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Activity Pattern of Polecats Mustela putorius L. in Relation to Food Habits and Prey Activity

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Abstract

The activity pattern of polecats *Mustela putorius* L. was studied by radiotracking five males and four females in the wetlands of western France from Jul. 1988 to Mar. 1992. Polecats were nocturnal throughout the year with no differences between males and females. The diel activity remained moderate (31 %). Seasonal food habits were characterized by the exploitation of anurans in spring, while rodents were preyed upon from summer to winter. Seasonal changes in the activity rhythm of polecats appeared synchronized with the activity of the main prey. It is suggested that the activity patterns exhibited in different periods of the year are a result of changes in feeding tactics.

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Introduction

Most European mustelids exhibit an activity rhythm closely related to photoperiod length (HAINARD 1961). However, numerous disturbances due to meteorological or physiological factors are likely to affect this pattern. For example, mustelids are known to reduce their outside activities during cold weather, to increase their movements during mating season (EWER 1968; SKIRNISSON 1986; RICHARDSON et al. 1987; BUSKIRK et al. 1988), and it could be that activity is scheduled to avoid dominant predators (POWELL 1973; RICHARDSON et al. 1987). Furthermore, because prey searching may be easier when prey are active, the existence of a synchrony between carnivores' activity and their main prey has been suggested (GERELL 1969; CURIO 1976; ZIELINSKI et al. 1983).

The wild European polecat Mustela putorius L. is a terrestrial mustelid which forages in woodlands and marshes (KRATOCHVIL 1952; DANILOV & RUSAKOV 1969; BLANDFORD 1987; WEBER 1989a; BRZEZINSKI et al. 1992; LODE 1993a).

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The diet includes a wide range of vertebrate prey (KRATOCHVIL 1952; DANILOV & RUSAKOV 1969; BALLARIN et al. 1980; BLANDFORD 1987; WEBER 1989a; LODE 1991, 1993b), but, despite its food eclecticism, the polecat mainly exploits rodents and anurans.

Available information on polecat activity patterns portrays a rather nocturnal predator showing variable activity throughout the year (NILSSON 1978; HERRENSCHMIDT 1982; BLANDFORD 1987; WEBER 1989b). If changes in activity rhythm exhibited by polecats in different periods of the year were adaptive, one would assume that polecats synchronize their activity rhythm with the activity of prey to make hunting more successful. Furthermore, changes in activity should be associated with dietary variations and prey availabilities. In order to test the hypothesis of a close association between feeding tactics and activity patterns, a detailed description of the activity rhythm was performed in relation to some environmental variables, to polecat food habits, and to prey activity period.

Methods

Study area

This study was carried out on wetlands and adjoining woodlands stretching along the banks of the river Loire, western France, i.e. the Brière Marshes (47°25 N, 2°15 W) and the Grand-Lieu Lake (47°05 N, 1°39 W). Peat-bogs and marshes have been formed behind the alluvial banks deposited by the Loire. Elsewhere, the landscape is characterized by a patchwork of small fields hedged by oaks and ashes. The climate is mild and humid (Table 1) with only 2 snowy days per year.

Study Methods

From Jan. 1989 to Mar. 1992, nine wild polecats (Table 2) were live-trapped and fitted with radiotransmitters (14 g, pulse rate 50–90, 148 MHz). The animals were repeatedly located using a handheld antenna and a portable receiver for periods of 6 h per d with location of each animal given every 45 m (instantaneous time-sampling: JACOBSEN & WIGGINS 1992) for a total of 24 h per wk (see LODE 1993 a). Only active fixes outside the dens, shown by the variations in radio-signal strength due to the movements, were considered. When the polecat activity was unclear, other fixes at 10-min intervals were monitored to confirm whether the animal was moving or resting, but only one fix was considered. Activity was defined as the percentage of active radio-fixes per h. Daily activity data of individuals were pooled for a 2-mo period of the year. X and SD values are given unless otherwise stated. A Kruskall-Wallis one-way analysis of variance by ranks was used. The Spearman rank-correlation coefficient was calculated monthly between mean activity level and temperature, photoperiod, and precipitation.

Diel activity rhythms of bank voles Clethrionomys glareolus, and meadow voles Microtus arvalis were investigated by direct observation. For each species, four females and two males were live-trapped and housed in two individual outside terrariums (natural conditions) that were grass-covered and contained a basin, a water bottle, and tree-bark, moss and nest compartments. Observation lasted 7 d after which the animals were released. The d 1 was considered to be an adaptation period.

The diel-activity rhythm of wild brown rats Rattus norvegicus was recorded by direct observation from a hidden spot at an artificial feeding site that had previously been baited for 2 d. The diel activity of six agile frogs, Rana dalmatina, and six common toads, Bufo bufo, was directly observed in the field. The animals were temporarily marked on the back with fluorescent powder to make the survey easier (LODE 1993 c). Activity was determined in periods of 8 h per d for 6 d by counting the number of individuals seen with a record every 15 min (n = six individuals \times (4 \times 15 min) \times 2 = 48 observations per h, except for n Rattus individuals = x, n observations = 48). A red spot light was used to observe the animals in darkness. All activities (feeding, locomotion, grooming, interactions) outside the dens

Table 1: Variations of mean monthly temperature and precipitation

				1989	68						1990		
	Jan.	Feb.	Mar.	Jul.	Aug.	Sep.	Oct.	Nov.	Jan.	Feb.	Mar.	Apr.	May
Temperature °C	5.9	7.7	10.5	21.2	20.1	17.4	14.7	9.0	7.6	10.8	9.6	10.9	17.6
minimum	2.1	3.7	5.9	15.1	13.7	10.8	9.4	5.3	4.5	9.7	3.9	9.0	11.4
maximum	8.6	11.7	15.1	27.4	26.5	24.0	20.0	12.8	10.7	14.1	15.3	15.9	23.8
Precipitation mm	36	8	108	33	26	٣	51	54	∞	122	5	54	∞
	1990				1991					19	1992		
	Jun.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Mar.	Apr.	May	Jun.	
Temperature °C	16.6	14.8	8.9	4.7	5.1	3.0	8.6	8.6	8.4	6.6	15.8	17.3	
minimum	11.6	6.6	5.3	1.5	5.0	6.0-	6.0	4.5	4.3	5.3	9.6	11.5	
maximum	21.5	19.6	12.4	7.9	8.1	6.9	13.6	15.1	12.5	4.5	22.0	23.0	
Precipitation mm	2,6	156	87	62	112	37	81	51	30	4	15	32	

Table 2.	Characteristics	οf	radiotracked	nolecate

Identification	Sex	Weight (g)	Survey period	Locations
M102	М	1260	15 Jul. 89–6 Oct. 89	224
M103	M	1580	29 Jan. 90–7 Jun. 90	235
M204	M	1500	27 Nov. 90-6 Apr. 91	306
M205	M	1430	8 Jan. 91–24 Mar. 91	210
M206	M	1600	10 Feb. 92-14 Jun. 92	224
F102	F	890	20 Jan. 89-24 Feb. 89	126
F103	F	605	21 Aug. 89-29 Nov. 89	276
F104	F	820	13 Feb. 90-12 May 90	132
F205	F	680	21 Oct. 90-8 Jan. 91	98

Table 3: Percentage of time polecats were active ($\bar{X} \pm SD$) during 2-mo periods between Jul. 1989 and Mar. 1992

	Diel a	ctivity	Nocturn	al activity
	Males	Females	Males	Females
JanFeb.	33.7 ± 7.4	31.8 ± 9.4	90.4 ± 9.9	91.1 ± 10.9
MarApr.	27.3 ± 6.8	29.5 ± 7.6	84.9 ± 15.1	79.6 ± 13.5
MayJun.	30.3 ± 7.5	37.5 ± 0.0	62.6 ± 21.2	44.4 ± 15.8
JulAug.	29.2 ± 4.6	34.1 ± 7.2	69.9 ± 12.7	68.5 ± 15.5
SepOct.	31.7 ± 6.3	31.1 ± 4.7	80.4 ± 12.6	80.2 ± 21.9
NovDec.	34.2 ± 4.6	31.8 ± 3.3	95.5 ± 6.2	95.5 ± 7.9

were considered. The concordance between activity rhythms of polecats and every prey species was estimated using the Kendall rank-correlation coefficient T with 24-h periods. Since some variables were interdependent relative to nocturnal habits, a cluster analysis was performed to point out dependencies (PCSM program, hierarchical ascending classification). Polecat food habits were studied by scat analysis. Scats were collected from telemetred polecats during a daily search following the nocturnal path of surveyed animals (LODE 1994) and remains identified using standard techniques by comparison with a collection and atlas (DAY 1966; RAGE 1974; DEBROT et al. 1982). The results are expressed as the relative frequency of occurrences. Some fish and molluscs or mammals and birds, assumed to be carrion, formed the 'other' categories.

Results

Activity Pattern

No difference was found in the distribution of mean activity between any individual polecats (H = 1.67, df = 8, ns). Polecats spent, on average, one third of their time (31.0 \pm 6.8 %) in activity, with no differences between males (30.6 % \pm 7.1 %) and females (31.6 \pm 6.4 %) (Mann-Whitney U = 8, ns). The mean rate of activity appeared remarkably stable throughout the year (Table 3) with no differences between the 2-mo periods (H = 10.54, df = 5, p = 0.06). Resting periods lasted between about 16 h and 30 min (68.9 %).

The activity was not, however, distributed in a homogenous pattern and

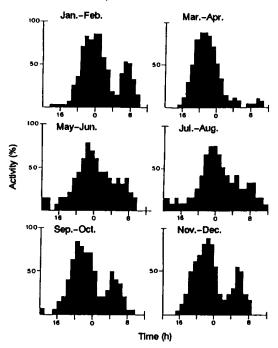


Fig. 1: Diel activity of polecats in western France. from Jul. 1989 to Mar. 1992

varied considerably from one hourly period to another. A peak of activity was recorded at 23 h (89.9 \pm 38.7 %). The activity generally occurred soon after sunset and ended at sunrise (Fig. 1). From Sep. to Feb., the animals showed two peaks in their activity with a resting period of about 2–3 h. In Mar. and Apr., the level of activity decreased after midnight. From May to Aug., the variations tended to be more moderate. All the surveyed polecats exhibited a pronounced nocturnality. The percentage of time polecats were active at night (darkness) averaged 82.3 % (\pm 17.6 %) with no differences between males (82.1 \pm 17.3 %) and females (82.5 \pm 18.2 %; U = 15.5, ns) but varied significantly throughout the year (H = 38.81, df = 5, p < 0.0001) both for males (H = 21.57, df = 5, p < 0.0001) and females (H = 18.42, df = 5, p < 0.002). The monthly diel activity did not correlate with precipitations (males: $r_s = -0.319$, df = 18, ns; females: $r_s = -0.408$, df = 14, ns) and was not related either to photoperiod ($r_s = 0.049$, $r_s = 0.230$, ns) or mean temperature ($r_s = 0.072$, $r_s = 0.212$, ns).

Relationships between Activity Rhythms of Prey and Diet of Polecats

The anurans studied were mainly nocturnal in relation to the daylight cycle but activity decreased rapidly after midnight (Fig. 2). Activity periods were restricted to the Mar.—Oct. period, but a relatively high diel activity occurred from dusk to midnight. A few activities were diurnal, occurring mainly in the early morning in summer. The bank voles showed several peaks in the activity

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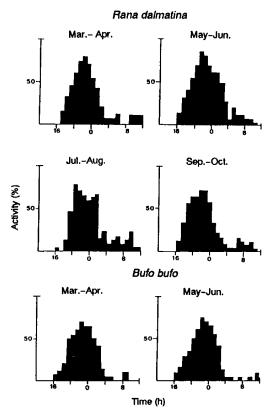


Fig. 2: Diel activity of main anuran prey of polecats in western France: agile frogs, Rana dalmatina, and common toads, Bufo bufo

pattern, generally more pronounced soon after sunset and before sunrise (Fig. 3). The level of activity was often very low around 0300–0400 h. The meadow voles had polyphasic rhythms because individual activity cycles were successively overlapping. Voles appeared to be more active during the day, soon after sunrise, but the pattern seemed rather irregular in the afternoon. The brown rats exhibited a strong nocturnal preference, but the youngest were more diurnal in short active periods, probably in relation to their social status. A prominent peak can be seen in the evening and a second one shortly before sunrise.

The distribution of active hourly periods showed the close synchrony with polecat activity (Table 4), except for *Microtus*.

Mammals, chiefly rodents (bank voles, meadow voles and brown rats) were the most important food in the diet of the polecats (Table 5) but amphibians, mainly terrestrial anurans (agile frogs and common toads) were equally important from Mar. to Jun. Birds and invertebrates formed secondary food categories. Dietary changes showed a clear seasonality. The consumption of brown rats increased significantly from Nov. to Feb. (H = 17.24, df = 5, p < 0.004). The

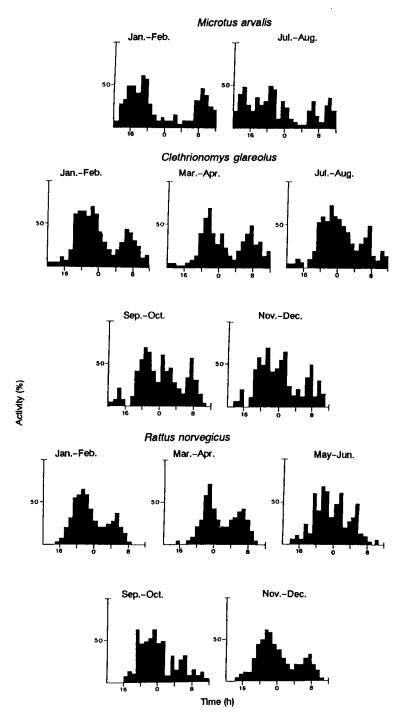


Fig. 3: Diel activity of main rodent prey of polecats in western France: meadow voles, Microtus arvalis, bank voles, Clethrionomys glareolus, and brown rats, Rattus norvegicus

Table 4: Concordance (Kendall rank coefficient) between distribution of active hourly periods in polecats (%) relative to distribution of active hourly periods

		in	in main prey species (%)		species (%)	cuve mounty periods
	JanFeb.	MarApr.	May-Jun.	JulAug.	Sep.—Oct.	Nov-Dec
Rana dalmatina	ı	0.728	0.756	0.620	079 U	
Bufo bufo	1	p < 0.0001	p < 0.0001	p < 0.0001	p < 0.0001	l
		p < 0.0001	0.889 p < 0.0003	ı	i	
Clethrionomys	0.689	0.438	: I	0.735	7.847	0
1	p < 0.0001	p < 0.003		p < 0.0001	0.04	0.330
Rattus	0.735	0.435	0.643		1000.0 × 4	P / 0.0003
;	p < 0.0001	p < 0.003	p < 0.0001		0.000	0.810
Microtus	-0.162	I	,	-0.187	1000 P	P 0.0001
	su			SU US	I	ı

Table 5: Relative frequency of occurrences (%) of different food categories in the diet of polecats in western France (number of prey in parentheses)

	JanFeb. (235)	MarApr. (253)	May-Jun. (104)	JulAug. (67)	SepOct. (101)	NovDec. (106)	Total (866)
Mammals	91.5	49.8	55.8	79.1	79.2	72.6	70.3
Sorex sp.	5.9	0	0	2.9	4.9	5.7	3.1
Ondatra z.	2.9	0	0	0	0	6.0	0.0
Rattus n.	25.1	7.5	4.8	0	6.9	26.4	12.5
Clethrionomys	31.9	22.1	26.9	32.8	31.7	28.3	28.1
Microtus sp.	25.1	19.4	20.2	22.4	13.9	15.1	20.1
Oryctolagus c.	4.0	8.0	3.8	20.9	21.8	5.7	5.6
Birds	0	2.4	3.8	11.9	1.9	9.9	3.1
Amphibians	4.7	47.4	40.4	1.5	11.9	9.4	22.6
Invertebrates	2.6	0.4	0	7.5	3.9	7.5	2.8
Others	1.3	0	0	0	2.9	3.8	1.2

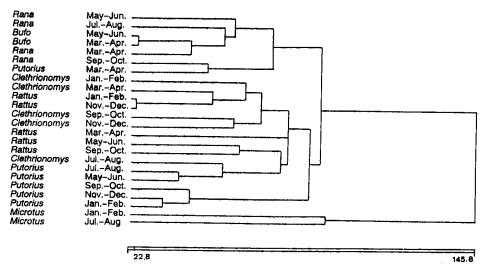


Fig. 4: Dendrogram resulting from the cluster analysis of seasonal activity rhythms of polecat and prey (weighed mean euclidian distances)

occurrence of bank voles varied throughout the year (H = 11.05, p < 0.05), while frequency of meadow voles did not, and the exploitation of anurans increased considerably in spring (H = 19.67, p < 0.001).

Cluster Analysis

Cluster analysis (mean euclidian distances D) allowed a clarification of the association between the polecats activity and that of their prey (Fig. 4). A first cluster (D = 71.74) was formed by frog and toad activity rhythms and the activity rhythm of polecats in Mar. and Apr. A second cluster (D = 75.14) included activity rhythms of the brown rat in May and Jun. and Sep. and Oct., bank voles in Jul. and Aug. and polecat in May and Jun. and Jul. and Aug. Polecat activity rhythm from Sep. to Feb. (D = 43.73) was indirectly related to other prey activities (D = 78.48), but also embraced the second cluster (D = 77.81). Activity rhythms of meadow voles appeared to be independent.

Discussion

Relationships between Activity Patterns and Diet

In western France, polecats exhibited a bimodal activity rhythm with a great agreement between males and females. The activity pattern of polecats was characterized by important variations in distribution of active hourly periods throughout the year. Changes in activity distribution correlated highly with main prey activity rhythms. As a result of this, from Mar. to Jun., changes in polecat

activity rhythm were strongly correlated with frog and toad activity patterns. In Europe, polecats are known to exploit frogs and toads intensively (KRATOCHVIL 1952; DANILOV & RUSAKOV 1969; BALLARIN et al. 1980; JEDRZEJEWSKI et al. 1989; WEBER 1989a; LODE 1991, 1993b) and may secrete surplus food when anurans are over-abundant near breeding sites (DANILOV & RUSAKIV 1969; LODE 1989). Agile frogs and common toads are nocturnal terrestrial anurans, although temperature might affect their activity (ANGEL 1947; FRAZER 1966; HEUSSER 1968; GEISSELMANN et al. 1971; BLAB 1986; PINSTON & GUEYETANT 1987). The degree of activity varies throughout the night, decreasing after midnight in both species. The relative humidity at dusk may be an important factor in maintaining the nocturnality in summer, as in *Rana sylvatica* (BELLIS 1962).

From Nov. to Dec., the strongest correlations were in the rat activity pattern. Although the animals might have become accustomed to a baited site, disturbing their natural rhythm, the nocturnal activity pattern shown by brown rats in this study was similar to that found in nature (TAYLOR 1978). Brown rats were generally nocturnal although there were wide individual variations, especially among the youngest individuals (TAYLOR 1978). Maximum activity occurred in the evening but the activity level remained high throughout the night.

In bank voles, activities were concentrated around dusk and dawn, sometimes

In bank voles, activities were concentrated around dusk and dawn, sometimes with another peak soon after midnight, and showed significant concordance with summer and winter activity rhythms of polecats. Previous investigations on bank-vole activity patterns (MILLER 1955; SAINT-GIRONS 1960, 1961; KIKKAWA 1964; GORECKI 1968; WOJICK & WOLK 1985) stressed that these small rodents were active chiefly during the night, with 2-3 peak periods. On the other hand, the polyphasic activity rhythm of *Microtus arvalis* was not connected with polecat activity pattern. Important individual variations occur in voles, some individuals being more nocturnal than others. Short-term rhythm and alternate resting and active periods have often been described in *Microtus arvalis* (DURUP 1956; LEHMANN & SOMMERSBERG 1980). Due to negative interactions, the activities of young voles in *Microtus* were particularly nocturnal (BÄUMLER 1975; LEHMANN 1976; LEHMANN & SOMMERSBERG 1980).

Significance of Changes in Activity Patterns

Physiological factors such as breeding could also affect the activity pattern of mustelids. Here, no female has been surveyed during the breeding, but SANDELL (1986) in stoat, SKIRNISSON (1986) in stone marten, and RICHARDSON et al. (1987) in black-footed ferret noticed increases in activity at this time. The activity rhythm was probably dependent on endogenous factors, as suggested by correlations between the different activity rhythms in animals studied. The circadian activity rhythm of numerous species was, however, synchronized by day-night cycle (ASCHOFF 1966). Most mustelids start their activity in close connection with the sunset (GERELL 1969; BIRKS & LINN 1982; KALPERS 1984; BLANDFORD 1987: WEBER 1989b). In polecats, nocturnal activities are predominant and the animals synchronize their activity rhythm with the day-night cycle. Similar observations

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on nocturnal preference have been previously reported (NILSSON 1978; HER-RENSCHMIDT 1982; BLANDFORD 1987; WEBER 1989b).

In western France, the level of total diel activity was moderate (31 %) and stable throughout the year. In more severe conditions, polecats are less active at very low temperatures (KORHONEN & HARRI 1986; BLANDFORD 1987; WEBER 1989b). Some authors have found that mustelids have a more reduced activity in the coldest months (SKIRNISSON 1986; RICHARDSON et al. 1987; WEBER 1989b). Polecats have been found to be predominantly nocturnal in winter and adopt diurnal activities in summer (DANILOV & RUSAKOV 1969; WEBER 1989b), but, they can also exhibit more diurnal activity in winter than in summer. BLANDFORD (1987) and LABHARDT (1980) observed that 'the weather had not any influence' on the night activity of a food-bringing female. In this study, the level of nocturnal activity was greater in autumn and winter than in spring or summer. In western France, mild meteorological conditions may have only a reduced effect and, hence, this suggests that prey availability might have a deciding influence on changes in polecat activity pattern. Changing their activity rhythm in spring, polecats maximized contact with anurans. That flexibility exhibited by polecats characterizes adaptive response to differences in availability can, therefore, be assumed.

The results of this study show that variations in polecat activities are clearly related to that of their main prey. Thus, it seems reasonable to suggest that the observed variations in the activity pattern of polecats in western France are closely associated with changes in the feeding tactics exhibited by this predator in different periods of the year.

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Literature Cited

ANGEL, F. 1947: Vie et Moeurs des Amphibiens. Biblio. sc. Payot, Paris.

ASCHOFF, J. 1966: Circadian activity with two peaks. Ecology. 47, 657-662.

BALLARIN, I., GARZON, J., PALACIOS, F., CUESTA, L. & CASTROVIEJO, J. 1980: Sobre la alimentacion del turon (Putorius putorius L. 1758) en Espana. I. Reunion Iberoamer. Zool. Vert., La Rabida, 625-627.

BÄUMLER, W. 1975: Activity of some small mammals in the field. Acta theriol. 20, 365-377.

BELLIS, E. D. 1962: The influence of humidity on wood frog activity. Am. Midl. Nat. 68, 139-148. BIRKS, J. D. S. & LINN, I. J. 1982: Studies of the home-range of the feral mink (Mustela vison). Symp. Zool. Soc. Lond. 49, 231-251.

BLAB, J. 1986: Biologie. Ökologie und Schutz von Amphibien. Kilda-Verl., Bonn.

BLANDFORD, P. R. S. 1987: Biology of the polecat Mustela putorius: a literature review. Mammal Rev. 17, 155-198.

Brzezinski, M., Jedrzejewski, W. & Jedrzejewska, B. 1992: Winter home-ranges and movements of polecats Mustela putorius in Bialowieza Primeval Forest, Poland. Acta theriol. 37, 181-191.

BUSKIRK, S. W., HARLOW, H. J. & FORREST, S. C. 1988: Temperature regulation in American marten (Martes americana) in winter. Nat. Geogr. Res. 4, 208-218.

CURIO, E. 1976: The Ethology of Predation. Springer Verl., Berlin.
DANILOV, P. I. & RUSAKOV, O. S. 1969: Peculiarities of the ecology of Mustela putorius in North-West districts of the European part of the U.S.S.R. (in Russian). Zool. 48, 1383-1394.

- 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. Instit. Zool., Neuchatel.
- DURUP, H. 1956: Observations sur le rythme de l'activité du campagnol des champs *Microtus arvalis* Pallas. Mammalia 20, 390—404.
- EWER, R. F. 1968: Ethology of Mammals. Logos Press Ltd, London.
- FRAZER, I. F. D. 1966: A breeding colony of toads (Bufo bufo L.) in Kent. Brit. J. Herpetol. 4, 236—252.
- GEISSELMANN, B., FLINDT, R. & HEMMER, H. 1971: Studien zur Biologie, Ökologie und Merkmalvariabilität der beiden Braunfroscharten Rana temporaria und Rana dalmatina. Zool. Jb. Syst. 98, 521—568.
- GERELL, R. 1969: Activity patterns of the mink Mustela vison Schreber in southern Sweden. Oikos 20, 451—460.
- GORECKI, A. 1968: Metabolic rate and energy budget in the bank vole. Acta theriol. 13, 341—365.
- HAINARD, R. 1961: Mammifères Sauvages d'Europe. Delachaux & Nièstlé, Neuchatel.
- 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.
- HEUSSER, H. 1968: Die Lebensweise der Erdkröte Bufo bufo L. Wanderungen und Sommerquartiere. Rev. Suisse Zool. 75, 927—982.
- JACOBSEN, N. K. & WIGGENS, A. D. 1982: Temporal and procedural influences on activity estimated by time sampling. J. Wildl. Manage. 46, 313—324.
- 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.
- KALPERS, J. 1984: Contribution à l'étude éco-éthologique de la Fouine Martes foina. Stratégie d'utilisation du domaine vital et des ressources alimentaires. II. Radiorepérage et discussion générale. Cahiers Ethol. Appl. 4, 11—26.
- KIKKAWA, J. 1964: Movement, activity and distribution of the small rodents Clethrionomys glareolus and Apodemus sylvaticus in woodland. J. Anim. Ecol. 33, 259—299.
- KORHONEN, M. & HARRI, M. 1986: Seasonal changes in energy economy of farmed polecat as evaluated by body weight, food intake and behavioural strategy. Physiol. Behav. 37, 777—783.
- Kratochvil, J. 1952: O potrave a rasachtchore tmaveho (*Putorius putorius L.*). Acta. Univ. Agr. Sylv. Brno 1, 43—60.
- LABHARDT, F. 1980: Zur Fütterungstätigkeit und über einige Verhaltensweisen einer freilebenden Iltisfähe, Mustela putorius Linné, 1758. Säugetierk. Mitt. 28, 247—251.
- LEHMANN, U. 1976: Short-term and circadian rhythms in the behaviour of the vole, *Microtus agrestis* L. Oecologia 23, 185—199.
- —— & SOMMERSBERG, C. W. 1980: Activity patterns of the common vole *Microtus arvalis*—automatic recording of behaviour in enclosure. Oecologia 47, 61—75.
- LODE, T. 1989: Le comportement de mise en réserve alimentaire des proies chez le Putois Mustela putorius. Cahiers Ethol. Appl. 9, 19—30.
- 1991: Evolution annuelle du régime alimentaire du Putois Mustela putorius L. en fonction de la disponibilité des proies. Bull. Ecol. 22, 337—342.
- 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.
- 1993b: Diet composition and habitat use of sympatric polecat and American mink in western France. Acta theriol. 38, 161—166.
- 1993c: Rythme d'activité et utilisation de l'espace chez le Grenouille agile Rana dalmatina B., 1840 dans l'ouest de la France. Bull. Soc. Herp. Fr. 67, 13—22.
- 1994: Environmental factors influencing habitat exploitation by the polecat *Mustela putorius* in western France. J. Zool. Lond. 234, 75—88.
- MILLER, R. S. 1955: Activity rhythms in the wood mouse *Apodemus sylvaticus* and the bank vole *Clethrionomys glareolus*. Proc. Zool. Soc. Lond. 125, 505—519.
- NILSSON, T. 1978: Home-range utilization and movements in the polecat Mustela putorius during autumn. Congr. Theriol. Int. Brno, 173.

- PINSTON, H. & GUYETANT, R. 1987: Home fidelity in the common toad Bufo bufo L., Amphibia. Anura. Proc. 4th Ord. Gen. Meet. Soc. Europ. Herpetol., Nijmegen. pp. 317—320.
- POWELL, R. A. 1973: A model for raptor predation on weasels. J. Mammal. 54, 259—260.
- RAGE, J. C. 1974: Batraciens fossiles du quaternaire. Bull. Soc. Linn. Lyon 43, 276-289.
- RICHARDSON, L., CLARK T. W., FORREST, S. C. & CAMPBELL, T. M. 1987: Winter ecology of the black-footed ferret at Meetcetee, Wyoming. Am. Midl. Nat. 117, 225=239.
- SAINT-GIRONS, M. C. 1960: Le rythme nycthéméral d'activité du campagnol roux Clethrionomys glareolus (Schreber, 1780). I. Les mâles. Mammalia 24, 516—532.
- 1961: Le rythme nycthéméral d'activité du campagnol roux Clethrionomys glareolus (Schreber, 1780). II. Les femelles. Mammalia 25, 342—357.
- SANDELL, M. 1986: Movement patterns of male stoat Mustela erminea during the mating season: differences in relation to social status. Oikos 47, 63—70.
- SKIRNISSON, K. 1986: Untersuchungen zum Raum-Zeit-System freilebender Steinmarder (Martes foina Erxleben 1777). Hamburg, Beitr. Wildbiologie 6, 1—200.
- TAYLOR, K. D. 1978: Range of movements and activity of common rats (Rattus norvegicus) on agricultural land. J. Applied Ecol. 15, 663—677.
- WEBER, D. 1989a: Foraging in polecats (Mustela putorius L.) of Switzerland: the case of a specialist anuran predator. Z. Säugetierkd. 54, 377—392.
- 1989b: Beobachtungen zu Activität und Raumnutzung beim Iltis (Mustela putorius L.). Rev. Suisse Zool. 96, 841—862.
- WOJCIK, J. M. & WOLK, K. 1985: The daily activity rhythm of two competitive rodents Clethrionomys glareolus and Apodemus flavicollis. Acta theriol. 30, 241—258.
- 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.

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