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Foraging in polecats (*Mustela putorius* L.) of Switzerland: The case of a specialist anuran predator

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Abstract

Studied the foraging behaviour of 12 radio-tracked polecats (*Mustela putorius* L.) in a mountainous and a lowland area of Switzerland and of captive-held animals. Five different foraging options are described, of which at least three are self-excluding: 1. Hunting small mammals in and around houses; 2. Hunting rats in rubbish dumps; 3. Collecting anurans in suitable forests; 4. Collecting eggs, pet food or offal in and around houses; 5. Collecting offal in rubbish dumps. Mammals are easily found by polecats, but are difficult to seize. Anurans are difficult to find but easy to seize. Frog-collecting polecats seek intensively in one small area for one or more foraging bouts, and then leave for another, sometimes distant area. The resulting pattern can best be described as nomadic; a polecat may not return to a given area for some weeks or months.

It is hypothesized that Swiss polecats are specialized anuran foragers because they are awkward rodent hunters. There are two reasons for taking other foraging options: 1. extreme local concentrations of food (e.g. rubbish dumps, carcasses, hen houses), and 2. extreme travelling costs between resting sites and amphibian-hunting areas (in winter, when polecats are forced to rest inside houses).

Introduction

Polecats are usually described as relatively unspecialized carnivores (e.g. TSCHUDI 1858; BREHM 1879; GRASHEY 1894; HAINARD 1948; HERTER 1959; RAHM 1976; WALTON 1977). Some of these authors also mention a certain preference for fruits or honey. Food analyses from all over Europe confirm this (GOETHE 1939; KRATOCHVIL 1952; DANILOV and RUSAKOV 1969; RZEBIKKOWALSKA 1972; BRUGGE 1977; MERMOD et al. 1983). Recent investigations on the diet of polecats from Switzerland have revealed a dominance of anurans (WEBER 1988a). This was already mentioned by ROHRDORF (1853) and agrees with observations of LABHARDT (1980).

Prey-catching and related behaviour in polecats and ferrets has been intensively studied under laboratory conditions (GOETHE 1940; RÄBER 1944; HERTER 1953; EIBL-EIBESFELDT 1956; WÜSTEHUBE 1960; GOSSOW 1970; APFELBACH 1973; APFELBACH and EBEL 1975; APPELBACH and WESTER 1977). In contrast, we know almost nothing of the foraging behaviour of wild polecats. HERRENSCHMIDT (1982) and NILSSON (1978) radio-tracked some individuals, but did not investigate the feeding habits of these animals.

The present study attempts to close this gap, in describing the foraging behaviour of the only specialized predator of anurans among the mammals of central Europe.

Material and methods

The lowland study area

The "Leimental" is a lowland valley on the Franco-Swiss border south-west of Basle (47° 30' N, 7° 29' E; altitude 300–450 m). Compared to the rest of Switzerland, the climate is mild with warm winters (January mean 0°C). The vegetation period is approximately 210 days. Snow-cover occurs only on few days of the year, most often in February.

The dominating land use of the Leimental is arable farming. The main structuring elements of the countryside are strips of woodland along brooks. Between the fields there are locally a few drainage ditches, which in summer are overgrown by shrubs. The hilltops are mostly covered with patchy and irregular-shaped forests of various areas, crossed by many small brooks. These forests consist of old oak, beech and other deciduous trees with local occurrence of conifers (mainly old plantations of silver fir). Clear-cuttings are small, and often left to natural succession. Where the canopy is thin, the ground is covered with large thickets, dominated by bramble.

Farmhouses are mostly concentrated in the villages. Near Basle the rural character of the valley changes to a suburban one, with industrial areas, densely built-up centres and large areas with houses and gardens.

The mountain study area

The mountains of La Brévine (46° 58' N, 6° 39' E; altitude 1000–1300 m) are a chain of the Swiss Jura mountains south of the village of La Brévine. For the geographical latitude, the climate is cold with harsh and long winters and a vegetation period of about 140 days (January mean -4°C , annual mean $+4^{\circ}\text{C}$). Temperatures below -30°C occur regularly.

About half the area is covered with mountain forests, with spruce, fir and sycamore as dominant tree species. Locally, there are almost pure stands of spruce to be found. Forestry operates without clear-cutting; only selected individual trees are cut, and there are no plantations. This results in richly-structured stands on a small scale and in a highly uniform appearance of the woodlands on a large scale. The forest's floor is densely covered with shrubs, bushes, young trees and dead branches.

The rest of the area is mainly covered by grassland and wooded pastures, which are divided by stone walls, hedges, and combinations of both. Farmhouses and stables are isolated and scattered; not all of them are used in winter. There is almost no surface water in this study area.

Methods

Polecats were captured in wooden box traps ($85 \times 16 \times 24$ cm) baited with mice or tinned sardines. Captured specimens were sedated with an intramuscular injection of 20 mg Vetalar® (Parke, Davis and Co, Detroit, USA) and equipped with a collar containing a transmitter (type MV/A, Karl Wagener, Cologne, West Germany). The weight of the radio collars was about 30 g, transmitting frequencies around 148 MHz. A female reared in captivity was also radio-tracked after her release. Systematic observations of this individual started 5 weeks after her release. During this period, she had mated, and her behaviour showed no obvious differences to that of wild individuals. All radio-tracked polecats were adults (Table 1).

Table 1. Radio-tracked polecats, study areas and observation periods

Identification (name)	Sex	Study area	Start of observation	Last observation
Viva	f	Leimental	15. 9. 83	17. 9. 83
Dickkopf	m	Leimental	22. 12. 83	12. 6. 84
Phlegma	m	Leimental	2. 3. 84	16. 3. 84
Methusalem	m	Leimental	27. 3. 84	11. 4. 84
Schaggeli	f	Leimental	27. 4. 84	14. 7. 84
Müllä	f	Leimental	24. 7. 84	23. 8. 84
Micro	f	Leimental	3. 9. 84	27. 10. 84
Urs	m	Leimental	21. 10. 84	25. 11. 84
Jean-Marc	m	La Brévine mountains	1. 6. 84	18. 8. 84
Claude	m	La Brévine mountains	12. 2. 85	27. 2. 85
Paul	m	La Brévine mountains	12. 2. 85	16. 4. 85
Philippe	m	La Brévine mountains	14. 4. 85	3. 5. 85

The animals were located with a receiver and a hand-held H-type aerial (Karl Wagener, Cologne, West Germany). The constancy of signal strength showed whether an animal was resting or moving. Two types of observation were made: 1. During daytime I located the sites of resting polecats and searched there for scats and prey remains. I recorded location (50 m coordinate grid), date, time, weather and the type of resting place. 2. Periodical monitoring of individuals for (normally) 6 hours was performed by following animals on foot, at close distance. Every 10 minutes, coordinates (50 m grid), habitat, weather, activity of the animal and special observations were recorded. In the Leimental area, distances to active polecats could usually be kept at about 50 m or less; in the La Brévine

mountains, due to the difficult topographical situation or to snow-cover, distances were often greater. The animals often made so much noise while moving around that I was able to follow them simply by listening. Monitoring usually took place at night, during the period of highest activity (WEBER 1987).

The habitat types available to individual polecats were quantified by means of 50 m or 100 m gridpoints, which were laid over the minimum-convex-polygon (TREVOR-DEUTSCH and HACKETT 1980) of all locations of the individual concerned.

Techniques of scat analyses and quantitative treatment of these findings are given elsewhere (WEBER 1988a). Results are calculated as weighted relative frequencies of occurrence. Note that prey remains of less than an estimated 25 % of scat volume have been disregarded.

Some direct observations and experiments regarding hunting behaviour were made in an enclosure of 200 m², with two hand-reared, adult male polecats. Experiments to investigate hunting success in relation to prey species and vegetation cover were made in a 2 × 2 m cage within the enclosure. Polecats were trained to expect prey in this cage and to hunt it there. They could enter and leave this cage at will. The prey animals were not able to escape from this smaller cage.

The hunting experiments were performed in the following manner: A prey animal was placed in the hunting cage. Then, presumably attracted by scent, a polecat would enter the cage and attempt to catch the prey. Based on definitions of Gosow (1970), I protocolled on a tape-recorder the following phenomena: 1. The beginning of the searching phase, which is marked by signs of positive excitement, hasty, undirected movements and sniffing around on the ground; 2. The moment of attack (raised head, jumping instead of walking, visual or acoustical orientation); 3. The end of the attack (either grasping the prey, or beginning another searching phase, if the prey has escaped by jumping away or by immobility); 4. The success of the attack; 5. The number of grasping attempts during the attack; 6. Special events depending on situations. Later, the durations of searching phases and attacks were timed with a stopwatch while playing the protocol tapes. Details of these experiments and their results are given elsewhere (WEBER 1987). Here, only successes of attacks are reported (successful = grasping the prey; unsuccessful = attack without grasping, followed by a new searching phase).

Results

Hunting techniques

Direct observations of wild polecats catching prey were rare. This was mainly due to the strong connection of polecats with dense vegetation: Even at distances of 2 or 3 metres I could not normally see foraging polecats. In some cases, information on hunting techniques resulted from tracks. Therefore, most results presented in this chapter stem from experiments with the two captive polecats, to which I fed more than a dozen anurans and over 100 small rodents of different species (WEBER 1987). Additionally, some experiments with dead prey were performed.

The smell of mice or voles stimulated the captive polecats to excited searching behaviour at distances of about five metres and more. Dead mice thrown into the enclosure were normally found after several minutes of undirected searching. The polecats sometimes rummaged only a few centimeters from the prey without detecting it. Prey finding was greatly eased by pulling the dead mice some metres over the ground with a kind of fishing rod (to produce a scent track): When they first crossed the track while searching, they immediately stopped and followed the scent, keeping the nose to the ground, until they reached the mouse. They hereby often followed a trace in the wrong direction until the starting point, and had to turn back. Living rodents presented in the experimental cage where found in the same way.

Compared to natural conditions, mice and voles in the 4 m² experimental cage were handicapped in avoiding polecat attacks: They were confronted with an unfamiliar environment with no sure escape routes (e.g. holes, trees). However, they often successfully escaped from polecats approaching on their track by jumping away (*Apodemus*), or by remaining motionless until the polecat had run over them (*Apodemus*, *Clethrionomys*). Especially in dense vegetation structure, polecats showed a high rate of unsuccessful attacks on rodents (Table 2). A wild polecat was observed catching a vole (*Microtus agretis*) by "ploughing" with its muzzle along the vole's tunnel.

I never observed any reaction by polecats to the presence of immobile anurans nearby.

Table 2. Rodent-hunting success of 2 polecats under experimental conditions (2 × 2 m cage)

	Only leaf-litter on ground			Cage structured with heap of twigs		
	N _a	N _s	% S	N _a	N _s	% S
<i>Apodemus</i>	128	84	65.6	88	36	40.9
<i>Clethrionomys</i>	17	17	100.0	17	12	70.6

N_a is the total number of attacks, N_s the number of successful attacks (ending with grasping the prey) and % S is the proportion of successful attacks (percent). Different hunting successes are significant ($p < 0.001$ for *Apodemus*; $p < 0.02$ for *Clethrionomys*; χ^2 -tests). Note that there were no holes or other protected places for the rodents in the experimental cage

There was no sign of stimulation by odour or scent tracks. Frogs were found by chance while the polecat was searching at suitable places. To provoke attacks, immobile frogs had to be touched with the nose, the mouth or the vibrissae. When polecats approached, frogs (*Rana temporaria*) and toads (*Bufo bufo*) often avoided detection by pressing themselves to the ground. I never saw an attacked anuran attempt to jump away; once detected, they were always caught.

In winter, polecats also eat anurans when these are hibernating underground. Several times, I found places where polecats had dug up frogs or toads during winter. Such holes were normally not deeper than about 30 cm. I never made an observation that gave me any idea of how polecats are able to detect hibernating anurans. Surprisingly, they found them even in frozen soil and under snowcover of more than a metre.

I once observed an encounter between a radio-tracked female polecat and a hedgehog (*Erinaceus europaeus*). She sniffed with excitement at the rolled-up animal, but made no attempt to bite it. After a few minutes, she lost all interest and continued rummaging around for other prey. Remains of small birds found on polecat snow-tracks never showed blood. I therefore assume that the birds had been found already dead and frozen.

The polecats regularly found eggs in barns and stables where poultry was allowed to range freely during daytime. Often the farmers did not know that eggs had been taken, as the polecats found only those eggs which had been missed by the farmers in the evening. I never observed attacks on chickens, even when these were sleeping in the same barn as the polecat. The ability of polecats to enter hen-houses was poor; they only succeeded when there was an entrance at ground-level.

I once observed a male polecat who tried to enter a poultry yard, for 30 minutes without success, until he was chased away by some geese. The same individual was able to steal eggs from brooding turkeys during the night.

The polecats always took their prey to a hidden and undisturbed place before feeding. The captive polecats in the enclosure could be prevented from feeding by continuous offers of food; they did not start feeding, as long as there was still food to be hidden. When they knew each other's food-hiding, they often performed long reciprocal stealing behaviour before starting to feed.

Sometimes, polecats catch and hide more food than they will eat afterwards. Following radio-tagged animals, I found nine heaps of anurans (which had only partly been eaten) in different numbers near polecat hiding-places. Some had not been eaten, but only killed or injured by bites in the head or neck.

The largest heap was one of 16 common frogs (*R. temporaria*), of which some were still alive. When there are sufficient anurans available, polecats eat only the leg muscles (Fig. 1). In other cases, even toads were eaten entirely, which was also indicated by the regular occurrence of cranial bones in polecat scats.

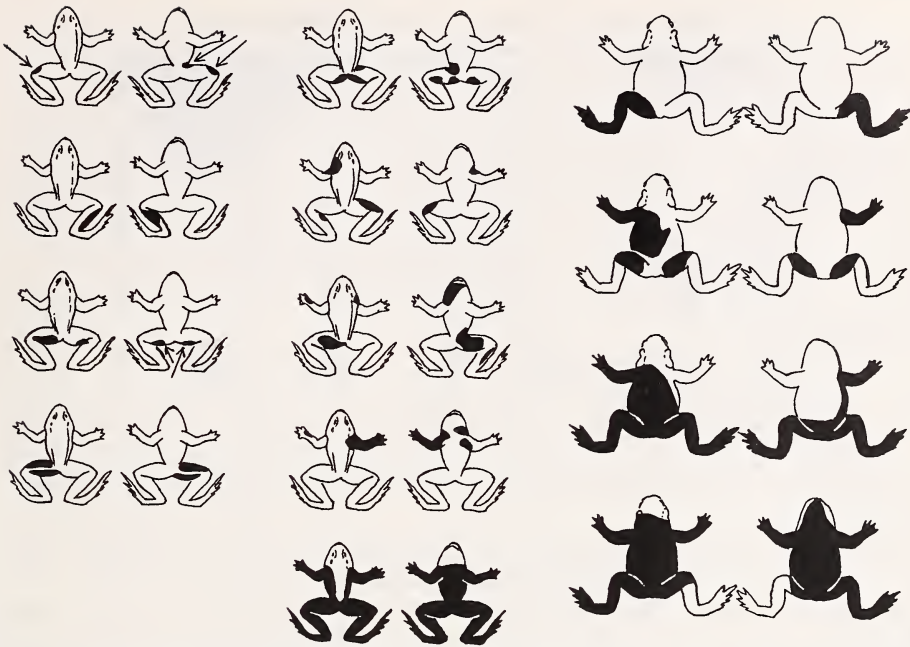


Fig. 1. Anurans killed by polecats but not completely eaten. Common frogs *Rana temporaria* and common toads *Bufo bufo*. Parts eaten in black. View from above (left) and below (right) on the same individuals

Hunting grounds

Table 3 shows all records of active polecats in different habitat types (pooled data from single daytime observations and 10-minute-interval localisations during consecutive monitoring). Forest, farmhouses and refuse dumps make up nearly 90 % of the records, and can be considered as typical polecat habitats. Within the agricultural land category, polecat presence was nearly always restricted to special structures between fields and meadows. Some of the farmhouses used by polecats were situated in the centres of large villages. Records from gardens originate mainly from places near forests. The category "forest" was not subdivided for this analysis, as it was often impossible to attribute a localisation to one of the different forest types available; often, the patches were too small and the localisations not precise enough. According to my subjective impression, the most attractive forest stands were shrubby thickets, and the least attractive those with bare ground below the canopy.

All individuals with such areas within their ranges avoided agricultural areas (Table 4). Rubbish dumps were a rare but attractive resource in the Leimental study area. The three polecats which had dumps within their range spent 83 % (Micro), 40 % (Phlegma) and 19 % (Urs) of their recorded activity at these places.

Forests and houses were within the range of every animal. In the lowland study area, houses were mainly used during winter and spring, whereas in the mountain area, the polecats were mostly active in forests during these seasons also (Fig. 2).

The bulk of food passes through the polecat gut within a few hours (GOETHE 1940), which allows prey remains in fresh scats to be attributed to the foraging of the previous night. Within a single foraging bout, the polecats usually concentrated their activities on one of the three habitat categories forest, buildings and dumps: In 112 of 133 activity bouts, they were recorded to more than 80 % within only one of these three habitats.

Table 3. Records of active polecats in different biotopes

Biotope	Leimental		La Brévine mountains		Total	
	N	%	N	%	N	%
Woodland	572	56.5	329	80.4	901	63.4
Agricultural land	67	6.6	49	12.0	116	8.2
hereof: fields	7	0.7	0	0	7	0.5
grassland	8	0.8	3	0.7	11	0.8
wooded pastures	0	0	18	4.4	18	1.3
marsh, bank	6	0.6	0	0	6	0.4
fallow grounds	23	2.3	0	0	23	1.6
hedges, ditches	23	2.3	28	6.9	51	3.6
Settlements, houses	197	19.4	31	7.6	228	16.0
hereof: farms, vegetable gardens	164	16.2	31	7.6	195	13.7
gardens	28	2.8	0	0	28	2.0
centre of town or village	3	0.3	0	0	3	0.2
industrial area	2	0.2	0	0	2	0.1
Rubish dumps	177	17.5	0	0	177	12.4
Total	1013	100.0	409	100.0	1422	100.0

Table 4. Use of agricultural areas by active polecats

Individual	Total records active	% of records in agricultural area	% of home range agricultural area	χ^2
Dickkopf	468	1.07	42	187.1
Phlegma	30	0.00	a	—
Methusalem	74	6.76	67	40.5
Urs	154	0.00	45	69.0
Schaggeli	77	0.00	20	12.0
Müllä	147	3.40	66	85.3
Micro	163	0.00	0	—
Jean-Marc	130	6.15	27	20.8
Paul	243	5.35	44b	82.6
Claude	22	0.00	44c	10.0
Philippe	14	0.00	44c	6.0

a: All records in a barn and a rubbish dump in a distance of about ca. 2 km; in-between agricultural land; b: Polygon calculated excluding an excursion of about 8 km; c: Offer assumed to be the same as for "Paul" within whose polygon they were recorded.
It is assumed that all areas within the minimum-convex-polygon of its records are potentially accessible to an individual polecat. Significance of avoiding agricultural areas was calculated by χ^2 -tests ($\chi^2_{(1;p 0.02)} = 5.4$; $\chi^2_{(1;p 0.01)} = 10.8$)

Thus, prey remains from different habitat types would not be expected to be found in a single scat.

For 51 daytime resting places there are monitoring data from the previous night, with more than 80 % use of only one habitat type. Table 5 shows that resting sites were mostly found in the same habitat where the activity of the previous night had taken place. Scats which were found in forests or dumps therefore contain with a high probability remains of prey which had been hunted in the same habitat. Scats from buildings may also contain prey remains from other habitats.

It follows that habitat-specific food spectra can be calculated, based on the habitats in which scats of radiotracked polecats were found (Fig. 3). As eggs do not often leave recognizable remains in scats (BRUGGE 1977; WEBER 1988a), their proportion in the

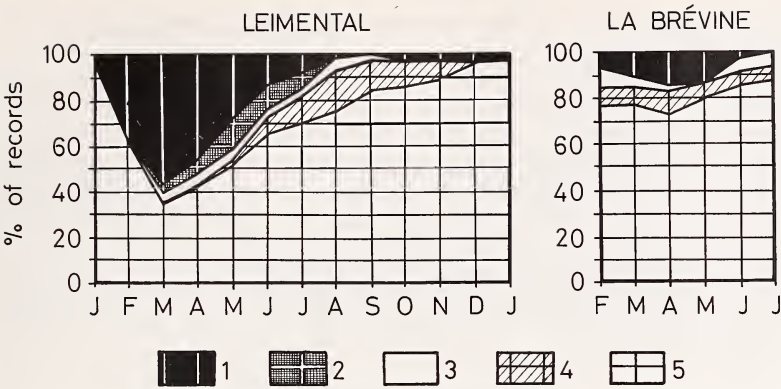


Fig. 2. Use of different biotopes by active polecats through the year. Given are gliding means over three months, excluding rubbish dump records. 1 = farms; 2 = other human settlements; 3 = agricultural land; 4 = hedges, ditches, fallow land; 5 = forest. Numbers of records for single months (Leimental/La Brévine mountains): J 121/0; F 43/68; M 114/90; A 76/118; M 24/3; J 117/37; J 65/93; A 84/0; S 0/0; O 48/0; N 75/0; D 40/0

Table 5. Habitats where polecats had their daytime resting places and habitats of activity in the previous nights

Resting site	Forest, fallow	Activity bout Farm, house	Rubbish dump
Forest, fallow	30 (27)	0	0
Farm, house	6 (4)	8 (6)	1 (1)
Rubbish dump	0	0	6 (4)

The table contains the number of activity bouts with more than 80 % of records within the same habitat category. Numbers of activity bouts with all records in the same habitat are given in brackets

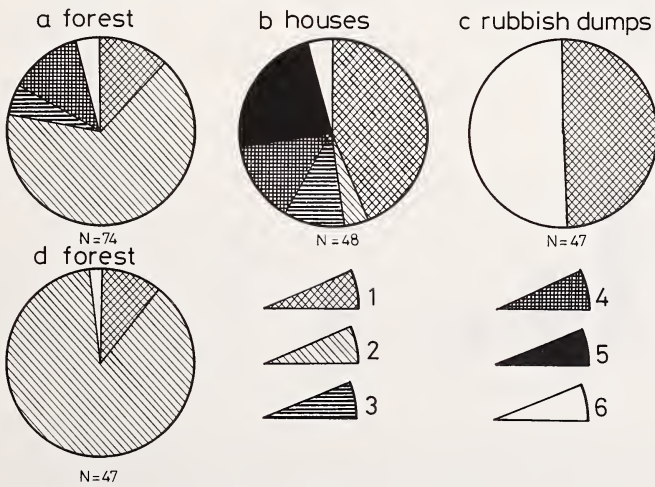


Fig. 3. Habitat-specific food spectra of polecats from Switzerland. 1 = small mammals; 2 = anurans; 3 = other vertebrates; 4 = invertebrates, fruits; 5 = eggs; 6 = carrion, offal. The circle segments are in proportion to the concerned food category in the total diet. Lowland study area: a, b, c; and mountain area: d

"buildings" spectrum is underestimated. On the other hand, this spectrum also contains prey from forests and dumps.

In the Leimental area, the anurans were mainly common frogs (*R. temporaria*), in the La Brévine mountains mainly common toads (*B. bufo*). Frogs and toads dominate the "forest" spectrum throughout the year. Their proportion is in winter (Dezember to February) only slightly less important than during the rest of the year (60 % compared to 69 %; $\chi^2 = 0.47$; $p > 0.1$). Mammals are mostly hunted in and around buildings, with woodmice (*Apodemus* sp.) being the most frequent species. 14 of 19 *Apodemus* and 4 of 6 *Microtus* were found in scats from buildings. Mammals from dumps are mostly rats (14 *Rattus norvegicus*; 5 *Apodemus* sp.; 2 *Microtus* sp.; 2 *Glis glis*).

I also found the following uneaten remains of polecat meals: 6 chicken- and 3 turkey-eggs in barns; 4 passerine birds, 25 common frogs and 5 or 6 common toads in forests.

Foraging movements

All radio-tracked polecats were mostly nocturnal (WEBER 1987). Daytime activity occurred in summer and autumn. Activity bouts alternated with resting periods also during night-time. To describe foraging, only data from activity bouts of at least 30 min will be used in this section.

The polecats rarely moved by bounding in the typical mustelid manner. Most of their activity was spent "rummaging" ("stöbern", HERTER 1959). Hereby they walk in a hasty, irregular and undirected way, holding their head near the ground. They often change direction and investigate even the smallest holes with the muzzle, or move it under the vegetation and leaf litter. This kind of movement is accompanied by much rustling, snuffling, snorting and sneezing which allows rummaging polecats to be easily detected. I never saw polecats leave the ground to climb trees or other structures.

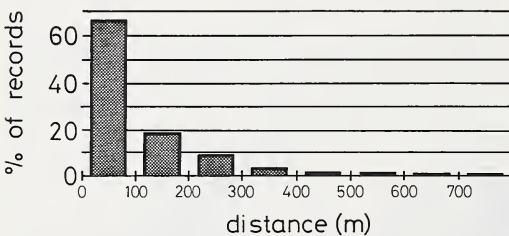


Fig. 4. Minimal distances between consecutive (10 min.) locations of active polecats (N = 1192)

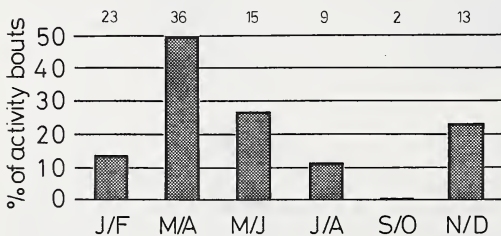


Fig. 5. Proportions of activity bouts during which at least once a distance of ≥ 300 m was run by male polecats. The total numbers of activity bouts observed for each two month period is given at the top of the columns. The difference between the period March to June to the rest of the year is significant ($\chi^2 = 9.73$; $p < 0.01$)

Long distance, strongly directed locomotion was seldom observed (Fig. 4). Only in 3 of 36 observed activity bouts of females distances of at least 300 m were crossed within 10 min. Male polecats showed such behaviour especially during the mating season in spring (Fig. 5). During this period they do not eat much, but live mainly of fat reserves (WEBER 1988b). Longdistance, fast and directed movements were also associated with habitat

Table 6. Characteristics of polecat foraging bouts in different habitat types

Habitat	Activity bouts (N)	Duration (min)	Total distance (m)	Mean speed (m/min)	Range (ha)
Forest	58 (25)	86 ± 51	508 ± 436	6.16 ± 3.51	3.118
Farms, houses	19 (4)	59 ± 31	76 ± 125	1.22 ± 2.25	0.120
Rubbish dump	16 (6)	86 ± 61	128 ± 293	0.94 ± 1.78	0.068
Mixed	7 (2)	90 ± 50	494 ± 431	5.82 ± 4.76	3.732

Arithmetic means and standard deviations are given. Activity bouts were attributed to the habitat in which at least 80 % of the records were registered. The beginning or the end of an activity bout was often missed. The number of such bouts is given in brackets. Durations, distances, speeds and ranges were calculated including such bouts. Therefore, these data represent minimum values rather than exact means. Ranges were calculated using the standard-circle method (TREVOR-DEUTSCH and HACKETT 1980)

changes (6 of 12 activity bouts with habitat changes showed distances of ≥ 300 m within 10 min, compared to 26 of 121 bouts within the same habitat type; $\chi^2 = 4.86$; $p < 0.05$).

Activity bouts without movements of ≥ 300 m within 10 min are interpreted as foraging bouts. Some characteristics of foraging bouts are given in Table 6. As distances were calculated on the basis of a 50 m-grid protocol, total distance and speed values are minima. These data are presented to illustrate the fact, that during a single foraging bout, small areas are intensively exploited, whereby the polecats do not go far from their starting point. This is most extreme while foraging in and around houses.

When foraging in forests, the areas in which a polecat rummaged changed with foraging bouts more or less continuously. This resulted in long-term home ranges much larger than the ranges of single activity bouts (Fig. 6). Extended stays in human settlements were

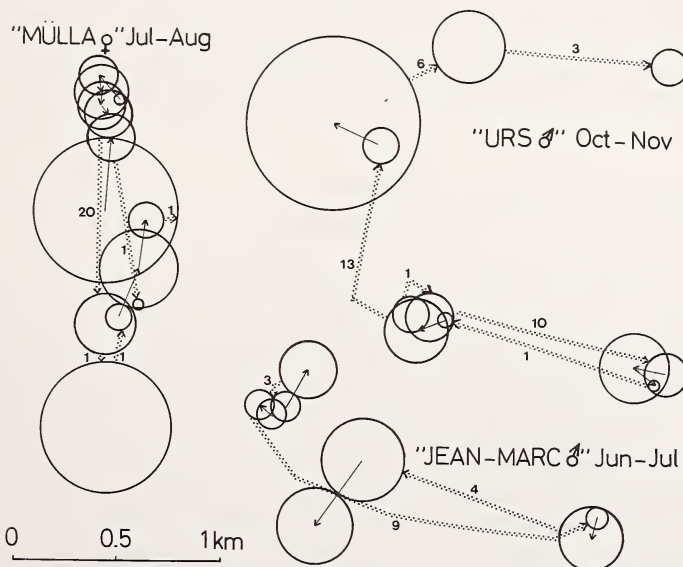


Fig. 6. Ranges of three different polecats during activity bouts in forests (standard circles, TREVOR-DEUTSCH and HACKETT 1980). Each circle represents one activity bout. Consecutive bouts during each period of observation are connected by solid arrows. Non-observed movements between area of activity are represented by dotted arrows. Numbers beside dotted arrows give periods between observations in days

nearly always restricted to the interior and the nearest surroundings of single houses or farms. Hereby, the polecats concentrated their activities on a limited number of places: During 18 foraging bouts the male "Dickkopf" used only three different barns. He did not leave one barn during all 5 bouts observed in February and early March, and he was not found resting anywhere else during this period. The use of rubbish-dumps was similar to that of buildings. During 14 of 17 monitored activity bouts the female "Micro" used one single dump exclusively and the male "Urs" did not leave another dump during one week for all 4 observed bouts.

Table 7. Ranges of individual polecats during single foraging bouts and over longer periods

Individual	Observation period	N foraging bouts	Single bout range (ha)	Total range (ha)	"Good habitat" (ha) within total range
Dickkopf	22. 12.– 9. 6.	33	2.3	1178.6	312.8
Methusalem	27. 3.–11. 4.	5	0.4	238.2	63.3
Urs	21. 10.–29. 11.	9	1.8	368.6	197.8
Schaggeli	24. 4.–14. 7.	6	0.6	8.3	5.2
Müllä	24. 7.–23. 8.	10	3.1	237.8	69.4
Micro	5. 9.–25. 10.	18	0.3	8.3	8.3
Jean-Marc	13. 6.– 9. 7.	12	3.4	69.0	50.6
Paul	12. 2.–16. 4.	6	1.3	346.3	193.8

Mean single bout ranges calculated as standard circles, total ranges as minimum-convex-polygons (TREVOR-DEUTSCH and HACKETT 1980). "Good habitat" is the total surface of forest, fallow, and rubbish dumps within individual total ranges (see Table 3)

The small areas used during single foraging bouts are in contrast to the large home ranges calculated for longer periods (Table 7). This is also valid when only forests and the parts of villages actually exploited within the polygons are considered. The restricted range of the female "Schaggeli" may be due to her cub-rearing during the observation period. She was bound to her den and could not nomadize like the other individuals. During the 7 weeks of observation, the activities of female "Micro" were almost restricted to one single dump.

Discussion

Prey-specific foraging

The predatory behaviour of captive polecats, ferrets and hybrids thereof has been studied by different authors (GOETHE 1940; RÄBER 1944; HERTER 1953; EIBL-EIBESFELDT 1956; WÜSTEHUBE 1960; GOSSOW 1970; APFELBACH 1973; APFELBACH and EBEL 1975; APFELBACH and WESTER 1977). According to GOSSOW (1970), the behavioural sequence can be divided into 7 units: 1. Searching; 2. Acoustical, visual or olfactorical perception of prey stimulus; 3. Localisation of stimulus, approaching; 4. Aimed leap at the prey or short pursuit and grasp, repeated if necessary; 5. Killing-bite and follow-up bites; 6. Holding the prey as long as this is still able to wriggle; 7. Carrying away, eating or hiding the prey. As in other mustelids (e.g. POWELL 1979 for *Martes pennanti*), foraging economics in polecats may depend chiefly on the success in finding and grasping prey, whereas the killing and eating can be regarded of neglectable importance. Different prey types impose different foraging problems.

My polecats reacted with excitement and appetite behaviour to the scent of rodents. This was already observed by APFELBACH (1973). When mouse or vole scent-tracks were crossed, they were followed, and the prey was found with high probability (see also HERTER 1959). Attacks are mainly provoked by visual or acoustical short-distance stimuli

(APFELBACH and WESTER 1977; HERTER 1959). Rodents avoid being attacked by immobility (GOETHE 1940) or by escaping into holes or up trees and shrubs. In my experimental environment similarly structured to the sites where polecats forage outside houses, mice and voles showed a high success rate in avoiding polecat attacks. It must be stressed that this occurred in an experimental environment which facilitated polecat hunting success, as there were no secure escape routes for the prey, and the rodents were unfamiliar with the environment. Under natural conditions, rodent-hunting by polecats may be even less successful, as polecats move around noisily, which allows the prey to escape to secure places even before an attack occurs.

One can conclude that for polecats, finding rodents is a smaller problem than catching them. The hunting experiments show, that rodent-catching is easier on unstructured, bare ground. The radio-tracked polecats hunted rodents mainly inside barns and other buildings, sometimes foraging in the same farm for several weeks.

Although I made no such observations, I believe that rats are followed into their tunnels and caught there, as this has been observed for rabbits (GOETHE 1940).

Catching frogs or toads raises completely different problems. Once found and attacked by a polecat, anurans never attempted to escape and were grasped as if they were dead. This is confirmed by observations of HERTER (1953). He also emphasizes that polecats do not find frogs by following scent tracks, but more or less by chance, while rummaging around. This is confirmed by my observations and those of Gossow (1970). Sometimes, especially in winter, frogs were dug from their holes in the ground. It remains unclear how the polecats found these sites, especially during winter, with snow-depths of more than one metre. However, anurans are the most important component of polecat winter diet in mountainous areas of Switzerland (WEBER 1988a).

One can conclude that anuran hunting for polecats is principally a problem of finding, not of catching. Anurans are not hunted, but collected. Anuran collecting occurred mostly in forests. Hereby, the polecats foraged in small areas, which were intensively searched for frogs and toads during one or more activity bouts, and then abandoned. Consequent foraging bouts concentrated on other areas. The next visit to an abandoned anuran foraging ground may only occur after several weeks or months. This suggests that anuran-collecting polecats are exhaustive predators, that empty a site and then forage elsewhere. This assumption is supported by the radio-tracking results of NILSSON (1978) and HERRENSCHMIDT (1982).

Other important food for Swiss polecats, apart from rodents and anurans, are carrion, offal and eggs. These pose problems of locating and not catching, which is also the case for the seldom eaten birds (found dead) and invertebrates.

Surplus killing

Polecats are known to store prey, mostly anurans, in caches (DANILOV and RUSAKOV 1969; for other authors see GROSSENBACHER and NEUENSCHWANDER 1978). In those frog-heaps found during this study, some of the prey animals were still alive. Similar observations led to the conclusion that polecats bite frogs in a special way producing paralysis, which can be considered as a sophisticated technique of prey-caching (WÜSTEHUBE 1960). Gossow's (1970) findings suggest however that paralysis is rather an accidental occurrence.

However, even when the frogs are killed, the question of the function of frog-caching remains. One crucial point is the fact that frog-caches are often not revisited and used as food (e.g. GROSSENBACHER and NEUENSCHWANDER 1978). HERTER (1959) therefore interpretes anuran caching as a non-adaptive consequence of an unusual stimulus situation in cases of local concentrations of frogs: Polecats would not stop killing as long as the according releasing mechanism is elicited by the sign stimulus "prey". But OKSANEN (1983) and OKSANEN et al. (1985) show convincingly that surplus killing can be adaptive, even

when surplus prey is only rarely eaten at all, when this does not significantly reduce future prey availability, and when hunting efforts are not too high.

These conditions are probably fulfilled in the case of polecats and anurans. When a frog is already found, the only effort to kill (or immobilize) is a bite. As the finding of frogs is difficult, the chance of encountering the same frog later is not high. The polecat will presumably not return to the same place until some weeks or months later, and frog mortality is high (about 50 % per year in adult *R. temporaria* according to HEUSSER 1970). *R. temporaria* needs at least 3 years to maturity in lowlands (ASHBY 1969) and up to 9 years in Swiss mountains (GROSSENBACHER pers. comm.), and even longer to reach maximum size. Additionally, the number of metamorphosed frogs may depend more on the ecological parameters of the spawning pond than on the number of spawning adults (HINTERMANN 1984). Therefore, killing surplus frogs probably does not strongly influence frog availability in future years. The killing and hoarding of already located anurans may therefore cost a polecat only the time spent, and could be adaptive, even if the prey is rarely eaten. Frog-caches could functionally be considered as a short-term insurance against food shortages. Additionally, surplus killing allows a polecat to eat only the best-tasting parts of anurans, which are, according to my observations, the legs.

The need to decide

KORHONEN et al. (1983) found no difference in the basal metabolic rates of polecats and mink (*Mustela vison*). According to FARRELL and WOOD (1968), a mink of 1 kg needs about 250 kcal of metabolizable energy per day. Assuming that 75 % of the energy intake is metabolizable (as found by MOORS (1977) for mice fed to weasels, *Mustela nivalis*), a mean polecat of 1 kg would need approximately 8 to 10 wood mice or voles, the same number of adult common frogs or toads, 4 chicken eggs or 350 g of commercial cat food per day (Energy contents of prey estimated from data from ROBBINS 1983 and MOORS 1977). This corresponds roughly to the food consumption of my captive polecats, and is more than the quantities proposed by USINGER (1960).

A hungry polecat must decide where to go, what to search and which foraging behaviour to perform. Unspecialized, erratic foraging will probably not result in a sufficient food intake, as different foods must be found and caught in different ways, as different food types occur in different habitats, and as foraging efficiency on the same prey might differ according to the habitat where a polecat hunts. That polecats do not forage randomly is suggested by the demonstration of a searching image in ferrets (*Mustela putorius furo*) by APFELBACH and EBEL (1975).

As discussed in the section above, a polecat following mouse tracks will have only minimal chances of finding a sufficient number of frogs. On the other hand, a frog-hunting polecat ploughing with its nose under leaf-litter and rummaging around will chase away potential small rodent prey. As indicated by the food spectra from forests, polecats concentrate on anuran prey there throughout the year. Even in early winter, when rodent numbers are still high and anurans hibernate underground, rodent predation rarely occurs in forests.

Foraging in barns and around houses minimizes the chances of finding frogs. Here, a polecat has to decide whether to search for eggs or pet food, or whether to hunt rodents. Which option he takes will depend on the relative availability of these potential foods. The food spectra show that all these resources are exploited, and I speculate that polecats only rarely hunt rodents if there are eggs and meat available. However, I do not have the data to support this idea.

In rubbish dumps the polecats must decide whether to kill rats or to search for offal. Again, there are no data to illustrate the relative attractivity of these options.

It follows that Swiss polecats must choose between 5 foraging options, which mutually

exclude one another. There are two hunting options, namely 1. small rodents inside or around houses and 2. rats in rubbish-dumps; and three collecting options, 3. anurans in forests, 4. eggs or meat in or around houses and 5. offal in dumps. In other areas a further option exists: hunting rabbits in their burrows (GOETHE 1940; BRUGGE 1977). The observed foraging behaviour reflects the decisions among these possibilities, and for an understanding of the decisions it is sensible to assume that they are the result of an optimisation of related fitness costs and benefits (KREBS and DAVIES 1981).

Swiss polecats as specialized anuran foragers

The food spectra of the radio-tracked polecats are very similar to those resulting from gut analysis of 120 polecat carcasses from all over Switzerland (WEBER 1988a). This is as valid for the relative importance of different food components as for seasonal and altitudinal differences in diet. Therefore, some generalisations on foraging can be formulated on the basis of the results presented here.

Rubbish-dumps were used without obvious seasonal preferences. A female almost never left a small dump during two months of observation. Around this dump was a forest where another female lived on anurans. Rubbish dumps were the best places for catching polecats (author's unpublished data), as many different individuals from the surrounding area visited them regularly. I conclude that, throughout the year, foraging on rubbish dumps may be the most attractive option for Swiss polecats. However, such dumps are rare in our country and only small number of polecats has a dump available. I have no information on the relative attraction of rats and offal at these places.

According to NIETHAMMER and KRAPP (1982) and GEUSE et al. (1985), the total biomass of ground-living rodents in a European lowland deciduous forest can be estimated as approximately 6000 g/ha in late autumn. Locally, this figure may be several times higher. The biomass of adult common frogs (*R. temporaria*) in Swiss lowland forests would be about 250 g/ha, reaching 750 g/ha in the best places (GROSSENACHER 1974, 1980). Thus, the specialisation on anurans by polecats foraging in forests cannot be explained by the quantity of prey available. It must be a result of difficulties in rodent-hunting, as is suggested by the results of my hunting experiments. Finding hibernating anurans in winter may be facilitated by local concentrations of these animals near spawning sites.

The seasonal habitat change in polecats was already known by TSCHUDI (1858). Further references are given by GAUTSCHI (1983). This habitat change is also a dietary change: In late winter and spring my polecats ceased to forage for amphibians in forests, at least partly, and lived on eggs, offal and small mammals, which they found in and around houses. This is confirmed by seasonal food spectra from Switzerland which resulted from gut analysis (WEBER 1988a). At a first glance, this may well be explained by a low availability of frogs and toads during winter, and by concentrations of small mammals in barns during this period. However, for two reasons, I do not consider food availability to be the ultimate cause of the seasonal habitat change in polecats:

1. The habitat change is not synchronous with relative anuran and rodent availability: Anurans hibernate from December to mid-March, their availability probably being highest at spawning sites during March. Rodents may enter human buildings in December, and their numbers will decline until spring, as no reproduction occurs, and as predators, e.g. cats and Beech martens, will kill a certain proportion. If food availability were the cause of habitat change one would expect polecats to enter barns in December and leave them in March. The data of this study show that they entered the buildings during January and partly remained there until early summer.
2. In the mountainous regions, where frog-hunting during winter is especially difficult due to deep snow, the polecats continued to forage for anurans, but used barns for

resting and sleeping. There, the seasonal habitat change takes also place, but the dietary change only to a lesser extent. Consequently, each night, the polecats were obliged to travel longer distances between hunting grounds and resting sites than in summer, when a polecat may sleep near its prey in forests (WEBER in press).

My conclusion is that Swiss polecats are specialized anuran foragers, and that other prey is found accidentally while hunting frogs or toads. Only two reasons for specialised foraging on other prey occur: First, extreme local concentrations of potential food (e.g. rubbish dumps, carcasses, hen houses with eggs, peaking microtine populations) can prevent a polecat from frog-hunting throughout the year. Second, a food availability at the barn used for resting in winter (because of thermoregulatory problems, WEBER in press) that outweighs the travelling costs between the barn and potential anuran hunting grounds. This situation is more often found in the lowlands, where farms are occupied all year, and therefore offer eggs, pet food and offal in winter, than in the mountains, where stables and barns are sometimes only used during summer. Additionally, in the lowlands higher rodent densities in barns can be expected than in the mountains, as arable farming results in higher food availability for rodents than hay-cutting.

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Zusammenfassung

Zum Ernährungsverhalten des Iltisses (Mustela putorius L.) in der Schweiz

Das Ernährungsverhalten wurde bei 12 sendermarkierten Iltissen in einem Berggebiet und einem tiefliegenden Feld-Wald-Siedlungs-Mischgebiet in der Schweiz beobachtet. Zusätzliche Informationen lieferte die Beobachtung einiger Iltisse, die in einem Freiland-Gehege gehalten wurden. Mit diesen Tieren wurden auch einige einfache Experimente durchgeführt.

Es werden fünf verschiedene Möglichkeiten beschrieben, die den Iltissen zur Ernährung offenstehen: 1. Jagd auf Kleinsäuger in und um Gebäude; 2. Jagd auf Ratten auf Müllkippen; 3. Sammeln von Fröschen oder Kröten in geeigneten Wäldern; 4. Sammeln von Eiern, Haustierfutter oder Fleischabfall in und um Gebäude; 5. Sammeln von Fleischabfall auf Müllkippen.

Mindestens drei dieser Optionen können nicht gleichzeitig wahrgenommen werden, weil dazu verschiedene Biotope aufgesucht werden müssen. Außerdem muß ein Iltis entsprechend der jeweiligen Beute sein Jagdverhalten wählen: Kleinsäuger sind leicht zu finden, aber schwer zu fangen, während Froschlurche schwer zu finden, aber leicht zu fangen sind. In den meisten Fällen sind schweizerische Iltisse Froschfresser. Dementsprechend verhalten sie sich nicht wie Jäger, sondern wie Sammler: Ein kleinflächiges Gebiet wird intensiv abgesucht und anschließend verlassen. Es kann mehrere Wochen oder Monate dauern, bis der Iltis wieder zurückkehrt. Das resultierende Raumnutzungsmuster kann am treffendsten mit dem Begriff „nomadisch“ charakterisiert werden.

Das beobachtete Auftreten der verschiedenen Ernährungsmöglichkeiten wird diskutiert und mit der folgenden Hypothese erklärt: Schweizerische Iltisse sind Anuren-Spezialisten, weil sie für die Kleinsäugerjagd zu ungeschickt sind. Es gibt zwei Gründe, von dieser Spezialisierung abzuweichen: 1. Extreme lokale Konzentrationen anderer Nahrung (z. B. Müllkippen, Tierkadaver, Hühnerhäuser) können ergiebiger sein als Wälder mit Fröschen. 2. Im Winter, wenn Iltisse aus Gründen der Thermoregulation in Gebäuden ruhen, können die Weg-Kosten zwischen Versteck und Amphibien-Jagdgründen so hoch werden, daß es sich mehr lohnt, in unmittelbarer Umgebung des Versteckes Kleinsäuger zu jagen oder nach Eiern, Fleischabfall oder Haustierfutter zu suchen.

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