



ELSEVIER

Behavioural Processes 47 (1999) 11–18

BEHAVIOURAL  
PROCESSES

www.elsevier.com/locate/behavproc

# Time budget as related to feeding tactics of European polecat *Mustela putorius*

Thierry Lodé

*Laboratoire d'Ecologie Animale, Université d'Angers, 49045 Angers, France*

Received 13 May 1998; received in revised form 5 May 1999; accepted 6 May 1999

## Abstract

The time budget of five male and four female European polecats was studied in western France through radiotracking surveys. Their activity level averaged 7 h and 31 min without any significant differences between males and females. However two phases, foraging and travelling, were not similarly distributed in both sexes. Despite a strong sexual dimorphism, females spent more time foraging than males. Travelling, i.e. time devoted to linear movements was more important in males than females. Variations in activity phase duration were correlated with the proportions of food categories, suggesting that the dispersion of available resources directly influenced polecat activity. The exploitation of prey showing an aggregative distribution such as anurans led to a decrease in general activity whereas the consumption of rodents, which were more regularly distributed, was correlated to the foraging activity. Mating and breeding also affected the activity duration. Thus it seems that the time budget of polecats resulted from a compromise between social organization and trophic constraints. © 1999 Published by Elsevier Science B.V. All rights reserved.

*Keywords:* Time budget; *Mustela putorius*; Polecat; Feeding tactics

## 1. Introduction

Most mustelids adopt rather nocturnal habits (Hainard, 1961; Ewer, 1968), and it seems that the photoperiodism is the exogenous factor that most affects the circadian rhythm of small Canivores (Ashoff, 1966; Saint-Girons, 1966). However, severe meteorological conditions, extreme cold, drought or catastrophic events such as floods, can modify activity rates and rhythms, especially at extreme latitudes. During coldest periods, animals

can stay several days in their dens (Price, 1971; Skirnrison, 1986; Richardson et al., 1987; Robitaille and Baron, 1987; Burskirk et al., 1988; Weber, 1989a). During breeding, general activity and movements can increase (Sandell, 1986; Skirnrison, 1986; Richardson et al., 1987; Robitaille and Baron, 1987). Animals may also limit their outside activity to avoid predators (Powell, 1979; Richardson et al., 1987). Finally, mustelids synchronise their activity rhythm to that of their main prey (Zielinski et al., 1983; Lodé, 1995).

Polecats are confronted to and must face seasonal changes in prey availability. The duration of

*E-mail address:* thierry.lode@univ-angers.fr (T. Lodé)

the hunting bouts depends on the latency to find, detect or capture the prey (Sargeant et al. 1973). The polecat's diet includes prey such as anurans and rodents which show different spatial distribution. The selection of anurans by polecats (Weber, 1989b; Jedrzejewski et al., 1993) may be explained by the availability of large breeding congregation of this type of prey (Lodé, 1997). By contrast, Bank vole, *Clethrionomys glareolus*, is a common small forest rodent which shows a homogeneous distribution (Mermod, 1969), and this prey is regularly observed in the polecat diet (Lodé, 1997). It may be predicted that the foraging activity duration decreases when the predator exploits an aggregated resource.

Moreover, because of the important sexual size dimorphism in polecats (Moors, 1980; Blandford, 1987), sexual differences in foraging, therefore in time budget are likely to occur (Bekoff et al., 1984; Raymond et al., 1990; Vaudry et al., 1990).

The aim of this study was to determine the influence of some biotic and abiotic factors on the time budget in European polecats *Mustela putorius*, based on both the distribution and the duration of activity phases of five radiotracked males and four radiotracked females. I examine how the time budget is influenced by (1) the photoperiod, the temperature and the precipitation, (2) the sex and the reproductive state of animals, and (3) the dietary occurrences of different prey types.

## 2. Materials and methods

The study was carried out in the lake of Grand-Lieu (47°05'W, 1°39' N) and the Brière (47°25' W, 2°15' N) and their adjoining wooded areas near the Loire estuary in western France. These two wetlands developed in caving-in basins of the old eroded Hercynian Massif, the Armorican peneplain. Grand-Lieu is an eutrophic lake bordered with peat-bogs, reeds (*Phragmitetum*), and small woods of willows (*Salix* sp.). The Grande-Brière is a peat-bog drained by numerous canals. Paludal areas of the Brière and Grand-lieu give way to natural meadows lined by oak *Quercus* sp., and ash *Fraxinus* sp. hedges with small deciduous woods. The climate is mild and humid influenced

by the nearby ocean. Precipitation average 800 mm with less than 3 snowy days yearly. Mean of maximum temperature was 21°C in July 1989 and mean of minimal temperature was 3°C in February 1991 during the study period.

In western France, male polecat sexual activity begins in February and is revealed by an increase in the size and weight of testicles. Males reach for a mate in February and March. Female sexual receptivity is reached in March and April, and is revealed by a conspicuous congestion of the vulva reflecting the state of follicular maturation. Birth occurs in June and young are weaned in August (Lodé, 1990).

Data were collected between 1988 and 1992 from radiotracking nine adult European polecats (Lodé, 1993a, 1994, 1995). The animals caught in trap-boxes were sexed, weighed, fitted with a radio-collar transmitter, and further localised by triangulation on a grid map 50 × 50 m. One localisation was obtained at least every 45 min during surveys of 6 consecutive hours for a total of 24 h/week as suggested by Jacobsen and Wiggins (1982). The monthly survey averaged 150 h (SD 118 h) for the males ( $n = 5$ ) totalling 696 h in winter, 768 h in spring, 192 h in summer and 144 h in autumn. The monthly survey averaged 104.3 h (SD 50.3h) for the females ( $n = 4$ ) totalling 360 h in winter, 312 h in spring, 144 h in summer and 384 h in autumn. Animals were often noisy while foraging and easily detectable. The polecats used with varying regularity numerous places ( $n = 149$ ) as diurnal resting sites (an average of 13.5 dens per surveyed individual) for 1 or 3 days (sometimes 10 days), from shelters under roots (43%), rabbit warrens (18%) to shrubs (20%) (Lodé 1993a). Nocturnal resting sites were only used for some hours (Lodé 1993a). On the basis of the signal intensity and the distance variations between two successive locations, I distinguished (1) two phases of stationary activity: diurnal rest in the den and nocturnal rest in temporary dens, and (2) two phases of locomotory activity: foraging characterised by repetitive and sinuous movements on very small areas, and travelling, longer and regular linear movements. Various activities such as comfort behaviour or feeding may occur in the den but were not distinguished from rest

phases. Monthly duration of foraging, travelling and total locomotory activity were measured for each individual according to its sex. Variations of activity durations (in hours) were tested by an ANOVA followed by Duncan Test while the differences of activity rates between males and females were tested by the *U* of Mann–Whitney.

The chosen abiotic variables were the mean monthly duration of the photoperiod; the monthly precipitation (in mm), the number of frosty days, and, since polecats remained mainly nocturnal (Weber, 1989a; Lodé, 1995), the monthly average of minimal temperatures. A pluviothermic quotient *Q* (Dajoz, 1974) was calculated as  $Q = \text{precipitation in mm}/(1/\text{monthly mean temperature} \times 1000)$  and temperatures (maximal and minimal). Kendall's *Tau* were computed to examine relationships between abiotic factors and the duration of bouts of foraging, travelling and total locomotory activity. Multifactorial correlation analysis were also computed (PCSM program).

The diet was based on the analysis of numerous faeces collected on the paths of animals ( $n = 849$  identified preys) and results were given as monthly relative frequency of occurrences (Lodé, 1993b, 1994). Kendall's *Tau* was used to evaluate the relationship between the activity durations and monthly proportions of the predominant food categories in the polecats' diet: shrews (*Sorex* sp.), bank voles (*Clethrionomys gareolus*), meadow

voles (*Microtus arvalis*), brown rats (*Rattus norvegicus*), rabbits (*Oryctolagus cuniculus*), birds, anurans (mainly agile frogs *Rana dalmatina* and common toads *Bufo bufo*), or invertebrates.

### 3. Results

#### 3.1. Organisation of the time-budget

Polecats spent an average of 7 h 31 min per day ( $\pm 62$  min) active without any significant differences among individuals ( $F = 0.48$ ,  $n = 9$ , Duncan test  $P > 0.05$ ). Animals were resting more than two thirds of the time (68.5%). Polecats were mainly nocturnal since animals were active 52.0% of the night compared to 11.1% of the day without any significant difference between males and females (nocturnal activity,  $U = 111.5$ ,  $P > 0.05$ ; diurnal activity  $U = 119.0$ ,  $P > 0.05$ ).

The duration of total locomotory activity varied seasonally and remained significantly more important in winter than in other seasons (Table 1, Duncan test, winter versus spring, summer, autumn,  $P < 0.05$ ). Females dedicated more time to forage (4 h 50 min) and less time to travel (2 h 52 min) than males (foraging: 3 h 71 min; travelling: 3 h 64 min, Table 1). Foraging activity lasted significantly longer than travelling in females (paired  $t = 6.01$ ,  $P < 0.0001$ ) but not in males (paired  $t = 0.87$ ,  $P > 0.05$ ). Time spent travelling

Table 1  
Variations in the duration of various activities in European polecats

Duration (min)						Factor	<i>F</i>	<i>P</i>
<i>Total locomotory activity</i>								
	Winter	Spring	Summer	Autumn	SD	Sex	1.734	0.197 NS
Males	516	397	415	442	63	Season	4.007	0.018 <sup>a</sup>
Females	495	442	495	463	56	Interaction	1.739	0.183 NS
<i>Foraging activity</i>								
						Sex	22.540	0.0001 <sup>a</sup>
Males	243	223	229	228	40	Season	1.474	0.050 <sup>a</sup>
Females	285	285	375	290	52	Interaction	1.135	0.107 NS
<i>Travelling</i>								
						Sex	16.354	0.001 <sup>a</sup>
Males	271	173	184	240	53	Season	10.395	0.001 <sup>a</sup>
Females	213	157	120	172	42	Interaction	0.884	0.534 NS

<sup>a</sup> Indicates the significant relationships.

was significantly longer in winter, summer and autumn than spring for males ( $F = 8.66$ ,  $P < 0.02$ , Duncan test, winter versus spring, summer and autumn *versus* spring) and only in winter for females ( $F = 4.19$ ,  $P < 0.03$ , Duncan test, winter *versus* spring, summer,  $P < 0.05$ ). Females spent more time foraging in summer than in autumn or in winter ( $F = 3.07$ ,  $P = 0.07$ , Duncan test, summer *versus* autumn, winter,  $P < 0.05$ ). In males, foraging duration did not vary seasonally ( $F = 0.29$ ,  $P < 0.05$ ).

During the breeding period, the duration of travelling increased significantly in males (rut:  $276 \pm 40$  min, out of rut:  $207 \pm 52$  min;  $t = 2.17$ ,  $P = 0.044$ ). In females, the foraging activity was significantly longer during the breeding period reaching 370 min, ( $\pm 46$ ) than in other months (271 min,  $\pm 30$ ) ( $t = 4.68$ ,  $P < 0.0004$ ).

### 3.2. Environmental factors

The duration of the total locomotory activity was negatively correlated with the photoperiod length in both sexes ( $r = -0.362$ ,  $df = 31$ ,  $P < 0.04$ ). Nevertheless, the travelling duration well correlated with the photoperiod length ( $r = -0.594$ ,  $df = 31$ ,  $P < 0.0003$ ) whereas the foraging activity did not. Furthermore the duration of travelling was negatively correlated with minimal temperatures ( $r = -0.460$ ,  $df = 31$ ,  $P = 0.007$ ) and with the number of freezing days ( $r = 0.354$ ,  $df = 31$ ,  $P < 0.043$ ).

The photoperiod length was the factor that contributed more clearly to the duration of travelling either in males (multiple correlation coefficient  $r = 0.811$ ) or females (multiple correlation coefficient  $r = 0.807$ ) as shown by the multifactorial correlation analysis (Table 2). By contrast, the foraging activity was influenced by meteorological factors such as variations in the pluviothermic quotient and precipitation for males (multiple correlation coefficient  $r = 0.607$ ) while minimal temperatures affected the foraging activity in females (multiple correlation coefficient  $r = 0.807$ ).

### 3.3. Trophic factors

Mammals constituted the chief food category in winter while anurans were mainly consumed

in spring (males  $\chi^2 = 106.6$ ,  $df = 3$ ,  $P < 0.0001$ , females  $\chi^2 = 79.0$ ,  $df = 3$ ,  $P < 0.0001$ , considering only three dietary categories, mammals, anurans and others) (Table 3). The diet did not differ between males and females ( $\chi^2 = 9.29$ ,  $df = 4$ ,  $P < 0.050$ , based on the five main categories, mammals, birds, anurans, invertebrates and others). But females ate significantly more rabbits and less rats than did males ( $\chi^2 = 19.33$ ,  $df = 4$ ,  $P < 0.001$ , considering only mammalian prey).

The duration of travelling was positively correlated with the proportion of shrews ( $P < 0.004$ ) and rats ( $P < 0.001$ ) for both sexes (Table 4). On the other hand, there was a negative correlation between the travelling activity and the predation of anurans ( $P < 0.034$ ) and birds ( $P < 0.05$ ). In fact, the foraging activity clearly decreased when the polecat ate a lot of anurans ( $P < 0.032$ ) whereas it increased with the consumption of voles ( $P < 0.012$ ). The duration of the total locomotory activity is inversely correlated with the variations of anurans in the diet both in males ( $P < 0.003$ ) and females ( $P < 0.03$ ). The duration of travelling was positively associated with an increase of rats in the diet of both sexes.

## 4. Discussion

Polecats exhibited either (a) movements located on restricted areas or (b) more or less linear movements within the home range. This space use was generally regarded as a selective exploitation of environment with long travelling between intensively exploited sites (Weber, 1989b; Lodé, 1993a, 1994). This pattern of space use was often observed in mustelids (Gerell, 1967; Erlinge, 1979; Burskirk et al., 1988; Marchesi, 1989). It could be predicted that the duration of different activities varies with the prey type. The time spent in foraging may decrease when prey were available, vulnerable or easily detectable. Travelling movements may increase when prey were patchily distributed but other circumstances as breeding or weather could also affect movements.

Table 2  
Multifactorial correlation analysis between polecats' activity and abiotic variables

<i>Foraging in males</i>			
Factors	Regression coefficient	<i>F</i> (df 1,12)	<i>P</i>
Pluviothermic quotient	−3.520	6.63	0.023 <sup>a</sup>
Precipitation	+0.036	6.21	0.027 <sup>a</sup>
Minimal temperature	+0.08	1.02	0.334
Photoperiod length	+0.004	0.85	0.621
Number of frosty days	−0.025	0.35	0.573
Multiple correlation coefficient	+0.607		0.292
<i>Foraging in females</i>			
Factors		<i>F</i> (df 1,9)	<i>P</i>
Minimal temperature	+0.235	5.13	0.048 <sup>a</sup>
Number of frosty days	+0.133	3.86	0.077
Pluviothermic quotient	−2.222	2.29	0.161
Precipitation	+0.022	1.34	0.276
Photoperiod length	+0.004	0.62	0.543
Multiple correlation coefficient	+0.807		0.054 <sup>b</sup>
<i>Travelling in males</i>			
Factors		<i>F</i> (df 1,12)	<i>P</i>
Photoperiod length	−0.013	11.53	0.005 <sup>a</sup>
Number of frosty days	+0.046	1.22	0.291
Minimal temperature	+0.076	0.98	0.655
Precipitation	−0.012	0.70	0.575
Pluviothermic quotient	+1.008	0.58	0.532
Multiple correlation coefficient	+0.811		0.014 <sup>a</sup>
<i>Travelling in females</i>			
Factors		<i>F</i> (df 1,9)	<i>P</i>
Photoperiod length	−0.010	6.35	0.031 <sup>a</sup>
Precipitation	−0.013	0.75	0.595
Pluviothermic quotient	+0.257	0.05	0.827
Number of frosty days	+0.006	0.01	0.915
Minimal temperature	+0.002	0.00	0.981
Multiple correlation coefficient	+0.807		0.052 <sup>b</sup>

<sup>a</sup> Indicates the significant relationships and

<sup>b</sup> indicates a marginal significance.

Trophic factors obviously influenced polecats' activity. Indeed, foraging and travelling clearly decreased during anuran exploitation by polecats in western France as predicted. The capture of anurans was easy for polecats (Weber, 1989c), and the aggregation of anuran on spawning sites in spring (Blab, 1986; Guyétant, 1986) probably facilitated the predation. By contrast, polecats increased their travelling related to the consumption of brown rats. Rats provided an appreciable biomass. However their difficult capture (Wusthehube, 1960; Gossow, 1970) probably led the predator to change hunting ground more often.

When polecats fed on bank voles, they increased their foraging. The predation on voles remained relatively easy (Wusthehube, 1960; Gossow, 1970). Nonetheless, the increase of the foraging activity suggested that its duration was affected by the regular dispersion of *Clethrionomys glareolus* in woods. Predators generally avoided shrews because of toxic glands they have on their flanks (Moors, 1975). Here, their winter consumption probably indicated a decrease of resource availability as suggested by the correlation between the duration of travelling and the proportion of this particular prey in their diet. The diet

pattern of polecats was directly affected by the availability of dietary resources (Lodé, 1994) but time budget was also influenced by the dispersion of available resources in the environment.

Polecats were mainly nocturnal and spent an average of 7 h 30 min in activity, duration slightly comparable to that of other mustelids such as badgers *Meles meles* (8 h 20 min, Rodriguez et al., 1998). During coldest periods, mustelids may remain several days in their den (Skirnrison, 1986; Richardson et al., 1987; Robitaille and Baron, 1987; Weber, 1989d). In western France, the mildness of climatic conditions allowed polecats to have an outside activity in winter. Rut began as soon as the end of February (Lodé, 1990) and was accompanied by extended movements as shown by the duration of male travelling.

Although total activity level did not vary among individuals or between the sexes, females spent significantly more time forag-

ing than males. Sexual size dimorphism has been presumed to allow animals to exploit different sized prey (Marti et al., 1993; Paton et al., 1994). The smaller size of female compared to male polecats may reduce food requirements. But, here the foraging duration of females considerably exceeded that of males despite a sexual size dimorphism. In females, the duration of foraging increased in summer during breeding period. Because the females have to provide prey for their cubs, the increase of this activity was probably associated with the breeding. By contrast, travelling duration was more important in males than in females. This difference may be attributed both to the search for mate in males and their need to defend large exclusive home range.

Therefore it appears that the organisation of budget time in *M. putorius* resulted from a compromise between the requirements of breeding and trophic constraints.

Table 3

Seasonal variations in the occurrences of each prey category in the diet of polecats (relative frequency percentages)

	Winter	Spring	Summer	Autumn	Total
<i>Males</i>					
Shrews	6.3	0.0	2.2	4.1	3.3
Rats	25.8	6.1	1.7	6.1	13.6
<i>Clethrionomys glareolus</i>	27.4	24.1	22.8	32.9	26.3
<i>Microtus arvalis</i>	23.3	21.1	25.3	23.1	22.9
Rabbits	0.4	0.0	16.7	12.5	3.3
Birds	0.0	2.2	11.9	0.0	2.0
Anurans	4.2	45.9	15.0	18.4	23.9
Invertebrates	4.8	0.6	4.4	4.3	2.3
Others	7.8	0.0	0.0	0.0	2.3
<i>Females</i>					
Shrews	6.4	0.0	2.4	4.0	3.0
Rats	22.8	8.5	0.0	10.7	11.3
<i>Clethrionomys glareolus</i>	37.9	23.8	36.7	27.0	30.1
<i>Microtus arvalis</i>	16.7	15.8	20.5	10.0	16.1
Rabbits	0.0	4.9	19.6	21.6	9.3
Birds	5.0	3.6	10.5	5.5	5.1
Anurans	2.0	43.4	3.4	11.9	19.7
Invertebrates	6.9	0.0	7.2	4.0	3.6
Others	1.7	0.0	0.0	5.2	1.8

Table 4  
Concordance (Tau Kendall) between polecats' activity and categories of prey

	General activity duration			Foraging duration			Travelling duration		
	<i>Tau</i>	<i>Z</i>	<i>P</i>	<i>Tau</i>	<i>Z</i>	<i>P</i>	<i>Tau</i>	<i>Z</i>	<i>P</i>
<i>Males</i>									
Shrews	0.532	3.084	0.002 <sup>a</sup>	0.188	1.089	NS	0.286	01.656	NS
<i>Clethrionomys</i>	0.281	1.628	NS	0.208	1.204	NS	0.116	0.671	NS
<i>Microtus</i>	0.007	0.039	NS	-0.124	-0.720	NS	0.123	0.711	NS
Rats	0.298	1.725	NS	0.042	0.243	NS	0.424	2.459	0.014 <sup>a</sup>
Rabbits	0.017	0.098	NS	-0.154	-0.891	NS	0.071	0.413	NS
Birds	-0.332	-1.922	0.055 <sup>b</sup>	-0.063	-0.368	NS	-0.303	-1.757	NS
Anurans	-0.505	-2.928	0.003 <sup>a</sup>	-0.193	-1.119	NS	-0.397	-2.300	0.020 <sup>a</sup>
<i>Females</i>									
Shrews	0.000	0.000	NS	-0.130	-0.678	NS	0.433	2.248	0.025 <sup>a</sup>
<i>Clethrionomys</i>	0.390	2.028	0.043 <sup>a</sup>	0.327	1.698	NS	0.259	1.340	NS
<i>Microtus</i>	0.193	1.003	NS	0.060	0.313	NS	0.051	0.262	NS
Rats	0.011	0.053	NS	-0.230	-1.195	NS	0.463	2.403	0.016 <sup>a</sup>
Rabbits	-0.065	-0.335	NS	0.128	0.664	NS	-0.343	-1.779	NS
Birds	0.086	0.447	NS	0.245	1.273	NS	-0.149	-0.790	NS
Anurans	-0.429	-2.231	0.03 <sup>a</sup>	-0.301	-1.562	NS	-0.240	-1.245	NS
<i>Males + females</i>									
Shrews	-0.289	2.361	0.018 <sup>a</sup>	0.023	0.184	NS	0.351	2.875	0.004 <sup>a</sup>
<i>Clethrionomys</i>	0.355	2.923	0.004 <sup>a</sup>	0.324	2.649	0.008 <sup>a</sup>	0.091	0.745	NS
<i>Microtus</i>	0.008	0.065	NS	-0.220	-1.799	NS	0.190	1.552	NS
Rats	0.287	1.859	NS	-0.004	-0.033	NS	0.407	3.331	0.001 <sup>a</sup>
Rabbits	0.005	0.037	NS	0.091	0.747	NS	-0.198	-1.717	NS
Birds	-0.042	-0.342	NS	0.154	1.257	NS	-0.244	-1.999	0.05 <sup>a</sup>
Anurans	-0.483	-3.955	0.0001 <sup>a</sup>	-0.297	-2.427	0.015 <sup>a</sup>	-0.259	-2.119	0.034 <sup>a</sup>

<sup>a</sup> Indicates the significant relationships and

<sup>b</sup> indicates a marginal significance.

## References

- Ashoff, J., 1966. Circadian activity with two peaks. *Ecology* 47, 657–662.
- Bekoff, M., Daniels, T.J., Gittleman, J.L., 1984. Life history patterns and the comparative social ecology of Carnivores. *Annu. Rev. Ecol. Syst.* 15, 191–232.
- Blab, J., 1986. *Biologie, Ökologie und Schutz von Amphibien*. Kilda Verlag, Bonn, Bad Godesberg, 150 pp.
- Blandford, P.R.S., 1987. Biology of the Polecat *Mustela putorius*: a literature review. *Mammal Rev.* 17, 155–198.
- Burskirk, S.W., Harlow, H.J., Forrest, S.C., 1988. Temperature regulation in American marten (*Martes americana*) in winter. *Nat. Geo Res.* 4, 208–218.
- Dajoz, R., 1974. *Précis d'écologie*, Dunod, Paris, 505 pp.
- Erlinge, S., 1979. Movements and daily activity patterns of radio tracked male stoats (*Mustela erminea*). In: Amler, C.J., Mac Donald, D.W. (Eds.), *Handbook on Biotelemetry and Radiotracking*. Pergamon, Oxford, pp. 703–710.
- Ewer, R.F., 1968. *Ethology of Mammals*. Logos Press, London, 418 pp.
- Gerell, R., 1967. Food selection in relation to habitat in mink *Mustela vison* in Sweden. *Oikos* 18, 233–246.
- Gossow, H., 1970. Vergleichende Verhaltensstudien an Mardeartigen I Über Lautäusserungen und zum Beuteverhalten. *Z. Tierpsychol.* 27, 405–480.
- Guyétant, R., 1986. Les Amphibiens de France. *Revue Française d'Aquariophilie-Herpéthologie* 13, 1–62.
- Hainard, R., 1961. *Mammifères Sauvages d'Europe*. Delachaux & Niestlé, Neuchâtel, p. 332.
- Jacobsen, N.K., Wiggins, A.D., 1982. Temporal and procedural influences on activity estimated by time sampling. *J. Wild. Manag.* 46, 313–324.
- Jedrzejewski, W., Jedrzejewska, B., Brzezinski, M., 1993. Winter habitat selection and feeding habits of polecats (*Mustela putorius*) in the Białowieza National Park, Poland. *Z. Säugetierk.* 58, 75–83.
- Lodé, T., 1990. Reconnaissance du congénère et comportement sexuel chez le putois. *Bull. Soc. Sc. Nat. Ouest France* 12, 105–110.
- Lodé, T., 1993a. 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.

- Lodé, T., 1993b. Diet composition and habitat use of sympatric polecat and American mink in western France. *Acta Theriol.* 38, 161–166.
- Lodé, T., 1994. Environmental factors influencing habitat exploitation by the polecat *Mustela putorius* in western France. *J. Zool. Lond.* 234, 75–88.
- Lodé, T., 1995. Activity pattern of polecats *Mustela putorius* L. in relation to food habits and prey activity. *Ethology* 100, 295–308.
- Lodé, T., 1997. Trophic status and feeding habits of the European polecat *Mustela putorius* L. 1758. *Mammal Rev.* 27, 177–184.
- Marchesi, P., 1989. Ecologie et comportement de la Martre (*Martes martes* L.) dans le Jura Suisse. Thesis, University of Neuchâtel, Neuchâtel, 185 pp.
- Marti, C.D., Steenhof, K., Kochert, M.N., Marks, J.S., 1993. Community trophic structure: the roles of diet, body-size, and activity time in vertebrate predators. *Oikos* 67, 6–18.
- Mermod, C., 1969. Ecologie et dynamique des populations de trois rongeurs sylvicoles. *Mammalia* 33, 1–57.
- Moors, P.J., 1975. The food of weasels (*Mustela nivalis*) on farmland in north-east Scotland. *J. Zool. Lond.* 177, 455–461.
- Moors, P.J., 1980. Sexual dimorphism in the body size of mustelids (carnivora): the roles of food habits and breeding systems. *Oikos* 34, 147–158.
- Paton, P.W.C., Messina, E.J., Griffin, C.E., 1994. A phylogenetic approach to reversed size in dimorphism in diurnal raptors. *Oikos* 71, 492–498.
- Powell, R.A., 1979. Mustelids spacing patterns: variations on a theme by *Mustela*. *Z. Tierpsychol.* 50, 153–155.
- Price, E.O., 1971. Effect of food deprivation on activity of least weasel. *J. Mammal.* 52, 636–639.
- Raymond, J.M., Robitaille, J.F., Lauzon, P., Vaudry, R., 1990. Prey-dependent profitability of foraging behaviour of male and female ermine, *Mustela erminea*. *Oikos* 58, 323–328.
- Richardson, L., Clark, T.W., Forrest, S.C., Campbell, T.M., 1987. Winter ecology of the black-footed ferret at Meteete, Wyoming. *Amer. Mid. Nat.* 117, 225–239.
- Robitaille, J.F., Baron, G., 1987. Seasonal changes in the activity budget of ermine, *Mustela erminea* L. *Can. J. Zool.* 65, 2864–2871.
- Rodriguez, A., Martin, R., Delibes, M., 1998. Space use and activity in a mediterranean population of badgers *Meles meles*. *Acta theriol.* 41, 59–72.
- Saint-Girons, M.C., 1966. Le rythme circadien d'activité chez les mammifères holarctiques. *Mém. Mus. Nat. Hist. Nat. Zool.* 40, 101–187.
- Sandell, M., 1986. Movement patterns of male stoat *Mustela erminea* during the mating season: differences in relation to social status. *Oikos* 47, 63–70.
- Sargeant, A.B., Swanson, A., Doty, H.A., 1973. Selective predation by mink, *Mustela vison*, on waterfowl. *Am. Nat.* 89, 208–214.
- Skirnirson, K., 1986. Untersuchungen zum Raum Zeit-System freilebender Steinmarder (*Martes foina* Erxleben 1777). *Hamburg Beit. Wildbio.* 6, 1–200.
- Vaudry, R., Raymond, M., Robitaille, J.F., 1990. The capture of voles and shrews by male and female ermine *Mustela erminea* in captivity. *Holarct. Ecol.* 13, 265–268.
- Weber, D., 1989a. Beobachtungen zu Aktivität und Raumnutzung beim Iltis (*Mustela putorius* L.). *Rev. Suisse Zool.* 96, 841–862.
- Weber, D., 1989b. Foraging in polecats (*Mustela putorius* L.) of Switzerland: the case of a specialist anuran predator. *Z. Säugetierk.* 54, 377–392.
- Weber, D., 1989c. The diet of polecats (*Mustela putorius* L.). *Z. Säugetierk.* 54, 157–171.
- Weber, D., 1989d. The ecological significance of resting sites and the seasonal habitat change in polecats (*Mustela putorius*). *J. Zool. Lond.* 217, 629–638.
- Wusthehube, C., 1960. Beiträge zur Kenntnis besonders des Spiel- und Beuteverhaltens einheimischer Musteliden. *Z. Tierpsychol.* 17, 579–613.
- 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.