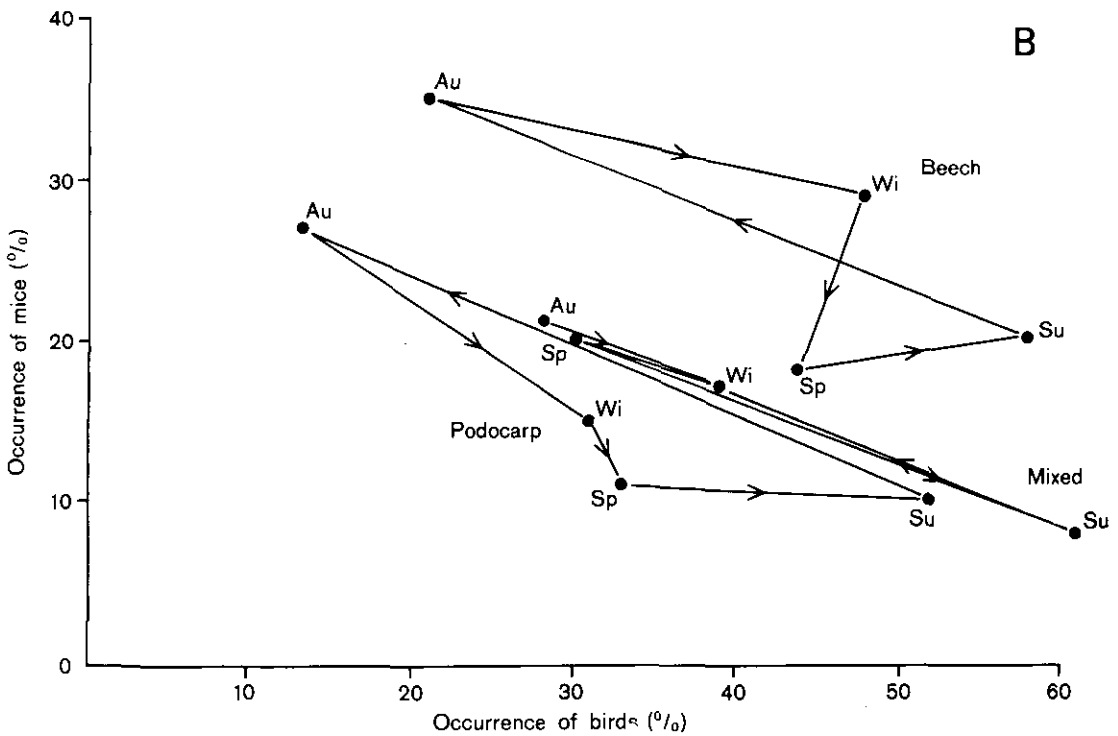
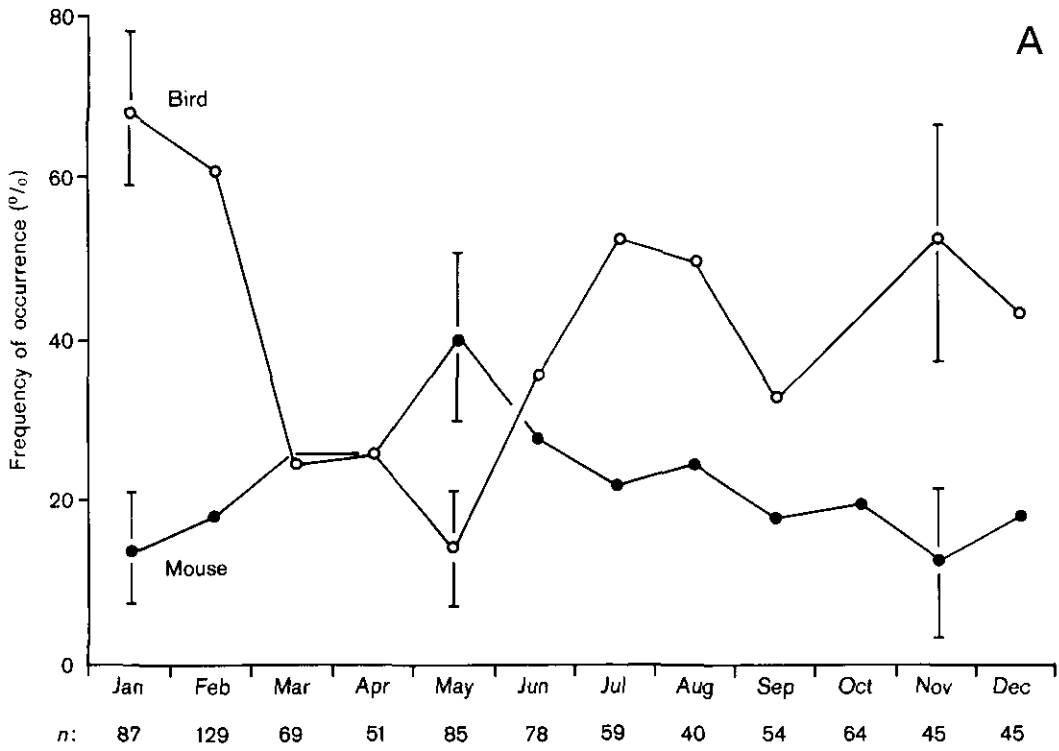


Fig. 10 Predator damage to starlings' eggs, and correspondence between placing of toothmarks on egg and spacing of canines in a stoat skull. Photos: J. E. C. Flux.

(1964) illustrated similar damage to ducks' eggs done by *M. frenata*. On the other hand, eggs containing advanced embryos could not be eaten without ingestion of some shell; and B. M. Fitzgerald (pers. comm.) states that droppings of stoats that had fed on dotterels' eggs had a distinctly yolky appearance, and always contained some fragments of shell.

Fig. 11 (A) Monthly occurrence of birds and mice in forest stoat guts (sexes and ages pooled),  $\pm$  95% confidence intervals at extremes. (B) Seasonal variation in the occurrence of birds and mice in stoat guts (ages and sexes pooled) in different kinds of forest.



### Seasonal variation

The gross patterns of seasonal variation in diet show a striking decline in the frequency of birds in autumn, matched by an increase in the occurrence of mice (Fig. 11A). This occurs in all types of forest (Fig. 11B), and was found also by Fitzgerald (1964), and by Roser & Lavers (1976) in ferrets in a marsh area in the North Island.

Stoats of both sexes ate more lagomorphs in summer and fewer in winter. Young rabbits and leverets are especially vulnerable to stoats, and are most readily available in summer, less so in spring and autumn, and least in winter (although, in fact, we could not tell the age, or even the species, of most of the lagomorphs identified). The breeding season of rabbits is long in New Zealand; most young appear from July to January (Watson 1957), continuing for another 2–3 months in certain conditions (e.g., low population density imposed by control measures). Young hares are available from August to March (Flux 1967).

### Opossums

Opossums are large (2–4 kg) climbing marsupials, introduced to New Zealand for their fur and now very common, particularly in podocarp and mixed forests. The extent to which stoats eat them is difficult to judge, for two reasons. On the one hand, our method of identifying prey species from hairs could underestimate the number of opossums eaten, because it would not detect the skinned carcasses of opossums discarded by fur trappers. Not all opossums made available to stoats by trappers were skinned (trappers reported stoats taking live young from the pouches of dead females, or chewing at carcasses before the night's kill could be collected), but adult opossums contain so much meat that a stoat could avoid ingesting much hair even when eating from a fully furred carcass. This may explain why the distribution of unidentified hair (usually in small quantities) parallels that of opossums in our data.

On the other hand, we may have overestimated the importance of opossums by collecting stoats trapped along roadsides. Road-killed opossums are commonly seen being eaten by stoats, and most stoats in the samples from Egmont, Westland, and the Eglinton Valley were collected within 20 m of traffic which, by the standards of rural New Zealand, was often moderately heavy.

We cannot tell whether stoats killed opossums as well as eating them as carrion, but 3 points suggest that many—perhaps most—were scavenged.

(1) Male stoats living in 3 podocarp forests intensively worked by opossum trappers tended to eat fewer opossums in summer ( $0.10 > P > 0.05$ ), although opossums are common there all the year round.

(2) On the research block studied by DSIR'S Ecology Division in the Orongorongo Valley, near Wellington, where opossums are common but where there is no fur-trapping and no traffic, no opossum remains were found in the 46 scats of stoats collected in summer and autumn 1972 (King, unpubl. data). Stoats were caught there only during a period of unusually high population density of mice in the forest; when the numbers of mice declined the stoats disappeared, although living opossums remained abundant.

(3) Opossums are strong, can be aggressive when threatened, and certainly are less helpless than the typical 'stoated' rabbit. Killing a 2–3 kg opossum free to defend itself would be a risky undertaking for a 300 g stoat.

### Sexual dimorphism and food habits

The extent and development of sexual dimorphism in New Zealand stoats is documented by King & Moody (1982b). On average, adult males are longer than females by 11% in head plus body length and by 10% in the condylobasal length of the skull, and they are heavier by 57%.

Current information on male/female differences in the food habits of stoats and other mustelids has been reviewed by Moors (1980). Many general observations, mostly from Europe, have suggested that the small females of strongly dimorphic species might eat more small prey species and correspondingly fewer large ones. For the present samples, in which variation due to season and habitat was controlled, this expectation is confirmed when prey species are grouped as large, medium, or small; but this is not necessarily because females are unable to tackle larger prey. The group of large prey categories (listed in the upper section of Table 5) comprises 6 items, of which carrion and hedgehogs were relatively unimportant, rats and lagomorphs occurred equally often in both sexes, and only opossums and unidentified mammals (probably including many skinned opossums – see above) were eaten more often by males. Erlinge (1979) found that female stoats in Sweden ate significantly fewer lagomorphs than did males, probably because there they are better able to subsist on small rodents. In New Zealand this option is unreliable, and although females do eat small prey (mice and insects) more often than males, the more nutritious larger prey, such as rats and young rabbits, may often be the only alternative to starvation. The scarcity of small rodents, and the larger mean size of other mammalian prey (King & Moors 1979), may explain why female stoats in New Zealand have become larger than their British ancestral stock (King & Moody 1982b), and those that we sampled ate lagomorphs as often as did males.

The status of opossums as large prey is uncertain, since it seems likely that many were scavenged. The higher incidence of opossums in the guts of male stoats may simply reflect the higher absolute food requirements of larger predators relative to smaller ones (Moors 1977, 1980). There are few other large prey species in the podocarp and mixed forests where opossum carrion is most readily available; or, if males have larger home ranges than females, they might have more opportunity to find carrion. The size relationship between a predator and its prey is influenced not only by the killing power of the predator but also by the size, distribution, and energy content of the available prey.

#### Use of carnivore gut analysis in surveys of small animal distribution

Brunner et al. (1976) and Friend (1978) showed that several species of small mammals were identified in the scats of Australian feral cats, foxes, and dingoes which were not detected by conventional survey techniques used in the same area. They suggested that analysis of the diet of predators could be a useful complement to conventional methods in documenting the distribution of their prey. Table 2 and Appendix 3 list the prey of stoats which could be identified at least to genus. Although these lists are the result of analysis of a very large number of stoat guts, few rare species were identified, so it appears that faunal surveys in New Zealand would be better conducted by more direct methods.

#### Food habits in New Zealand and Britain

The spectrum of prey for stoats in New Zealand differs from that in Britain, principally in that there are no voles and only 1 species of mouse here. Since voles and mice are frequently eaten by stoats in Britain, it has been stated—e.g., by Gibb & Flux (1973)—that stoats in New Zealand compensate for the lack of voles by eating more insects and birds. Table 9 compares the diets of New Zealand and British stoats.

The data for Britain are recalculated from the original appendix table in Day (1963); the published figures in Day (1968) are not comparable with ours, for 3 reasons. Day assumed that remains of a given prey species found in stomach and intestine represented 2 individuals; he counted vegetation as prey; and he expressed his results as the frequency of occurrence of a given item as a percentage of all items identified, rather than of all guts with food.

The lower section of Table 9 displays the frequency of occurrence of the 4 principal groups of vertebrate prey of stoats common to both countries, segregated by sex and season. Variation in habitat has been minimised as far as possible by using only the data from New Zealand forests; hence, the comparison is really only between the New Zealand

and British habitats (forests and farmland respectively) which were best sampled by the collections examined. The extent of regional variation in the food of stoats is less well known for Britain than for New Zealand, but 2 localised studies of the food habits of stoats, in Sussex (Potts & Vickerman 1974) and Yorkshire (Howes 1977), give results essentially similar to those of Day.

Table 9 shows that birds did not in fact appear significantly more frequently in the New Zealand sample. The cells of the sex/season table for Britain get down to very small numbers, so a  $2 \times 2 \chi^2$  test on the simple gross frequencies of birds in the total British and New Zealand samples has also been tried. This is not too misleading, since the proportion of stoats collected in autumn—when, at any rate in New Zealand, birds were eaten least often—is 25% and 26% respectively in the 2 samples. This result too was not significant ( $\chi^2 = 1.30$ ).

The only marginally significant difference found among the vertebrate prey species common to both countries is that there were fewer lagomorphs in our samples. This is probably a simple habitat difference. Lagomorphs are rare or absent in many of the New Zealand forests sampled, where their place as large mammalian food for stoats is taken by opossums (Fig. 7). At Mount Cook, where there is open grassland without opossums (more like Britain than the solid forests in the other Parks), lagomorphs were eaten more often than in Britain by both sexes in every season ( $P = 0.008$ ). Other vertebrate prey species were eaten in only one country or the other (squirrels, opossums, lizards) or very rarely (hedgehogs), and the difference in occurrence of insects as a group is too obvious to require testing.

In Ireland too stoats subsist on a prey fauna lacking voles. A small sample of Irish stoats examined by Fairley (1971) contained about the same proportion of birds as in Britain (Table 9). In Holland, Brugge (1977) identified 61 food items of stoats, including 51% mice and voles, 23% lagomorphs, and 21% birds and eggs. Elsewhere in their enormous range stoats live in an environment entirely different from temperate western Europe and New Zealand. The northern Holarctic has a severe climate; stoats are small (adult males average < 210 g throughout the U.S.S.R. and North America—Corbet & Southern 1977) and adapted to hunting a fauna rich in voles and lemmings, which are pursued in their burrows and under the snow. Birds and lagomorphs together seldom contribute more than 10% of the prey of stoats in either winter or summer (e.g., Aspisov & Popov 1940, Aldous & Manweiler 1942).

Day (1968) stated that 90% of the stoat guts he examined contained only one type of prey. In our

Table 9 Comparison of the diet of stoats in New Zealand and Britain.

(A) Total samples	Frequency of occurrence (%)		
	New Zealand	Britain	Ireland
Small rodents <sup>(1)</sup>	19.3	29.9	17.2
Rats	6.4	3.4	3.4
Lagomorphs	17.5	34.5	34.5
Birds (excl. eggs)	42.6	41.4	37.9
Squirrels	—	2.3	0
Opossums	10.0	—	—
Insectivores <sup>(2)</sup>	0.2	1.1	0
Lizards	4.5	—	0
Insects	40.9	6.9	0
Guts with food	1250 <sup>(3)</sup>	87	29
Source	Table 2	Day (1963)	Fairley (1971)

<sup>(1)</sup> *Mus musculus*, *Apodemus sylvestris*, *Microtus arvalis*, *Clethrionomys glareolus* and other unidentified small rodents, as applicable  
<sup>(2)</sup> Only hedgehogs present in N.Z.; hedgehogs and pigmy shrews in Ireland  
<sup>(3)</sup> 1216 for opossums, 1214 for lagomorphs

(B) Relative distribution, by sex and season, of occurrence of four principal vertebrate prey categories in New Zealand and Britain (sources: Table 5, and Day (1963)). Seasons for Britain taken as 3-month groups opposite those for New Zealand given in Appendix 2.

	Frequency of occurrence (%) of			n
	Small rodents	Rats	Lagomorphs	
Summer, males	NZ	13	20	53
	GB	15	54	38
females	NZ	19	16	62
	GB	66	0	66
Autumn, males	NZ	24	11	25
	GB	27	27	36
females	NZ	39	13	15
	GB	13	38	25
Winter, males	NZ	18	7	39
	GB	38	0	42
females	NZ	34	3	48
	GB	33	0	50
Spring, males	NZ	11	4	41
	GB	20	0	40
females	NZ	35	12	42
	GB	50	0	50
P (2-tailed signs test)	0.29	0.29	0.07	0.29

material this proportion was 49% in Fenn-trapped stoats and 59% in gin-trapped stoats. This difference is perhaps due to British stoats eating few very small prey items. The only prey species averaging less than 10 g in Day's sample were insects, which occurred in 7% of guts with food (Table 9). In our samples a higher proportion of guts contained such small items—insects in 41%, lizards in 5%, and freshwater crayfish in 2%. It would be interesting to know whether this higher incidence of small items really represents an adjustment in foraging strategy on the part of New Zealand stoats. Large cave wetas and tree wetas (2–4 g each) and lizards (7–8 g) could compensate for the lack of voles if they have a high enough caloric content and can be found in adequate numbers, but otherwise the energetics of foraging would make them profitable only incidentally.

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#### Appendix 1 Estimation of biomass composition of diet of stoats in this study.

The relative contribution of the major prey categories to the total diet was estimated by loading the raw frequencies according to the size of the prey. A single meal was taken to be 10 g of food (Day 1968), and all types of prey were assumed to remain in the gut for equal periods. The contribution of small items (< 1 per meal) to the diet was estimated by multiplying the minimum number found and their approximate mean weight, taken as follows: wetas 3 g; other insects 1 g; lizards 7 g; birds' eggs 7 g. Medium-sized prey items were weighted as 1 meal (10g) each; these included mice, birds, crayfish, and fish. Large prey items were weighted as 2 meals (20 g) each; these included opossums, lagomorphs, rats, carrion, unidentified mammals (mostly opossums and rats; see Methods), and hedgehogs. We assume that if a stoat feeds repeatedly off a single carcass, the appropriate weight is the average amount of food in the gut at one time—about 20 g fresh weight, according to Day (1968). The logic and the weights assigned differ from those used by Fitzgerald & Karl (1979) for calculating the percentage contribution of virtually the same prey fauna to the total diet of feral cats, estimated from scats.

(Appendix 2 et seq. overleaf)

Appendix 2 Numbers of stoat guts examined.

	UW	TG	EG	MB	AT	NL	AP	CB	MC	WL	MA	TK	FL	KK	
SEASON	Number of guts with food (excluding 58 undated)														
Spring (Sep–Nov)	6	12	16	1	2	26	16	35	18	12	7	4	55	—	210
Summer (Dec–Feb)	3	11	7	20	2	19	7	63	66	44	2	21	153	23	441
Autumn (Mar–May)	1	12	16	8	—	15	34	40	53	52	4	16	56	—	307
Winter (Jun–Aug)	5	4	37	2	4	10	16	13	7	15	5	19	97	—	234
SEX RATIO	Percentage of guts with food														
% males	67	64	68	42	63	67	53	51	46	54	72	55	57	52	56
$\bar{n}$	15	39	76	31	8	70	73	151	144	123	18	60	361	23	1192
AGE RATIO <sup>+</sup>	Percentage of stoats with guts containing food also classified by age														
% young + subadult	13	26	20	65	29	32	22	40	50	45	21	29	38	83	
$\bar{n}$	15	39	66	31	7	69	69	150	141	119	14	58	348	23	1149
HABITAT	Number of guts analysed														
Beech	1	37				83	34	166	1		23	79	267		691
Podocarp			87							112					199
Mixed	20						17				5		113		155
Scrub	1				8	3									12
Grass					1	4	7		133	5			12		162
Alpine		1	3			1	10								15
Villages		6		51		3	12		47	23			21		163
Rubbish tip							4			12			33		49
Other or unknown	1		3			8	13			12	2		5	24	68
$\bar{n}$	23	44	93	51	9	102	97	166	181	164	30	79	451	24	1514

<sup>+</sup> *Young*: first-year stoats caught between November and February. *Subadult*: first-year males caught between March and August (no equivalent category for females). *Adult*: all stoats caught in September and October, and all but those defined above caught from November to August.

Appendix 3, Table 1 Insects and other arthropods identified from stoat gut samples.

Order	Family	Genus (and species if known)	Common name	Total no. found
Orthoptera	Rhaphidophoridae	—	small cave wetas	100
		—	large cave wetas	104
	(incl. 42 <i>Gymnoplectron edwardsii</i> , 15 <i>G. longipes</i> , and 13 <i>G. sp.</i> )			
	Stenopelmatidae	<i>Hemideina</i>	tree wetas	122
		<i>Hemiandrus</i> , <i>Zelandosandrus</i>	ground wetas	277
—	—	—	unidentified wetas	22
—	—	—	grasshoppers	1
Coleoptera	Carabidae (incl. 2 <i>Megadromus ballatus</i> , 4 <i>Megadromus sp.</i> , 1 <i>Mecodema laterale</i> , 1 <i>Mecodema sp.</i> , 8 <i>Anchomenus sp.</i> )			68
	Scarabaeidae	<i>Odontria</i>	chafer beetles	2
		<i>Chlorochiton</i>	chafer beetles	2
		<i>Pyronota</i> (incl. 2 <i>P. festiva</i> ,	manuka beetle)	4
		<i>Costelytra</i>	grass grub	3
		—	unid. melolonthines	2
	Cerambycidae	<i>Prionoplus reticularis</i>	huhu beetle	1
		<i>Hexatracha pulverulenta</i>	squeaking longhorn	1
	Buprestidae	<i>Nascioides enysi</i>	beech buprestid	2
	Lucanidae	—	stag beetle	1
	Tenebrionidae	—	unidentified	2
	Staphylinidae	—	carion beetles	11 <sup>+</sup>
—	—	unidentified beetles	54	
Lepidoptera	Hepialidae	<i>Wiseana</i> (incl. 1 <i>W. characterifera</i> )		
		<i>Aenetus virescens</i>	porina moth	64
		—	puriri moth	14
		—	unidentified	13
	Noctuidae	—	unidentified	16
	—	—	unid. moths	12
—	—	unid. caterpillars	37	

(continued on next page)

Order	Family	Genus (and species if known)	Common name	Total no. found
Hymenoptera	Vespidae	<i>Vespa germanica</i>	German wasp	96
	Formicidae	—	unid. ants	2
Odonata	—	—	unidentified dragonflies (1 unid.)	5
	—	<i>Uropetala carovei</i>	—	2
Diptera	Calliphoridae	<i>Calliphora</i>	blowfly	20
	—	—	unidentified flies	9
Trichoptera	—	—	caddisfly	1
Hemiptera	Cicadidae	—	unid. cicadas	15
Dermaptera	—	—	earwig	1
Phasmatodea	Phasmidae	<i>Acanthoxyla geisovii</i>	stick insect	1
Plecoptera	—	—	unid. stoneflies	2
Thysanura	Lepismatidae	—	unid. silverfish	1
		—	unid. insects	15
Araneida	—	—	unid. spiders	21
—	—	—	unid. centipede	1
				<b>1127</b>

† All in one stoat

**Appendix 3, Table 2** Total numbers of lizards, crayfish, and insects identified to genus or species, by collection area.

	UW	TG	EG	MB	AT	NL	KK	AP	CB	MC	WL	MA	TK	FL
<b>WETAS</b>														
<i>Gymnoplectron longipes</i>		2	1	11							1			<b>15</b>
<i>Gymnoplectron edwardsii</i>			6	1	2	5		3	10	1	3			<b>42</b>
<i>Gymnoplectron</i> sp.			1		1						1			<b>13</b>
<i>Hemideina</i> sp.		2	8	2	0	2	6	0	2	5	71	6	0	<b>122</b>
<i>Hemiandrus</i> sp.		5	1	3	2	2	2	0	7	19	2	53	10	<b>277</b>
<b>OTHER INSECTS</b>														
<i>Pyronota festiva</i>									1	1				<b>2</b>
<i>Megadromus ballatus</i>														<b>2</b>
<i>Mecodema laterale</i>														<b>1</b>
<i>Prionoplus reticularis</i>											1			<b>1</b>
<i>Hexatracha pulverulenta</i>														<b>1</b>
<i>Nascioides enysi</i>									2					<b>2</b>
<i>Aeneus virescens</i>		2	9	3										<b>14</b>
<i>Vespa germanica</i>						21			74		1			<b>96</b>
<i>Uropeta carovei</i>											1			<b>1</b>
<i>Acanthoxyla geisovii</i>														<b>1</b>
<i>Wiseana characterifera</i>			1											<b>1</b>
<i>Odontria</i>										1	1			<b>2</b>
<i>Chlorochiton</i>				1							1			<b>2</b>
<i>Pyronota</i>									2					<b>2</b>
<i>Costelytra</i>										3				<b>3</b>
<i>Megadromus</i>														<b>4</b>
<i>Mecodema</i>														<b>1</b>
<i>Anchomenus</i>				2		2		2	1					<b>8</b>
<i>Wiseana</i>			25	13				5	2		9			<b>63</b>
<i>Calliphora</i>						2	1		1	2	3		1	<b>10</b>
<i>Melampsalta</i> <sup>(1)</sup>				1	1					3	4		1	<b>5</b>
<b>CRAYFISH</b>														
<i>Paranephrops planifrons</i>			4	12	2	5								<b>23</b>
<i>Paranephrops zealandicus</i>														<b>2</b>
<b>LIZARDS</b>														
<i>Leiopisma zelandica</i> <sup>(2)</sup> or sp.						7		3		5			8	<b>24</b>
<i>L. lineocellatum</i>						1 <sup>(3)</sup>								<b>1</b>
<i>Hoplodactylus maculatus</i> <sup>(2)</sup> or sp.				1				2		14				<b>17</b>

<sup>(1)</sup> Members of this defunct taxon are now placed in various other genera<sup>(2)</sup> These are the two commonest species of their respective genera<sup>(3)</sup> Within known range of species

**Appendix 4** Distribution of birds eaten, by habitat and season (sexes and ages pooled).

Habitat	Collection area	Spring		Summer		Autumn		Winter		n (seasons combined)
		f	%	f	%	f	%	f	%	
Beech forest	TGw	6	86	7	70	3	25	3	75	33
	NL	10	43	10	59	4	29	1	25	58
	APe	2	40	—	—	4	27	2	29	28
	CB	9	26	44	70	6	15	4	31	151
	MAe	2	29	2	100	2	50	—	—	13
	TK	4	100	8	38	—	—	9	47	60
	FLe	25	49	29	49	8	31	38	53	208
Podocarp forest	EG	3	19	2	29	2	13	12	34	73
	WL	6	55	13	59	5	12	3	23	87
Mixed forest	UW	—	—	—	—	—	—	—	—	14
	APw	2	67	3	75	—	—	1	25	13
	MAw	—	—	—	—	—	—	3	60	11
Disturbed habitats	FLh	1	50	40	63	8	31	3	75	96
	MB	1	100	11	55	1	13	—	—	29
	WL + FL	—	—	17	44	4	44	1	20	53
Grassland	MC	5	28	26	39	12	23	4	57	144
Seashore	KK	—	—	21	91	—	—	—	—	23