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The diet of polecats (*Mustela putorius* L.) in Switzerland

By D. Weber

Museum of Natural History, Basel, Switzerland

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Abstract

Studied the diet of polecats in Switzerland by gut-analysis of 120 individuals and by analysis of 354 scats from 12 radiotracked individuals. Carcasses were collected from 1982 to 1987 from all over Switzerland and adjoining areas of France. Scats originate from a mountainous (1000–1300 m) and a lowland (300–450 m) study area. Results are given as weighted frequencies of occurrence, disregarding items of less than 25 % estimated sample volume.

The diet of polecats is almost exclusively carnivorous. Some fruits are also taken, mainly by juveniles. 43 animal species, 8 plant species, offal and pet food occurred as polecat food. Anurans (mainly *Rana temporaria* and *Bufo bufo*) are the staple food. Further elements of importance are small mammals (mainly Muridae, but also Microtidae and Soricidae), carrion, and eggs. The annuran proportion of the diet is higher in summer than in winter and higher in the mountains than in the lowlands. In mountainous regions, anurans are also the most important food in winter. Juveniles eat more fruits and invertebrates and fewer mammals than adults. Sex-related differences in the importance of the main food categories were not detected. Within the mammal and arthropod category, females showed a significant preference for larger prey.

Methods and results are discussed in various contexts. The diet of Swiss polecats differs strikingly by its high amphibian component from what has been published on the species until now. Possible reasons for this discrepancy are mentioned. The food niche of polecats overlaps only to a small extent with those of sympatric *Mustela erminea, Martes foina* and *M. martes*, which themselves show considerable niche overlap. The diet of polecats gives an additional argument in the debate on the origin of sexual dimorphism of mustelids.

Introduction

As elsewhere, polecat populations have declined in Switzerland during this century (Eiberle 1969; Mermod et al. 1983). In a thesis directed by Prof. U. Rahm at the Unsiversity of Basle, I tested several hypotheses which would explain this decline. One striking fact was the discription of the diet of polecats in literature, which is usually given as similar to that of stone martens *(Martes foina).* Considering the decline of polecats and the recent increase of stonemarten populations in Switzerland (Müri 1982), this similarity suggested a food competition conflict as a possible reason for the decline of the polecat. On the other hand, if the increase of the stone marten was insufficient to explain the decrease of the polecat, why could other carnivores with similar diets increase their numbers, and not the polecat?

To answer these questions, it was necessary to obtain data on polecat diet in Switzerland, as all information on the subject came from countries with different ecological conditions. This paper presents the results of my study. I have discussed them in the context of the polecat decline elsewhere (Weber 1987). Here, they will be discussed in some contexts of more general interest.

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Material and methods

Material and study areas

This study is based on scats and gut contents of polecats from Switzerland and adjoining areas of France.

The guts are from 84 carcasses, which I obtained from many sources (mainly taxidermists, gamekeepers and hunters). Additional 25 stomachs were made available by the Institute of Veterinary Bacteriology of the University of Berne and further 11 stomachs by the Veterinary Service Lons-le-Saunier, France. All animals died between the years 1982 and 1987. The causes of death were traffic (54), hunting (9), dogs (3), others (3) and unknown (51). The polecats were sexed and aged (mainly by means of cementum-annuli-counts, Weber 1987. Specimens which diet between June and November and were younger than one year are called juveniles in this paper; all others are called adults. Polecats from the Institute of Veterinary Bacteriology were aged and sexed by the staff of the institute. A list of the origin of all but five guts analysed for this paper is given in Weber (1987). In some cases, not all information about a carcass could be obtained.

The scats of radio-tracked polecats were collected at resting sites from 1983 to 1985 in two different areas (for a more extensive discription see Weber 1987): 1. Leimental (47°30′ N, 7°29′ E; altitude 300–450 m). A lowland valley with mainly arable farming and scattered deciduous forests of different areas. Many brooklets cross the area, which to the north-east, the city of basle, has an increasingly suburban character. The climate is warm compared to the rest of Switzerland, with mild winters (January mean 0 °C). In the Leimental area, 197 scats from 8 individuals were collected.

2. La Brévine mountains (46°58′ N, 6°39′ E; altitude 1000–1300 m). A chain of the Swiss Jura mountains south of La Brévine. About half the area consists of mountain mixed forests with *Picea abies* and *Abies alba* as dominant tree species. The rest is mainly covered with grassland and wooded pastures, which are structured by stone walls, hedges and combinations of both. There is virtually no surface water in this study area. Farmhouses and stables are isolated and scattered; only a fraction of them are used in winter. For the geographical latitude, the climate is cold with harsh and long winters and a vegetation period of approximately 140 days (January mean −4 °C, annual mean +4 °C). In the La Brévine area, 88 scats from 4 polecats were collected.

Snow-tracking provided some additional scats. In 5 cases, droppings were found scats stacked in "latrines". These heaps were frozen and cut into pieces of approximately 3 ml (the mean volume of 40 random-selected individual scats beeing 3.1 ml), trying to separate individual droppings as well as possible. By this procedure, I obtained 21, 10, 9, 8 and 6 samples, which are not identical with individual scats.

All faeces from radio-tracked polecats and most of those found on snow-tracks could be dated with an accuracy of a few days. However, for a pile of 71 scats from a stable in the La Brévine area this was not possible.

Treatment of the samples

The volume of the stomach contents was measured to the nearest ml. All samples were washed in a sieve (mesh width 0.8 mm). A second sieve (mesh width 0.14 mm) was used to retain potential earthworm chaetae and small molluscan radulae (Ashby and Elliot 1983). After the treatment of 354 scats the fine sieve was no longer used, as I found small numbers of chaetea in only 4 samples and no radulae. Washed prey remain types were macroscopically observed in suspension and, according to their visually estimated relative volume, assigned to one of the following categories: >50 %, 50 %, 25 %, 10 %, <10 %.

For identification of hairs, medulla and scale patterns were observed microscopically and compared with the atlas of Debrot et al. (1982) and a collection of hairs of domestic mammals. Colour, macroscopical form or size also assisted identification in some cases. Mammals could often be identified by jaws or teeth according to Stresemann (1974) and Brohmer (1971). Amphibian bones were compared to reference skeletons. Where appropriate bones were found, species were identified according to Schaefer (1932). No attempts were made to identify fish remains. R. Winkler helped with the identification of some feathers. Other animal and fruit components could be attributed to species or higher taxonomic entities with the help of common field guides, reference collections and the personal experience of the author.

Three categories of prey remains are treated as carrion: 1. Animals which are too large to be killed by polecats (ungulates, dogs, cats, martens); 2. Animal remains which were found together with maggots; 3. Cases where radio-tracking revealed the food source (e.g. a polecat foraging on a rubbish-heap containing remains of slaughtered chickens). Some items were identified, but not considered as food remains (e.g. polecat hair, grass, dry leaves) and therefore not used to describe polecat diet.

The identification of prey remains was greately facilitated by the knowledge of the distribution of potential prey species in Switzerland, and especially in the radio-tracking study areas. This made it possible to exclude for example wild rabbit and, depending on the sampling site, several anuran species as potential prey.

A fundamental problem arises from the presence of gut contents of prey animals in carnivore droppings and guts (ROSER and LAVERS 1976). I often found small, intact arthropods, which presumably originated from anuran stomachs: Of 79 samples with arthropods in small proportions (≤ 10 % estimated volume), 78 contained also anuran bones. These 78 arthropod recordings are considered as anuran prey remains; a list of them is given in table 7.

Calculation of diet composition

Diet composition is given as relative frequency of occurrence (%) in the relevant sample. Every dropping, stomachal and intestinal content is thereby considered as an independent sample of a polecat meal. As most of the samples showed only one dominant prey type, this simple approach should give a representative image of food composition (DAY 1968).

To prevent the overestimating of mammals and birds (compared to amphibians), all prey forming an estimated 10 percent or less or remains in an individual sample, and all stomach contents with less than 1 ml, were not used to calculate diet composition. Thus, the analysis is restricted to items which form the bulk of individual samples; single hairs or feathers which can be found in a gut several days after ingestion of a mouse or a bird (ROSER and LAYERS 1976) were disregarded.

The distribution of remains used for frequency calculations over categories of estimated volume was as follows: > 50 %: 467 identified prey types; 50 %: 64 i. p. t.; 25 %: 29 i. p. t. As frequencies are given as percentages of samples, remains in the 50 % category were scored as 0.5 and those in the 25 % category as 0.25 (ERLINGE 1981). The method underestimates the importance of eggs, meat from rubbish-heaps or pet food and other food with few undigestible components, when they occur together with other prey (BRUGGE 1977).

A food-niche breadth index was calculated according to Simpson's formula (MÜHLENBERG 1976): $N_B = 1/\Sigma\ p_i^2$. were p_i is the proportion of food category i in the diet. Niche breadth is therefore dependent on the number of defined food categories with values from 1 (only one category exploted) to i (all categories evenly exploited). In this paper, all niche breadth indices are based on the following 7 food categories: mammals, amphibians, other vertebrates, invertebrates, carrion/offal, eggs, fruits. This allows N_B values from 1 to 7.

When not specified, the statistical tests used are chi^2-tests (MÜHLENBERG 1976). Other tests were used according to SIEGEL (1956).

Results

Food components

In 34 of 120 stomachs no food remains were detected. A further 9 contained less than 1 ml and are also desregarded. In 11 of 83 intestines and 2 of 354 scats no food remains could be identified. A list of all individual samples including origin, place, date and main prey remains identified is given in WEBER (1987).

A list of all food items forming more than an estimated 10 % of the sample concerned is given in Tab. 1. As the samples are not randomly distributed over seasons, regions, age-groups or sexes, Tab. 1 does not give a representative figure of an average polecat diet in Switzerland. Therefore, no frequencies are given.

In the mammal group, most small ground-living species of the region are present. The considerable number of shrew records is remarkable. Ungulate and carnivore remains were interpreted as carrion. Remains of domestic rabbits were almost exclusively found in the droppings of a female polecat that foraged on a rubbish-heap with many carcasses available. Hare remains were once recorded together with several maggots. This item was considered as carrion. Having observed foraging polecats for several years, I believe that most of the hare records and all hedgehogs aught to be placed in this category. However, as I can not prove this, they have been retained in the "mammal" category for further analysis.

Chicken eggs are broken by feeding polecats and the contents are licked. Therefore, they often leave no traces in scats or intestines. Sometimes, when polecats had been observed while foraging, identification of bird species by fragments of eggshell was possible. The proportion of eggs in the polecat diet is certainly underestimated in this

Table 1. **Recorded food items of swiss polecats**

Food items		Rel. volume in sample > 50 %	50 %	25 %
Mammalia	*Erinaceus europaeus*	1	1	–
Insectivora	*Sorex minutus*	1	–	–
	Sorex araneus	2	5	–
	Sorex/Neomys sp.	3	–	–
	Crocidura russula	3	–	–
	Crocidura sp.	3	–	–
	unid. Soricidae	1	–	–
	Talpa europaea	1	–	–
Lagomorpha	* *Oryctolagus cuniculus* f. dom.	10	3	–
	Lepus capensis	16	2	–
	* *Lepus capensis*	1	–	–
Rodentia	*Glis glis*	3	1	–
	Clethrionomys glareolus	8	3	–
	Arvicola terrestris	4	–	–
	Microtus arvalis	2	–	–
	Microtus agrestis	9	3	2
	Microtus/Pitymys sp.	10	3	1
	Ondatra zibethicus	1	1	–
	Apodemus sylvaticus	7	–	–
	Apodemus sp.	23	2	3
	Rattus norvegicus	11	4	1
	Mus musculus	3	–	–
	unid. Rodentia	1	–	–
Carnivora	* *Canis lupus* f. familiaris	1	–	–
	* *Martes martes*	2	–	–
	* *Felis sylvestris* f. catus	5	–	–
Artiodactyla	* *Sus scrofa*	1	–	–
	* *Capreolus capreolus*	3	1	–
	* *Capra aegagrus* f. hircus	5	–	–
Unid. Mammalia		–	1	–
Aves	*Gallus gallus* f. dom.	5	1	–
Eggs	*Meleagris gallopavo* f. dom.	1	–	–
	Gallus/Anas f. dom.	4	1	2
Wild birds	*Turdus viscivorus*	–	1	–
	Unid. Passeriformes	3	1	–
	Unid. Aves	4	2	–
Poultry	*Gallus gallus* f. dom.	5	1	1
	* *Gallus gallus* f. dom.	11	–	–
	Meleagris (?) f. dom.	1	–	–
Reptilia	*Lacerta agilis*	–	1	–
	Podarcis muralis	1	–	–
Amphibia	*Salamandra salamandra*	1	–	–
	Bufo bufo	135	9	4
	Rana "esculenta"	4	1	–
	Rana temporaria	39	2	1
	Rana sp.	43	6	5
	Unid. *Anura*	9	–	–
Pisces	Unid. fish	8	–	–
Invertebrata	*Arion* sp.	2	–	–
Mollusca	Tettigonioidea	1	–	1
Arthropoda	*Gryllotalpa gryllotalpa*	2	2	2
	Acridoidea	–	–	2
	Dermaptera	–	–	2
	Coleoptera	2	3	–
	Vespoidea	1	–	–
	Lepidoptera (mites)	–	2	–
	unid. Arthropoda	2	–	–

Table 1 (continued)

Food items		Rel. volume in sample >50 %	50 %	25 %
Annelida	Lumbricidae	–	–	2
Other Meat	Commercial catfood	1	–	–
	Meat/carrion	14	–	1
Plants	Apple	5	1	–
	Pear	1	–	–
	Plum	4	1	–
	Cherry	–	–	1
	Fig	1	–	–
	Tomato	2	–	–
	Unid. fruit	–	–	2
	Peanut	1	–	–
	Salad leaves	2	–	–

Items interpreted as carrion or offal are indicated with *. Not interpreted as food remains and therefore not included in this table: polecat hair, dirt, grass, hay, straw, tree-leaves, paper, rubber, trap-bait, tapeworms

paper. This can be illustrated by the following episode: One of the radiotracked polecats used a resting-site in a barn for two weeks. I collected there 6 droppings and the shells of 7 chicken eggs. None of these scats contained detectable egg remains. Similar observations were made several times.

11 scats with chicken remains (mainly skin from the legs and cervical vertebrae, no feathers) originate from a polecat who was observed taking offal behind a house. These samples will be considered as "carrion" in the following.

"*Rana esculenta*" is actually considered as two or three species, which were not distinguished appropriately in the identification key used. Most of the frogs mentioned as *Rana* sp. are probably *Rana temporaria*; other possible species (*R. lessonae, esculenta, ridibunda* and *dalmatina*) are rare or even absent in most of those areas from which samples originated.

No special attempts were made to identify fish and bird species, as these types of prey occurred only rarely. These animals are normally not hunted, but found as carrion (pers. observations). All in all, the "carrion/offal" category is surely underestimated in this paper, but not as extremely as the eggs.

Seasonal variations

Seasonal variation of diet composition is shown in fig. 1. In summer and autumn, amphibians (*Rana temporaria* and *Bufo bufo*) form the bulk of the food of Swiss polecats. Carrion/offal is of particular importance in winter, when the proportion of anurans is smaller. Considering the relative importance of these two food categories, I distinguish in the following the seasons "winter" (December to April) and "summer" (Mai to November).

The seasonal importance of food categories is given in tab. 2. Significant differences of the proportion in polecat diet were found for amphibians ($p<0.001$ for scats; $p<0.05$ for guts), carrion ($p<0.001$ in both samples) and mammals ($p<$ .01 in scats; $p<0.05$ in guts). Other categories are of minor importance throughout the year, except possibly eggs.

Due to the dominance of anurans, the food niche is markedly narrower in summer than in winter. However, amphibians are also an important food in winter (48 % in december, 28 % in january, pooled data), when their activity is reduced or nil. Only in february was

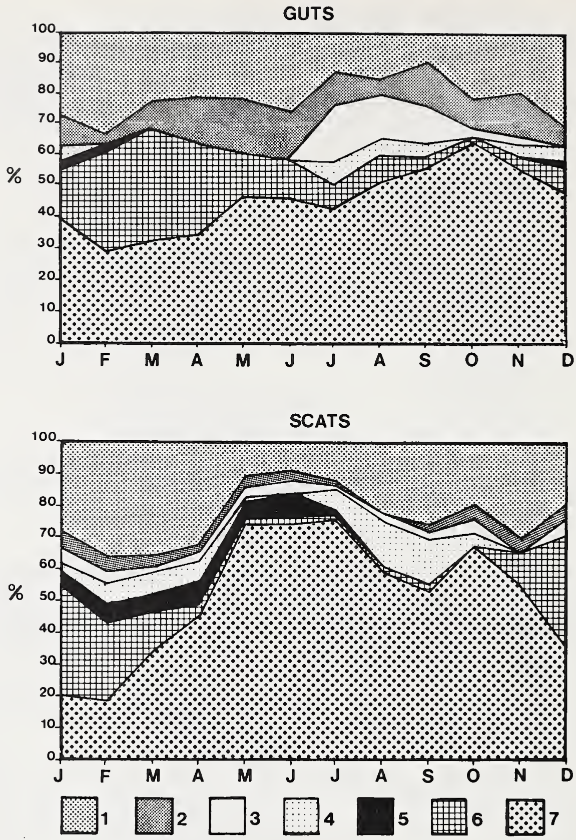

Fig. 1. Seasonal proportions of different food categories in polecat diet. Given are Gliding values over 3 months. Food categories given are mammals (1), birds/reptiles/fish (2), invertebrates (3), fruits (4), eggs (5), carrion/meat (6) and amphibians (7). Sample sizes (N) for single months are (guts/scats): J 12/26; F 5/34; M 9/34; A 8/30; M 14/21; J 8/47; J 3/8; A 16/20; S 17/15; O 15/8; N 18/1; D 15/11

this proportion slightly below 20 %. The reduced anuran contribution to diet is mainly compensated by an increase of the carrion/offal category. Monthly proportions of these two categories are strongly correlated ($r_s = -0.767$; $p < 0.001$).

Different treatment of scats (255 samples, 12 individuals) and guts (139 samples, 88 individuals) in tab. 2 shows that the above-mentioned seasonal differences in polecat diet are a general phenomenon in Switzerland; local specialities will be shown below.

Age- and sex-specific diets

The diet of juveniles is compared to that of adults (>1 year old) in the months of July to October, as juveniles occur per definitionem only during this period (tab. 2). There are significant differences for the occurrence of mammals ($p < 0.001$) and fruits ($p < 0.01$). The difference in the category of invertebrates is not significant ($p < 0.12$), presumably due to the small sample size. Reduced exploitation of mammals and compensation of this by feeding on fruits and invertebrates leads to a broader food niche in juveniles.

Scats were not used to investigate sexual differences in the diet, as there are no female

Table 2. **Dietary differences according to season, age and sex**

Period	Winter (XII.–IV.)		Summer (V.–XI.)		July–October		Whole year	
Sample	Guts All	Scats All	Guts All	Scats All	Guts/Scats pooled Juveniles	Adults	Guts Females	Guts Males
Mammals	24.5	31.5	19.8	15.2	6.5	32.2	25.0	24.2
Amphibians	34.4	34.1	53.8	66.7	55.6	54.4	44.3	44.0
Other vertebrates	10.4	4.1	12.1	2.7	8.6	8.9	14.3	9.7
Carrion/offal	25.0	18.5	5.5	2.5	5.1	2.2	11.4	19.0
Invertebrates	0.0	2.6	6.6	3.6	10.3	2.2	2.9	0.0
Eggs	1.6	3.9	0.0	4.2	0.0	0.0	2.1	0.0
Fruit	4.2	5.4	2.2	5.0	13.8	0.0	0.0	3.2
Sample size (N)	48	135	91	120	58	45	35	62
Niche breadth	3.94	3.90	2.85	2.11	2.83	2.45	3.41	3.35

The percentages of occurrence are given for seven main food categories. 28 scats of a female which lived exclusively on a rubbish-heap and foraged there on carrion and rats (all in October) are omitted in this table

droppings from winter and only those of three individuals in summer. This database would not allow individual variation to be separated from sex-specific variation. To obtain a sufficient sample-size, data from the whole year were pooled (Tab. 2). The data let not suspect sex-specific diets.

As polecats show a prominent sexual dimorphism, corresponding differences in prey size might be expected. An analysis of prey size was unfortunately not possible for anurans, the main dietary component: Intraspecific variation in the size of adult frogs and toads is considerable compared to mammals (HINTERMANN [1984] found in the Leimental area spawning *Rana temporaria*-females from 22 to 99 g), but the small anuran bone fragments could rarely be correlated to the size of the victim. Sex-specific proportions of different-sized prey species of mammals and invertebrates are given in tab. 3.

The table shows that male polecats do not exploit larger mammals than females. A statistical test (Kolmogorov-Smirnov-test for 2 samples) shows even the contrary ($D = 0.400$; $p < 0.025$). Pooling murids and microtids does not fundamentally change the image ($p < 0.05$). It must be stressed however, that the database is restricted, that the main prey (anurans) is not considered and that most hares are probably not killed, but found as carrion.

Table 3. **Occurence (%) of different-sized prey from the mammal/arthropod group in females and males**

Prey	Males	Females
Arthropoda	9.4	9.8
Soricidae	18.3	7.3
Apodemus, Mus	38.0	20.7
Microtus, Clethrionomys, Pitymys	25.8	25.6
Talpa, Glis, Arvicola	3.8	9.8
Rattus norvegicus	1.9	0.0
Erinaceus europaeus	0.9	0.0
Lepus capensis	1.9	31.8
Sample size (N)	53.25	20.5

Pooled data from all individuals exept one female, which lived on a rubbish-heap and foraged exclusively on rats and carrion. Size-classification of prey according to BRUGGE (1977) and VAN DEN BRINK (1975).

Regional variations in diet

Due to the mountain chains of the Alps and the Jura, ecological conditions in Switzerland range from arctic to submediterranean, altitude being the most important factor. I therefore investigated regional variations in polecat diet. The study areas "Leimental" and "La Brévine mountains" are described above. Guts were obtained from the whole country, which for the following analysis is divided into areas above and below 500 m of altitude.

The resulting four regions with different ecological conditions and human land use can be characterized as follows (Note that 1 and 4 are relatively homogenous; 2 and 3 very heterogenous areas):

1. 1000–1300 m: harsh winters (January mean −4 °C), conifer and mixed mountain forests, mountainous pastures, few, isolated farms (partly not used in winter).
2. 500–1000 m: cold winters (January mean −1 to −3 °C), mixed forests, dairy-farming, dispersed farms and habitats.
3. 250–500 m: mild winters (January mean +1 to −1 °C) decidous and mixed forests, mainly arable farming, farms and habitats concentrated in villages.
4. 300–450 m: similar to 3), but almost exclusively decidous forests and arable farming.

Polecat diets in these 4 regions are presented in fig. 2. Differences between regions are most pronounced during winter, when the food-niche in the mountains is narrower than in the lowlands. In the La Brévine mountains, anurans are the staple food throughout the year, with *Bufo bufo* dominating clearly. The relationship between altitude and the importance of anurans as polecat food was tested by a Mann-Whitney-U-test using all guts. This test confirms the impression from fig. 2 ($U = 2644$; $Z = 1.79$; $p < 0.05$). A multivariate approach, taking account of seasonal, sex- and age-related biases, would probably reveal a correlation of higher significance.

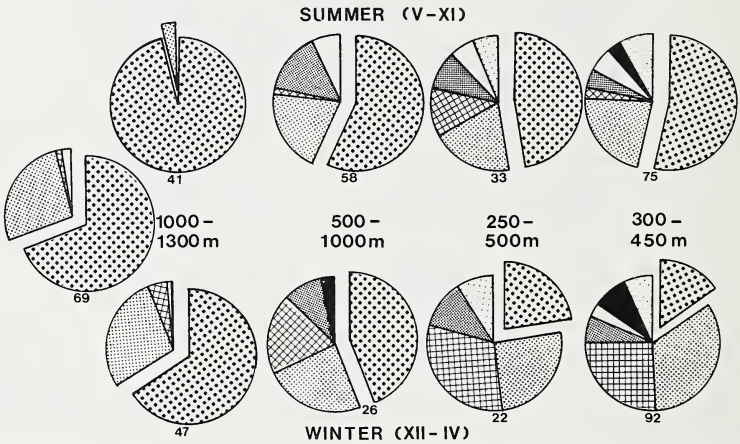

Fig. 2. Polecat diet in regions of different altitudes. Circle segments are proportional to frequency of occurrence. Categories identical to fig. 1. Amphibian segments are cut out. Data from scats (1000–1300 m; 300–450 m) and guts (500–1000 m; 250–500 m). At left 69 scats from autumn to winter which could not be dated exactly. Sample sizes (N) below circles

Discussion

Methodical weaknesses

Several authors have tried to correlate absolute quantities of food remains in scats and guts to quantities of food ingested (e.g. Erlinge 1981; Lockie 1961; Goszczynski 1976; Holisova and Obrtel 1982; Waechter 1975; Zielinsky and Spencer 1983). Correction factors for different items are thereby established on the basis of feeding trials. For four reasons, such attempts were not undertaken in the present study: i) The digestability of specific items can depend on the presence of other items. For example, polecats fed with pure meat excrete undigested meat cells; when meat is fed together with whole mice, no remains of the meat are found in the scats (pers. obs.). ii) Depending on the circumstances, different parts of the same prey-type with different proportions of undigestable matter may be eaten (Erlinge 1981): When many frogs are available, polecats may eat only the muscles of the hind legs, whereas in other circumstances the whole animal is eaten (Weber 1987). iii) The same prey type may occur in different sizes (e.g. hares, rats, anurans), which can not necessarily be assessed using undigested remains. iv) In this study I was interested in the composition of typical polecat diets and not in the absolute amount of prey items eaten.

Thus, polecat diet was investigated by means of frequency analysis, which has often been used to evaluate mustelid diets (Amores 1980; Brugge 1977; Danilov and Rusakov 1969; Erlinge and Jensen 1981; Kalpers 1983; Rasmussen and Madsen 1985; Raymond et al. 1984; Roser and Lavers 1976; Rzebik-Kowalska 1972; Tapper 1976 and others). Each scat and the contents of each stomach or intestine is considered as one independent sample of a polecat meal. Diet composition (not numbers of prey eaten) can be assessed accurately by this method, if only one prey-type is found per sample (Erlinge 1981; Debrot 1981; Moors 1975; Day 1968). In the present study this was mostly the case.

The occurrence of different prey types in the same sample presents the fundamental problem of frequency analysis. Some authors have tried to solve it by treating every identified prey item as the independent sample and by calculating frequencies of occurrence as the proportion of total items identified (e.g. Debrot 1981; Danilov and Rusakov 1969). A known disadvantage of this approach is the overestimation of small and rare dietary components (Debrot 1981).

A lesser-known bias of the above mentioned approach is the overestimation of prey-types whose remains are defaecated over long periods. Roser and Lavers (1976) mentioned for ferrets *(Mustela putorius* f. furo) that anuran bones are defaecated more rapidly than mammal hairs. This is also supported by the observation during the present study that hair and feathers were more often found in small quantities than anuran bones (Tab. 4). Further support for this is given by the following observation: In 8 almost empty stomachs (< 1 ml) hairs were recorded but not amphibian bones, whereas in 77 stomachs with more than 1 ml of contents, anuran bones were present 34 times and hairs 20 times ($p < 0.001$). Dearborn (1932) found feathers in the scats three days after feeding a sparrow to a mink *(Mustela vison)*. Meat remains would be defaecated by polecats within a few hours (Goethe 1940). Thus, one mouse could leave detectable traces in dozens of scats, whereas the bones of a frog might be defaecated in one single dropping.

Table 4. **Occurrence of hairs, feathers and amphibian bones as bulk and as trace in guts and scats**

Estimatet percentage of sample volume	≥ 25 %	≤ 10 %
Hair/feather	149/16	47/8
Amphibian bones	255	13
$Chi^2 = 41$; $p << 0.001$		

Attempts to overcome these disadvantages by use of relative volume or weight of different items in a sample (Rzebik-Kowalska 1972; Hargis and McCullough 1984) only make sense when all prey types have comparable proportions of undigestable matter. Amphibians and mammals do not fulfil this condition (Brugge 1977).

I have tried to minimize the biases mentioned above by disregarding stomach contents of less than 1 ml, and prey remains of less than an estimated 25 % of sample volume. Equal treatment of every identifiable item would have resulted in higher proportions of mammals and invertebrates. However, because only a minority of the samples contained more than one prey-type, such methodical differences are not sufficient to explain the differences of the results presented here to those of other studies.

The diet of polecats in Switzerland and elsewhere

Like other european *Mustela*-species (e.g. Debrot 1981; Erlinge 1981; Moors 1975; King 1980; Cuthbert 1979) and in remarkable contrast to other mustelids of the region (Waechter 1975; Tester 1986; Marchesi 1985; Born 1974) Swiss polecats are almost totally carnivorous.

The present study shows a dominance of anurans (mainly *Rana temporaria* and *Bufo bufo*) in the diet, which is most pronounced in summer and autumn. During this period more than half the prey are frogs and toads. In winter and spring, amphibians are partly replaced by carrion, and to a minor extent by mammals, but remain an important dietary component even during the coldest months. In the mountains, anurans are also the staple food in winter; specialization on amphibians is positivly correlated with altitude.

Invertebrates and fruits are taken mainly by juveniles, which show a correspondingly lower proportion of mammals in their diet than adults. Eggs have not often been found, but this may be due to a methodical bias. Personal observations of radio-tracked polecats (Weber 1987) suggest a higher importance of this dietary component, especially in winter and spring.

These findings do not correspond very well to those of other authors in other countries, where far smaller percentages of anurans were found (Tab. 5). A proportion of more than 30 % was found only in the summer diet in northwest Russia. Mermod et al. (1983) and Weber (1986) out of 24 scats of Swiss polecats only found amphibian remains in one case.

Table 5. **Polecat diets from Germany (Goethe 1939), Poland (Rzebik-Kowalska 1972), Northwest Russia (Danilov and Rusakov 1968). Czechoslovakai (Kratochvil 1952) and the Netherlands (Brugge 1977)**

	Winter			Summer		Whole year	
	Russia	Poland	Germany	Russia	Poland	Czechosl.	Netherlands
Small mammals	51	17	37	52	14	47	32
Lagomorphs	1	2	4	0	7	10	29
Amphibians	19	11	18	32	19	18	20
Other vertebrates	9	20	14	11	25	14	20
Carrion/meat	18	27	2	2	10	0	0
Invertebrates	0	1	10	0	10	12	0
Eggs	0	17	17	0	14	0	0
Fruit	3	5	0	2	2	0	0
Sample size (N)	65	220*	57	26	44*	35	41

* 62 empty stomachs included. – All data from gut contents, partly recalculated to give % frequencies of occurrence.

Only Labhardt (1980) observed in the Leimental area a female which brought 61 % anurans to her young (61 prey identified). Goethe (1939) mentions that amphibians may dominate polecat diet in summer.

I see three factors that may explain the discrepancy of my results with most published data on polecat diet: i) methodical biases, ii) sampling biases, iii) local dietary specialization of polecats.

Danilov and Rusakov (1968), Rzebik-Kowalska (1972), Brugge (1977) and Kratochvil (1952) have certainly overestimated the importance of mammals and birds in relation to amphibians, using also almost empty stomachs and considering all identified remains as single samples, regardless of their relative contributions to the sample volume (see discussion above). These biases have already been recognized and mentioned by

Brugge. However, this explanation is not sufficient to explain all discrepancies; a calculation of the diet composition of Swiss polecats using the methods of the papers cited above, still shows anurans as the staple food.

Radio-tracked polecats foraged exclusively in forests and in and around human buildings. In forests, mainly anurans were taken; in settlements none (Weber 1987). The gut collections of other authors were possibly habitat-biased. The high proportions of eggs found by Rzebik-Kowalska may be an indication of such a bias. As the studies mentioned in tab. 5 are based on gut analysis, presumably from shot or trapped polecats, a habitat bias in polecat hunting could explain the small numbers of amphibians.

It is not clear, why Swiss polecats should specialize on other prey than those elsewhere. Only the polecats in the Netherlands intensively use a ressource, which does not exist in Switzerland (rabbits). After declining during the last 50 years (Baumgartner 1986), amphibians do not seem to be more abundant in Switzerland at present than in Central and Eastern Europe dozens of years ago. However, the data from Switzerland show in winter low proportions of anurans in the lowlands. In these regions, foraging during the cold season is concentrated in and around barns and farmhouses. High anuran proportions in the mountains can be explained by poor food resources around farmhouses and, as a consequence, continued foraging in forests also during winter (Weber 1987). Therefore, at least in winter, a lower significance of frogs and toads as polecat food can also in Switzerland be expected outside mountainous areas, as has been shown in fig. 2.

Sexual dimorphism and diet

Sexual dimorphism of body size is a characteristic feature of mustelids, males always being larger than females. Two different theories were proposed to explain this dimorphism (for an extensive discussion hereon see Moors 1980): The first theory (e.g. Brown and Lasiewski 1972) claims that sexual dimorphism is a strategy for avoiding intraspecific competition, allowing each sex to exploit different food-resourcers. A more recent theory explains sexual dimorphism by different sex-specific pressures (females being selected for small size because of lower maintenance costs, and males being selected for successful intrasexual competition for mates; Erlinge 1979; Moors 1980; Raymond et al. 1983).

Discussion on the significance of the two competing theories concentrated until now on theoretical arguments and data from *Mustela erminea* and *M. nivalis*. Unfortunately, as far as is known, these species show not only the polygynous mating system with no male assistance in cub-rearing (argument for the second hypothesis), but also sex-specific diets with males killing larger prey than females (argument for the first hypothesis). So far, it is not clear whether food specialization is the cause or simply one consequence of sexual dimorphism.

The data presented here are, as those of Brugge (1977), arguments against the Brown and Lasiewski theory. The smaller females do not prey on smaller animals than males. It is highly probable that the situation is even inverse ($p < 0.025$). If polecats showed a similar mating system to that of stoats, *Mustela putorius* would be a stronger argument for the theory of Erlinge and Moors than *Mustela erminea*. Such a mating system may be indicated by the observation of a dramatic fat loss of male polecats during the mating season, whereas females loose their reserves during cub-rearing (Weber 1987).

The food niche of polecats and other mustelids

Polecats occur in Switzerland together with closely related (stoat, *Mustela erminea*) and similar-sized (pine marten, *Martes martes*, stone marten, *M. foina*) mustelids. According to "Gause's hypothesis" (Krebs 1978) long-term coexistence of different species is only possible where their niches differ significantly. Rosenzweig (1966) explained the coexist-

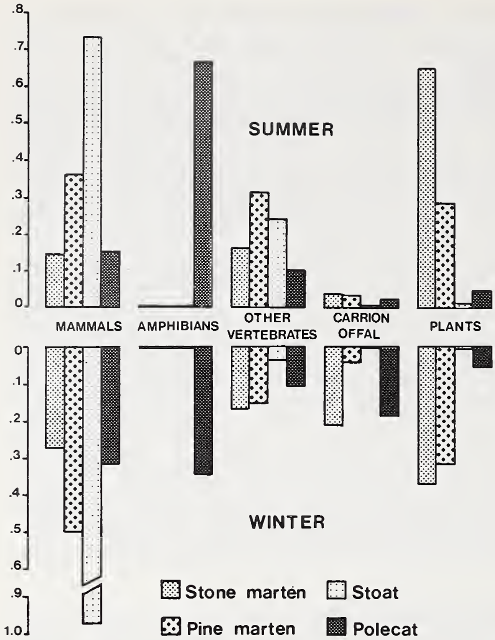

Fig. 3. Diet of 4 mustelids from Switzerland. Proportions of each of the five food categories are given for every species in summer and winter (sources see tab. 6)

ence of three species of weasel in North America with size-specific food specialization. Local dietary differences have been described for European *Mustela nivalis* and *M. erminea.* POWELL and ZIELINSKI (1983) have however shown theoretically that even partly overlapping food-niches make the long-term coexistence of two or more *Mustela*-species impossible, if no other fundamental biological differences occur. Newer theories explain the coexistence of *M. erminea* and *M. nivalis* with other interspecific differences than ROSENZWEIG (SIMMS 1979; KING and MOORS 1979). As rabbits occur only locally in Switzerland, there is no larger prey-class available for polecats than for stoats. Stoats are morphologically better adapted to vole-hunting than polecats. On the other hand, all resources used by polecats are also accessable to stone martens and pine martens.

Fig. 3 shows that polecats probably escape competition for food by

Table 6. **Overlap of food-niches of polecat (present study, gut contents), stone marten (Waechter 1975; Tester 1985), pine marten (Marchesi 1986) and stoat (Debrot 1981) in Switzerland**

Summer data of stone marten are means from WAECHTER and TESTER, winter data are from TESTER. Niche overlap is calculated as $O_{xy} = 1-0.5\,\Sigma\,|p_{ix}-p_{iy}|$ (MÜHLENBERG 1976), based on food-categories mammals, birds, reptiles, amphibians, fish, invertebrates, carrion/offal, fruit/plant

	Winter/Spring			Summer/Autumn		
	M. putorius	*M. foina*	*M. martes*	*M. putorius*	*M. foina*	*M. martes*
Martes foina	0.535	–	–	0.339	–	–
Martes martes	0.374	0.760	–	0.390	0.623	–
Mustela erminea	0.265	0.286	0.526	0.358	0.318	0.533

Table 7. **Records interpreted as amphibian gut contents**

Item	N records	Item	N records
Pulmonata	4	Formicidae	19
Diplopoda	1	Div. Hymenoptera	4
Tettigonioidea	2	Lepidoptera	2
Grylloidea	1	Nematocera	3
Dermaptera	7	Brachycera	4
Heteroptera	4		
Coleoptera	29	Unid. Arthropoda	15

specialized preying on frogs and toads, which are not systematically exploited by other mammals (Note that all data in fig. 3 originate from the polecat-study areas Leimental [Waechter 1975; Tester 1986] and La Brévine mountains [Debrot 1981; Marchesi 1985] or nearby sites). The realized food niches of stoats, stone martens and pine martens show larger overlaps between themselves than with that of the polecat (Tab. 6). The only exception to this is the apparent niche overlap in winter between stone marten and polecat. This is due to an undifferentiated analysis of the mammalian component of their respective diets. A more detailed comparison shows that the bulk of mammals eaten by stone martens are voles (70 %), whereas voles only account for about 30 % of the mammals in the polecat diet.

One can conclude that Swiss polecats considerably reduce potential food competition with other mammals by specialising on frogs and toads. On the other hand one has to note that the consequence of this freedom from competition is the highest trophic position of all terrestrial mammals in the region.

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Zusammenfassung

Zur Nahrung des Iltisses (Mustela putorius L.) in der Schweiz

Die Nahrung schweizerischer Iltisse wurde durch die Analyse von Magen-Darm-Inhalten von 120 zwischen 1982 und 1987 gestorbenen Individuen sowie durch die Analyse unverdauter Reste in 354 Losungen von mindestens 12 Individuen untersucht. Iltiskadaver erhielt ich aus der ganzen Schweiz und angrenzenden Gebieten Frankreichs. Fast alle Losungen stammen von 12 mit Radiosendern markierten Tieren aus dem Leimental bei Basel (300–450 m) und dem Neuenburger Jura (1000–1300 m). Reste von Iltismahlzeiten bilden eine weitere Informationsquelle. Quantitative Aussagen erfolgen auf der Basis gewichteter Frequenzen, wobei Reste, die deutlich weniger als 25 % der einzelnen Stichprobe (Losung, Mageninhalt, Darminhalt) ausmachten, nicht berücksichtigt wurden.

Schweizerische Iltisse ernähren sich fast ausschließlich carnivor. In einem geringen Ausmaß werden, hauptsächlich von Jungtieren, auch Früchte aufgenommen. Als Nahrungsbestandteile konnten 43 Tierarten, 8 Pflanzenarten sowie Fleischabfall und Haustierfutter nachgewiesen werden. Die dominierende Nahrungskomponente bilden Anuren. Weitere Nahrungskomponenten von Bedeutung sind Kleinsäuger (hauptsächlich Muridae, aber auch Microtidae und Soricidae), Aas und Fleischabfall aller Art und Eier von Hausgeflügel.

Der Anurenanteil der Nahrung ist im Winter geringer als im Sommer und in Berggebieten höher als im Tiefland. In Berggebieten sind Anuren auch im Winter die wichtigste Nahrungskomponente. Jungtiere fressen häufiger Invertebraten und Früchte, dafür seltener Kleinsäuger als adulte Iltisse. Eine unterschiedliche Bedeutung der Nahrungskategorien Amphibien, Säuger, andere Vertebraten, Invertebraten, Aas/Fleischabfall und Früchte in der Nahrung der beiden Geschlechter zeigte sich nicht. Weibchen bevorzugten innerhalb der Gruppe Säugetiere/Arthropoden größere Beutetiere als männliche Iltisse.

Die angewandten Methoden und die Ergebnisse werden unter verschiedenen Gesichtspunkten diskutiert und mit Literaturangaben verglichen. Die Nahrung schweizerischer Iltisse unterscheidet sich durch den hohen Anurenanteil stark von Befunden aus anderen Gebieten. Die Nahrungsnische schweizerischer Iltisse überlappt nur wenig mit denjenigen anderen Musteliden, welche untereinander dagegen teilweise starke Nischenüberlappung zeigen. Iltisse besetzen die höchste trophische Position aller terrestrischen Carnivoren des Gebietes. Die Ernährung des Iltisses bildet ein wichtiges Zusatzargument in der Debatte um die Ursachen des Geschlechtsdimorphismus in der Gattung *Mustela*.

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Author's address: Dr. Darius Weber, Ökologische Beratung und Systemanalysen, Talackerstraße 23, CH-4153 Reinach, Schweiz