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Food preference, optimal diet and reproductive output in stoats *Mustela erminea* in Sweden

Sam Erlinge

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Field data on the diet of stoats in relation to different prey density were used to examine food preference and selective feeding and to test predictions from optimal foraging theory. The relationship between diet and reproductive output was also examined in three food environments. Stoats concentrated on voles (their basic food) when vole density was high or moderately high. Male stoats showed a high preference for the larger water voles. Selective hunting for them increased with their relative abundance but the males specialized less on water voles at overall high density of rodents. This was probably due to high relative density of the prey second in preference (field vole). The data are in agreement with the theory predicting relative density of prey to be important in determining optimal diet. Females did not show any clear preference for water vole relative to field vole and no long term change occurred in selective hunting relative to changes in vole density. The difference between males and females was ascribed to different fitness set functions, implying a combination of large and small voles to be the optimal diet for females and large prey as water vole as optimal diet for males. No consistent difference in reproductive success was found in the different food environments, but the highest reproductive output occurred in areas with relatively high water vole density.

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Данные полевых исследований состава пищи у горностая в зависимости от различий плотности жертв использовали для анализа пищевого предпочтения и пищевой избирательности, а также для проверки оптимальной фуражировочной теории. Изучали также зависимость между составом пищи и эффективностью размножения в трех местообитаниях с разным составом пищи. Горностаи в основном питались полевыми (их основная пища), если плотность полевок была высокой или умеренно высокой. Самцы предпочитали крупных водных полевок. Селективность охоты за ними повышалась при увеличении их относительной плотности, но самцы меньше специализировались на водных полках при общей высокой численности грызунов. Это очевидно определялось высокой относительной плотностью жертв, занимающих второе место в рядах предпочтительности (пашенные полки). Результаты согласуются с теорией, предсказывающей, что относительная плотность жертв имеет важное значение при определении оптимальной диеты. У самок нет четкого предпочтения водных полевок в сравнении с пашенными и не отмечены долговременные изменения в избирательности охоты в зависимости от плотности полевок. Различия между самцами и самками были описаны разными уравнениями функциональных зависимостей, в которых комбинируются крупные и мелкие полки для оптимальной диеты самок и отмечены крупные жертвы в виде водных полевок как оптимальная пища самцов. Не было отмечено существенных различий в плодовитости в разных местообитаниях, но наибольшая скорость размножения установлена в участках с относительно высокой плотностью водных полевок.

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1. Introduction

In recent years there has been an increasing interest in analysing the feeding ecology of animals from evolutionary aspects (for review see Pyke et al. 1977). Mathematical models on optimal foraging behaviour have been presented which make predictions on how an animal's foraging should be performed in various situations (e.g. Emlen 1966, 1968, MacArthur and Pianka 1966, Schoener 1969, 1971, Pulliam 1974, Charnov 1976, Stenseth and Hansson 1979, Stenseth 1980). However, the predictions have only in a few cases been tested against field data (Krebs 1978). This paper aims to present field data on the feeding ecology of the stoat *Mustela erminea* and examine it in the light of optimal foraging theory. Also the relationship between optimal diet and reproductive output is examined – an important subject which has been discussed in theory but rarely tested by field data.

General information on feeding and reproductive biology of the stoat

The stoat, ('short-tailed weasel' in North America) is a carnivore adapted morphologically and behaviourally to feed on small mammals; its long and thin body permits it to enter the narrow burrows of small rodents, and it kills prey according to a fixed behavioural pattern (Wüstehube 1960, Gossow 1970, Müller 1979 and own observations). Analysis of scats and stomach contents has shown that small rodents usually are its main prey (Ognev 1935, Klimov 1940, Novikov 1962, Maher 1967, Stroganov 1969, Fitzgerald 1977, Simms 1978). Shrews (in North America), lagomorphs and birds are alternative prey (Hamilton 1933, Aldous and Manweiler 1942, Day 1968, Potts and Vickerman 1974, Tapper 1976, Brugge 1977).

The stoat – like the weasels in general – shows a pronounced sexual dimorphism in size; females are much smaller than males (Erlinge 1979, Simms 1979, Moors 1980). Females rear the young without assistance from males, and the small body size of the females probably is an adaptation for maximizing food exploitation at breeding time (Erlinge 1979, Moors 1980). There seems to be a close relationship between body size of female weasels and size of their predominant prey (Simms 1979).

2. Study area and methods

2.1. The study area

The main study area of about 4000 ha was the Revinge area in Skåne, southern Sweden. The area contains extensive wet meadows for the most part inhabited by the field vole *Microtus agrestis* and the water vole *Arvicola terrestris*; drier parts are inhabited by rabbits; and open fields grazed by cattle support a few small rodents, mainly the wood mouse *Apodemus sylvaticus*. The wet

meadows with surrounding drier areas were the preferred habitat of the stoat. For comparative purposes an adjoining farmland containing stone walls overgrown by grass, bushes and trees was also examined.

2.2. Estimating small rodent numbers

Data on small rodent numbers in the Revinge area were obtained by L. Hansson according to the Standard-Minimum method (Hansson unpubl.). Trapping was performed in early summer, midsummer and autumn in each of the years 1974–77 in two randomly selected areas in each of the ungrazed and grazed wet meadows on peat soil. During most periods trapping was also carried out in grazed fields and on ungrazed fields on mineral soil. The captures provided information on density of small rodents (the field vole and the wood mouse) in various seasons and habitats.

When estimating numbers of water voles, larger snap traps were used (Jeppsson and Schlyter unpubl.). Three kinds of habitats were examined, i.e. ungrazed and grazed wet meadows and grazed fields on mineral soil. In each habitat two randomly selected sample plots were examined during each of five trapping periods. The plots were 50 × 50 m in ungrazed meadows and 50 traps were placed in a grid on the ground connected with runways and burrow entrances of water voles. In the other two habitats where the water voles live in underground tunnels 20 traps were placed in the tunnels in sampling plots of 25 × 25 m. These data provided information on density of water voles in various habitats in autumn 1975. Complementary observations on water vole occurrence were carried out throughout the study and since 1978 a detailed analysis of local water vole populations has been carried out (Jeppsson unpubl.). There were considerable local variations in water vole density but judging from water vole activity and food analysis of predators in an integrated study (Erlinge et al. unpubl.) the total water vole population of the area did not show any pronounced between-year variations during the study period. Therefore, the data in 1975 were considered representative for the period 1974–77. The seasonal decrease in water vole number during the non-reproductive period from October to April was calculated from data on total mortality due to predation (Erlinge et al. unpubl.; see also Appendix 1). It was assumed that the main losses during this period were due to predation.

At hedgerows in the farmland, information on numbers of small mammals was obtained by trapping according to the Small Quadrangle method (Myllymäki et al. 1971, Hansson 1972, 1975). Ten sampling plots, each with 4 × 4 snap traps were covered at the hedge rows and in the fields on each side in a five day trapping period in autumn 1975.

2.3. Examining the diet and hunting behaviour of stoats

Stoat diet was examined by scat analysis, while hunting behaviour and food preferences were studied both in the field and in an enclosure containing simulated habitats with live prey. Habitat use was examined by radio-tracking (Erlinge 1977). Scats were collected throughout the year from August 1973 to March 1977. Prey were identified on hair in the scats by examining the medulla, scale pattern and the appearance of guard hairs in transverse section (Day 1966). Guard hair remains in scats were assessed on the basis of their frequency of occurrence (Day 1968) and on their quantities.

2.4. Testing the method of food analysis

Feeding experiments were performed to test the accuracy of these two methods. Large and small prey in various combinations were offered to caged stoats. The scats were collected and analysed and prey hair remains recorded. Frequencies of occurrence showed that large prey such as rabbit, starling, and water vole was underestimated, whereas the small rodents *Clethrionomys glareolus*, *Microtus agrestis*, and *Apodemus* sp. were overestimated (Tab. 1). In order to adjust this bias, a quantitative evaluation was used with correction factors. The following procedure was adopted. Each scat was considered one unit as they were all of similar size. A sample of guard hairs from each scat was randomly

selected and prepared for transverse sections. When more than one prey species was present, they were either classified as being equally present or one of them was clearly dominant. The sum of transverse sections in a scat was scored 1.0. When two categories were equally present, scoring was 0.50 for each; in cases with one category clearly dominant the scoring was 0.75 and 0.25 (two items) or 0.50, 0.25 and 0.25 (three items). The scores for each prey category was then summed. The ratio of quantity of remains to amount of food offered or consumed was used to provide correction factors. Two kinds of correction factors were used: One obtained from the ratio of quantity of remains relative to amount of food *consumed*, i.e. 0.192 for small rodents (the average of obtained values) and prey of similar size i.e. *Soricidae* and *Mustela nivalis*, 0.101 for *Arvicola terrestris*, *Sciurus vulgaris* and *Rattus norvegicus*, 0.098 for birds, and 0.075 for *Oryctolagus cuniculus* (Tab. 1). These factors were used to calculate the relative importance of various prey categories in the diet (Tabs 2 and 3). The other correction factors were obtained from the ratio of the quantity of remains to amount of food *offered*. In this case the remaining uneaten parts of prey animals, other than hairs, were included; large prey such as rabbit, starling and water vole were not eaten completely like small rodents were. Calculated correction factors were then 0.192 for small rodents, 0.087 for *Arvicola*, 0.079 for birds, and 0.055 for *Oryctolagus*. The latter were used for *Arvicola*, *Microtus* and *Apodemus* (Tab. 5) and for *Arvicola* and

Tab. 1. Amount of various prey species offered to and consumed by stoats in feeding experiments and the hair remains of the prey in the scats recorded by frequency of occurrence and in a semi-quantitative way. In the latter case the quantitative estimate was based on scoring according to the formula $P_i = n_i/n$, where P_i (the scoring of prey species i) is the relative quantity (number of cross-sections) of prey species i , n_i in relation to the total amount, n , of observed cross-sections in a sample.

Test	Prey	Amount of food offered	Amount of food consumed	Frequency of occurrence %	Relative quantity No. of scores	Quantity of remains/food offered	Quantity of remains/food consumed
1	<i>Microtus agrestis</i>	45 g	45 g	25 (52 scats)	10.00	0.222	0.222
	<i>Apodemus</i> sp.	36	36	33	11.75	0.326	0.326
	<i>Oryctolagus cuniculus</i>	550	395	69	30.25	0.055	0.076
2	<i>Clethrionomys glareolus</i>	32	32	29 (31 scats)	4.25	0.132	0.132
	<i>Apodemus</i> sp.	37	37	32	6.25	0.168	0.168
	<i>Oryctolagus cuniculus</i>	410	310	68	19.50	0.047	0.062
3	<i>Microtus agrestis</i>	28	28	30 (27 scats)	3.75	0.133	0.133
	<i>Clethrionomys glareolus</i>	25	25	37	5.00	0.200	0.200
	<i>Apodemus</i> sp.	28	28	26	5.00	0.178	0.178
	<i>Arvicola terrestris</i>	144	124	70	13.25	0.092	0.106
4	<i>Clethrionomys glareolus</i>	32	32	62 (24 scats)	6.25	0.195	0.195
	<i>Apodemus</i> sp.	20	20	46	5.50	0.275	0.275
	<i>Arvicola terrestris</i>	146	126	71	12.25	0.083	0.097
5	<i>Clethrionomys glareolus</i>	76	76	83 (23 scats)	17.25	0.226	0.226
	<i>Sturnus vulgaris</i>	102	70	43	5.75	0.056	0.082
6	<i>Clethrionomys glareolus</i>	18	18	6 (49 scats)	1.75	0.097	0.097
	<i>Apodemus</i> sp.	15	15	14	3.00	0.200	0.200
	<i>Oryctolagus cuniculus</i>	555	410	86	36.50	0.065	0.089
	<i>Sturnus vulgaris</i>	75	67	20	7.75	0.103	0.115

Microtus (Figs 2–4) when examining food preference. The method is approximate but is considered to provide more accurate information on the relative importance of the various prey categories than is recording frequency of occurrence, especially so as a considerable number of scats (32% of the examined 1402) contained more than one prey item.

The following procedure was used to analyse the field data. The remains were recorded quantitatively in the way described for the feeding experiments. The scored quantities for each prey category were summed and divided by the correction factor to give the relative quantities of various prey categories. These were then recalculated as percentages in a food spectrum.

3. Results

As a background for examining the stoats’ food preference and their tendency for selective feeding, data are presented on local and seasonal variations of their diet.

3.1. Food spectrum in various habitats

In the Revinge area, 80% of the food was provided by the water vole and the field vole (Tab. 2). Lagomorphs (mainly young rabbits) were important during some periods. The wood mouse, the bank vole *Clethrionomys glareolus* and certain birds played a smaller role. Shrews, the rat *Rattus norvegicus*, the squirrel *Sciurus vulgaris* and the weasel *Mustela nivalis* occurred occasionally. No remains of reptiles, amphibians or invertebrates were found.

The relative importance of water vole and field vole varied in the wet meadows (Tab. 2). In meadows in the western part of the study area “W wet meadows” the field vole was the primary food, whereas in “E wet

meadows” (meadows in the eastern part of the study area) the water vole was the main food.

Stoats exploiting hedges on the farmland had a more varied diet (Tab. 2). *Apodemus* sp. and lagomorphs (primarily rabbits) were the primary food followed by field vole, bank vole, and water vole. Birds played a greater parts here than in the wet meadows ($\chi^2 = 8.25$, $p < 0.01$). Shrews, the mole *Talpa europaea*, rat and squirrel occurred occasionally. The varied diet was reflected in a considerably higher niche breadth index than for stoats exploiting wet meadows (Tab. 2).

3.2. Seasonal changes in feeding habits

This was examined in the Revinge area (Tab. 3). As the same trend appeared each year, the material from 1973–77 was pooled. In January and February the stoats concentrated on water voles and field voles and the food niche was narrow. In March and April the diet became more varied and there were considerable local variations. Besides in wet meadows the stoats hunted in grazed fields, in groves of deciduous and coniferous trees, at abandoned farms and other buildings (data from trapping and radio-tracking). Rabbits and wood mice were sometimes taken besides field voles and water voles. In some areas the stoats concentrated on water voles, which were hunted in their tunnels (radio-tracking). In May young rabbits became available and were preyed upon especially by the males (Erlinge 1979). In the spring the food niche was wider than in winter (Tab. 3). In June and July the diet was also more varied and birds and lagomorphs occurred beside small rodents. Among them, the water vole was the staple food whereas the field vole occurred at a relatively low frequency. In August and September the field voles appeared more and more in the diet, and in October and November they provided the bulk of the

Tab. 2. Diet of the stoat in various localities in Sweden as indicated by scat analysis. The figures show the relative importance of the various prey categories from the analysis with the described quantitative evaluation; frequency of occurrence values recalculated to relative occurrence are given in brackets. Niche breadth indices are calculated on the frequency of occurrence values according to Simpson’s formula $N_B = 1/\Sigma p_i^2$.

Locality	Food						
	N	<i>Arvicola</i>	<i>Microtus</i>	<i>Clethrionomys</i>	<i>Apodemus</i> sp.	<i>Mus</i>	Unidentified small rodents
Revinge area (Wet meadows, ditches and dry habitats)	1006	40.0 (32.2)	40.0 (51.6)	1.3 (2.6)	3.3 (4.4)	– –	1.1 (1.3)
Revinge area Western wet meadows	539	23.7 (22.1)	56.9 (61.3)	2.3 (3.8)	4.9 (5.6)	– –	0.9 (1.0)
Eastern wet meadows	258	67.1 (51.6)	21.2 (36.7)	0.3 (0.9)	1.6 (2.5)	– –	1.5 (1.9)
Hedgerows in a farmland, S Sweden	396	7.8 (9.1)	13.8 (19.4)	8.6 (12.4)	31.9 (36.3)	1.5 (2.1)	0.9 (1.2)

food together with the water voles. The more varied diet indicated for December (Tab. 3), was probably due to bias in the material; the high frequency reported for the wood mice and the bank vole was mainly based on scats obtained from a few localities in 1973 and 1977.

3.3. Food niche breadth of stoats in relation to vole abundance

The niche breadth of the stoats was inversely correlated with vole density (Fig. 1); the stoats fed almost exclusively on voles when vole density was high or moderately high in autumn and winter. With decreasing vole numbers in spring, the niche breadth increased, especially in May. The widening of the niche breadth was largely due to a change in the males' diet from a field vole-water vole diet in autumn-winter to a water vole-rabbit diet in later spring (Erlinge 1979); female stoats fed largely on voles also in spring and summer.

The relationship of niche breadth to vole density (Fig. 1), indicated that above a certain vole density (about 20 voles per ha) the stoats fed almost exclusively on voles. Below that density alternative prey as birds and rabbits were increasingly included in the diet (especially for males).

Considering that small rodents – taken as one prey category – are preferred prey of the stoat, the field data are in agreement with the theory on optimal diet (Emlen 1966, 1968, Schoener 1971, Pyke et al. 1977).

3.4. Food preference

3.4.1. At hedgerows

The preference for different species of small rodents of equal size was examined at the hedgerows by comparing the proportion of the various species in the diet and in the habitat (Tab. 4). The stoats showed a high preference for field voles and wood mice, whereas bank voles were eaten to a low extent relative to their numbers in the snap-trap captures. The figures also indicated a low

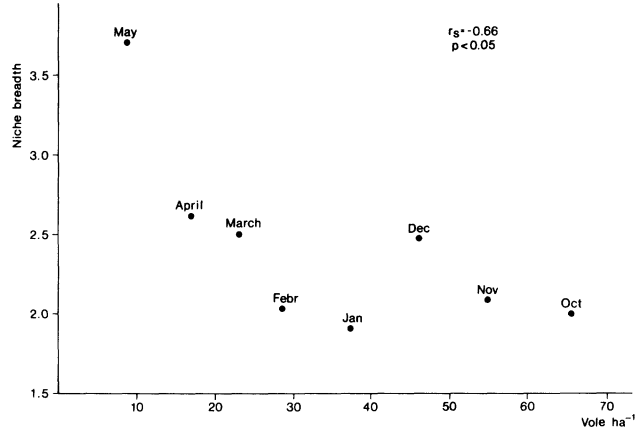


Fig. 1. Food niche breadth of stoats in relation to estimated vole density from October to May (non-reproductive season). The niche breadth was calculated as in Tab. 2. Vole numbers are from L. Hansson and B. Jeppsson. Statistical analysis according to Spearman's rank correlation test.

preference for shrews. In terms of relative density in the habitat the figures for field voles and bank voles were probably underestimated in the small sampling units, as these species, especially field voles are less easily trapped than wood mice. Thus, preference values for wood mice might have been higher and for the bank vole lower than the figures indicate.

3.4.2. In wet meadows and grazed fields

Stoats exploiting the wet meadows showed a preference especially for water vole but also for field vole (Tab. 5). The high preference for water vole could be related to its large size; the average weight (about 120 g) is about four times that of a field vole (30 g). The preference for water vole was pronounced in male stoats (Fig. 2), whereas for the females the overall data indicated only a slight preference for the water vole relative to the field vole (Fig. 2). The low preference value for the wood mouse (Tab. 5) was probably due to the different

items									
<i>Rattus</i>	<i>Sciurus</i>	Lagomorpha	Soricidae	<i>Talpa</i>	<i>Mustela nivalis</i>	Birds	Fish	Invertebrates	N _B
0.3 (0.4)	0.1 (0.1)	10.3 (4.8)	0.4 (0.5)	— —	0.1 (0.2)	3.0 (2.0)	— —	— —	2.66
0.1 (0.1)	0.2 (0.1)	8.1 (3.4)	0.3 (0.3)	— —	0.3 (0.3)	2.3 (1.7)	— —	— —	2.32
0.7 (0.9)	— —	4.0 (2.5)	0.7 (0.9)	— —	— —	2.9 (1.9)	— —	— —	2.48
0.6 (0.4)	0.1 (0.2)	28.2 (13.6)	0.3 (0.4)	0.1 (0.2)	— —	6.2 (4.7)	— —	— —	4.66

Tab. 3. Seasonal variations in the diet of stoats in the Revine area as indicated by the analysis of 1006 scats obtained in 1973–77. The figures are presented as in Tab. 2.

	N	<i>Arvicola terr.</i>	<i>Microtus agr.</i>	<i>Clethrionomys glareolus</i>	<i>Apodemus sp.</i>	Unidentified small rodents	<i>Rattus rattus</i>	<i>Sciurus vulgaris</i>	Lagomorphs	Soricidae	<i>Mustela nivalis</i>	Birds	N _b
Jan.	30	46.8(38.6)	53.2(61.4)	—	—	—	—	—	—	—	—	—	1.90
Feb	77	47.8(41.8)	50.0(55.7)	0.3(0.8)	1.0(0.8)	—	—	—	—	—	1.0(0.8)	—	2.06
Mar	86	4.1(3.7)	52.9(58.3)	1.2(3.5)	15.7(21.3)	1.4(2.8)	—	—	24.1(10.2)	—	—	0.5(0.9)	2.51
Apr	32	60.1(45.5)	26.3(40.9)	1.6(2.3)	5.3(6.8)	—	—	—	6.8(4.5)	—	—	—	2.62
May	65	28.2(25.0)	16.7(32.5)	1.3(7.5)	—	—	—	—	50.2(31.3)	—	—	—	3.66
Jun	53	54.3(44.8)	24.1(38.8)	—	—	1.2(1.5)	—	—	9.9(6.0)	—	—	3.7(3.8)	2.76
Jul	122	66.9(50.3)	22.6(39.5)	0.3(1.3)	0.8(1.3)	2.1(2.5)	—	—	3.4(1.9)	0.5(1.3)	—	10.5(9.0)	2.44
Aug	203	39.4(32.4)	41.2(51.7)	1.4(2.7)	2.7(3.5)	1.1(1.2)	0.2(0.4)	—	7.4(3.1)	1.4(1.5)	—	3.4(2.5)	2.66
Sep	113	36.7(32.0)	44.5(53.1)	0.3(1.4)	3.2(3.4)	2.7(2.7)	0.3(0.7)	—	7.7(4.1)	0.7(0.7)	—	5.3(3.5)	2.58
Oct	97	31.1(24.8)	60.2(66.1)	0.8(3.3)	0.2(0.8)	0.8(0.8)	2.0(1.7)	—	4.8(2.5)	—	—	3.9(2.0)	2.00
Nov	50	42.3(35.5)	51.7(57.9)	0.4(1.3)	4.8(3.9)	—	0.8(1.3)	—	—	—	—	—	2.16
Dec	78	23.2(16.5)	53.0(59.2)	6.0(7.8)	10.3(10.7)	1.4(1.9)	—	1.6(1.0)	3.0(1.9)	—	0.8(1.0)	—	2.53

Tab. 4. The stoats' preference for various species of small mammals at hedgerows in a farmland. The preference value (α) for each one species was calculated according to the formula

$$\alpha = r \cdot n^{-1} \cdot \left(\sum_{j=1}^m r_j \cdot n_j^{-1} \right)^{-1},$$

(Chesson 1978), where r means the proportion in the diet and n the proportion in the environment; the subscript j means that the summation should be done for all m prey categories. The proportion in the diet was obtained by recording remains quantitatively; the scored quantities for each prey category are given in brackets. These figures were then recalculated in percentages. The biomass of captured small mammals during the study in autumn 1975 was 2032 g (109 specimens) and the number of stoat scats collected during the same period was 104 specimens.

Prey species	Proportion in the diet (%)	Proportion in habitat (%)	Preference value
<i>Microtus agrestis</i>	17(14)	11	0.45
<i>Apodemus sp.</i>	63(52)	44	0.41
<i>Clethrionomys glareolus</i>	20(17)	43	0.14
Soricidae	—	2	0.00

habitat utilization by the stoats and the wood mice; the stoats primarily exploited the wet meadows – which were the preferred habitat of the water vole and the field vole – whereas the wood mouse occurred mainly in the grazed fields. (Information on stoats' habitat utilization was from radio- and snow tracking and the data on small rodents' distribution from captures by L. Hansson.) As was found at the hedgerows (Tab. 4) the stoats showed a low preference for shrews also in wet meadows (Tab. 5).

Water voles were more important in the diet of the stoats than in that of other small rodent predators in the area (Tab. 6). For the stoat the consumed prey biomass of water voles was estimated to be equal to that of field voles, whereas for the long-eared owl and the kestrel the calculated water vole consumption was only one fifth to one third of the field vole consumption.

3.4.3. Feeding experiments

To examine the reasons for the low preference for the bank vole and the shrews experiments were performed with two specimens each of bank voles, wood mice and shrews (*Sorex araneus* or *S. minutus*). The prey animals were released simultaneously into an enclosure of about 30 m², containing simulated grassland and woodland habitats. The small rodents were caught to a similar extent and no tendency to hunt selectively was observed (Tab. 7). The shrews on the other hand were only occasionally taken.

When seven stoats were offered a choice of feeding on recently killed wood mice, bank voles and shrews, no definite preference was shown for any of the rodent

Tab. 5. The stoats' preference for various species of small mammals in wet meadows and grazed field habitats in the Revinge area at two periods of the year. The preference values were calculated as in Tab. 4. Adopted correction factors in dietary calculations were 0.192 for *Microtus*, *Apodemus* and *Sorex* and 0.087 for *Arvicola*. The number of field voles, wood mice and shrews (recalculated to biomass) was from captures by L. Hansson according to the Standard Minimum Method (the average sampling in 1974–77), and the number of water voles in autumn (given in biomass) from captures by B. Jeppsson and F. Schlyter in 1975; data on losses due to predation from autumn to spring (Erlinge et al. unpubl.) were used to calculate the biomass of water voles in April/May, see Appendix 1. The figures in brackets give the number of stoats' scats and the estimated total biomass of small mammals.

Prey species	October–November			April–May		
	Proportion in the diet (147 scats)	Proportion in the en- vironment (2946 kg)	Preference value (α)	Proportion in the diet (97 scats)	Proportion in the en- vironment (728 kg)	Preference value (α)
<i>Arvicola terrestris</i>	39	33	0.47	65	49	0.55
<i>Microtus agrestis</i>	58	54	0.43	32	39	0.34
<i>Apodemus sylvaticus</i>	3	12	0.10	3	11	0.11
<i>Sorex araneus</i>	0	1	0.00	0	1	0.00

Tab. 6. Small rodents and insectivores as food for three predators feeding mainly on small mammals in the Revinge area. The figures are calculated prey biomass in %. The diet data of kestrel (*Falco tinnunculus*) obtained by G. Högstäd and long-eared owl (*Asio otus*) by I. Nilsson, were from various seasons of the years 1974–77 and based on analysis of 373 pellets of the kestrel and the identification of 7811 prey individuals in pellets of the long-eared owl.

	<i>Arvicola terrestris</i>	Prey species <i>Microtus agrestis</i>	Other small rodents	Insectivores (Soricidae and <i>Talpa</i>)
Stoat	46.4	46.4	6.7	0.5
Long-eared owl	14.9	70.5	13.7	0.9
Kestrel	21.7	73.6	1.4	3.2

Tab. 7. Sequence of capturing prey animals by the stoats (seven males and five females) in feeding experiments. *Clethrionomys glareolus*, *Apodemus sylvaticus* or *A. flavicollis*, and *Sorex araneus* or *S. minutus* (two specimens of each species) were used in 47 experiments.

Order of capture	<i>Clethrionomys glareolus</i>	<i>Apodemus</i> sp.	<i>Sorex</i> sp.	Unidenti- fied
1	20	24	0	3
2	13	10	1	–
3	5	6	1	–
Total	38	40	2	3

For *Clethr.* and *Apod.* $\chi^2 = 0.80$, $p > 0.05$.

Tab. 8. Sequence of consumption of first-captured *Clethrionomys glareolus* and *Apodemus* sp. by stoats in 47 feeding tests.

	1st captured	1st consumed
<i>Clethrionomys glareolus</i>	20	11
<i>Apodemus</i> sp.	24	18

$\chi^2 = 1.93$, $0.20 > p > 0.10$.

species (Tab. 8). The wood mice tended to be eaten first more frequently than bank voles, but this was not statistically significant. A distaste for shrews was clearly demonstrated. In twelve tests where individual stoats (eight specimens) were offered one bank vole, one wood mouse and one shrew, the small rodents were consumed the following day, whereas in all tests the shrew was left uneaten.

3.5. Selective feeding in relation to vole density

Optimal foraging theory predicts that a predator should increase its selectivity on preferred prey with increased overall prey density (Emlen 1966, Schoener 1971, and references given in Pyke et al. 1977). This prediction was tested for male and female stoats feeding on water voles and field voles in the wet meadows. The females did not show any change in selectivity with changing vole density, whereas in male stoats there was an inverse correlation between selectivity for preferred prey (water vole) and overall vole density (Fig. 2). The same pattern appeared when comparing selectivity in relation to the density of the preferred prey (water vole) (Fig. 2). On the other hand the selectivity for water vole by male stoats was positively correlated with the water voles' relative abundance (Fig. 3). Regarding prefer-

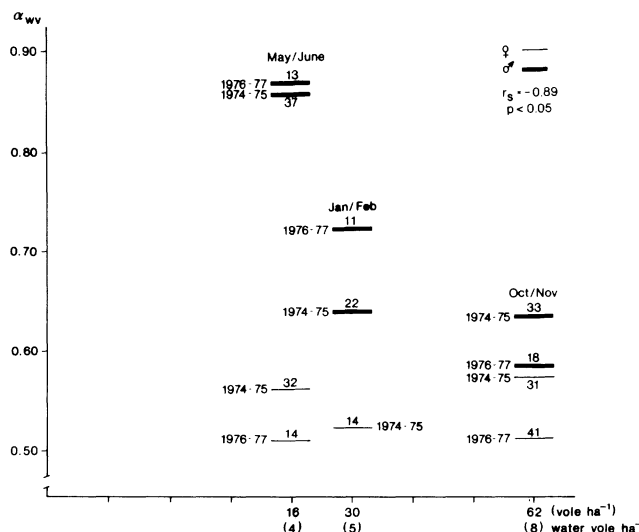


Fig. 2. The tendency of selective feeding on preferred prey (water vole) by male and female stoats in relation to overall vole density and to water vole density in wet meadows (the figures in brackets). The preference values (α), indicating the tendency of selective feeding, were calculated according to Chesson's formula (see Tab. 4). Field data underlying the calculations are given in Appendix 1. The figures above the horizontal bars denote the number of scats examined at three periods of the years 1974–75 and 1976–77. Statistical test for males as in Fig. 1.

ence values for the field vole (the less preferred prey of the male stoats) in relation to changes in the field vole density there was a positive correlation in males (Fig. 4). In females no change in selectivity for the field vole was found over the year.

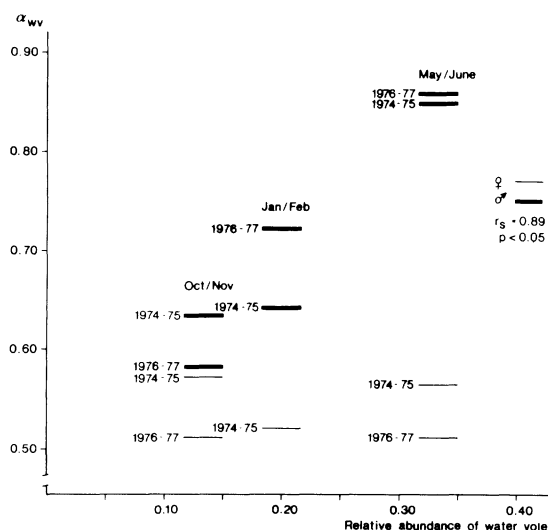


Fig. 3. The tendency for selective feeding on preferred prey (water vole) in relation to the relative abundance of the water voles (per cent water vole of total vole biomass). The α values are the same as in Fig. 2.

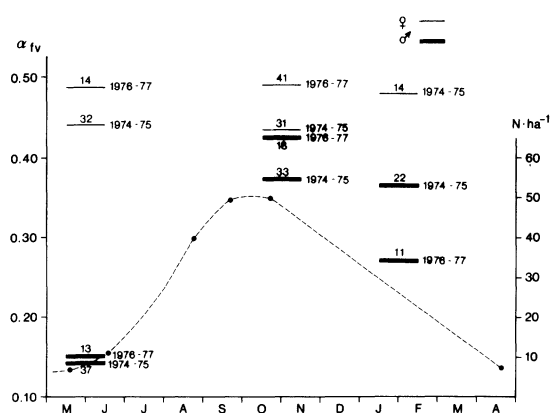


Fig. 4. The tendency of male and female stoats to feed on field voles as indicated by the α values at different field vole density. The α values were calculated as in Tab. 4. The seasonal variations in the field vole density with low density in spring – early summer and peak density in autumn, were similar from year to year (Hansson unpubl.). Statistical test as in Fig. 1, for males: $r_s = 0.89$, $p < 0.05$.

3.6. Optimal diet and reproductive output

The examined stoat population was distributed in four areas separated by open fields, i.e. the hedgerow area, “W and northern wet meadows” (dominated by field voles) and “E meadows” dominated by water voles (Erlinge 1977). Between these areas very little exchange of individuals occurred among the females (only one female out of 31 moved from one meadow to another). Also juvenile females showed a high tendency to stay in or close to their native area during their first summer and autumn; all 18 females marked as juveniles in July/August 1973–78 in a separate area were recaptured in the same area after a lapse of more than one month.

The number of captured juvenile females per breeding female was taken as an index for reproductive output in the separate areas and two types of wet meadows were compared (water vole-dominated meadows and field vole-dominated meadows). There was on an average higher reproductive output in the water vole-dominated meadows, where the diet of the females also contained a higher proportion of water vole (Tab. 9).

The number of captured young females per captured breeding female was also examined for separate sub-areas included in the E and W meadows. There were some dispersal movements of juvenile females (three individuals out of 18) to adjacent subareas (where no breeding female was captured), but most juvenile females remained in the area of a breeding female where they were initially captured in July/August (at a time when the family group splits up). The average number of captured young females per breeding female in the various water vole-dominated meadows was higher than for the field vole-dominated meadows (Fig. 5), but the difference was not statistically significant (U

Tab. 9. Reproductive output as indicated by the number of captured juvenile females per captured breeding female in three food environments. The figures in brackets include individuals captured in spring and assumed to be present preceeding year in the same area as juveniles.

No. captured	Water vole-dominated meadow	Field vole-dominated meadow	Hedgerows in farmland
Juvenile ♀	27(30)	14(20)	7(8)
Breeding ♀	11	16	7
Juv/ad (\bar{x})	2.45 (2.73)	0.88 (1.25)	1.00 (1.14)

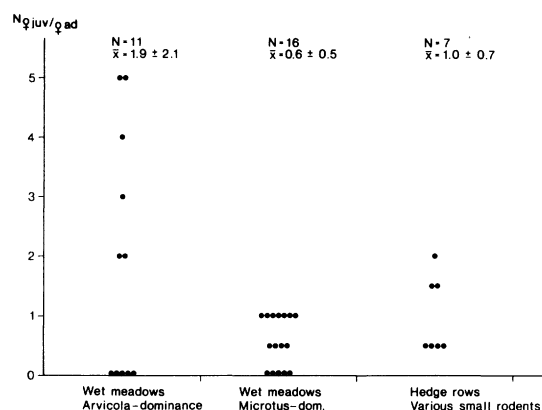


Fig. 5. Reproductive output as indicated by the number of captured juvenile females per breeding female in the two types of wet meadows examined and at hedgerows in a farmland. The dots denote the number of recorded litters of each size category. When two breeding females were captured in one area (six cases) the average number of juvenile females per breeding female was calculated. N is the total number of recorded breedings and \bar{x} the average number of captured young females per breeding female.

= 67.5 > 47; $\alpha > 0.05$, Mann-Whitney two tailed U-test). A considerable number of breeding females with no captured juvenile females was recorded in both types of wet meadows. In water vole-dominated meadows, a high reproductive output (5 and 4 juvenile females per breeding female) was especially found in areas with high local density of water voles (apparent from signs of vole activity and trapping data, Jeppsson unpubl.).

The index values from the hedgerows indicated a recruitment similar to that in the field vole-dominated meadows (Tab. 9, Fig. 5).

4. Discussion

4.1. Accuracy of obtained preference values

The calculated preference values in Tabs 4, 5 and Figs 2–4 are based on estimates on vole biomass (recalculated from numbers) in the habitats and in the stoats' diet.

4.1.1. Changes in absolute and relative numbers of field voles and water voles

The methods of estimating vole numbers provide only approximate values, and are useful when analysing large-scale changes in vole numbers. The dynamics of the field vole population was characterized by a seasonal pattern with peak density in autumn (about 50 voles per ha in wet meadows) and low density in spring and early summer (about 5–10 voles per ha). No significant between-year variations occurred (Hansson unpubl.). The marked decrease in numbers from autumn to spring (non-breeding season) was related to hard winter predation (Erlinge et al. unpubl.). For the water vole on the other hand the main predation occurred in summer time (April to October), whereas winter predation was less intense; 19% of the annual predation was calculated for the period November to April, compared to 70% of the annual predation for field voles (Erlinge et al. unpubl.). The low predation rate on water voles in winter was probably due to their life in underground tunnels at that time which made them less susceptible to predation. Thus summarising: During the voles' non-breeding season (from October up to the beginning of the new breeding season in May/June) there was a continuous decrease in vole numbers; a marked decrease in field vole numbers and a moderate decrease in water vole numbers caused a change in their relative abundance from autumn to spring (Figs 2–4).

4.1.2. Dietary analysis

The method of analysing the diet includes some uncertainties e.g. in quantifying the remains (hairs) of different prey species and the unequal amount of remains from different prey. Day (1968), Moors (1975) and King (1980) used frequency of occurrence when examining weasels' diet from scat remains, and argued that the method could be used, as important prey of the weasels had similar size and as the scats usually contained remains of only one prey species. In this study a considerable number of the stoats' scats (32%) contained remains of more than one prey species and the two species of basic importance – field vole and the water vole – differ greatly in size. Feeding tests confirmed that small species (field vole) was greatly overestimated relative to the large water vole when estimated by frequency of occurrence (Tab. 1). Therefore, correction factors derived from the feeding tests were adopted. In spite of this improvement, the diet data are considered to give only approximate information on the relative importance of the prey species. When comparing the males' and females' diet and their seasonal changes, the data are considered to be unbiased and directly comparable.

4.2. Factors influencing prey preference

The stoat catches its prey by pursuit. The prey size is remarkably large in relation to the size of the stoat

(Hewson and Healing 1971). For females having an average body weight of 130 g, the range of recorded prey size was about 10 to 150 g and occasionally more than 150 g (rabbits); for males weighing on average 250 g the upper limit of prey size was about 400 g and occasionally even higher (rabbits). It has been suggested that for prey with different size, a preference order should generally correspond to the order of size (Schoener 1971, Werner 1974, Pyke et al. 1977). Field data in this study are in agreement with this suggestion, i.e. regarding rodents: water vole (100–150 g) > field vole and wood mice (20–30 g) > bank vole (15–20 g) (Tabs 4 and 5). However, other factors than size are important and the preference can vary due to many factors. Bank voles were clearly less preferred than wood mice at hedgerows, but no such difference appeared in the enclosure experiments with grassland habitats (Tabs 4 and 6). Also, at hedgerows in Britain the bank voles were subject to low predation by weasels, although the bank voles were quite common (Moors 1975). On the other hand bank voles were the most common prey for weasels in a deciduous forest in Britain (King 1980) and they were also eaten by weasels in the same proportion as they were caught in snap-traps in woodland habitats in Sweden (Erlinge 1975). It might be that the small body size of bank voles allow them to take refuge in narrow places difficult to reach for the stoat and possibly also for the weasel, when they exploit habitats such as stone walls or hedgerows. Distaste can also influence prey capture (Macdonald 1976). This was evidently the case for the shrews (Tab. 6), as was found also in other studies on the diet of stoat and weasel in Europe (Day 1968, Erlinge 1975, Moors 1975, Tapper 1976, King 1980).

4.3. Optimal foraging theory and food choice of male and female stoats

In optimal foraging theory a predator is assumed to maximize the difference between foraging gains and costs (Pianka 1974). One important foraging decision concerns which prey species (or prey type) to hunt (MacArthur 1972). The prey species providing the greatest net energy yield should usually be preferred. For stoats in wet meadows the choice is mainly between two rodent species, water vole and field vole. The energy cost for catching and handling the two species is probably rather similar (enclosure observations) and search time is probably largely related to the density of the two species. As the energy content is several times higher in water voles one would expect a preference for them. This was the case for the males (Fig. 2). In females a preference for water voles could not be established with any certainty, but the overall data consistently indicated at weak preference for them (Fig. 2). Also the comparison with the food choice of other small rodent predators (kestrel and long-eared owl, Tab. 6) emphasizes this preference for water voles in stoats. The

difference in diet between the sexes might be due to different fitness set functions of males and females. (The concept of fitness set implies that all evolutionary variables cannot be maximized simultaneously; e.g. a consumer which specializes on one food type has to accept a reduced ability to utilize other food types or it can be adapted to exploit two similar food types each less efficiently than the specialist, Levins 1968.) Stenseth's model (unpubl.) predicts that the shape of the fitness set function is important for predicting the performance of foraging. For a consumer exploiting similar food types, the function will be convex and gradual changes in the diet is predicted. For a consumer exposed to different prey types the fitness set function will be concave and specialization and abrupt changes in diet are predicted. Concerning the small rodent diet of female stoats one would expect a convex fitness set. The females have high food requirements when rearing the young and they have to restrict their hunting to an area around the nest site. Their morphology and behaviour also make the suggestion of a convex fitness set function reasonable; their small body size permits them to enter narrow tunnels and to exploit efficiently small voles, and the females' small body size is compensated for by a well-developed fighting spirit so they can capture also large voles (Erlinge 1979). Food preference values for females (Fig. 2) support the suggestion that they are adapted to feed on a combination of large and small voles, and a gradual change in their diet was found (Figs 2–4) which is predicted for a consumer with a convex fitness set (Stenseth unpubl.).

In male stoats the fitness set function might be concave. In accordance with their large body size the males might be adapted to feed preferably on large prey such as water voles, whereas smaller voles are less efficiently utilized; the males' body size prevents them from entering the small voles' tunnels. (Concerning the evolution of large body size in male stoats, see Erlinge 1979.). The males' diet showed a high preference for water voles (Fig. 2). Selective feeding on them was connected with extensive movements of males, especially at mating time (May to August) and hunting was concentrated to patches with water voles, spaced out over the ranges (data from radio-tracking). Also the marked changes in diet which was found in male stoats (Figs 2–4, and Erlinge 1979) is in agreement with predictions for a consumer with a concave fitness set (Stenseth unpubl.). A similar pattern implying significant seasonal change in diet of males but not in females occurred also in weasels (Erlinge 1975, Tapper 1979).

4.4. Importance of the prey types' relative abundance for optimal diet

One principal disagreement in optimal foraging theory concerns the importance of the relative abundance of the prey types on the optimal diet. Models by Pulliam (1974) and Charnov (1976) predict that the relative

abundance of the non-preferred prey is unimportant for the optimal diet; only the absolute abundance of the preferred prey is important. On the other hand models by Emlen (1966), Rapport (1971), Estabrook and Dunham (1976), and Stenseth and Hansson (1979) predict that the relative abundance can have an influence on the optimal diet; a non-preferred prey type can be included in the diet by becoming relatively very abundant. Further Stenseth (unpubl.) claims, that models on optimal diet should incorporate a fitness set and this matter changes some predictions of the models, e.g. the relative density of different food types becomes important in determining the optimal diet. The observed inverse correlation between males' selectivity for preferred prey and overall vole density (Fig. 2), and the positive correlation between preference values for the field vole (less preferred prey) and its density (Fig. 4) is contrary to predictions in models where the optimal diet depends only on the absolute abundance of the preferred prey type (Pulliam 1974, Charnov 1976, Pyke et al. 1977). On the other hand the observations are in agreement with models where the relative abundance of the prey types is predicted to be important and where a non-preferred food item could be added to the diet by becoming relatively very abundant (see references above). At a high relative abundance of water vole (preferred prey) in May–June and low density of field voles, the male stoats hunted selectively on water voles (Fig. 3 and evidence from radio-tracking). With increased absolute and relative abundance of field voles (less preferred prey) in autumn (Figs 3 and 4) this prey item was considerably more included in the diet. Besides a change in relative abundance, reduced accessibility of water voles at peak densities in autumn might be important. The water voles change from a life in shallow tunnels and feeding above ground to a life in deeper underground tunnels from late autumn to spring-early summer (Jeppsson pers. comm.). Stoats hunt water vole also in tunnels, but this hunting might be more energy demanding and so could reduce the cost-benefit ratio for hunting water voles. However, the change in water vole behaviour does not seem to be the determining factor behind the change in the male stoats' diet. The males changed to field vole diet in September/October (Fig. 4) when the water voles still had summer-time behaviour and the male stoats selectively hunted for water voles in April when the voles were in tunnels (evidence from radio-tracking).

4.3. Diet and reproductive output

A characteristic feature in stoats' reproduction is a great variation in litter size. In ten examined females from southern Sweden the number of unimplanted blastocysts varied between 1 and 15 (average 6.7) (Andersson unpubl.). Correspondingly large variations were found also in other studies (Rowlands 1972). Also the index values on recruitment in various localities indicated a

great variation (Fig. 5). The differences are probably mainly due to variations in abundance of important prey (small rodents), and possibly also to the relative abundance of large and small voles. On energetic grounds one would expect the large water vole to be a preferred prey for the females (although to a lesser extent than for the males). Field data indicated only a weak preference for water vole relative to field vole (Fig. 2). This can be explained by constraints associated with the fitness set of females (see above) and as an adaptation of females to the size of predominant prey in the area (see also Simms 1979). Female stoats in Sweden are remarkably small compared to female stoats in Denmark, Central Europe and Britain (Moors 1980, Southern 1964) and small voles are the predominant vole species in many habitats exploited by stoats in Sweden.

The average reproductive output was higher in the water vole-dominated meadows than in the field vole-dominated meadows and at hedgerows (Tab. 9). The difference was due to high reproductive success in some water vole-dominated meadows with local high water vole density. Klimov (1940) also reported concentrations of stoats in western Siberia in places where water voles were common. Low reproductive success or failure occurred in some other places in the examined meadows (Fig. 5). The failure might in some cases be due to predation. The wet meadows and especially those providing fairly high density of water voles attracted several other predators in the area, e.g. foxes, polecats, domestic cats, tawny owls and common buzzards which were potential predators on the stoats: Remains of stoat and/or weasel were found in scats or pellets of these predators (Erlinge et al. unpubl.) and two nests of breeding females in meadows were dug out by a predator.

The low reproductive rate indicated in the field vole-dominated meadows (where the females' diet also consisted primarily of field voles, Fig. 5 and Fig. 6 in Erlinge 1979) was probably due to the low field vole density in spring and early summer in the area (Fig. 4 and Erlinge et al. unpubl.). At peak densities of cyclic small rodents in northern Sweden, high density of stoats has been observed, indicating good reproductive success by female stoats having access to high numbers of small voles (own observations).

At hedgerows where the stoats' diet greatly varied (Tab. 2), a recruitment similar to that in the field vole-dominated meadows was indicated (Tab. 9, Fig. 5). No consistent inverse relation between food niche breadth and reproductive success was found, but the highest reproductive success was recorded in areas where the females specialized on water voles.

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Appendix 1. Field data and estimates underlying the calculation of preference values for water vole and field vole in Figs 2–4. The preference values were calculated according to the formula given in Tab. 4; N is the number of scats.

	Water vole	Oct–Nov Field vole	N	Water vole	Jan–Feb Field vole	N	Water vole	May–Jun Field vole	N
<i>Water vole and field vole in the diet as indicated by the analysis of scats</i>									
Males									
1974–75									
Scored quantities	9.5	18.0	33	9.5	12.5	22	16.0	5.0	37
Corrected value	109.2	93.8		109.2	65.1		183.9	26.0	
%	54	46		63	37		88	12	
1976–77									
Scored quantities	4.5	10.5	18	5.5	5.0	11	5.5	1.5	13
Corrected value	51.7	54.7		63.2	26.0		63.2	7.8	
%	49	51		71	29		89	11	
Females									
1974–75									
Scored quantities	8.5	20.0	31	4.5	9.5	14	12.0	16.0	32
Corrected value	97.7	104.2		51.7	49.5		137.9	83.3	
%	48	52		51	49		62	38	
1976–77									
Scored quantities	9.0	27.5	41				4.5	7.5	14
Corrected value	103.4	143.2					51.7	39.1	
%	42	58					57	43	
<i>Water vole and field vole in wet meadows</i>									
Density (No. ha ⁻¹)	8	54		5	25		4	12	
Biomass (g ha ⁻¹)	800	(8x100) 1134	(54x21) 500	(5x100) 525	(25x21) 460	(4x115) 360	(12x30) 44		
%	41	59	49	51	56				

Estimates of vole density in wet meadows.

Water vole

The average density in October–November 1975 was estimated at 8 ind per ha (Jeppsson and Schlyter unpubl.). The changes from autumn to spring was calculated from data on mortality due to predation. For 1975 and 1976 complete estimates were available which showed that 21800 water voles were consumed by the predators each year (Erlinge et al. unpubl.). During the period October to February the consumption was 4400 voles, reducing the water vole number from 12300 to 7900, i.e. 64% of the October number remained in January–February, which recalculated to average density is 5 ind per ha. During the period February to May the water vole consumption by the predators was estimated at 3000 voles (from 7900 to 4900) i.e. 62% of the number in February remained at the beginning of May or on average 3 voles per ha. In May reproduction started and the density of catchable water voles in June was estimated at 5 voles per ha and as an average for the May–June period 4 voles per ha.

Field vole

Average density in autumn was 54 voles per ha and there was no significant differences between the years 1974–77 (Hansson unpubl.). The density of adult voles in May–June (average for 1974–77) was 8 ind per ha; juveniles occurred to a variable number in catches in June and 12 voles of catchable size per ha were taken as an average density for the May–June period. From autumn to spring there was a steady decrease in numbers (see Fig. 4); the calculated density in January–February was 25 ind per ha.

References

- Aldous, S. T. and Manweiler, J. 1942. The winter food habits of the short-tailed weasel in Northern Minnesota. – *J. Mammal.* 23: 250–255.
- Brugge, T. 1977. Prooidierkeuze van Wezel, Hermelijn en Bunzing in Relatie tot Geslacht en Lichaamsgroter. (Prey selection of weasel, stoat and polecat in relation to sex and size). – *Lutra* 19: 39–49.
- Charnov, E. L. 1976. Optimal foraging attack strategy of a mantid. – *Am. Nat.* 110: 141–151.
- Chesson, J. 1978. Measuring preference in selective predation. – *Ecology* 59: 211–215.
- Day, M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoat and weasels. – *J. Zool., Lond.* 148: 201–217.
- 1968. Food habits of British stoats (*Mustela erminea*) and weasels (*Mustela nivalis*). – *J. Zool., Lond.* 150: 485–497.
- Emlen, J. M. 1966. The role of time and energy in food preference. – *Am. Nat.* 100: 611–617.
- 1968. Optimal choice in animals. – *Am. Nat.* 102: 385–389.
- Erlinge, S. 1975. Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. – *Oikos* 26: 378–384.
- 1977. Spacing strategy in stoat *Mustela erminea*. – *Oikos* 28: 32–42.
- 1979. Adaptive significance of sexual dimorphism in weasels. – *Oikos* 33: 233–245.
- Estabrook, G. F. and Dunham, A. E. 1976. Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. – *Am. Nat.* 110: 401–413.
- Fitzgerald, B. M. 1977. Weasel predation on a cyclic population of the Montane vole (*Microtus montanus*) in California. – *J. Anim. Ecol.* 46: 367–397.
- Gossow, H. 1970. Vergleichende Verhaltenstudien an Marderartigen. I. Über Lautäusserungen und zum Beuteverhalten. – *Z. Tierpsychol.* 27: 405–480.
- Hamilton, W. J. 1933. The weasels of New York. – *Am. Midl. Nat.* 14: 289–344.
- Hansson, L. 1972. Evaluation of the Small Quadrant method of censusing small mammals. – *Ann. Zool. Fennici* 9: 184–190.
- 1975. Comparison between small mammal sampling with small and large removal quadrats. – *Oikos* 26: 398–404.
- 1980. Small mammal dynamics and production in a heterogeneous grassland landscape in South Sweden (submitted).
- Hewson, R. and Healing, T. D. 1971. The stoat *Mustela erminea* and its prey. – *J. Zool., Lond.* 164: 239–244.
- King, C. M. 1980. The weasel *Mustela nivalis* and its prey in an English woodland. – *J. Anim. Ecol.* 49: 127–159.
- Klimov, Yu. N. 1940. Materialy po biologii gornostaya. (Data on the biology of the ermine: in Russian). – *Trudy Biologicheskogo Instituta.* 7: 80–88. In King: Biology of mustelids. Some Soviet Research. British Library Lending Division.
- Krebs, J. R. 1978. Optimal foraging: Decision rules for predators. – In: Krebs, J. R. and Davies, N. B. (ed.), *Behavioural ecology – an evolutionary approach*. Blackwell, Oxford, pp. 23–63.
- Levins, R. 1968. *Evolution in changing environments*. – Princeton Univ. Press, Princeton, N.J.
- MacArthur, R. H. 1972. *Geographical Ecology*. – Harper and Row, New York.
- and Pianka, E. R. 1966. On optimal use of a patchy environment. – *Am. Nat.* 100: 603–609.
- Macdonald, D. W. 1976. Food caching by red foxes and some other carnivores. – *Z. Tierpsychol.* 42: 170–185.
- Maher, W. J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. – *Can. Field – Nat.* 81: 248–250.
- Moors, P. J. 1975. The food of weasels (*Mustela nivalis*) on farmland in north-east Scotland. – *J. Zool., Lond.* 177: 455–461.
- 1980. Sexual dimorphism in the body size of mustelids (Mammalia: Carnivora): The roles of food habits and breeding systems. – *Oikos* 34: 147–158.
- Müller, H. 1970. Beiträge zur Biologie des Hermelins. – *Säugetierk. Mitteil.* 4: 293–380.
- Myllymäki, A., Paasikallio, A., Pankakoski, E. and Kanervo, V. 1971. Removal experiments on small quadrats as a means of rapid assessment of the abundance of small mammals. – *Ann. Zool. Fennici* 8: 177–185.
- Novikov, G. A. 1962. *Carnivorous mammals of the fauna of the U.S.S.R. – Israel Program for Scientific Translations.* Jerusalem.
- Ognev, S. I. 1935. *Mammals of U.S.S.R. and adjacent countries. – Israel Program for Scientific Translations,* Jerusalem.
- Pianka, E. R. 1974. *Evolutionary Ecology*. – Harper and Row, New York.
- Potts, G. R. and Vickerman, G. P. 1974. Studies on the cereal ecosystem. – *Adv. Ecol. Res.* 8: 107–197.
- Pulliam, H. R. 1974. On the theory of optimal diets. – *Am. Nat.* 108: 59–74.
- Pye, G. H., Pulliam, H. R., and Charnov, E. L. 1977. Optimal foraging: A selective review of theory and tests. – *Quart. Rev. Biol.* 52: 137–154.
- Rapport, D. J. 1971. An optimization model of food selection. – *Am. Nat.* 105: 765–768.
- Rowlands, I. W. 1972. Scientific report: Zoological Society. Reproductive studies in the stoat. – *J. Zool.* 166: 574–576.
- Schoener, Th. W. 1969. Models of optimal size for solitary predators. – *Am. Nat.* 103: 277–313.
- 1971. Theory of feeding strategies. – *Ann. Rev. Ecol. Syst.* 2: 369–404.
- Simms, D. A. 1978. Spring and summer food habits of an ermine population (*Mustela erminea*) in the central Arctic. – *Can. Field – Nat.* 92: 192–193.
- 1979. North American weasels: resource utilization and distribution. – *Can. J. Zool.* 57: 504–520.
- Southern, H. N. (ed.) (1964). *The Handbook of British mammals*. – Blackwell, Oxford.
- Stenseth, N. C. 1980. Evolutionary stable strategies (ESS) in food selection models with fitness sets. – *Am. Nat.* (submitted).
- and Hansson, L. 1979. Optimal food selection: a graphic model. – *Am. Nat.* 113: 373–389.
- Stroganov, S. U. 1969. *Carnivorous mammals of Siberia. – Israel Program for Scientific Translations.* Jerusalem.
- Tapper, S. C. 1976. The diet of weasels, *Mustela nivalis* and stoats, *Mustela erminea* during early summer, in relation to predation on gamebirds. – *J. Zool., Lond.* 179: 219–224.
- 1979. The effect of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland. – *J. Anim. Ecol.* 48: 603–617.
- Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. – *J. Fish. Res. Bd Can.* 31: 153–156.
- Wüsthube, C. 1960. Beiträge zur Kenntnis besonders des Spiel- und Beuteverhaltens einheimischer Musteliden. – *Z. Tierpsychol.* 17: 578–613.