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Source: *Journal of Animal Ecology*, Vol. 49, No. 1 (Feb., 1980), pp. 127-159

Published by: British Ecological Society

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## THE WEASEL *MUSTELA NIVALIS* AND ITS PREY IN AN ENGLISH WOODLAND

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### SUMMARY

(1) In a 27 ha deciduous woodland at Wytham, near Oxford, 344 samples (scats) were collected from live-trapped weasels, principally from September 1968 to March 1970. The home ranges and fleas of these weasels were described previously (King 1975, 1976).

(2) In 215 samples containing wild-caught prey, 245 vertebrate items were identified: fifty-one birds or eggs; one rabbit; one mole; and 192 small rodents (including eighty-nine bank voles (*Clethrionomys glareolus*), forty field voles (*Microtus agrestis*), and thirty-four wood mice (*Apodemus sylvaticus*)). The ages of the prey, and the species of the birds eaten, were unknown.

(3) The most marked feature of the seasonal variation in the prey taken was the large number of eggs eaten in spring.

(4) The differences in diet between six individual male weasels reflected differences in the habitats of their home ranges.

(5) The density of bank voles and wood mice together varied from twenty-one to thirty-nine individuals per ha from September 1968 to October 1969. During this time the weasels were estimated to have eaten an average of 8–10% per month of the total populations of each species. Lagomorphs were rare in the wood; insectivores were common but almost never eaten.

(6) Seasonal and local variations in the survival of wood mice bore no relationship to the distribution of resident weasels.

(7) Predation by weasels usually accounted for only a small proportion of the wood mice and bank voles disappearing from the study area.

(8) Weasels ate bank voles and wood mice in approximate proportion to their availability. Relatively more bank voles were taken in winter, when more weasels were present, because of differences between bank voles and wood mice in their preference for cover, and reactions to being hunted. The difference might have been biologically significant, although statistically insignificant.

(9) The ecological efficiency of the rodent-weasel food chain averaged 0·6%.

(10) The size of the territory occupied by weasels seems to be related to the density of prey rather than to, e.g., the hunting skill of the owner.

(11) Predation by weasels appeared to have no observable effect on the density or survival of small rodents in Marley Wood, but its effect on tits (Paridae) nesting in boxes is greater, for reasons discussed.

(12) Weasels and tawny owls, the two principal resident predators in Marley Wood, are complementary in their hunting strategies, prey selection, and life-history tactics,

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but their common food resource is not renewed rapidly enough for them to avoid exploitation competition altogether. Weasels are more active by day than by night in Marley Wood, possibly because they are vulnerable to predation by owls.

## INTRODUCTION

This paper is the third of three describing the weasels (*Mustela nivalis* L.) of Marley Wood, part of Wytham Woods, near Oxford. The first (King 1975), gave details of the home ranges of the resident weasels, and what was known of the activity and population biology of resident and non-resident weasels in the wood. The second (King 1976), derived some conclusions on the hunting and denning behaviour of the woodland weasels from the distribution of their fleas. The present paper describes the diet of the weasels, and their relationships with their principal rodent prey, and with the other important predators in the wood, the tawny owls (*Strix aluco* L.). The relationship between the weasels and the tits (Paridae) nesting in boxes in the wood has been analysed by Krebs (1970) and Dunn (1977).

The study area and some of the work previously done in Wytham was described by King (1975). Weasels were live-trapped only in and around Marley Wood, and their consumption of, and impact on the wood mice (*Apodemus sylvaticus* L.) and bank voles (*Clethrionomys glareolus* Schr.) was estimated by reference to past and current studies of these small mammals there. To help interpret these field data, important background information is available from laboratory studies on the energy metabolism of weasels (Moors 1977), and from behavioural observations of the responses of weasels to different types of prey (Erlinge, Jonsson & Willstedt (1974), summarized in English but in less detail by Erlinge (1975)). Previous studies on the food habits of weasels have been published by Nasimovich (1949), Parovschchikov (1963), Day (1968), Barbu (1968), Walker (1972), Potts & Vickerman (1974), Erlinge (1975), Moors (1975), Tapper (1976), Brugge (1977) and Howes (1977). Most of them show that *Microtus* is the principal prey of the weasel: but in woodland, *Microtus* is relatively scarce.

## MATERIAL AND METHODS

### *Weasels: home ranges and habitats*

The distribution of the resident weasels in the wood was described by King (1975). Figure 1 shows the distribution of habitats in and around the wood, the locality names mentioned in the text, and the positions of the two rodent trapping grids.

### *Small rodent prey species: estimation of numbers*

Southern (1970) has given a general description of the prey available in Wytham for weasels and tawny owls. The two commonest small rodents are wood mice and bank voles. Field voles (*Microtus agrestis* L.) are also present, but rarely appear in traps set in the wood. Data on the density of wood mice and bank voles in Marley Wood during this study were kindly provided by Flowerdew (1972 and unpublished data), whose fieldwork in Marley Wood overlapped with mine between September 1968 and December 1969. Flowerdew's Area C (control trapping grid) occupied 1.5 ha (Fig. 1), and he used Longworth live-traps and a modified version of the 'calendar of captures' method to arrive at the population estimates shown in Fig. 2. On the experimental grid (1.1 ha)



PLATE 1. Marley Wood from the air, July 1968 (Crown Copyright reserved).

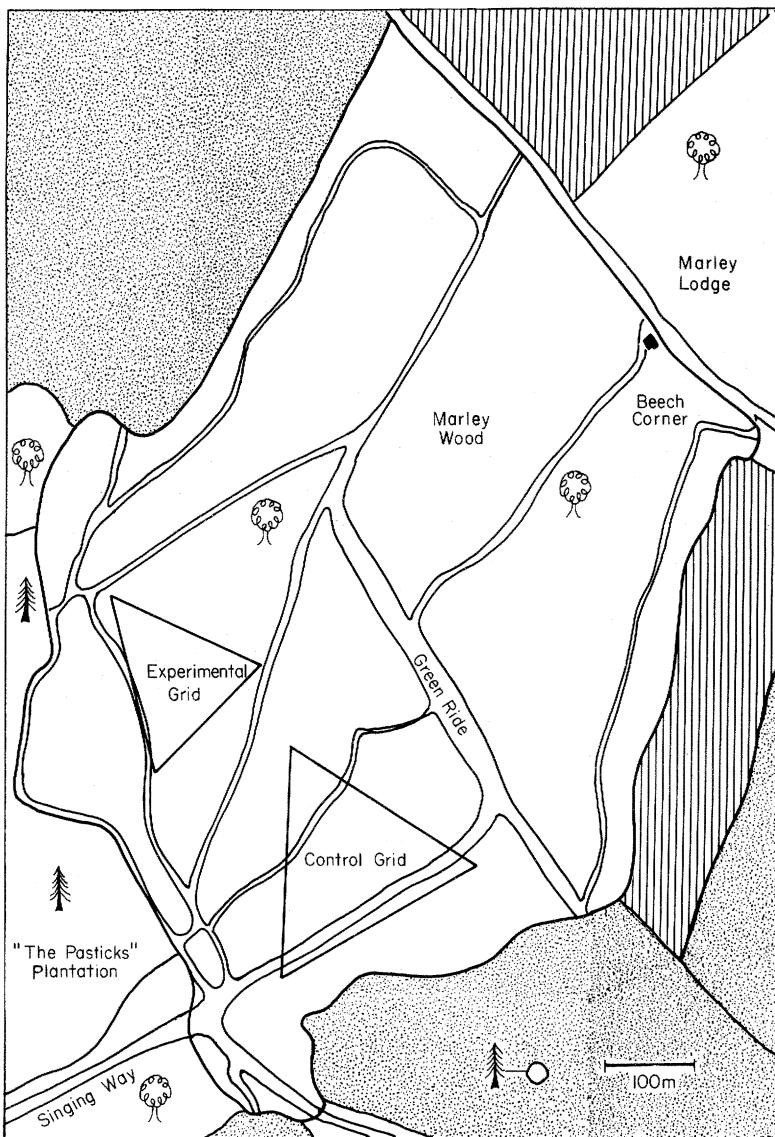


FIG. 1. Map of Marley Wood and environs, showing the distribution of adjacent habitats, the positions of the rodent trapping grids, and the place-names mentioned in the text.

■ Arable, ▨ pasture.

he supplied extra food for the small rodents, which caused minor local changes in the density and population dynamics of wood mice, so I have used the density estimates for the control grid alone to represent the rodent populations of the whole wood.

The study area was a nearly isolated patch of woodland: little migration of small rodents in and out of it (Watts 1970), or of weasels (King 1975) was detected.

Methods of censusing small rodents are all unreliable to some extent. The figures supplied by Flowerdew for Marley Wood in 1968–69 are probably rather low for the following reasons:

(a) In autumn 1968 there was a good seed crop, and mice came less readily to traps at that time.

(b) During the breeding season certainly, and perhaps at other times, the 5-weekly spacing of the trapping periods could allow many rodents to enter and leave the population without ever being exposed to traps.

(c) A proportion of the population never enters traps at all, so population estimates based on trapping results are usually too low. Ryszkowski, Gosczynski & Truszkowski (1973) overcame this problem by increasing some of their population estimates by a standard 25%, but I have not done this because (i) Boonstra & Krebs (1978) showed that the underestimate given by live-traps was not constant through all densities of *Microtus*, and (ii) it adds nothing to the information given by Flowerdew's figures. The reader may do it himself if he wishes, or alternatively, he may keep the probable underestimate in mind. The point is that the rodents missed by the traps may not be missed by the weasels, and these uncounted rodents, in *Microtus* at least, can comprise more than half the population (Boonstra & Krebs 1978).

(d) The vegetation on Flowerdew's control grid could not represent the relative distribution of cover types over the whole study area: it contained few thickets of dense cover such as occurred in some other parts of the wood. The extrapolation of the density estimates for wood mice from the control grid to the whole area is probably reasonable, as their distribution is fairly independent of cover (Southern & Lowe 1968), but the density of bank voles increases in thicker cover (*loc. cit.*). The extent of the potential error here, at least in some years, can be gauged from the difference found by Smyth (1968) in the density of bank voles in two areas of Marley Wood in January 1961. However, there were no large discontinuities in the distribution of rodents through the wood (Watts 1970).

#### *Origin of material*

From the woodland study area, 344 samples of weasel scats were collected from live-traps during trapping sessions or when resetting after the interval between sessions, when the traps were locked open. Most of the samples (289) were obtained from known individuals at known dates and times between September 1968 and June 1970; there were also a few extra samples of scats left by unknown individuals, and for these (fifty-five) the date was known only to within 17 days. The two classes of samples contained 243 and forty-two identifiable items of wild prey; 26 and 29% respectively contained only bait. A 'scat' is defined as the equivalent of one faecal pellet; a 'sample' is a scat or group of scats collected at the same time and place.

The samples were not evenly distributed through the year. Rather few were available in summer because (1) trapping success was lower then, and also the best results were obtained from September 1968 to March 1970, through two winters and one summer (King 1975); and (2) the number of extra scats collected from traps after each non-trapping period was lower in summer because dung beetles often destroyed scats in warmer weather.

#### *Identification of prey remains*

Prey items were identified under the microscope by the hair and feather characteristics described by Day (1966). Birds could not be identified nearer than to Order. Mammals could be identified, from the hairs, down to genus, and from known geographical distribution, to species.

Traps were provided with food, usually a dead laboratory mouse (*Mus musculus* L.). This had two functions: to sustain the captured weasel, and to stimulate peristalsis. The first scats eliminated from the gut should contain the remains of natural prey eaten before the weasel entered the trap. When no food was provided (e.g. in hot weather) fewer scats were collected. If the scat contained only the food provided, the weasel's gut was considered to have been empty. On the few occasions when there were no mice available, cubes of ox heart were used instead.

Although I would have preferred to place only white mice in the trap, often I had to use brown ones. When this happened, I found, under the microscope, traces of brown hair of wild-caught prey tended to escape attention against a background of brown *Mus*, whereas they stood out clearly against albino hair. I calculated, by proportions, that eight trace identifications (about 2% of all the items identified) of wild small mammals could have been missed because of this. Birds were not underestimated in the same way, since feathers are conspicuous against any background. Clearly, it is an advantage to use only albino *Mus* as food for trapped weasels: and it saves time, since it takes longer to identify and reject the hair of a brown *Mus* than that of an albino one.

The results have been presented as the percentage frequency of occurrence of scats containing a given item among the 215 scats containing vertebrate prey or eggs. Scats containing only bait or invertebrates were excluded. This method is simple and rapid, and in weasels is no less accurate than more complex methods which involve measuring the weight or volume of undigested remains. In predators which live mostly on prey items of similar size, each larger than its stomach capacity, the contents of the gut or scats will usually contain one, or at most two species of prey only, and each will be represented by one individual. The weasel lives very largely upon prey animals of one size class (small mammals and birds, mostly weighing about 20 g); the capacity of the stomach is about 10–12 g (Heptner *et al.* (1967), and personal observations). Few smaller items of 10 g each or less are eaten. Hence, the usual disadvantages of the frequency method, that of overestimating small items and underestimating large ones, do not apply. (No correction has been made for the much larger size of lagomorph prey, since these comprised only a small proportion (0.4%) of the total number of prey animals identified.) Day (1968) and Moors (1975) showed that most of the guts of stoats and weasels contained only one species of prey. Gosczynski (1972) concluded that this convenient character of weasels justified the use of the percentage frequency of occurrence method for them. In the present material, 77% of the 215 scats containing wild prey yielded only one vertebrate species; 14% contained a vertebrate with an invertebrate or an egg, and only 9% contained remains of two vertebrate prey species.

#### *Quantitative estimation of prey*

Few samples contained teeth or recognizable fragments of bone, since the scats collected comprised only a small sample of all the indigestible parts of the prey eliminated, and weasels do not always eat the front of the skull and the teeth (Heidt 1972). There was therefore no opportunity to obtain a direct tally of the number of prey eaten from counts of teeth in the scats, and no weasel dens were found where uneaten remains with teeth might be left (Fitzgerald 1977), so another method had to be devised.

Each prey item recorded was considered to represent one prey animal killed, even if only a trace of hair was detected. The validity of this assumption depends upon the probability of counting, in two samples, the same prey animal twice or, in one sample, two prey as one. Since most weasel guts contain only one prey individual (see above)

the probability of counting two as one is not high. But many of the weasels from which these samples were taken were caught daily or even twice a day, and in them the same prey could be counted twice unless the gut is quickly cleared after each meal. Experiments in captivity show that food does pass quickly through the gut, as the first scat of a given meal reaches the rectum in about 3 h (Short 1961): in Marley Wood, where the live-traps were inspected twice daily, the *Mus* provided in them appeared in 81% of the scats collected. This rapid digestion is probably because the gut of carnivores is relatively short: even in larger species such as mink, transit time is still only 1–3·5 h (Sibald *et al.* 1962). But there is no information in the literature on the time taken for the gut to be cleared of all traces of a meal.

On sixty-five occasions, the same weasel was caught on two consecutive inspection rounds, and left scats containing identifiable items in both traps. To calculate the percentage of occasions on which the same individual prey animal could have been present in both sets of scats, the following rules were applied: (i) the *Mus* provided was considered an item; (ii) if the trapping records showed that the weasel ate the *Mus* in the first trap, then wild rodent remains in the second trap were considered to be from a separate individual even if from the same species as was found in the first trap; (iii) if the records showed that little or no *Mus* was eaten in the first trap, then rodent remains of the same species produced in both traps could have been from the same individual prey animal. I found that the same prey animal could have been represented twice in only six (9·2%) of sixty-five cases. Hence, in over 90% of the cases, a whole meal had passed through without trace within an average of 12 h. The small potential error of 10% has been neglected in the following calculations.

A whole prey animal has been counted for each identification, even if only a trace was found. I considered it unlikely that a weasel would ever eat fur or feathers except in the course of eating the animal to which they were attached.

The daily food consumption of weasels in the wild is not known. From measurements of the food eaten by weasels in metabolism cages, Moors (1977) estimated daily averages of  $0\cdot33 \pm 0\cdot06$  g/g/day for males ( $n = 7$ ), and  $0\cdot36 \pm 0\cdot08$  g/g/day for females ( $n = 7$ ). The body weights of live resident weasels in Marley Wood were  $109 \pm 13\cdot4$  g for males ( $n = 7$ ), and  $65 \pm 4\cdot4$  g for females ( $n = 3$ ) (King 1975). Hence their daily food requirements would be about 36 and 23 g respectively. For the present purposes, the consumption of male weasels has been taken as two small rodents (averaging 20 g each) per day, and of females, one per day.

I also assumed that few prey were killed but not eaten (weasels are known to do this, but only when prey is extremely abundant (Heidt 1972)); hence, one prey animal detected in the scats was taken to represent one individual removed from the population of prey.

#### *Estimation of the proportion of each prey species eaten by weasels*

The total number of each prey species present per month on the study area has been estimated by multiplying Flowerdew's density figures for the density of rodents on his control grid by 26·8, the area of the wood in hectares. The total number of each prey species eaten by weasels per month, between September 1968 and October 1969 inclusive, was estimated from the number found in the scats by simple proportions:  $n_{Cl} = (a \times c)/b$ , where  $n_{Cl}$  = estimated total number of bank voles (*Clethrionomys*) eaten by all resident weasels in all parts of the wood per month:  $a$  = number of bank voles detected in the scats;  $b$  = number of weasel-kills sampled;  $c$  = estimated total number of weasel-kills (calculated at the rate of two kills per day for males and one for females, each consisting

of the equivalent of an 'average mouse' of 20 g). As the evidence of breeding by the weasels resident in the wood during the study was only circumstantial (King 1975), no allowance has been made for the increased food consumption of a pregnant or lactating female, or for the requirements of small young. The main assumption in this calculation is in the term '*c*', that the weasels killed a constant number of rodents per day at all densities of prey. If they ate less when food was scarce and more when it was abundant, these estimates would be wrong, but as the actual number of rodents killed was not known, there is no way to correct them. However, the range of variation in the density of prey available through the study was not extreme (Fig. 2). A second assumption is that the scats represented the true proportions of the various prey types in the weasel's diet. During the 14 months when weasel and rodent data were comparable and usable, I estimated that the scats sampled 11% of all the prey killed in the wood (Table 5, cols 3 & 4). Though this is not a bad sample as predator food analyses go, it is still small enough to be biased.

From these estimates I calculated the proportion of the population of each prey species eaten by weasels each month. Unfortunately, the actual numbers of prey identified each month are small (Table 5, cols 5 & 9) so possibly subject to some random variation: and the normal methods for estimating the standard error of a proportion cannot be applied, since each monthly estimate is a compound of two other estimates (number present and number killed), each with a separate, unknown, error. These data should therefore be regarded only as reasonable approximations.

Estimates of consumption of prey were calculated only from the number of resident weasels, even though, during the 14 months in question, one or more non-residents were caught in eleven of twenty-four trapping sessions (King 1975). The non-residents could have contributed to the total pressure of predation by weasels on the rodents, though practically nothing was known about them. Since attempts to include the non-residents would qualify only as guesswork, I have omitted them. There was no reason to believe that these weasels were living in the wood but evading the traps, so I have assumed that their infrequent captures means that they were infrequently present, and that their omission from the calculations would not be serious.

## RESULTS

### *Potential prey species present*

Up to 1970, eighteen species of mammals had been recorded in Wytham, but of these, only five are commonly recorded in the literature as prey of weasels: the bank vole, the wood mouse, the field vole, the house mouse (*Mus musculus* L.), and the rabbit, *Oryctolagus cuniculus* (L.). Of these, bank voles and wood mice were common in the wood, and field voles, though mainly confined to the fields and plantation adjacent to the wood, also occurred there, especially along the Green Ride (Fig. 1). House mice may be regarded as absent from the wood, and rabbits were kept down to very low numbers by the gamekeeper. Shrews (*Sorex araneus* L., *S. minutus* L., and *Neomys fodiens* Pennant), moles (*Talpa europaea* L.), grey squirrels (*Sciurus carolinensis* Gm), and brown rats (*Rattus norvegicus* Berkenhout) were present.

On the control grid, the combined density of wood mice and bank voles varied from twenty-one to thirty-nine individuals per ha (mean  $30 \pm 6/\text{ha}$ ) during the study (Fig. 2). The normal range of density for these species together, measured in another part of

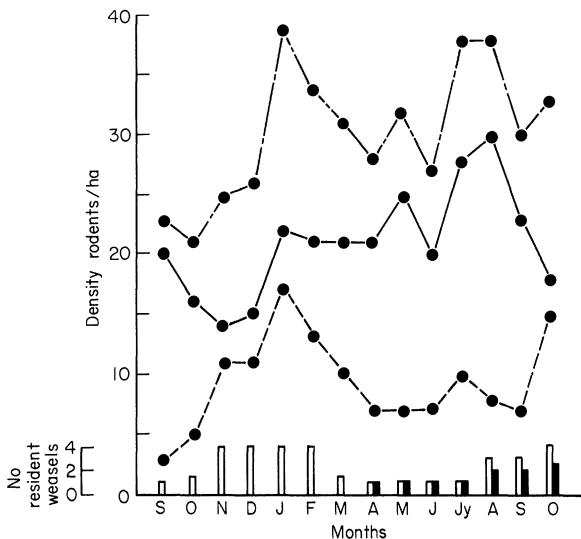


FIG. 2. Density per hectare of *Apodemus* (---) and *Clethrionomys* (—) on Flowerdew's control grid, September 1968 to October 1969. (---) Combined density of both species. Number of resident weasels are shown at the bottom, ■ females; □ males.

Wytham over twenty years by Southern (1970) was  $21 \pm 12/\text{ha}$ . Likewise, the density of titmice breeding in nestboxes (mostly *Parus major* L. and *P. caeruleus* L., with some *P. ater* L. and *P. palustris* L.) in the seasons 1969 and 1970 (1.93, 1.68 pair/ha) was near the long-term average for Wytham (Dunn 1977). The study was not therefore carried out during a period of exceptional numbers of these important prey species, though the numbers of the other potential prey were not measured.

In addition to the titmice, there was a high density of other birds breeding in spring, and, for a short period from May to about August, there was probably a higher biomass of small birds than of rodents as potential prey. The total spring population of breeding birds in Marley Wood was at least 415 pairs, of forty-two species (Perrins personal communication) which is well within the range quoted for oak woodlands in southern England, of comparable area to Marley Wood, surveyed by Flegg and Bennett (1974).

#### *The prey taken by weasels*

Of the total of 344 samples available for analysis, ninety-six (27.9%) contained only the *Mus* provided: 285 items were identified in the remaining 248 samples, of which forty were invertebrates. The invertebrates (twenty-six earthworms, thirteen insects and one slug) have been excluded from the following analyses because (a) Most of the identifiable invertebrates were dung- or carrion-inhabiting types (*Staphylinus*, *Catops*, *Lucilia*), which may have entered the provided food before it was eaten, or the scat after it was deposited, or else were too small to have been eaten deliberately (one seed mite (*Phthiracaridae*); two molluscs, *Carychium tridentatum*; three spiders); and (b) where an invertebrate was present in the same scat as another prey species, it could have been ingested in the stomach of the prey. Nevertheless, the number of earthworms found is interesting in view of Osgood's (1936) suggestion that *Mustela* sp. may turn to

TABLE 1. List of vertebrate prey items identified

Prey	Number found	Frequency of occurrence % (in 215 scats)
Small rodents	192	89
Voles	144	67
<i>Clethrionomys</i>	89	41
<i>Microtus</i>	40	19
Unidentified voles	15	7
Mice ( <i>Apodemus</i> )	34	16
Unidentified small rodents	14	7
Birds	51	23
Passerines	25	12
Non-passerines	5	2
Unidentified birds	7	3
Eggs	14	7
Lagomorph (probably rabbit)	1	0.5
Mole	1	0.5
	245	

them when short of food. Omission of scats containing only invertebrates reduced the number of useful samples to 215.

Rodent prey were found in the same order of frequency as they occurred in the wood: bank voles were always the commonest rodent available there, followed by wood mice (Fig. 2). The overall results (Table 1) show, rather surprisingly, that field voles were eaten more often than wood mice, but this is mainly because of particular individual and seasonal variations in the record, discussed below. Lagomorphs were uncommon, both in the wood and in the scats. Birds were probably eaten rather less in proportion to their numbers than rodents, though the seasonal flux of their eggs was faithfully reflected (Fig. 3). Insectivores (shrews and moles) were common in the wood, but almost completely avoided by weasels. The number of prey species included in the diet of the weasel is small by comparison with larger carnivores, and plant foods are not deliberately eaten. This considerably simplified identification and analysis.

On two occasions a weasel was found to have eaten a *Mus* which could not be accounted for as bait provided. As weasels were sometimes able to steal the bait without getting caught, these records were ignored.

#### *Variation between seasons*

The results are presented bimonthly, to allow comparison with Southern (1954). Figure 3 shows that the principal food of weasels in Marley Wood at all seasons was the bank vole, found in 27–45% of the scats collected every 2 months. The most remarkable feature of the annual pattern is the increase in the proportion of avian prey eaten in May and June, most of which was in the form of eggs. Statistical tests on these data (Appendix 1) confirm that eggs were the only item varying significantly with season.

#### *Variation between individuals*

Of the twenty-five weasels caught in the wood, six males (Table 2) were recaptured a total of 253 times, and they supplied 60% of the 245 prey items analysed. The variation in the composition of their individual records (Fig. 4: data in Appendix 1) could be accounted for by the season during which each was trapped, and the habitat in each of their home ranges.

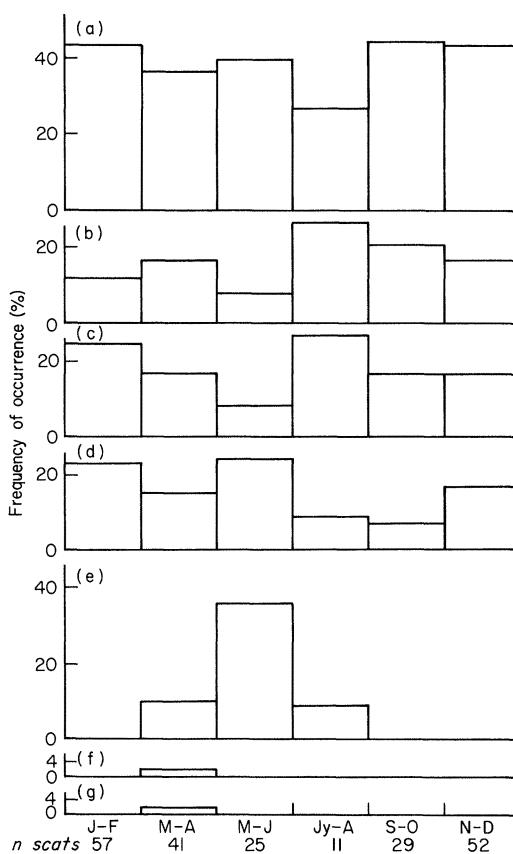


FIG. 3. Seasonal variation in the prey taken by weasels in Marley Wood. (a) *Clethrionomys*, (b) *Apodemus*, (c) *Microtus*, (d) birds, (e) eggs, (f) lagomorph, (g) mole.

#### Season

Eggs were found only in the scats of ♂11, which was the only weasel of the five which was regularly caught between April and August.

#### Habitat

Two weasels of the six (♂10 and ♂24) had ranges which extended into The Pasticks, a young plantation adjacent to the wood. Both ate a larger than average number of field voles, each in proportion to the extent that his home range was estimated to include grassland habitat: ♂10 had about half his in the young plantation, and ate 31% field voles, and ♂24 lived almost entirely in the plantation and ate 61% field voles. ♂7 and ♂11 were the only two whose home ranges were thought to be entirely in the wood; the woodland rodents *Apodemus* and *Clethrionomys* together formed 64 and 58% of their known diets. Both also took some field voles, but these may have been caught in the Green Ride and do not necessarily imply that these weasels hunted outside their trap-revealed home ranges, though of course they could have done so. (But field voles may also be more common in the wood than the trapping records suggest: at least, tawny owls which had no grassland on their territories were still able to catch many field voles (Southern 1954)). The two 'woodland' residents, ♂7 and ♂11 together, ate significantly more of the 'woodland' prey (*Apodemus* plus *Clethrionomys*) than did the two 'plantation'

TABLE 2. Capture records of weasels used for individual diet comparisons (see King 1975)

Tag. no.	Total captures	Total prey items ident.	Span of months caught	Season	Size of home range or part of it in Wood (ha)	Habitat type of home range	
						Probably entirely in wood; pasture at edge may have been visited	At least half in young plantation
♂7	55	36	6	Sept.-March	16.2		
♂10	20	13	5	Oct.-March	4.3		
♂11	109	39	12	(a) Nov.-March	3.2	At least half in wood or fields beyond Lodge	
♂22	28	25	10	(b) March-Oct. Aug.-June	12.2-24.3 6.9	Entirely in wood Up to half in fields and thick brambles; possibly also partly in young plantation	
♂24	20	19	7	Aug.-March	1.7 (strip at edge only)	Mostly in young plantation; regularly visited five border traps on wood boundary	
♂28	21	17	5	(a) Oct.-Dec. (b) Jan.-March	Beech Corner only 8.5	?	Mostly in wood

TABLE 3. The influence of the habitat of a weasel's home range on the composition of its diet (% frequency of occurrence)

	<i>Clethrionomys</i> and <i>Apodemus</i>	<i>Micromys</i>	Birds (excl. eggs)	No. of samples examined	
Woodland	Plantation <sup>1</sup>	Woodland	Plantation	Woodland	Plantation
Jan./Feb.	60	25	20	63	25
Mar./Apr.	57	50	0	38	14
July/Aug.	60	0	20	50	0
Sept./Oct.	73	0	0	100	9
Nov./Dec.	53	50	27	30	13

1-tailed signs test:

$$P = 0.031$$

No test<sup>a</sup><sup>1</sup> 'Woodland' residents: ♂♂7 and 11. 'Plantation' residents: ♂♂10 and 24 (neither caught in May or June).<sup>a</sup> Test requires >4 contrasts.

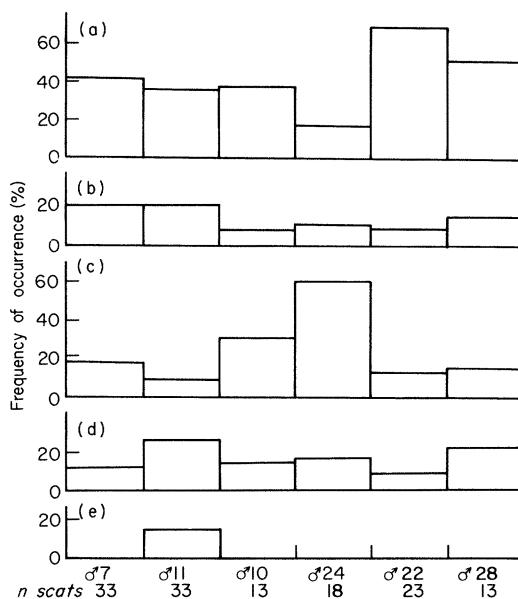


FIG. 4. Individual variation in the prey taken by six male weasels in Marley Wood. (a) *Clethrionomys*, (b) *Apodemus*, (c) *Microtus*, (d) birds, (e) eggs.

residents ( $\sigma 10$  and  $\sigma 24$  together), in every two-month period of the year tested (Table 3). Likewise,  $\sigma 10$  and 24 together took more *Microtus* than did  $\sigma 7$  and 11. The home range of  $\sigma 22$  probably extended into the overgrown brambles along the Singing Way, which was good habitat for bank voles: they comprised 65% of his recorded diet. Obviously the distribution of capture dates and the proportions of the total record contributed by these individuals will influence the general results (Table 1) and the seasonal variation (Fig. 3).

#### Variation between the sexes

Female weasels were recaptured much less frequently than the males: the sex ratio of all individuals marked was 67% males, but of recaptures of residents, 91% males (King 1975). The samples for females are therefore very small, but so far as they go they show that male and female weasels in the wood ate *Clethrionomys*, *Apodemus* and birds equally often (Table 4). No females were recorded eating *Microtus*, largely because no females were caught in the plantation.

#### The proportion of each rodent population eaten by weasels

On the assumption that, at least through the range of rodent densities observed during the study period, the weasels each ate a constant number of rodents per day, the proportion of the total available population of the two species of rodents eaten by weasels each month was estimated (Table 5). The lack of confidence limits for these estimates (see Methods) reduces their value somewhat, but from other evidence we can at least point to the most likely direction of the unknown error. The monthly predation estimates could not be higher unless there were undetected residents or a great deal of surplus killing, both considered unlikely (King 1975). The estimates could be lower if the known residents occasionally hunted outside the wood or had bad hunting days, or if the populations of prey were significantly underestimated, all of which seem quite likely.

TABLE 4. Composition of the diet by sex (% frequency of occurrence)

	<i>Clethrionomys</i>		<i>Apodemus</i>		<i>Microtus</i>		Unidentified rodents		Bird		Egg	No. samples examined
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Jan./Feb.	47	50	9	25	28	0	9	0	21	25	0	43
Mar./Apr.	38	0	23	25	12	0	8	50	12	25	12	26
May/June	33	100	6	0	11	0	22	0	33	0	39	25
July/Aug.	22	50	22	50	33	0	11	0	11	0	0	18
Sept./Oct.	35	100	26	0	17	0	17	0	9	0	0	9
Nov./Dec.	38	80	21	0	23	0	13	20	18	0	0	23
2-tailed signs test:			>0.05		0.032		>0.05		>0.05		No test	
P												

*Predation by woodland weasels*

TABLE 5. Monthly estimates of the proportions of two small rodent populations eaten by weasels in Marley Wood

Month	Weasels resident ♂♂	Weasels resident ♀♀	Weasels			Clethrionomys			Apodemus		
			Total number prey killed	No. prey sampled	Total found	Est. total killed	Est. total available	% killed	Total found	Est. total killed	Est. total available
1968											
Sept.	1	0	60	5	2	24	536	4	1	12	80
Oct.	1.5	0	90	10	1	9	429	2	3	27	134
Nov.	4	0	240	27	4	36	375	10	1	9	295
Dec.	4	0	248	22	7	79	402	20	4	45	295
Jan.	4	0	248	46	14	75	590	13	5	27	456
Feb.	4	0	224	13	3	52	563	9	0	—	322
Mar.	1.5	0	92	23	4	16	563	3	1	4	268
Apr.	1	1	90	31	4	12	563	2	3	9	188
May	1	1	93	16	3	17	670	3	1	6	188
June	1	1	90	10	2	18	536	3	1	9	188
July	1	1	90	2	0	—	750	—	0	—	268
Aug.	3	2	248	19	3	39	804	5	3	39	214
Sept.	3	2	240	16	3	45	616	7	2	30	188
Oct.	4	2.5	326	24	7	95	482	20	0	—	402
			264						Mean	7.8	9.7

<sup>1</sup> See King 1975, Appendix 1.

<sup>2</sup> 20-gram prey killed at the rate of two per day for males, one per day for females. Succeeding columns calculated as follows. September: 1 male resident killed 2 prey a day for the month (= 60 prey killed), of which 5 were sampled (= 5 scats collected): 2 of the scats contained bank voles, ∴ (2 × 60)/5 = 24 bank voles killed in September. Density of bank voles on control grid = 20/ha (Table 6); total area of wood 26.8 ha; ∴ 536 voles available, of which 4% were killed.

The percentage predation estimates given therefore probably lie near the upper end of the range of error of the true mean, if not above it.

Although there were fewer wood mice present than bank voles, similar proportions of both populations were eaten by weasels, averaging 8% per month for bank voles and 10% per month for wood mice. The seasonal variation in the percentage of the population removed was also similar in both species; it was high in the winter of 1968–69 and the autumn of 1969, and low in the intervening summer (Fig. 5). This was because the number of resident weasels in the wood was lower in the summer of 1969 than in the winters preceding or following (Fig. 2). The significant relationship which can be calculated between the percentage predation and the density of weasels should not be taken to mean anything, as it simply retrieves the above assumption (p.140).

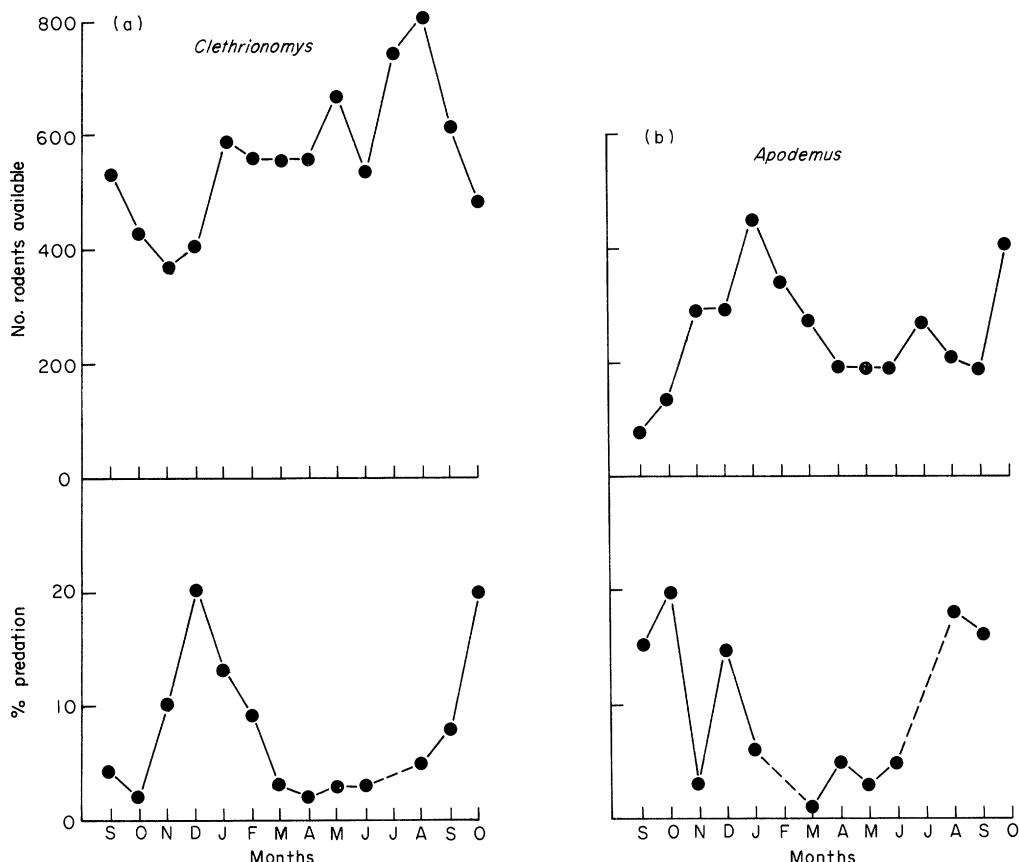


FIG. 5. Proportion of the total populations of *Clethrionomys* (a) and *Apodemus* (b) estimated to have been eaten by weasels. Upper curves: estimated total populations; lower curves: percentage eaten.

There was no numerical response by weasels to the density of prey, either in time or locality. Figure 2 shows no definite relationship between the populations of weasels and rodents; and the area of Flowerdew's experimental grid, where in the autumn of 1968 the density of wood mice was much higher than on the control grid (Flowerdew 1972), was at that time unoccupied by any resident weasel. Non-resident weasels (? potential immigrants) could be caught at any time (King 1975).

The method of calculating predation rate meant that the possibility of a functional response could not be investigated from these data.

#### *Mortality of rodents attributable to weasels and other causes*

Flowerdew (1972 and unpublished) estimated the minimum survival of the mice and voles known to be alive on his grids, and the reciprocal of this figure can be used to indicate the maximum rate of disappearance of marked individuals, by death or emigration. Table 6 shows the approximate proportion of each month's total disappearance which could be attributable to predation by weasels. The figures are not exactly comparable, as Flowerdew estimated the survival of rodents every 5 weeks, whereas predation was estimated per calendar month, but for most of the period covered this error would not much affect the large difference between the two series of figures. For example, in September 1968, 55% of bank voles known to be alive on the control grid disappeared, whereas only about 4% of the total population of bank voles estimated to be present in the whole wood were eaten by weasels (Table 5). Hence, assuming that the rate of disappearance observed on the control grid was representative, the weasel's share in the mortality of voles that month was probably less than one tenth.

From November to February 1968–69, few bank voles disappeared (13–30% per 5 weeks), and upwards of one-third of those that did could have been eaten by weasels. The estimates for December appear to show that more voles were eaten (20% of the population) than died (12%), but this was the time when the vole population was most underestimated, because of the good seed crop. During the rest of the year, before November 1968 and from February to September 1969, the rate of disappearance of the voles was higher (20–55% per 5 weeks) and less than one-fifth of it could be attributed to the weasels. It seems that more of the voles lost from the population during that breeding season were removed by other agencies than by predation by weasels.

A similar pattern is shown by the slimmer data for wood mice. The highest rate of loss per 5 weeks reached 64%, but the weasels probably were not responsible for more than about a third of this. For most of the year the total rate of disappearance was 22–49%, of which usually less than a third could be attributed to the weasels, except in December 1968, when the mice, like the voles, were probably most badly underestimated.

The pattern of loss in both rodent species appears to be related to season, but in fact is specific to this study. The months when the weasels' share in disappearance of rodents was high coincided with the months when most weasels were present (Fig. 2).

#### *The survival of wood mice in relation to the distribution of weasels*

Predation would not necessarily be expected to influence density in a stable, unenclosed habitat such as Wytham, since removal of individuals is always followed quickly by immigration (Smyth 1968). But the presence or absence of a predator could influence the mean survival of the prey, and this possibility was examined by comparing Flowerdew's (1972) 5-weekly survival values for wood mice on the two grids in Marley Wood, with the distribution of the resident weasels.

(a) On the control grid, wood mice survived for longer in winter than in summer, yet more weasels were present in the wood in winter than in summer (Fig. 2).

(b) From July to November 1969, cohorts of overwintered mice survived for longer on the control grid than on the experimental grid; yet there was a female weasel (♀25) living on the control grid at that time, and no resident weasel on the area of the experimental grid (King 1975).

TABLE 6. Approximate proportion of the 5-weekly estimates of maximum rate of disappearance of small rodents which could have been due to predation by weasels

Date	Density/ha	<i>Clethrionomys</i> Percent disappeared <sup>1</sup> $\pm$ se(p)	Approximate proportion of the total disappearance possibly due to weasels <sup>2</sup>		Density/ha	<i>Apodemus</i> Percent disappeared $\pm$ se(p)	Approximate proportion of the total disappearance possibly due to weasels
			All	All			
9 Sept. 1968	20	55 ± 4.7	<0.1	3	64 ± 14.5	0.2-0.3	
10 Oct.	16	45 ± 5.9	<0.1	5	64 ± 14.5	0.2-0.4	
16 Nov.	14	30 ± 6.5	0.3-0.4	11	29 ± 11.0	0.1-0.2	
13 Dec.	15	12 ± 5.0	All	11	28 ± 7.5	0.4-0.7	
21 Jan. 1969	22	13 ± 5.0	All	17	22 ± 6.9	0.2-0.4	
27 Feb.	21	27 ± 5.3	0.3-0.4	12	40 ± 6.7	0	
12 April	21	20 ± 5.0	>0.1	7	47 ± 8.3	c. 0.1	
10 May	25	16 ± 4.2	0.1-0.2	7	30 ± 8.8	c. 0.1	
11 June	20	31 ± 4.8	<0.1	7	44 ± 9.6	0.1-0.2	
15 July	28	19 ± 4.6	0	10	44 ± 9.6	0	
25 Aug.	30	45 ± 5.1	0.1-0.2	8	49 ± 8.2	0.3-0.4	
26 Sept.	23	50 ± 4.8	0.1-0.2	7	64 ± 9.1	0.2-0.3	
31 Oct.	18	49 ± 5.6	0.3-0.4	15	48 ± 9.6	0	

<sup>1</sup> Percentage of the minimum number alive on the control grid, taken to represent the maximum disappearance rate over the whole population.<sup>2</sup> Percentage of the total population killed by weasels (Table 5) expressed as a proportion of the total disappearance rate (see text).

(c) In The Pasticks, an enclave of woodland within the plantation, Flowerdew (1974) showed that minimum survival of mice improved after adult males were removed. One of the periods of improved survival (September–October 1969) coincided with the settling in that area of ♂24 (Table 2).

Flowerdew (1972) concluded that factors other than food supply affected the populations of wood mice he studied. These meagre data suggest that, at least in 1968–69, the unknown factors were unlikely to have included predation by weasels.

#### *Selection by weasels between alternative rodent prey*

If the weasels were taking a similar proportion of each of the two rodent prey species, regardless of the difference in their densities (Fig. 5), the ratio of one species to the other in the scats should be the same as that ratio in the populations. This relationship can be expressed by Ivlev's Index of Electivity, as modified by Jacobs (1974):

$$D = \frac{r - p}{r + p - 2rp}$$

where  $D$  = Jacob's modified index of electivity,  $r$  = the fraction of a species in the diet,  $p$  = the fraction of that species in the population.

Because wood mice are fairly strictly nocturnal, whereas bank voles are active day and night (Corbet & Southern 1977), bank voles may be more available to weasels, which are also active both day and night (King 1975), than wood mice. If bank voles are exposed to predation for twice as long as wood mice, direct comparison would be invalid. There are no specific data on this, but if weasels were unable to find and catch wood mice in their nests during the day, and food remains pass rapidly through the guts, wood mouse remains should be found only in scats collected on the morning round. In fact, there was no significant difference between the number of wood mice found on the morning and the evening rounds ( $\chi^2 = 0.18$ , 2 df,  $P > 0.05$ ), so it appears that both species were liable to be eaten by weasels at any time of day, a result also found by Moors (1975). An alternative explanation, that the wood mice eaten in the daytime were not captured but retrieved from caches, is unlikely as weasels store uneaten prey only in times of superabundance. Therefore, no allowance has been made in the calculations

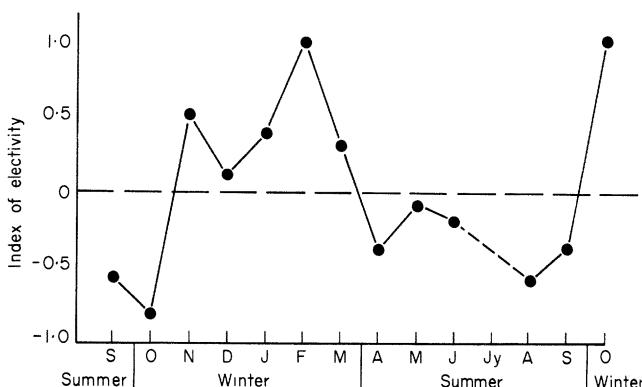


FIG. 6. Ivlev's index of electivity, calculated for *Clethrionomys*. Positive figures indicate that voles are being taken more frequently, relative to *Apodemus*, than would be expected at random. Values for *Apodemus* are the reciprocals.

for the difference in activity patterns of the two species. Jennings (1975) describes the burrow systems of wood mice, in which the runways were about 3 cm diameter. Weasels, especially females, would easily be able to negotiate these.

The results (Fig. 6) show that weasels tended to favour bank voles more than wood mice in the winter, and vice versa in summer, a pattern which was consistent, but not significant ( $r_s = 0.48$ ,  $0.1 > P > 0.5$ ). However, it is possible for an observation to be statistically insignificant and yet biologically significant, and there are two possible reasons to suspect that might be so here.

(1) The periods when bank voles were preferred coincides with the periods when weasels were most numerous. This would occur if, when predation pressure was high, weasels were able to kill proportionately more of the bank voles they encountered, or conversely, more of the wood mice escaped.

(2) The periods when bank voles were preferred were in winter. At that time of year, the distribution of bank voles becomes more restricted as the ground cover dies down (Kikkawa 1964), which might make it easier for weasels to find them in the remaining patches of cover. By contrast, the distribution of wood mice is independent of cover, and not affected by season in the same way.

## DISCUSSION

The results presented in this paper are a somewhat preliminary estimate of the relationship between weasels and small rodents in Wytham. As a study of predator-prey interactions in general, my data bear no comparison with those of Southern (1970), but together with his, they do make a contribution to our understanding of the total vertebrate predator-prey interactions in the Wytham woodland community. The discussion below is divided into five sections, concerned with the factors influencing the diet of the weasels; the ecological efficiency of the observed food chain; a comparison between weasels and tawny owls, the principal resident vertebrate predators in Wytham; the function of territory in weasels; and the effect of predation by weasels on their prey.

### *Factors influencing the diet of weasels in Marley Wood*

In most respects the weasels observed fed as unselective, opportunistic predators. The patterns of diet observed could be explained in terms of the relative abundance of different kinds of prey, their escape reactions, and the hunting strategy of weasels.

The weasels obviously made good use of the sudden flux of immobile prey, in the form of birds' eggs, in spring. The peak on Fig. 3 is impressive, and probably an underestimate, since the finding of eggshells in a scat does not tell us how many nests had been raided, or how many destroyed eggs are represented. I have a vivid memory of a weasel in a livetrap in April, his white shirt-front spattered with yellow yolk. By contrast, birds were taken least often in Wytham in the autumn, when rodents are generally most abundant—a pattern found also by Day (1968). On the Swedish study area of Erlinge (1975), where birds were few, weasels switched from lagomorphs to rodents in autumn.

Erlinge, Jonsson & Willstedt (1974) reported that the female weasels they observed in the enclosure tended to spend more time hunting in tunnels than did the males. There were no differences between the sexes in the data from Marley Wood alone, but the combined data from Marley and some other study areas analysed previously by King (1977), showed that females had eaten significantly more small rodents than had the males ( $\chi^2 = 5.9$ ;  $0.05 > P > 0.01$ ). This difference in hunting methods is perhaps part of the reason why female weasels can live on disproportionately smaller home

ranges than males (in Marley Wood, ranges of males were about 7–15 ha, and of females, about 1–4 ha; King 1975). Incidentally, it also implies that female weasels tend to eat fewer lagomorphs (Day 1968, Erlinge 1975, King 1977, Brugge 1977) because they meet fewer, not because they cannot tackle them. At least two types of lagomorphs, the nestlings and those found dead (which are usually not distinguished from live adults in diet analyses) should present no more difficulties for a female weasel than for a male. The common assumption that female weasels are too small to kill rabbits is persuasive, but has not, so far as I know, been tested.

One whole order of potential prey in the wood, the insectivores, was completely ignored. Shrews are quite common in Wytham (Pernetta 1976) but were never found in scats. Individuals of all three mainland species (*Sorex araneus*, *S. minutus* and *Neomys fodiens*) were occasionally caught in both Longworth and weasel traps throughout the study, yet none was found in 344 samples of scats examined. Moles were also common, but only one mole was identified, even though the fact that weasels often carry specific mole fleas suggests that they use mole runways and nests regularly, and may often have the opportunity to kill one (King 1976). Because of the alleged implication (Hansson 1967) of shrews in the transmission of *Skrjabingylus nasicola*, an important nematode parasite of weasels, very common in Wytham (King 1977), a careful watch was kept for shrews throughout this analysis, and since insectivore hairs are highly distinctive, it is unlikely that any were missed or were included in the 'unidentified small rodent' category. There is no obvious reason why the Marley wood weasels did not eat shrews, except the common observation that carnivores seem to find them distasteful. Weasels observed by Erlinge, Jonsson & Willstedt (1974) hesitated to kill shrews when offered live ones as prey and Hansson (1967) could get hungry weasels to eat them only with great reluctance. Rubina (1960) found shrews relatively more often stored dead in weasel caches than alive in the surrounding habitat, suggesting that weasels rarely eat what shrews they do kill.

Other than insectivores, the small mammal prey of weasels in Marley Wood seemed to be taken more or less in proportion to their availability. Likewise, the captive weasels observed by Erlinge, Jonsson & Willstedt (1974) ate all three small rodent species equally readily when offered them, and, in a study area in Southern Sweden, caught them in proportion to their abundance (Erlinge 1975). On the other hand, Moors (1975) found that the weasels he studied in Aberdeenshire ate few bank voles, although they were apparently more common on the study areas than field voles. He interpreted this to mean that weasels preferred field voles even though they were less abundant, as other predators are said to do.

The observations made by Erlinge, Jonsson & Willstedt (1974) on the hunting behaviour of weasels in a large semi-natural enclosure suggest that the observed selection in winter of bank voles in Marley, though statistically insignificant, might still have been real. They watched the reactions of six male and two female weasels, twice each, when placed in the enclosure with wild-caught live small mammals. By the end of sixteen trials of 24 h each, the weasels had caught nineteen wood mice, twenty-three field voles and twenty-four bank voles, of the forty-eight of each species presented alive. The first one caught was usually the first one eaten, so there was no evidence for the common assumption that predators like to eat *Microtus* more than other kinds of small rodents. However, the first one caught was significantly most often a bank vole ( $P < 0.01$ ). The weasels began their hunt by trying to drive the rodents out from under cover, and the observers noted that bank voles were the most likely to expose themselves in the open. Individual

wood mice often escaped by climbing or 'freezing', and this reaction was more important to them than their well-known agility, because in the enclosure the weasels could in fact catch wood mice after several attempts (although, of course, in the wild the weasel may not have the chance to make more than one attempt). Hence, when the herbaceous cover was reduced in winter in Marley Wood, the bank voles really could have been easier to find, and then to catch, than wood mice.

Rapport & Turner (1970) have rightly criticized the simple comparison of species proportions in diet and environment as a means of determining predator food preferences, since the relative proportion of two species eaten reflects both availability and catchability. They suggest determining separately the minimum density of each prey species at which the predator is able to fulfil its requirements from that prey alone, and then control the mixed population so that each prey is present at half that minimum density. This suggestion is valid as an experimental procedure, but does not help in the observation of natural populations.

#### *Ecological efficiency of the rodent-weasel food chain in Marley Wood*

Slobodkin (1968) predicted that the ecological efficiency of a foodchain, calculated from the ratio (Food consumed by predator/Food consumed by prey) should be a constant of 5–10% according to the predation pressure, although McNeil and Lawton (1970) point out that the high respiratory cost of homiothermy means that such a figure would be applicable only to short-lived poikilotherms. Turner (1970) estimates that in homiotherms, the absolute maximum efficiency, in the most favourable habitat and assuming 100% assimilation and complete consumption of all new tissues by predators, can only approach 3% and is usually much less than 2%.

The production of small rodents is comparatively inefficient; the ratio of flesh produced to food assimilated is about 2.65% (Grodzinski *et al.* 1969) and as their assimilation efficiency is about 85%, their production measured against food consumed is about 2.2% (*loc. cit.*). Since the weasels apparently never took more than about 20% of the population of small rodents produced, the maximum yield to the predator in this situation is 20% of 2.2%, i.e. an ecological efficiency of 0.4%. The assimilation efficiency of the weasels observed by Moors (1977) was 70–80%, depending on sex and diet. Using the figures for calorific value of whole rodents given by Varley (1970), I estimated that, depending on the level of predation, the ecological efficiency observed ranged from 0.2 to 1.5%, with a mean of 0.6%.

Figures quoted in the literature for other predators are rather similar. For example, Rykiel & Kuenzel (1971) calculated 0.4% for wolves preying on moose; Richardson (1975) 0.2–1.1% for thrushes preying on snails in winter; and Ryszkowski, Gosczynski & Truszkowski (1973), who warn that they greatly underestimated the density of weasels, 0.06% for weasels preying on *Microtus arvalis* (Pallas). In Marley Wood, at the greatest predation pressure observed, when weasels took 20% of the wood mice present in October 1968, and 20% of the bank voles in December 1968, the ecological efficiency was 1.3% and 1.5%, well above the theoretical maximum of 0.4%. However, the number of each species identified per month was considerably too small to be statistically respectable (Table 5), and there are also grounds to be cautious about the density estimates for the rodents. Little information relevant to ecological theory can be deduced from these data, but for our present purposes it seems reasonable to suggest that the weasels in Marley Wood were fully utilizing their principal small rodent prey, and with rather little margin to spare. The cost in energy for a weasel of searching through the miles of

TABLE 7. Comparison between weasels and tawny owls as woodland predators in Wytham

	Weasel	Owl
Mean expectation of life	< 1 year	4.9 yr
Life history strategy (Stearns 1976)	'r-strategist'	'K-strategist'
Activity	24 h but mainly diurnal	Mainly nocturnal
Hunting strategy (Schoener 1969)	Searcher Type II	Sit-and-wait Type I
Territory size ♂♂ (ha/100 g body weight)	About 9	About 3
Tends to select	Bank voles	Wood mice
Activity of selected prey	24 h	Nocturnal
Data from	Present study and King (1975) and (in press)	Southern 1954, 1970; Southern & Lowe 1968

tunnels on his large home range to find one of between twenty-one and thirty-nine rodents per ha must have been great, but smaller home ranges would not have been viable (King 1975).

#### Comparison between weasels and tawny owls as woodland predators

The principal vertebrate predators resident in Marley Wood, the weasel and the tawny owl, both rely for more than half their diets on the three small rodents *Clethrionomys*, *Apodemus*, and *Microtus* (Southern 1954, and Fig. 3). But they have different hunting and breeding strategies, which give each an advantage in different circumstances (Table 7).

Current theory on life-history strategy is reviewed by Stearns (1976). The tawny owl is a 'K-strategist': it is long-lived, and can afford not to breed in bad seasons yet remain in possession of its territory (Southern 1970). The weasel is an 'r-strategist': it is short-lived, and the chances are much against any individual breeding more than once (King, in press). The population of tawny owls in Wytham is therefore much more stable than that of weasels, and an individual owl, once established in a territory, has a higher chance of contributing its genes to a future generation than has an individual resident weasel. This gives the long-term advantage to the owls.

In hunting strategy, the tawny owl is a Type I 'Sit-and-wait' hunter (Schoener 1969), limited to catching small rodents only when they are in the open, and it maintains a comparatively small hunting territory for its size. It is fairly strictly nocturnal and tends to select the nocturnal wood mice (Southern & Lowe 1968). The weasel is an efficient Type II searcher, maintaining, as predicted by Schoener (1971), a comparatively larger territory (at least, in the males: females may be different—see above). It hunts both day and night, above and below ground and into the nests of small rodents, where it has access to a large population of nestling rodents not available to other predators. This efficiency of hunting gives a short-term advantage to the weasels.

Competition between owls and weasels cannot be entirely avoided, because their common resource is not renewed rapidly enough. Rodents killed by weasels hunting below ground during the day cannot be replaced by evening, so owls hunting above ground at night must be affected to some extent by the activities of weasels, and vice versa. However, competition is reduced by the fact that some categories of prey are available

to weasels but not to owls (rodents in thick cover or in underground nests, and tits in boxes) and some are taken more often by owls than by weasels (moles, shrews and rats); but competition is probably still significant. It is interesting that one recent theoretical model of competition predicted that co-existence of two predators competing for a single resource would be possible (or, if there is more than one resource, more likely) if one were a *K*-strategist and the other an *r*-strategist (Hsu, Hubbell & Waltman 1978). However, the weasels have the further disadvantage of being themselves liable to predation by tawny owls (Southern, personal communication), whereas records of weasels attacking tawny owls (Timperley 1962) are, to say the least, rare. In Wytham, weasels were more active by day than by night (King 1975), and this may be because they need to avoid exposure to predation by owls. The weasel's advantage in exploitation is therefore counterbalanced by a considerable disadvantage in interference competition.

The different hunting strategies of weasels and owls may reasonably be expected to have different results for the common population of prey, for example, in the age structure of prey taken by, and the shape of the functional response curves calculated for, the two predators. Some of this information may be available for owls (Southern & Lowe unpublished), but matching data for weasels must await new methods of counting and classifying the prey of weasels. One of the largest problems in making any such comparison follows from the unequal sizes of the populations of prey available to the two predators, and the unequal consequences of errors in estimating them. Many young mice are available to weasels, but not to either traps or owls, so the same census technique will not be suitable in both cases, and errors in density estimates are more serious for estimates of predation by weasels than for similar calculations for owls.

#### *Territory size*

Lockie (1966) assumed that weasels need territories primarily for food-gathering. The data presented above show that much of the individual variation in diet can be explained from the distribution of habitat and prey types on each weasel's ground. Such a correlation is commonly found in territorial predators, e.g. tawny owls (Southern 1954), or great horned owls (*Bubo virginianus*) (McInvaille & Keith 1974). However, Lockie also suggested that weasels hold as much ground as they can, so as to avoid having to adjust to fluctuations in prey density. The individual ranges of weasels in Wytham were much larger than those observed in Lockie's study area (King 1975), yet I suspect that they were still only the minimum viable size, and that the weasels were often hungry. Residents accustomed to being trapped invariably ate the whole laboratory mouse provided, and allowed themselves to be trapped frequently; they were in relatively poor condition, and several died or disappeared after drastic loss of weight; secondary foods, such as earthworms, were not scorned; the rate of energy conversion from rodents to weasels was probably near the maximum; and (taking records over 13 years) a modest decline in density of rodents in spring and summer shortened rations for weasels enough to make them search more diligently for tit nests when they became available (Dunn 1977). The weasels in Marley Wood could not have survived on ranges of the size observed by Lockie, which suggests that his conclusion should be modified slightly: his weasels did not hold as much ground as they could, but as little as they needed. At the lowest prey densities observed, the smallest viable home ranges on Lockie's study area and in Wytham held approximately the same minimum number of prey, about 100–150 rodents per weasel (King 1975). The ermine in California studied by Fitzgerald (1977),

which are smaller than British weasels, set up their territories in autumn with a minimum of ninety-seven voles per ermine.

### *The effects of predation by weasels on populations of their prey*

Published studies of weasels and their prey fall into five categories: those which present their results as frequencies of the prey species identified (Day 1968); those which add a comparison with frequencies of prey present (Erlinge 1975); those which add a calculation of the proportion of the prey population taken (Ryszkowski, Gosczynski & Truszkowski 1973, Tapper 1976); short-term studies which further add a calculation of the proportion of the mean total mortality of the prey attributable to predation (Lockie, Charles & East 1962, Gosczynski 1977, present study); and long-term studies which relate changes in percentage predation to changes in the density of prey (Dunn 1977). Only the last type of work is able to determine whether or not predation by weasels is a controlling influence on the density of prey. Predation may affect population structure without determining density, but as there are no data on the ages and sexes of prey taken by weasels, only the influence of predation on density will be considered here.

The ability of a predator to reduce the density of its prey at any given time depends on factors such as, for example, the ratio of predator to prey, the predator's searching efficiency, the number of refuges for the prey, etc. Whether the predator can maintain a lowered density over a period of time depends more on how these factors vary in response to changes in the density of prey. For a predator to control the numbers of its prey, they must vary so as to lead to density-dependent mortality of the prey. Further, since predation does not act on density itself, but on the population processes determining density, it can be evaluated only in relation to these other processes. Hence, the evidence required to demonstrate whether or not weasels control their prey is complex, and it is not provided by calculations of how many rodents are killed by weasels each year (Linn 1961), the proportion of the population killed or the proportion of the total mortality due to predation (this study), or a correlation between an increase in survival of prey and a reduced density of weasels (Potts & Vickerman 1974). A predator can control its prey only if its consumption of that prey is sufficient and can increase by as much or more than the increase in density of prey, and vice versa when the prey decline (Hassell 1966). Proof of this in the field is extremely elusive, and usually shows that the proportion of the prey eaten is often small and decreases as the prey increase (Lockie, Charles & East 1962, Gosczynski 1977), increasing only when the prey are already declining (Pearson 1971).

The evidence presented in this paper does not meet these rigorous requirements, but it suggests that predation by weasels on the two small rodent populations in Marley Wood in 1968–69 was probably not heavy enough to influence the densities of the rodents observed, largely because the density of the weasels themselves was low. The weasels ate only about 8–10% per month of the two rodent populations, compared with a total disappearance rate per five weeks of 12–64%, and their predation had no apparent correlation with the local patterns of their density or survival. Smyth (1968) attempted artificially to reduce the density of bank voles in Marley Wood, but found that a removal rate of 24–83% (averaging about 50%) per month could not keep the density lower than on his control area, except during a short period in late winter when the rate of immigration was low. My estimates of the proportion of the total disappearance of rodents accounted for by weasels suffered from several errors, pointed out in the Methods section, but the most important one is that the density of rodents was probably underestimated,

and this would mean that Table 5 probably exaggerates the number of rodents eaten by weasels, so that the real rate of predation was probably less than 8–10% per month. This study does not prove that predation by weasels was having no effect on the density of rodents in Marley Wood in the years observed, and could not investigate the crucial point, changes in predation rate across a substantial change in rodent densities, as did Southern (1970). Further, we had rather little information about the other reasons for disappearance of the rodents, and whether, for example, predation by weasels was additional to, or replacing, other forms of mortality. In certain circumstances, predation need not be heavy to be effective. All the same, there is nothing in this study to support the idea that predation by weasels had any effect on the density or distribution of the rodents; rather, an accumulation of small signs consistently pointing to the reverse.

Evidence of the effect of weasels on tits breeding in the nest boxes studied each year in Wytham by the Edward Grey Institute is stronger, and has been analysed by Krebs (1970) and Dunn (1977). These two authors concluded that (1), annual variations in clutch size and hatching success are density-dependent and sufficient to regulate the population; (2), one of the main factors in hatching success is predation on eggs by weasels; and (3), the extent of predation on nests is related to the relative densities of tits and rodents, which is more significant than the self-advertising behaviour of hungry nestlings. Further, Bulmer & Perrins (1973) showed that the mean survival of female great tits is 48% per year, compared with 56% per year in the males. Only the females incubate, and one of the reasons advanced for the lower survival of females is that it reflects the greater risk of predation to which they are exposed. Taken together, these data suggest that predation by weasels is exerting a significant effect on the population of tits in Wytham, though other factors are important too. The other main regulating factor isolated by Krebs (1970) was the availability of food for the female at the time of laying, which could perhaps be related to the temperature at a critical period in early spring (Slagsvold 1975).

Why is the effect of weasel predation apparently so much greater on tits than on rodents? Several reasons may be suggested:

(1) Tit nests are found at a lower density than are individual rodents, so, in any given year, there are nearly always fewer tit nests per weasel than rodents per weasel. The long-term mean combined density of rodents in Wytham estimated by Southern (1970) was 21/ha, whereas the mean density of breeding pairs of tits in spring since 1947 has been 1.8/ha (Dunn 1977).

(2) The rate of predation by weasels on nests is often very high (over 50% per season in 1964, since when it has been between 11 and 39% every year: Dunn 1977). The weasels in Wytham observed in 1968–69 rarely removed so high a proportion of rodents over the same length of time (Table 5).

(3) Predation on tits occurs over a short season and lost clutches are rarely replaced more than once. By contrast, the breeding season of rodents presents a less sudden influx of vulnerable prey, and replacement of individual rodents removed is nearly continuous.

(4) Weasels are by far the most significant predators of tit nests in boxes, whereas they share the rodents with tawny owls, and may be less significant than tawny owls as predators of rodents.

(5) Nest boxes are not mobile and most are easily visible from the ground, whereas rodents hide from, and may escape from weasels.

(6) Nest boxes are artificial and provide nesting sites for tits at an unnaturally high

density. The Wytham results do not imply that predation by weasels necessarily has any effect on natural populations of songbirds. (The same comment might be made of estimates of the effect of weasels on managed populations of game birds, e.g. by Tapper 1976.)

All these factors, and probably others, help to explain why predation by weasels on eggs and young tits in boxes is not at all the same process as predation on rodents. For an exhaustive review of predator-prey relationships reaching the same conclusion, see Goszczynski (1974).

The analysis of Dunn (1977) illustrates the great value of long-term records. By the time he came to plot the rate of predation by weasels on tits against the rodent density index, there were thirteen years of records and the regression was significant. The same plot done in 1971 with ten years of records was not significant (King unpublished).

Flegg & Cox (1975), noting the erratic incidence of weasel predation on tits in boxes in Kent, expressed surprise that it has not developed into a regular pattern, since 'most weasels would be expected to survive over at least two consecutive tit breeding seasons'. In fact the mean expectation of life in weasels is less than a year (King in press) and the turnover of residents in both Wytham (King 1975) and Sweden (Erlinge 1974) ensures that few individuals who learn the habit of raiding boxes survive to do it again next year.

The influence of changes in mammal populations on the degree of attention paid by predators to birds is interesting. Such triangular relationships were described by Gerell (1967) in mink (*Mustela vison*), small rodents and birds; Myrberget (1970) in stoats (*M. erminea*), *Microtus* and willow grouse (*Lagopus lagopus*); McInvaille & Keith (1974) in great horned owls, snowshoe hares (*Lepus americanus*) and ruffed grouse (*Bonasa umbellus*); Goszczynski (1976) in martens (*Martes* sp.), *Microtus* and birds; and Ryabitsev, Rhyzhanovskii & Shutuv (1976) in arctic foxes (*Alopex lagopus*) and stoats, lemmings, and birds. This might also explain why predation on tits in Marley Wood became significant only after myxomatosis removed all the rabbits on the estate (Dunn 1977); and it also has consequences for the strategy of predator control on game estates and on reserves established for the protection of rare birds. If permanent predator control is not possible or not wanted, monitoring of small rodents may indicate the seasons in which a special effort is required. For example, the spring following a population crash of *Microtus* in Norway, and of feral *Mus musculus* in New Zealand, is the time when control of stoats would most benefit nesting populations of willow grouse, (Myrberget 1970) and takahē, *Notornis mantelli* (King 1978). In other seasons, the same effort expended in removing stoats would profit the birds much less.

By far the most relevant and realistic theoretical model of predator-prey relations is that of Maynard Smith & Slatkin (1973), who state quite specifically that the system they had in mind was the relationship between mustelids and small rodents in an isolated area. Nearly all their assumptions are quite reasonable and fit the picture observed in Marley Wood well, except for two. They assumed that young weasels are less efficient predators than old ones; but young weasels kill efficiently by the age of 2 months old, without being taught (East & Lockie 1964). The greater difference is more likely to be in the hunting skills of males and females, since Erlinge, Jonsson & Willstedt (1974) observed that males made a kill on the average within 12.5 min, whereas females took 50 min. Secondly, Maynard Smith & Slatkin assumed that the size of an individual's foraging area is a reflection of its skill and is maximized by selection. Observations presented above and in King (1975) suggest that foraging area is principally related to

the density of prey rather than to hunting skill. The model could perhaps be modified to include these corrections. The main conclusion of the model, that weasel-rodent relationships are stable only when predation does not greatly depress the density of the prey, accords well with what we can tell of the situation in Marley Wood; the converse, that heavy predation leads to instability, is perhaps illustrated by the study of Fitzgerald (1977). He estimated the pressure of predation by the small Californian ermine (*Mustela erminea* L.) on populations of overwintering montane voles (*Microtus montanus* (Peale)) in the Sierra Nevada. There was very little prey for the ermine besides voles, and when the rodents were at low density, the number of voles per ermine became very small and the rate of predation increased. His data support the hypothesis of Pearson (1971) that predation can be responsible for the timing and amplitude of microtine cycles.

Andersson & Erlinge (1977) classified weasels as resident specialist predators, which often have a destabilizing effect on populations of rodents. This certainly seems to be true in habitats in which the principal or only prey is a fluctuating population of voles or lemmings (Lockie, Charles & East 1962, Ryszkowski, Gosczynski & Truszkowski 1973, McLean, Fitzgerald & Pitelka 1974), but the situation in Wytham appears to be quite different. Two reasons may be suggested:

(a) The availability of several alternative prey species in and around the wood, which meant that when one species was temporarily at low density, the weasels were not forced by hunger to drive it lower still.

(b) The large size of weasel home ranges required by the generally low density of prey in the wood, which meant that the hunting of the weasels there was costly in energy and probably rather inefficient. The stability of a predator-prey relationship is greatly influenced by the relative dispersal of predator and prey (Hilborn 1975); if the predators hunt too efficiently, such as when they are introduced on to small islands, great reduction or even extermination of the prey may result (e.g. water voles on Terschelling Island became extinct after the introduction of stoats (van Wyngaarden & Bruijns 1961)).

## CONCLUSION

The data reported in this paper provide negative evidence consistently suggesting, though not proving, that predation by weasels on bank voles and wood mice in Marley Wood was not a controlling influence on their population densities. This conclusion is the opposite of those following from analyses previously made of (a) the effect of weasel predation on the eggs and young of tits nesting in boxes in the same study area (the contrast can be explained by the different spatial and temporal relationships between weasels and the two types of prey); and (b) the effect of weasel predation on fluctuating populations of voles and lemmings (the contrast can be explained by the greater diversity and lower density of prey for the woodland weasels). However, this does not mean that the population dynamics of the woodland rodents was not influenced by predation. That question can be considered only when information from weasels is set alongside that from tawny owls (Southern & Lowe, unpublished).

## ACKNOWLEDGMENTS

Financial support for this work was gratefully received from the Natural Environment Research Council, and Lady Margaret Hall, Somerville and St Cross Colleges, Oxford. I thank Oxford University for permission to work on Wytham Estate; Dr J. Phillipson,

for facilities made available in the Department of Zoology; Dr H. N. Southern, for patient supervision; Dr J. R. Flowerdew, for indispensable and generous co-operation; Drs D. G. Dawson and D. R. Lees, for statistical advice; and Drs Flowerdew, Southern and B. M. Fitzgerald for illuminating manuscript criticism.

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(Received 18 October 1978)

## APPENDIX 1

Distribution of prey found in the total sample of weasel scats examined

Total no. scats examined (1)	<i>Clethrionomys</i> <i>n</i>	<i>Apodemus</i> <i>n</i>	<i>Micromys</i> <i>n</i>	Unidentified small rodent <i>n</i>	Bird <i>n</i>	Egg <i>n</i>	Lagomorph <i>n</i>	Mole <i>n</i>
<i>Seasons</i>								
Jan./Feb.	57	25	7	14	6	13	0	0
Mar./Apr.	41	15	7	7	4	6	4	1
May/June	25	10	2	2	5	6	9	0
July/Aug.	11	3	3	3	1	1	1	0
Sept./Oct.	29	13	6	5	4	2	0	0
Nov./Dec.	52	23	9	9	9	9	0	0
$\chi^2$ (2)		1.26	1.29	2.02	1.88	3.74	37.07	—
<i>P</i> (4 d.f.)		NS	NS	NS	NS	NS	<0.001	—

(1) Excluding scats containing only bait, moultings, or invertebrates.

(2) Pooling the 4 summer months, because of small samples.

*Individuals*

♂7	33	14	7	6	4	4	0
♂11	33	12	7	3	3	9	5
♂10	13	5	1	4	1	2	0
♂24	18	3	2	11	1	3	0
♂22	23	15	2	3	3	2	0
♂28	13	6	2	2	3	3	0