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Environmental factors influencing habitat exploitation by the polecat *Mustela putorius* in western France

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(With 6 figures in the text)

Variation in habitat use was studied by radiotracking 11 polecats *Mustela putorius* in two wetlands in western France. Habitat selection showed a clear seasonality. Marshes were the most exploited habitat in spring while woods were mainly used in the coldest months and meadows were frequented in summer and winter. An analysis of scats showed that diet correlated with habitat utilization. The proportions of bank voles *Clethrionomys glareolus*, and meadow voles *Microtus* sp. were, respectively, related to the use of woods and meadows, while amphibians (mainly *Rana dalmatina* and *Bufo bufo*) were associated with marshes. Availabilities of rodents, assessed monthly by trapline success, were also significantly correlated to their occurrences. In contrast, no correlations were found between larger prey, such as brown rats *Rattus norvegicus* and rabbits *Oryctolagus cuniculus*, and any habitats or their abundance in the field. The occurrences of these prey and of some minor resources, such as shrews and birds, were correlated most with meteorological factors. The exploitation of marshes and amphibians increased when small rodents declined. Therefore, in the polecat, habitat selection was mostly influenced by trophic factors. Dietary diversity was greater in spring when food resources decreased, suggesting that polecats were optimal foragers. The study has emphasized that the polecat is a generalist feeder.

Contents

Introduction

In many mustelids the size of an animal's activity area depends mainly upon food distribution and abundance (Kruuk & Parish, 1982; Pulliainen, 1984; Kruuk & Macdonald, 1985; Kruuk, Wansink & Moorhouse, 1990). Space is not uniformly used and the activity of animals is

concentrated on certain restricted areas, whereas others seem to be deserted (Gerell, 1970; Erlinge, 1977; Zielinski, Spencer & Barrett, 1983; Pulliainen, 1984). Such selective utilization of space is usually considered as evidence of intensive feeding upon a single resource.

This spacing pattern has been shown in the polecat *Mustela putorius* Linnaeus 1758 (Nilsson, 1978; Herrenschmidt, 1982; Blandford, 1987; Weber, 1989*a*; Lodé, 1991*a*). Nevertheless, although good information is available on the diet of this mustelid (Chaigneau, 1947; Kratochvil, 1952; Danilov & Rusakov, 1969; Brugge, 1977; Ballarin *et al.*, 1980; Blandford, 1987; Weber, 1989*b*; Lodé, 1990, 1991*b*; Roger, 1991; Sidorovich, 1992), the influence of food availability on habitat use has not yet been investigated and little is known about relationships between movements, feeding habits and prey abundance. Furthermore, the trophic status of the species remains unclear because the predator shows great variations in the composition of the diet, depending on the study area (see above). Based on its dietary eclecticism, the polecat has been portrayed either as a generalist carnivore (Erlinge *et al.*, 1982, 1983; Libois, 1984; Erlinge, 1986; Blandford, 1987; Hanski, Hansson & Henttonen, 1991), or as a specialist anuran predator (Weber, 1989*a*; Jedrzejewski, Jedrzejewska & Szymura, 1989), or else as a specialist rabbit predator (Roger, 1991). Therefore, one might assume that environmental variables may have a deciding influence on the feeding ecology and habitat use in polecats.

The European polecat was formerly distributed throughout the Western Palaearctic and was found in various habitats such as woodland, forest, farmland, marsh and riverbank (see Blandford, 1987). However, numerous studies have referred to the polecat's preference for wetlands and riverbanks (Chaigneau, 1947; Walton, 1968; Danilov & Rusakov, 1969; Jensen & Jensen, 1972; Saint-Girons, 1973; Waechter, 1979; Libois, 1984; Brzezinski, Jedrzejewski & Jedrzejewska, 1992).

In the present study, variations in habitat selection were assessed through the survey of 11 radiotracked polecats in a natural heterogeneous environment and the diet in relation to prey availability is reported. The relationships between diet variations, habitat choice, main meteorological variables and food resource availabilities are reported and a more accurate assessment of the relationships between polecats and their prey is made.

Study area

The study was performed on two wetlands and adjoining farmland in western France. The lake of Grand-Lieu (47°05N, 1°39W) is a naturally eutrophic lake of 60 km^2 which lies in a basin filled by recent alluvium. It is supplied by several rivers, the Acheneau, the Boulogne, the Tenu and the Ognon. The swampy grasslands are dominated by *Scirpetum* gradually invaded by reed beds and willows (Marion & Marion, 1975). The flooded marshes give way to wooded farmland and some woods mainly composed of oak, ash and chestnut. Meadows alternate with small vineyards and a few cereal fields. The lake of Grand-Lieu has been classified as a nature reserve since 1980.

The marshes of Grande-Brière (47°25N, 2°15W) cover 67 km^2 out of a total of 400 km^2 belonging to the Brière Regional Nature Park. On the old crystalline rock, alluvial peat-bogs accumulated. Only one river, the Brivet, drains the marshes but numerous canals criss-cross them. A recent reduction of grazing and mowing has favoured the extension of reed beds and willows to the detriment of natural flooded grassland and its vegetation of *Carex*, *Glyceria* and *Typha* (Dupont, 1972). Marshes lie alongside wooded farmland with hedges of ash and oak, alternating with more wooded areas.

These wetlands are used by numerous species of waterfowl (Brosselin, 1973). The climate,

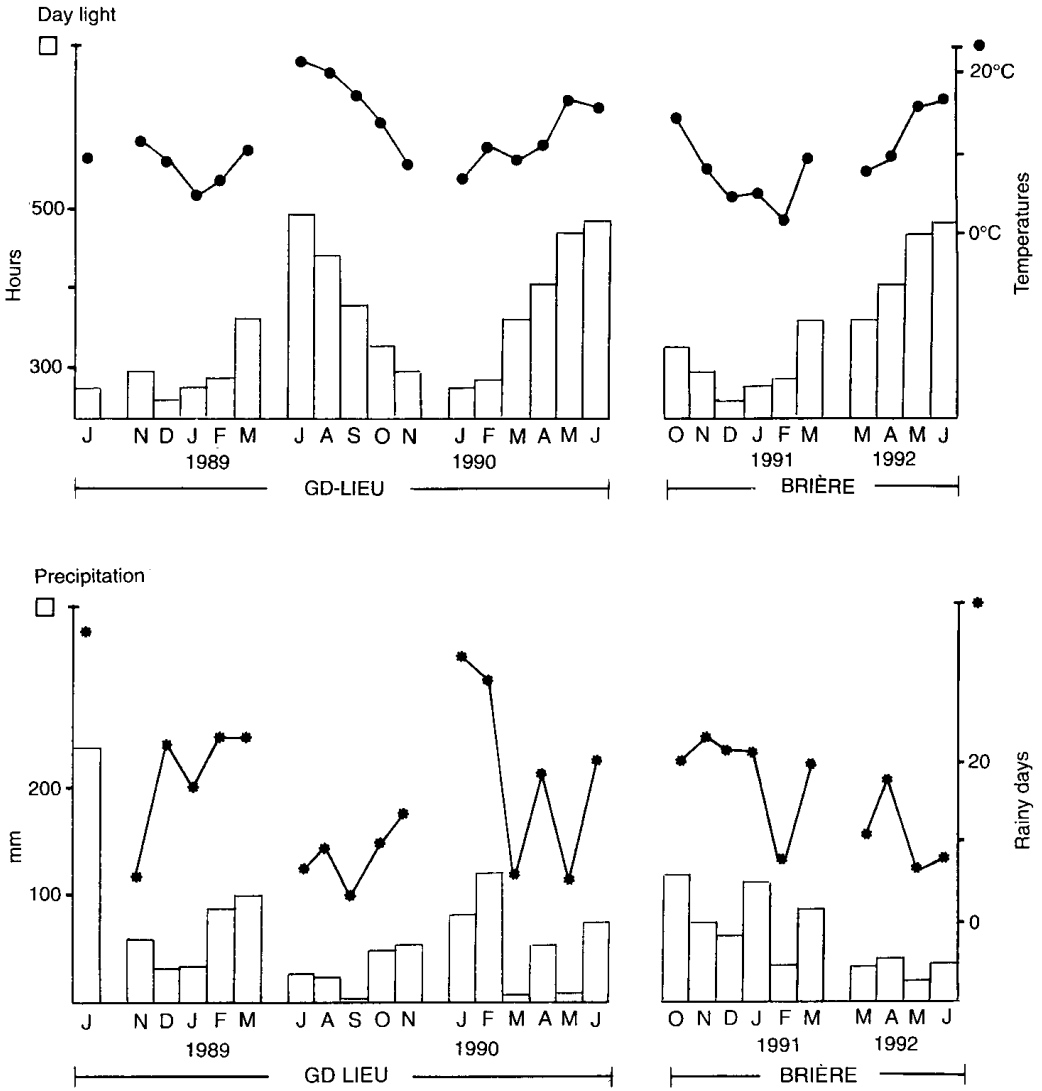

FIG. 1. Variations of main meteorological variables (mean temperature, photoperiod, precipitation and number of rainy days in the two study areas during the research period).

influenced by the nearness of the littoral, is mild and humid (Fig. 1) with a mean of three snowy days and 22 freezing days per year.

Materials and methods

From November 1988 through June 1992, movements of 11 wild polecats were recorded and their diet was studied by faecal analysis. The method was closely based on the one used by Cavallini & Lovari (1991) in the red fox.

Radiotracking survey

Wild polecats (6 males and 5 females) were live-trapped in wooden box-traps baited with dead white mice and were fitted with radiotransmitters (148 mHz). Table I indicates sex, age, survey period and number of active locations of each animal studied. The animals were located repeatedly by ground triangulation using a hand-held antenna (4 elements Yagi) and a portable receiver, in periods of 6 h per night with locations on each animal every 45 min for a total of 24 h per week. Most locations were recorded at night while polecats were active, but at least 3 observations during day-time were obtained 3 times a week (total = 9 h). Most of the animals were noisy when they foraged and were sometimes very easy to locate. Only fixes in which polecats were active were used in the analysis. The size of the animal's activity area was calculated by the minimum convex polygon method (Mohr, 1947). The percentage of occupied surface in each defined habitat was estimated on a monthly basis. The analysis was restricted to 3 main habitats which were the most used by polecats in western France (representing 99% of active fixes, Lodé, 1993), i.e. marshes (ditches, ponds, riverbanks, brooks and marshes), woods and meadows (often hedged by bushes and trees). Levins' (1968) index, $B = 1/\Sigma P_i^2$, where P_i is a proportion of a frequented habitat (as woods, meadows and marshes), was used to evaluate the monthly variation of habitat use. The Spearman rank correlation coefficient r_s was used to test correlations (Siegel, 1956). Differences between seasons (spring = March, April, May, $n = 8$; summer = June, July, August, $n = 4$; autumn = September, October, November, $n = 6$; winter = December, January, February, $n = 9$) and between 2 study areas (Grand-Lieu, $n = 17$ months, Brière, $n = 10$) were assessed by the χ^2 test.

Diet analysis

Following the nocturnal path of each surveyed animal, a daily search for faeces was made the morning after. Because only fresh faeces were collected and only in the area frequented by each studied animal, the probability of confusion with another individual was extremely low. Faeces were dried, weighed and washed. Food remains were examined, according to standard techniques, and were identified by comparison with a collection and the atlas (Day, 1966; Chaline *et al.*, 1974; Rage, 1974; Debrot *et al.*, 1982). Some food items, very large prey often associated with maggots, suspected or revealed during radiotracking as carrion (*Capreolus capreolus*, *Myocastor coypus*, *Felis catus*, *Tyto alba*, *Corvus corones*) and some rare items such as *Tinca tinca*, *Natrix natrix* or *Lepus capensis*, formed together the category named 'others'. Earthworm chaetae, found in only 12 samples, were assumed to have originated from amphibians or shrews and were discarded. The diet results are given as relative frequency of occurrences. The trophic niche breadth was calculated using Levins index $B = 1/\Sigma P_i^2$, where P_i was a percentage of a food category (as mammals, birds,

TABLE I

Characteristics of radiotracked polecats

	Sex	Age	Weight (g)	Survey period	Locations	Area
M1	male	ad	1380	16 XI 88–18 XII 88	73	Gd-Lieu
M2	male	sub	1260	15 VII 89–06 X 89	224	Gd-Lieu
M3	male	ad	1580	29 I 90–07 VI 90	235	Gd-Lieu
M4	male	ad	1500	27 XI 90–06 IV 91	306	Brière
M5	male	ad	1430	08 I 91–24 III 91	210	Brière
M6	male	ad	1600	10 III 92–14 VI 92	224	Brière
F1	female	ad	780	02 I 88–23 I 88	49	Gd-Lieu
F2	female	ad	890	20 I 89–24 III 89	126	Gd-Lieu
F3	female	sub	605	21 VII 89–29 XI 89	276	Gd-Lieu
F4	female	ad	820	13 II 90–12 V 90	132	Gd-Lieu
F5	female	sub	680	21 X 90–08 I 91	98	Brière

amphibians, invertebrates and others). Comparisons were made using 3 main food categories, mammals, amphibians and others which here included birds, invertebrates and the previous category 'others'.

Resource availabilities

An estimate of food availabilities was periodically conducted through monthly indices of relative abundance. The changes of rodent populations were assessed by trap-line success. Wire-mesh traps, spaced every 3 m in straight lines were set during 3 consecutive nights. The device and the method are described by Saint-Girons & Fons (1986, 1987). In each study area, Grand-Lieu and Brière, trapping was conducted monthly in 2 representative stations for each type of habitat, i.e. meadows (one transect line and one line along a hedge), marshes (one transect line and one line alone ditches) and woods (one transect line and one line along a boundary) with 192 trap-nights (TN) per habitat (576 trap-nights per month, except in November 1988, January 1989, March 1989, $n = 594$, December 1988 and August 1989, $n = 612$, February 1989, $n = 666$, July 1989, $n = 468$). Only the capture of shrews (*Sorex coronatus*, *S. minutus*, *Crocidura russula*, *C. suavolens*), brown rats (*Rattus norvegicus*), bank voles (*Clethrionomys glareolus*) and meadow voles (*Microtus arvalis* and *Microtus agrestis*) were considered because they formed the major mammal prey of the polecat. Each live-trapped animal was marked and released. Because trapping did not exceed 3 consecutive nights, the possible effect of rodent immigration was considerably attenuated. The relative abundance (Ra) of rodents and shrews was expressed as the number of individuals (n_i) captured per trap-night, $Ra = n_i/TN \times 1000$.

The relative abundance of rabbits was estimated by night countings in a run of 3 km during 2 nights monthly 1 hour after sunset, from July 1989 to June 1992. The results were expressed as the number of individuals seen per kilometre (Chapuis, 1979). The Spearman Rank correlation coefficient r_s was calculated between the relative abundance and the percentage of each concerned food category in the diet. When no precision was given, the degree of freedom was $d.f. = 15$ in Grand-Lieu, and $d.f. = 8$ in Brière. Finally, a summary of the activity period of the main anuran species present in the polecat's diet was made to give an idea of their accessibility. The periods of hibernation, breeding congregations, and when the juveniles left the water, were recorded for the main anuran species present in the polecat's diet; *Rana dalmatina*, *Rana* '*esculenta*' and *Bufo bufo*. *Rana lessonae*, *R. ridibunda* and their hybrid *R.* '*esculenta*' have not been discriminated. *Rana temporaria* was rare in the study areas.

Results

Habitat use

The activity area averaged a monthly surface of 38·3 ha (S.D. ± 16·7, $n = 6$) for the males and 18·7 ha (S.D. ± 10·8, $n = 5$) for the females. The most exploited habitat was marshes (45·2% of the frequented surface). Meadows and woods, respectively, represented 30·3% and 24·5% of the habitat used (Fig. 2). Seasonal variations in habitat selection was clearly apparent ($\chi^2 = 61{\cdot}18$, $d.f. = 6$, $P < 0{\cdot}001$). An increase in the use of marshes was shown from winter (23%) to spring (80·5%). The meadows were mainly used in summer (40%) and in winter (41%). The woods were chiefly utilized in winter (36%) and in autumn (36%) while they only represented 4·1% in spring. Habitat selection did not differ between males and females ($\chi^2 = 2{\cdot}59$, $d.f. = 2$, $P > 0{\cdot}2$). On the other hand, a difference between the two study areas was apparent ($\chi^2 = 7{\cdot}2$, $d.f. = 2$, $P < 0{\cdot}03$). In both areas, marshes were exploited most (45%) but woods were most used in Brière (Brière = 32·2%, Grand-Lieu = 20%) while meadows were most frequented in Grand-Lieu (Grand-Lieu = 34·9%, Brière = 22·5%).

The habitat use niche varied from $B = 1{\cdot}04$ in March 1991 to $B = 2{\cdot}59$ in October 1989 in

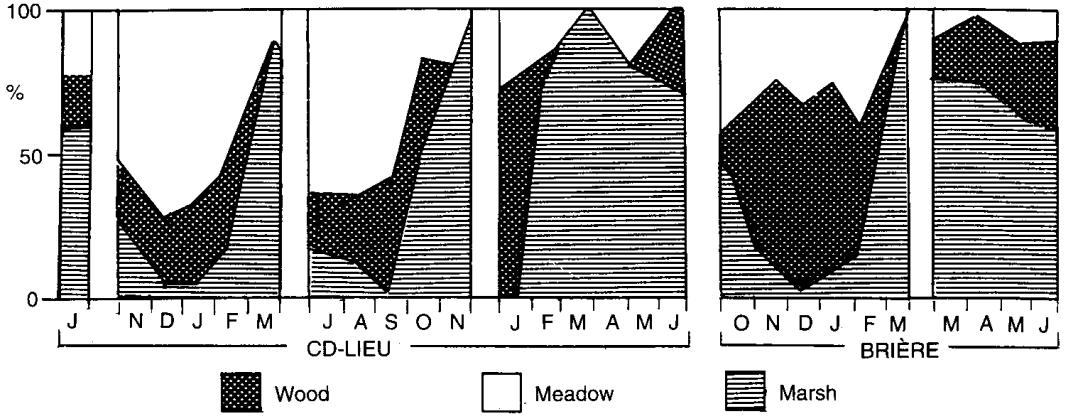

FIG. 2. Proportions of different habitats used by radiotracked polecats in western France.

Grand-Lieu, and from $B = 1{\cdot}09$ in November 1990 to $B = 2{\cdot}73$ in February 1991 in Brière. The index B was inversely correlated with the use of marshes ($r_s = -0{\cdot}628$, $P < 0{\cdot}01$) and positively with wood ($r_s = 0{\cdot}634$, $P < 0{\cdot}01$) in Grand-Lieu, but was not in Brière. The habitat use niche reached a mean of $B = 2{\cdot}121$ in winter (mean $B = 2{\cdot}015$, $n = 6$, in Grand-Lieu, $B = 2{\cdot}333$, $n = 3$, in Brière) while the index averaged $B = 1{\cdot}512$ in spring (Grand-Lieu, $B = 1{\cdot}334$, $n = 4$; Brière, $B = 1{\cdot}689$, $n = 4$), $B = 1{\cdot}931$ in summer (Grand-Lieu, $B = 1{\cdot}850$, $n = 3$; Brière, $B = 2{\cdot}174$, $n = 1$), $B = 1{\cdot}895$ in autumn (Grand-Lieu, $B = 2{\cdot}025$, $n = 4$; Brière, $B = 1{\cdot}636$, $n = 2$).

Diet composition

Mammals, chiefly rodents (bank voles, meadow voles and brown rats) formed the bulk of the diet with 72·3% (Fig. 3). Amphibians, mainly terrestrial anurans (*Rana dalmatina* and *Bufo bufo*), constituted an important food category with 21·1%. Birds (2·9%), invertebrates (2·6%) and others (1·1%) were of minor importance. No differences between the exploitation of mammals and amphibians by female and male polecats was apparent ($\chi^2 = 0{\cdot}96$, $d.f. = 2$, $P > 0{\cdot}3$). In the same way, there were no differences between the diets in Grand-Lieu and in Brière ($\chi^2 = 2{\cdot}78$, $d.f. = 2$, $P > 0{\cdot}2$).

Dietary changes clearly showed a seasonality ($\chi^2 = 20{\cdot}48$, $d.f. = 6$, $P < 0{\cdot}02$). The consumption of mammal prey increased from spring to winter while the proportion of amphibians decreased from spring to winter. The trophic niche breadth varied from $B = 1$ (January, November and December 1988, and January 1989) to $B = 2{\cdot}62$ (November 1989) in Grand-Lieu, and from $B = 1{\cdot}13$ (January 1991) to $B = 2{\cdot}41$ (June 1992) in Brière. The index reached a mean of $B = 2{\cdot}085$ in spring (Grand-Lieu, $B = 2{\cdot}97$, $n = 4$; Brière, $B = 2{\cdot}072$, $n = 4$) but decreased in summer $B = 1{\cdot}855$ (Grand-Lieu, $B = 1{\cdot}670$, $n = 3$; Brière, $B = 2{\cdot}41$, $n = 1$), in autumn $B = 1{\cdot}185$ (Grand-Lieu, $B = 1{\cdot}640$, $n = 4$; Brière, $B = 1{\cdot}775$, $n = 2$), with the lowest mean value in winter $B = 1{\cdot}192$ (Grand-Lieu, $B = 1{\cdot}138$, $n = 6$; Brière, $B = 1{\cdot}300$, $n = 3$). The index B correlated well with the proportion of amphibians in the diet (Grand-Lieu, $r_s = 0{\cdot}767$, $P < 0{\cdot}001$; Brière, $rs = 0{\cdot}830$, $P < 0{\cdot}005$) and negatively correlated with the proportion of mammals (Grand-Lieu, $r_s = -0{\cdot}968$, $P < 0{\cdot}001$; Brière, $r_s = -0{\cdot}976$, $P < 0{\cdot}001$).

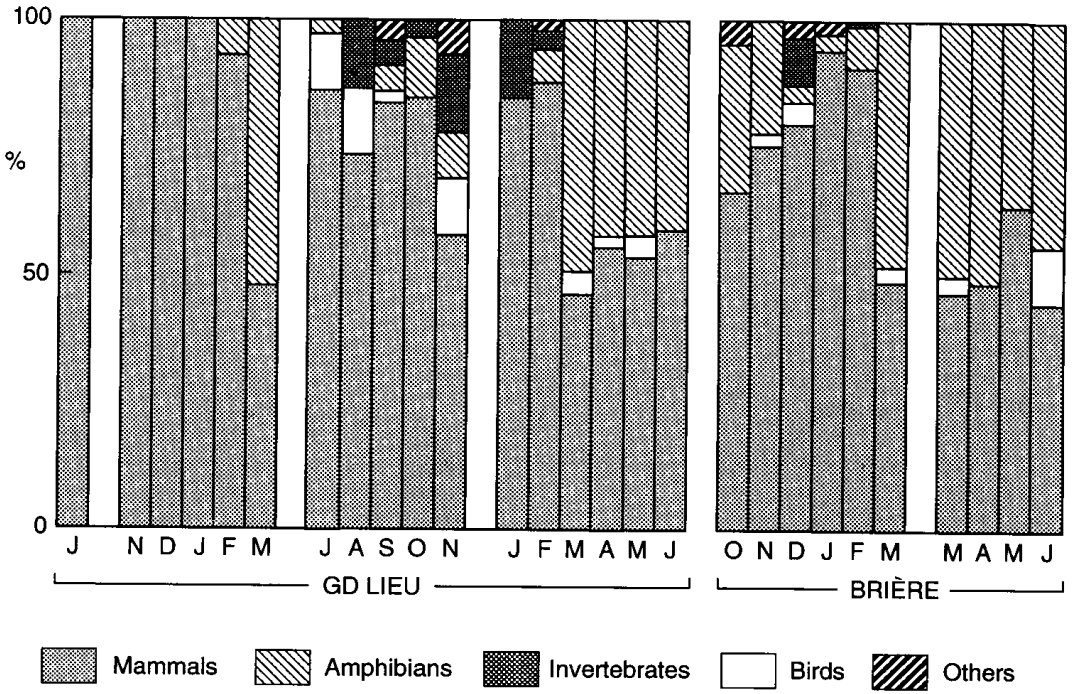

FIG. 3. Variations of occurrences of food categories in the polecat diet, western France. (Jan. *n* prey = 20; Nov. = 20; Dec. = 22; Jan. = 21; Feb. = 38; Mar. = 42; Jul. = 31; Aug. = 36; Sept. = 39; Oct. = 47; Nov. = 26; Jan. = 18; Feb. = 42; Mar. = 60; Apr. = 57; May = 37; Jun. = 17; Oct. = 15; Nov. = 32; Dec. = 48; Jan. = 63; Feb. = 53; Mar. = 43; Mar. = 26; Apr. = 25; May = 30; Jun. = 20).

Resource availabilities

Results of trap-lines showed that bank voles were almost exclusively found in woods whereas meadow voles were only caught in meadows, and, to a minor extent, in marshes (Table II). Brown rats were trapped near ditches and ponds, in marshes. A small number of shrews were present in woods and were almost absent in other habitats. Relative abundance of bank voles increased from spring to autumn (Fig. 4). Abundance of brown rats showed a similar increase from spring to autumn. Abundance of meadow voles declined in spring and increased from summer to winter.

TABLE II

Availability of mammal prey as revealed by trap-line success (mean Relative abundance, RA)

	GRAND-LIEU			BRIERE			
Ra	marsh	wood	meadow	marsh	wood	meadow	*n*
Shrews	0·9	9·4	1·8	0·5	10·4	1·6	*64*
Brown rats	31·8	—	—	21·9	—	—	*147*
Bank voles	—	78·2	29·7	0·5	69·3	16·7	*522*
Meadow voles	6·1	—	12·4	4·7	—	7·3	*84*
TN	*3300*	*3300*	*3300*	*1920*	*1920*	*1920*	

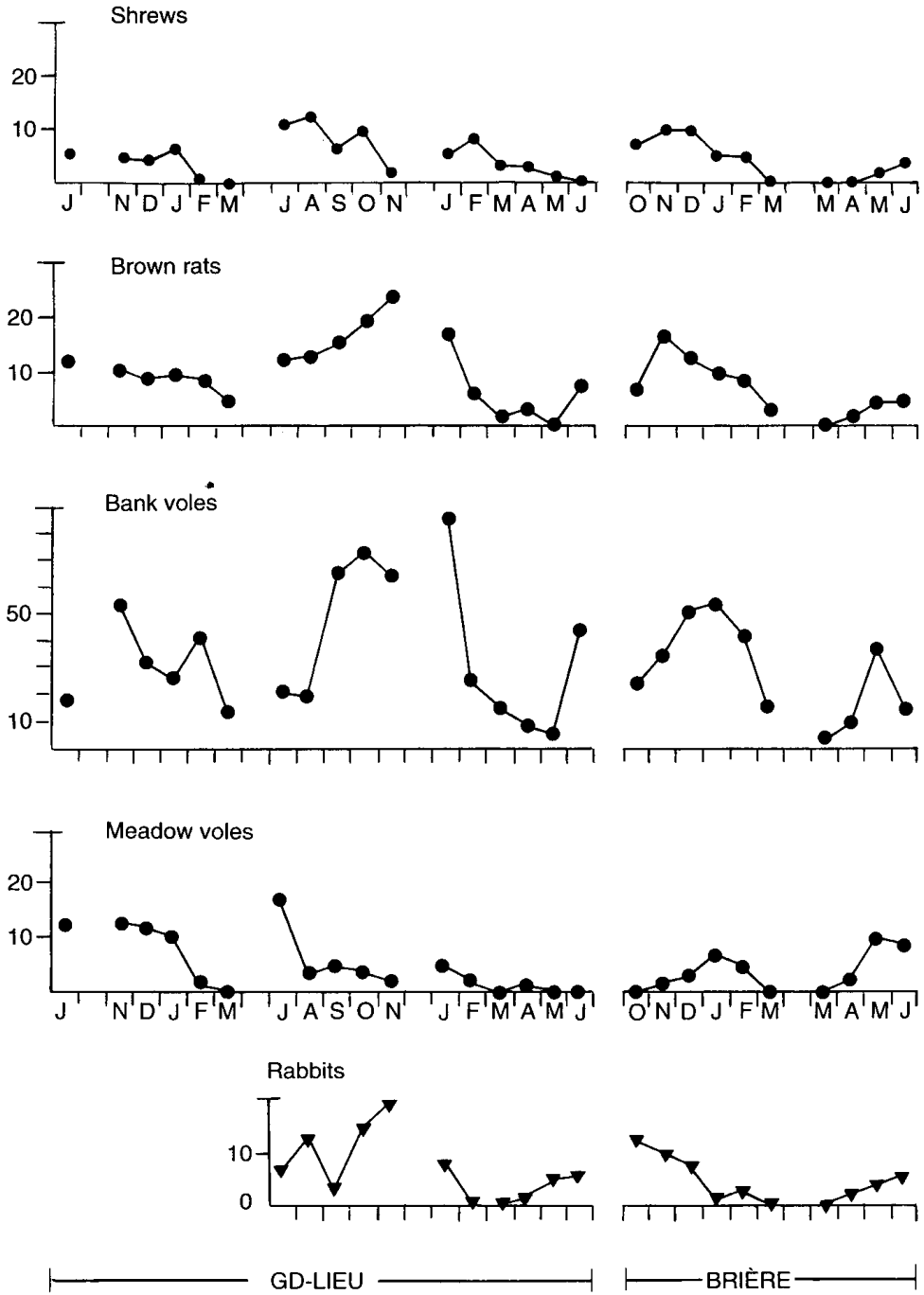

FIG. 4. Availabilities of main prey resources, expressed in individuals per trap-nights for rodents and shrews, and in individuals per km during night censuses for rabbits.

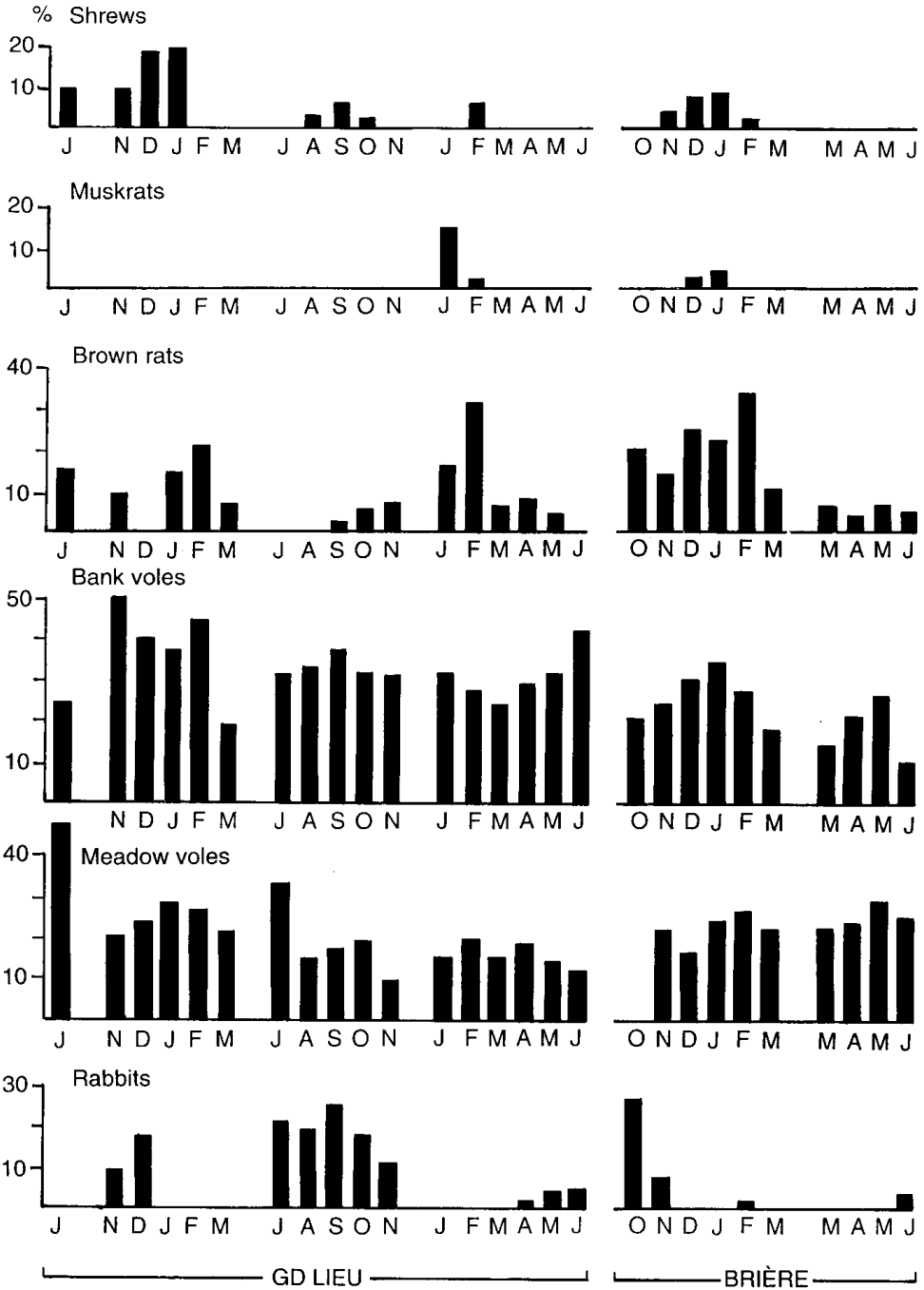

FIG. 5. Variations of mammal occurrences in the polecat diet, western France.

Shrews did not show clear variations but only a few individuals ($n = 22$) were caught. Night censuses showed that the availability of rabbits was greatest in summer and in autumn.

Dietary variations and correlations

Figure 5 shows the dietary variations of mammal prey. Meadow voles were present in the diet throughout the year and were significantly correlated neither with photoperiod nor mean temperature and precipitation. On the other hand, the dietary proportion of meadow voles correlated well with the use of meadows (Grand-Lieu, $r_s = 0{\cdot}589$, $P < 0{\cdot}02$; Brière, $r_s = 0{\cdot}782$, $P < 0{\cdot}02$) and with their availability (Grand-Lieu, $r_s = 0{\cdot}529$, $P < 0{\cdot}05$; Brière, $r_s = 0{\cdot}806$, $P < 0{\cdot}01$).

Bank voles were regularly eaten throughout the year and related neither to photoperiod (except Brière, $r_s = -0{\cdot}677$, $P < 0{\cdot}05$) nor temperature and precipitation. Their proportion in the diet was, however, correlated with the use of woods (Grand-Lieu, $r_s = 0{\cdot}654$, $P < 0{\cdot}01$; Brière, $r_s = 0{\cdot}754$, $P < 0{\cdot}02$), inversely correlated with the use of marshes (Grand-Lieu, $r_s = -0{\cdot}627$, $P < 0{\cdot}01$; Brière, $r_s = -0{\cdot}742$, $P < 0{\cdot}05$) and was associated with their availability (Grand-Lieu, $r_s = 0{\cdot}595$, $P < 0{\cdot}01$; Brière, $r_s = 0{\cdot}887$, $P < 0{\cdot}002$).

The high correlation between the occurrence of brown rats and the photoperiod (Grand-Lieu, $r_s = -0{\cdot}641$, $P < 0{\cdot}01$; Brière, $r_s = -0{\cdot}863$, $P < 0{\cdot}005$), mean temperature (Grand-Lieu, $r_s = -0{\cdot}655$, $P < 0{\cdot}01$; Brière, $r_s = -0{\cdot}782$, $P < 0{\cdot}02$) and precipitation (Grand-Lieu, $r_s = 0{\cdot}667$, $P < 0{\cdot}005$; Brière, $r_s = 0{\cdot}444$, NS) revealed that rats represented an important resource during the coldest months. No correlations were noted between the proportion of brown rats in the diet and any habitat or with their abundance.

Shrews were related to the photoperiod (Grand-Lieu, $r_s = -0{\cdot}562$, $P < 0{\cdot}05$; Brière, $r_s = -0{\cdot}877$, $P < 0{\cdot}005$) and temperature (Brière only, $r_s = -0{\cdot}730$, $P < 0{\cdot}05$) and appeared to be an occasional resource, mainly eaten in the cold months. They correlated with meadows in Grand-Lieu ($r_s = 0{\cdot}605$, $P < 0{\cdot}02$) but woods ($r_s = 0{\cdot}826$, $P < 0{\cdot}01$) and marshes ($r_s = -0{\cdot}887$, $P < 0{\cdot}002$) in Brière, and with their abundance (Grand-Lieu, $r_s = 0{\cdot}530$, $P < 0{\cdot}05$; Brière, $r_s = 0{\cdot}700$, $P < 0{\cdot}05$).

The occurrence of rabbits did not show clear correlations. It only correlated with mean temperature ($r_s = 0{\cdot}658$, $P < 0{\cdot}01$) and precipitation ($r_s = -0{\cdot}637$, $P < 0{\cdot}01$) in Grand-Lieu and abundance in Brière ($r_s = 0{\cdot}733$, $P < 0{\cdot}05$).

Although birds formed a minor food component, their occurrence in the diet was associated with photoperiod ($r_s = 0{\cdot}614$, $P < 0{\cdot}02$) and mean temperature ($r_s = 0{\cdot}523$, $P < 0{\cdot}05$), and negatively correlated with precipitation ($r_s = -0{\cdot}666$, $P < 0{\cdot}005$) in Grand-Lieu but not in Brière.

The amphibian frequency in the diet considerably increased in spring and a close relationship was shown between their occurrence and the use of marshes (Grand-Lieu, $r_s = 0{\cdot}784$, $P < 0{\cdot}001$; Brière, $r_s = 0{\cdot}927$, $P < 0{\cdot}001$) and photoperiod (Grand-Lieu, $r_s = 0{\cdot}542$, $P < 0{\cdot}05$; Brière, $r_s = 0{\cdot}802$, $P < 0{\cdot}05$), whereas their occurrence was inversely correlated with woods (Grand-Lieu, $r_s = -0{\cdot}518$, $P < 0{\cdot}05$; Brière, $r_s = -0{\cdot}903$, $P < 0{\cdot}001$) and meadows in Grand-Lieu, ($r_s = -0{\cdot}635$, $P < 0{\cdot}01$). A synchrony between the dietary proportion of amphibians and anuran breeding congregrations was noticed (Fig. 6).

Discussion

In western France, the use of space by polecats showed a clear seasonality. Marshes were exploited in spring while meadows were used in summer and winter, and woods were mainly

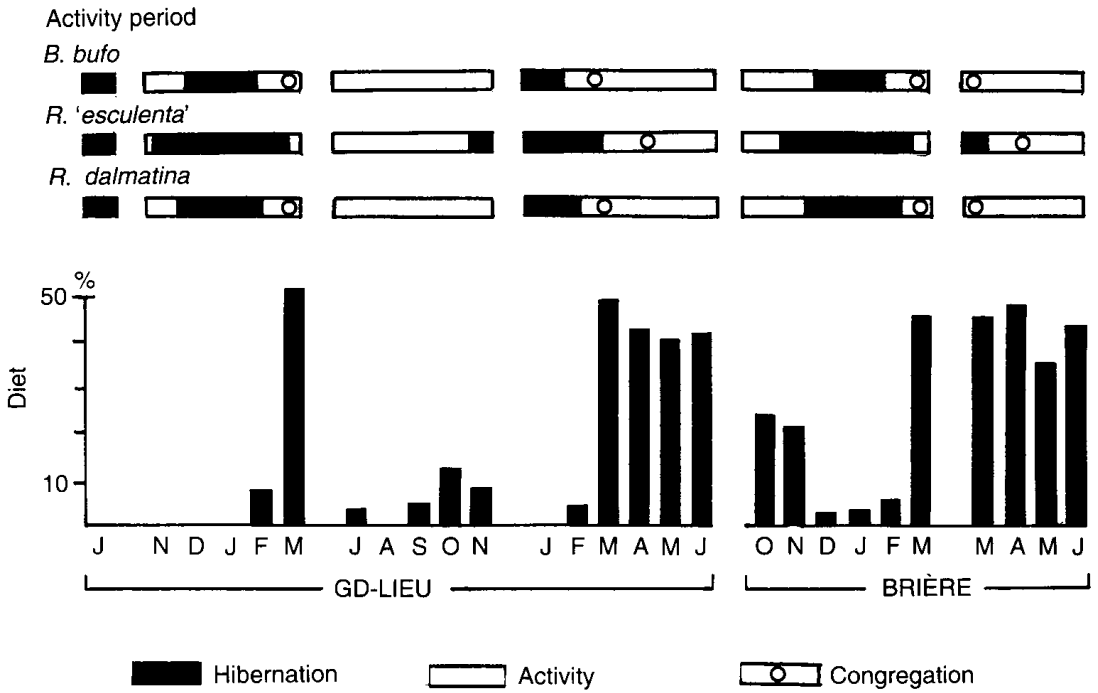

FIG. 6. Summary of main activity period in *Rana dalmatina*, *R. 'esculenta'* and *Bufo bufo*, in western France in comparison with the occurrences of amphibians in the polecat diet.

frequented in autumn and in winter. Wetlands, ponds and the banks of watercourses are known to be used by the polecat (Kratochvil, 1952; Walton, 1968; Danilov & Rusakov, 1969; Jensen & Jensen, 1972; Blandford, 1987; Lodé, 1988; Weber, 1989*a*; Brzezinski *et al.*, 1992), as well as wooded areas (Santos-Reis, 1983; Jedrzejewski *et al.*, 1989; Weber, 1989*a*). Here, the habitat selection was clearly correlated with seasonal dietary variations. Thus, the occurrence of amphibians, bank voles and meadow voles were, respectively, related to the use of marshes, woods and meadows. The utilization of different habitats was associated with prey distribution and the availabilities of small prey were directly correlated with their occurrences in the diet. In contrast, the dietary proportions of larger prey, such as rabbits and rats, were independent of their field abundance but were related to meteorological factors and mostly eaten in the coldest months. Furthermore, a synchrony between anuran breeding congregations and the predominance of amphibians in the diet was noticed. Therefore, the exploitation of different habitats was directly influenced by trophic factors. Severe climatic conditions may also play a role in habitat choice in the coldest areas, such as in Swiss mountains (Weber, 1989*c*), but in these marginal habitats, the resource dispersion greatly affected the ability to build up a territory (Weber, 1989*a*).

The increase of trophic niche breadth in spring showed that the diversity of the diet was dependent on dietary occurrence of amphibians. According to the optimal foraging hypothesis (Krebs, 1978), diet was more diversified when the availability of the main food resources (i.e. rodents) declined. Thus, the polecat behaved as a generalist feeder which shifted to another resource, increasing its diet diversity, in response to the decrease of food availability. Food

specializations reported by Weber (1989*a*) and Roger (1991) could rather be adjustments to local overabundance in food resources. The great variation of the polecat's diet from one area to another (Ballarin *et al.*, 1980) also supports the concept of opportunism in feeding strategy.

The habitat use niche was restricted in spring, while the trophic niche increased owing to the exploitation of marshes and amphibians. This opposite trend stressed the deciding role of habitat selection by the polecat when food resources declined. The successive utilization of different habitats disclosed the importance of the heterogeneity of available habitat for the polecat.

In fact, several concomitant elements allow specification of the feeding strategy of the European polecat. Evidence of correlations between dietary occurrences of small rodents and their availability, sudden predominance of amphibians in the diet in conjunction with the decline of rodent abundance in the field and with anuran breeding congregations, and the simultaneous increased use of marshes, suggested that habitat choice and prey selection has an adaptive significance and emphasized the special opportunism of this mustelid.

Summary

Habitat selection and dietary pattern showed a clear seasonality in the polecat and were correlated with small rodent availability, while larger prey was related to meteorological factors. Dietary occurrence of amphibians was associated with the use of marshes and a synchrony appeared between the variation in the diet and anuran breeding congregations. Therefore, in the polecat, the exploitation of different habitats was highly influenced by trophic factors.

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REFERENCES

Ballarin, I., Garzon, J., Palacios, P., Cuesta, L. & Castroviejo, J. (1980). [On the diet of polecats (*Putorius putorius* L. 1758) in Spain.] *Réun. Iberoamericana Zool. Vert.* **1:** 625–627. [In Spanish.]

Blandford, P. R. S. (1987). Biology of the polecat *Mustela putorius*: a literature review. *Mamm. Rev.* **17:** 155–198.

Brosselin, M. (1973). Valeur internationale pour l'avifaune migratrice des zones humides de la façade occidentale de la France. *Penn. ar bed* **74:** 185–194.

Brugge, T. (1977). Prey selection of weasel, stoat and polecat in relation to sex and size. *Lutra* **19:** 39–49.

Brzezinski, M., Jedrzejewski, W. & Jedrzejewska, B. (1992). Winter home ranges and movements of polecats *Mustela putorius* in Bialowieza primeval forest, Poland. *Acta theriol.* **37**(1/2): 181–191.

Cavallini, P. & Lovari, S. (1991). Environmental factors influencing the use of habitat in the red fox, *Vulpes vulpes*. *J. Zool., Lond.* **223:** 323–339.

Chaigneau, A. (1947). *Les animaux nuisibles à la chasse*. Paris: La Maison rustique.

Chaline, J., Baudvin, H., Jammot, P. & Saint-Girons, M.C. (1974). *Les proies des rapaces*. Paris: Doin.

Chapuis, J. L. (1979). *Le régime alimentaire du Lapin de garenne* ***Oryctolagus cuniculus*** *L. 1758 dans deux habitats contrastés: un lande bretonne et un domaine de l'île de France*. D. thesis, University of Rennes I.

Danilov, P. I. & Rusakov, O. S. (1969). [Peculiarities of the ecology of the polecat (*Mustela putorius*) in north-west districts of the european part of the USSR.] *Zool. Zh.* **48:** 1383–1394. [In Russian.]

Day, M. G. (1966). Identification of hair and feather remains in the gut and faeces of stoats and weasels. *J. Zool., Lond.* **148:** 201–217.

Debrot, S., Fivaz, G., Mermod, C. & Weber, J. M. (1982). *Atlas des poils de mammifères d'Europe*. Neuchatel: Institut Zoologique, Univer. Neuchatel.

Dupont, P. (1972). La végétation du Parc de Brière. *Penn. ar bed* **69:** 282–295.

Erlinge, S. (1977). Spacing strategy in stoat *Mustela erminea*. *Oikos* **28:** 33–43.

Erlinge, S. (1986). Specialists and generalists among the mustelids. *Lutra* **29:** 5–11.

Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, L., Nilsson, T., von Schantz, T. & Sylven, M. (1983). Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* **40:** 36–52.

Erlinge, S., Göransson, G., Högstedt, G., Liberg, O., Loman, J., Nilsson, L., Nilsson, T., von Schantz, T. & Sylven, M. (1982). Factors limiting numbers of vertebrate predators in a predator prey community. *Int. Cong. Game Biol.* **14:** 261–268.

Gerell, R. (1970). Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. *Oikos* **21:** 160–173.

Hanski, I., Hansson, L. & Henttonen, H. (1991). Specialist predators, generalist predators and the microtine rodent cycle. *J. Anim. Ecol.* **60:** 353–367.

Herrenschmidt, V. (1982). Note sur les déplacements et le rythme d'activité d'un putois, *Mustela putorius* L., suivi par radiotracking. *Mammalia* **46:** 554–556.

Jedrzejewski, W., Jedrzejewska, B. & Szymura, A. (1989). Food niche overlaps in a winter community of predators in the Bialowieza primeval forest, Poland. *Acta theriol.* **34:** 487–496.

Jensen, A. & Jensen, B. (1972). [The polecat *Putorius putorius* in Denmark 1969–1970.] *Dansk. Vildtunders.* **18:** 1–32. [In Danish.]

Kratochvil, J. (1952). [Diet and breeds of polecats (*Putorius putorius* L.)]. *Acta Univ. Agr. Silv. Brno* **1:** 43–60. [In Czech.]

Krebs, J. R. (1978). Optimal foraging: decision rules for predators. In *Behavioural ecology: an evolutionary approach*: 23–63. Krebs, J. R. & Davies, N. B. (Eds). Oxford: Blackwell Scientific Publications.

Kruuk, H. & Macdonald, D. W. (1985). Group territories of carnivores: empires and enclaves. In *Behavioural ecology: ecological consequences of adaptive behaviour*: 521–536. Sibly, R. M. & Smith, R. H. (Eds). Oxford: Blackwell Science Publications.

Kruuk, H. & Parish, T. (1982). Factors affecting population density, group size and territory size of the European badger *Meles meles*. *J. Zool., Lond.* **196:** 31–39.

Kruuk, H., Wansink, D. & Moorhouse, A. (1990). Feeding patches and diving success of otters *Lutra lutra* in Shetland. *Oikos* **57:** 68–72.

Levins, R. (1968). *Evolution in changing environments*. Princeton, N. J.: Princeton University Press.

Libois, R. (1984). Atlas des mammifères sauvages de Wallonie. Le genre *Mustela* L. en Belgique. *Cah. Ethol. appliq.* **4:** 279–314.

Lodé, T. (1988). Note préliminaire sur la biologie du comportement du putois (*Mustela putorius* L. 1766) dans les bocages humides de l'Ouest de la France. *Bull. Soc. Sci. Nat. Ouest Fr.* **10:** 58–67. [In French with English summary.]

Lodé, T. (1990). Le régime alimentaire d'un petit carnivore, le putois (*Mustela putorius*) dans l'ouest de la France. *Gibier Faune Sauvage* **7:** 193–203.

Lodé, T. (1991*a*). Exploitation des milieux et organisation de l'espace chez deux mustélidés européens, la fouine *Martes foina*, et le putois *Mustela putorius*. *Vie Milieu* **41:** 29–38.

Lodé, T. (1991*b*). Evolution annuelle du régime alimentaire du Putois *Mustela putorius* L. en fonction de la disponibilité des proies. *Bull. Ecol.* **22:** 21–26.

Lodé, T. (1993). Stratégies d'utilisation de l'espace chez le Putois européen *Mustela putorius* L. dans l'ouest de la France. *Rev. Ecol. Terre Vie* **48:** 305–322.

Marion, L. & Marion, P. (1975). Contribution à l'étude écologique du Lac de Grand-Lieu. *Bull. Soc. Sci. nat. Ouest Fr.* (Spec.): 1–611.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37:** 223–249.

Nilsson, T. (1978). Home range utilization and movements in polecat *Mustela putorius* during autumn. *Cong. Theriol. Int. Brno*: 173.

Pulliainen, E. (1984). Use of the home range by pine martens (*Martes martes* L.). *Acta zool. fenn.* No. 171: 271–274.

Rage, J. C. (1974). Batraciens fossiles du quaternaire. *Bull. Soc. linn. Lyon* **43:** 276–289.

Roger, M. (1991). Régime et disponibilités alimentaires chez le putois (*Mustela putorius* L.). *Rev. Ecol. Terre Vie* **46:** 245–261.

Saint-Girons, M. C. (1973). *Mammifères de France et du Benelux*. Paris: Doin.

Saint-Girons, M. C. & Fons, R. (1986). Le piègeage des micromammifères. I. Appâts et types de pièges. *Arvicola* **3:** 63–67.

Saint-Girons, M. C. & Fons, R. (1987). Le piègeage des micromammifères. II. Disposition des pièges. *Arvicola* **4:** 23–27.

Santos-Reis, M. (1983). Status and distribution of the Portuguese mustelids. *Acta zool. fenn.* No. 174: 213–216.

Sidorovich, V. (1992). Comparative analysis of the diets of the European mink *Mustela lutreola*, American mink *Mustela vison*, and Polecat *Mustela putorius*, in Byelorussia. *Small Carnivores Conserv.* **6:** 2–4.

Siegel, S. (1956). *Nonparametric statistics for the behavioural sciences*. New York: MacGraw-Hill.

Waechter, A. (1979). Note sur les mammifères d'Alsace: 2. Les carnivores. *Mammalia* **43:** 479–484.

Walton, K. C. (1968). The distribution of the polecat *Putorius putorius* in Great Britain. 1963–67. *J. Zool., Lond.* **155:** 237–240.

Weber, D. (1989*a*). Foraging in polecats (*Mustela putorius* L.) of Switzerland: the case of a specialist anuran predator. *Z. Säugetierk.* **54:** 377–392.

Weber, D. (1989*b*). The diet of polecats (*Mustela putorius* L.) in Switzerland. *Z. Säugetierk.* **54:** 157–171.

Weber, D. (1989*c*). The ecological significance of resting sites and the seasonal habitat change in polecats (*Mustela putorius*). *J. Zool., Lond.* **217:** 629–638.

Zielinski, W. J., Spencer, W. D. & Barrett, R. H. (1983). Relationship between food habits and activity patterns of pine martens. *J. Mammal.* **64:** 387–396.