

Functional response and area-restricted search in a predator: seasonal exploitation of anurans by the European polecat, *Mustela putorius*

T. LODE

Ecologie animale, UFR Sciences, Université d'Angers, 2 boulevard Lavoisier, 49045 Angers, France
(Email: thierry.lode@univ-angers.fr)

Abstract A study of the feeding habits and movements of 11 radiotracked polecats *Mustela putorius* in western France revealed that seasonal predation upon agile frogs, *Rana dalmatina*, was directly influenced by prey abundance and distribution. Although dietary structure showed the importance of mammalian prey (71.5%), polecats exploited nocturnal, terrestrial anurans in spring (31.6%). The periodic activity of anurans at spawning sites led both to a maximum density in spring and to a patchy distribution. The monthly variations in anuran dietary occurrences were associated with changes in frog availability. The functional response of polecats to frog density was sigmoidal shaped (type 3 response). Frog consumption rate increased more slowly than prey density but frogs were actively removed at higher density. It is therefore suggested that frog populations were moderately affected by the predator and this density dependent effect tends to stabilise anuran populations. Predation upon anurans was also correlated with a prey dispersion index as revealed by a polynomial regression. Polecats concentrated their predation on spawning congregations of the breeding adult frogs. Movements were smallest in spring and polecats changed their track length by increasing the difference between a succession of small movements and of longer journeys towards profitable sites. Changes in movements correlated with the anuran dispersion index and the response was sigmoidal (polynomial regression) revealing an area-restricted search. This response may be regarded as an 'aggregative response' according to the first part of the definition of Begon *et al.* (1996). Functional and area-restricted search responses to the frog abundance and dispersion constitute an original example of predator-prey coexistence strategies among vertebrates. I suggest that such predation could be favoured by the individualistic habits of the mustelid.

Key words: anuran, area-restricted search, carnivores, functional response, polecat, predation.

INTRODUCTION

Since Holling (1959a, 1959b) distinguished variations in numerical and functional responses of predators to prey availability, the predator's contribution to the regulation of small rodent population has been widely studied. For instance, predators influence the population cycles of microtines in northern areas (Krebs & Myers 1974; Hansson & Henttonen 1985, 1988) and in open-field agroecosystems (Spitz 1963, 1964; Butet & Leroux 1993; Jedrzejewski & Jedrzejewska 1996). In those systems specialized predators produce numerical responses to prey density (Andersson & Erlinge 1977; Erlinge *et al.* 1983; Korpimäki 1986; Erlinge *et al.* 1991; Hanski *et al.* 1991; Korpimäki *et al.* 1991; Jedrzejewski *et al.* 1995; Stenseth *et al.* 1996). In contrast, small rodents show less cycling in mid-European regions. The functional responses of non-specialised predators would influence the regu-

lation of microtines in such ecosystems (Andersson & Erlinge 1977; Erlinge *et al.* 1983; Erlinge 1986; Korpimäki 1987; Erlinge *et al.* 1988; Hanski *et al.* 1991; Krebs 1996). The availability of alternative resources would facilitate the ability of those predators to change prey (Krebs 1996).

In western France, the polecat *Mustela putorius* L. 1758 showed a functional response to changes in small rodent abundance (Lodé 1994). Particularly during resource decline phases, rodent predation was relieved by the consumption of lagomorphs, birds or carrion depending on the area (Lodé 1997). However, the polecat exploited amphibians regularly and intensively to such an extent that anurans sometimes predominated in the diet (Danilov & Rusakov 1969; Weber 1989; Jedrzejewski *et al.* 1993). Although other predators sometimes include amphibians in their diet (Gerell 1967; Henry 1984; Weber 1990; Feunteun & Marion 1994; Jedrzejewski *et al.* 1996), the polecat's assiduous predation upon anurans gives it a unique position within the biocoenoses of the Palearctic.

The responses of predators to changes in prey population are of great interest, especially when they involve both temporal and spatial variation. Furthermore, the demography of anurans is characterized by the complex features of their life history, associating aquatic and terrestrial phases with a strong mortality of larvae (Barbault 1984; Berven 1990). The intensity of aquatic predation considerably reduces tadpole populations (Calef 1973; Licht 1974; Walters 1975; Smith 1983; Berven 1990; Hero *et al.* 1998) but predation upon adult anurans may also have an important impact on population dynamic, particularly if it occurs during the breeding period. Periodic outbreaks in general activity and spawning congregations at laying sites may influence the dynamics of anuran populations, resulting in heterogeneous distribution. However, polecats concentrated their predatory activity on certain areas, ignoring other areas (Blandford 1987; Weber 1989; Jedrzejewski *et al.* 1993; Lodé 1994). Observations suggest that predators concentrate on profitable patches (cf. Krebs *et al.* 1978). Therefore, it is reasonable to assume that polecats may also exhibit an area-restricted search depending on the distribution of anuran prey. The responses of carnivores to prey dispersion have rarely been documented (Mellgren & Roper 1986). However, predator response to the dispersion of their prey is one of the fundamental components of predatory interactions, particularly in heterogeneous habitats. This response may have a decisive influence in maintaining prey population at stable density (Begon & Mortimer 1986).

I conducted a radiotracking survey of European polecats to study their feeding habits in the wetlands in western France, and to examine the exploitation of the agile frog, *Rana dalmatina* B. 1840. Simultaneously, I assessed availability of agile frogs both in terms of abundance and dispersion. The purpose of this work was to test the nature of the functional response of the predator to changes in agile frog abundance, and to determine whether polecats showed area-restricted

search in response to the patchy distribution of this anuran.

METHODS

Study site

I studied polecats from 1989 to 1992 in wetlands in western France, at lake Grand-Lieu (47°05' N, 1°39' W; 60 km²) and Brière (47°20' N, 2°10' W). Grand-Lieu is a naturally eutrophic lake encircled by populations of halophytes gradually overrun by reed beds. Floating forests invaded the reed bed and this gives way to swampy meadows alternating with deciduous wooded areas. Brière is a marshy depression drained by numerous canals associated with small deciduous wooded areas. The climate is mild and humid, influenced by the nearness of the littoral. The amplitude of the mean temperatures is low (mean temperature 21.5°C in August, 6°C in January). Precipitation reaches about 750 mm and is evenly distributed during the year with less than three snowy days per year.

Radiotracking survey

I performed a radiotracking survey of 11 European polecats (six males and five females, Table 1). Individuals were live-trapped in wooden-box traps baited with dead mice and traps were checked twice daily. Sex was determined and individuals were fitted with radiotransmitters (Biotrack). Polecats were then released and repeatedly located (one fix every 60 min) by triangulation (Lodé 1993, 1994, 1995). The range of the signal was 200–900 m and the position was estimated for periods of 6 h per day for a total of 24 h per week. The size of the activity area was calculated from the minimum convex polygon (Mohr 1947; White

Table 1. Characteristics of radiotracked polecats, *Mustela putorius*, at Lake Grand-Lieu and Brière, western France

No.	Sex	Survey period	No. of fixes used	Convex polygon (km ²)	Areas
M1	Male	Nov–Dec 88	73	0.541	Gd-Lieu
M2	Male	Jul–Oct 89	224	0.824	Gd-Lieu
M3	Male	Jan–Jun 90	235	1.608	Gd-Lieu
F1	Female	Jan 88	49	0.302	Gd-Lieu
F2	Female	Jan–Mar 89	126	0.731	Gd-Lieu
F3	Female	Jul–Nov 89	276	0.392	Gd-Lieu
F4	Female	Feb–May 90	132	0.441	Gd-Lieu
M1	Male	Nov 90–Apr 91	306	1.482	Brière
M2	Male	Jan–Mar 91	210	1.148	Brière
M3	Male	Mar–Jun 92	224	1.501	Brière
F1	Female	Oct 90–Jan 91	98	0.338	Brière

& Garrott 1990) Extent of movement was estimated by calculating the average of the minimum distances covered within 60 min for each individual. Individuals were compared by ANOVA. The dispersion index (*Id*) of the movements was defined by the ratio between the standard deviation and the mean value of an individual track length so that $\sigma^2 = \Sigma(x - X)^2/n$ and

$Id = \sigma^2/X$ (Snedecor & Cochran 1967; Barbault 1981; Frontier & Pichot-Viale 1993). The value of the index *Id* tends to be high when the length of tracks is variable, long distance tracks alternating with numerous small movements. By contrast, the index tends to be low when all movements are almost uniform either small, median or long distance. As fixes were located each 60 min, the value of the index *Id* is also an indirect estimate of the time spent in an area and was high when polecats spent more time in patches.

Table 2. Annual diet of polecats, *Mustela putorius*, at Lake Grand-Lieu and Brière, western France (percentage occurrence of prey categories)

	Males	Females
Shrews (<i>Sorex</i> sp., <i>Crocidura</i> sp.)	3.8	3.4
Brown rats (<i>Rattus norvegicus</i>)	12.6	11.3
Bank voles (<i>Clethrionomys glareolus</i>)	28.1	29.9
Field voles (<i>Microtus</i> sp.)	22.5	18.0
Rabbits (<i>Oryctolagus cuniculus</i>)	4.4	9.0
Total mammals	71.4	71.6
Birds	1.7	4.7
Agile frogs (<i>Rana dalmatina</i>)	15.5	13.8
Common toads (<i>Bufo bufo</i>)	5.8	4.5
Other anurans (<i>Rana</i> sp.)	1.4	0.9
Total anurans	22.7	18.9
Invertebrates	2.1	3.1
Other	2.1	1.7
Total no. of prey	573	355

Diet analysis

The polecats' diet was estimated through the analysis of faeces collected in the field, the morning after, by following the path of each animal (see Lodé 1994). The non-digested remains present in the faeces were examined (observation of bones, teeth, external characteristics of phaneres and microscopic sections) and identified by comparison with a reference collection and published atlas (Day 1966; Chaline *et al.* 1974; Rage 1974; Böhme 1977; Debrot *et al.* 1982). The results were given as monthly relative frequency of occurrence of each food category (mammals, birds, amphibians, invertebrates, and carrion). From the raw data, a χ^2 test was used to compare male and female

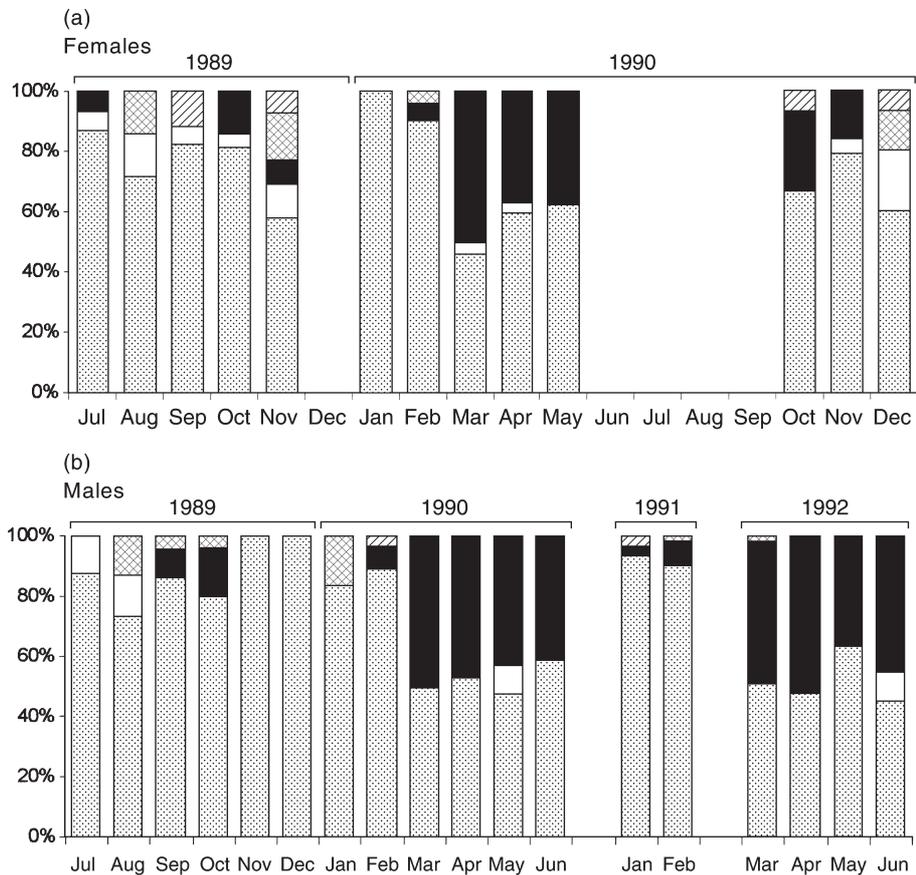


Fig. 1. Monthly variations of (a) female and (b) male polecats' (*Mustela putorius*) diet in wetlands at Lake Grand-Lieu and Brière, western France.
 ■, Mammals; □, birds; ■, amphibians; ▨, invertebrates; ▩, other.

diets, only considering four food categories (mammals, birds, amphibians and other). To test the seasonality of the diets, the Kruskal–Wallis (H) test was used for monthly occurrences.

Availability of anurans

The study of anuran availability was limited to one species, *Rana dalmatina*, which was the most common species in the polecats' diet in western France (Lodé 1994). Along three sample paths (two at Grand-Lieu, 800 m and 600 m long, respectively, one in Brière, 800 m long) from a laying site and transversely across the marsh, 40 control plots of 50 m² were defined (24 at Grand-Lieu, 16 at Brière). Samples were taken monthly at these plots, in the evening, by counting the number of frogs seen. These animals were marked with a temporary coloured pigment. A new count made the following morning at dawn allowed the application of Lincoln's index (Southwood 1966). I estimated density per hectare. Prey dispersion (Ad) was given as the ratio between the standard deviation and the mean value of average density so that $\sigma^2 = \Sigma(x - X)^2/n$ and $Ad = \sigma^2/d$ (Snedecor 1967; Barbault 1981; Frontier & Pichot-Viale 1993). The prey dispersion index Ad is high when the aggregate distribution of the animals was great and low when the individuals were distributed randomly in the environment.

Statistical tests and regressions were performed using the PCSM version 6 computer program (Delta-soft, Grenoble-Meylon, France). Variables were tested for normality (Gaussian distribution) with the Kolmogorov–Smirnov test (KS). Measures of correla-

tion and curve choice were based on an empirical search for the best R^2 and by testing the non-linearity of the slope. Regression slopes were compared to test their parallelism between the two study sites, Brière and Grand-Lieu.

RESULTS

Diet composition

In western France, the diet of polecats was composed mainly of small mammals (Table 2), notably rodents and lagomorphs. In this study, amphibians were the most common food items, mostly including the terrestrial anurans, *Rana dalmatina* and *Bufo bufo*. Dietary occurrences of *Rana dalmatina* averaged 14.7% of the total diet and represented 70.7% of ingested amphibians. Birds and invertebrates were also present. Diet composition did not differ between males and females ($\chi^2 = 7.64$, d.f. 3, $P > 0.05$) but the monthly variations of the categories showed a clear seasonality (Fig. 1). Anurans were mainly consumed in spring (Kruskal–Wallis $H = 12.48$, $P < 0.005$). The proportions of consumed *Rana dalmatina* did not differ significantly between males and females ($U = 122.5$, $P > 0.05$), nor between the Brière and Grand-Lieu (males $U = 11.0$, $P > 0.05$; females $U = 11.0$, $P > 0.05$).

Movements

The monthly movements of males were larger on average ($\bar{x} = 79.7$, $SD = 39.84$) than those of females

Table 3. Monthly changes in dispersion index of polecat, *Mustela putorius*, locations at Lake Grand-Lieu and Brière, western France

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Gd-Lieu	14.7	17.5	103.2	82.8	75.7		8.2	6.8	7.3	24.9	21.0	10.7
Brière	13.3	18.7	140.1	111.1	99.8	88.2				31.6	19.6	14.2

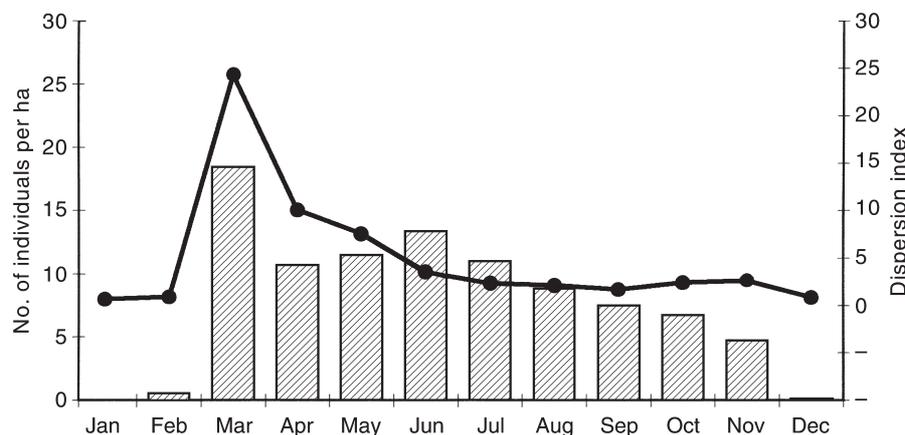


Fig. 2. Monthly changes in density (▨) and aggregation (●) in *Rana dalmatina* based on sample transects at Lake Grand-Lieu and Brière, western France.

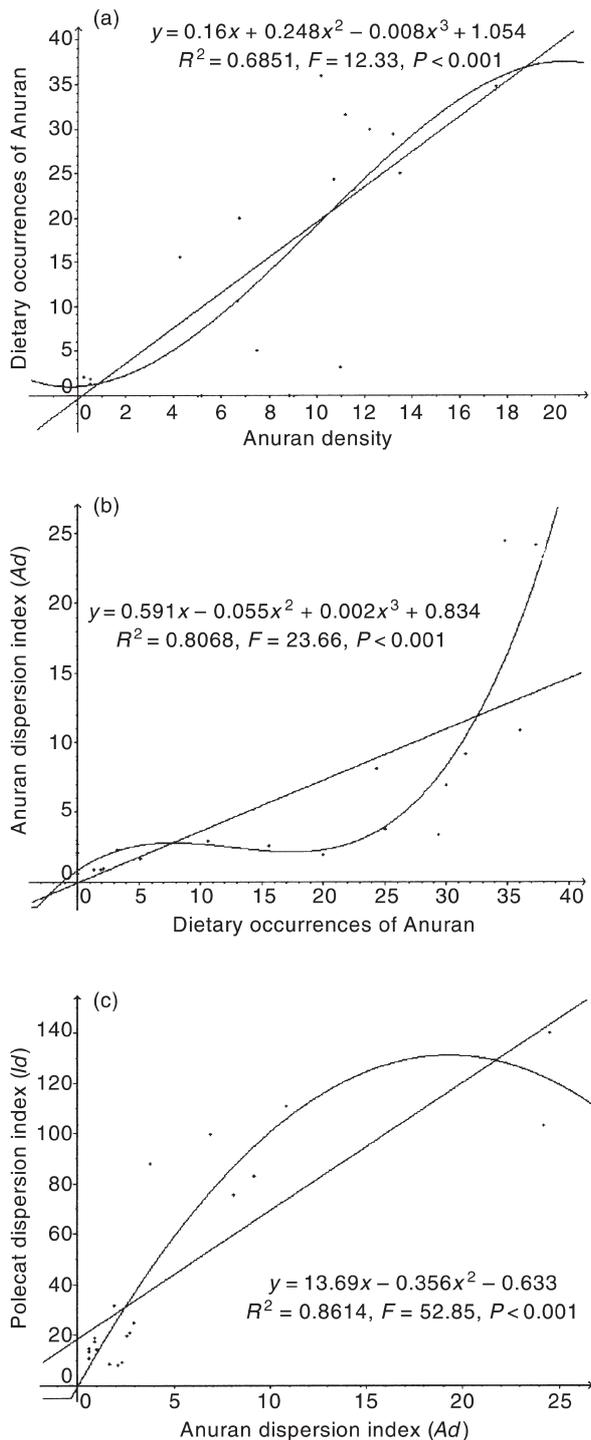


Fig. 3. Dietary (functional) and spatial responses of polecats, *Mustela putorius*, to *Rana dalmatina* density and dispersion at Lake Grand-Lieu and Brière, western France (polynomial regressions). (a) Relationship between monthly occurrences of *Rana dalmatina* in the polecat diet and the abundance (density) of frogs; (b) between monthly occurrences of *Rana dalmatina* in the polecat diet and the frog dispersion index and (c) between the polecat dispersion index and the frog dispersion index.

($\bar{x} = 53.67$, $SD = 13.31$, Student's t -test = 2.26, d.f. 30, $P < 0.05$) and varied significantly among seasons (males $F = 26.4$, $P < 0.001$, females $F = 4.25$, $P < 0.05$). The smallest tracks were recording in spring (males $\bar{x} = 44.5$, $SD = 10.8$; females $\bar{x} = 40.5$, $SD = 3.3$); then they increased during the summer (males $\bar{x} = 59.2$, $SD = 20.4$, females $\bar{x} = 53.6$, $SD = 7.9$) and in autumn for males ($\bar{x} = 72.5$, $SD = 23.5$), but not for females ($\bar{x} = 52.4$, $SD = 13.9$); they reached a maximum in winter (males $\bar{x} = 129.9$, $SD = 17.25$; females $\bar{x} = 61.1$, $SD = 2.7$).

In polecats, three types of locations characterized the space use, numerous locations in very restricted areas (ponds and marsh ditches), locations almost uniformly scattered (woods and meadows) and long distance locations. The movements of radiotracked polecats were relatively regular in autumn and in winter, but males exhibited long distance movements in February at the beginning of the mating season. Movements presented the biggest contrast in spring (males $Id = 114.5$, $SD = 17.6$; females $Id = 62.4$, $SD = 10.9$), a series of small sinuous tracks alternating with longer straight ones. This series of small tracks coincided with the beginning of frog breeding aggregations and polecats were mainly located in the vicinity of frog spawning sites.

The monthly index varied significantly among seasons ($F_{3,31} = 28.18$, $P < 0.001$; males $F_{3,18} = 29.15$, $P < 0.0001$; females $F_{3,12} = 21.9$, $P < 0.0001$) (Table 3). On the other hand, the dispersion index did not differ, neither between males and females (males $Id = 50.6$, $SD = 48.8$; females $Id = 26.35$, $SD = 22.4$, $t = 1.69$, d.f. = 30, $P > 0.05$), nor from one site to another (for males, Grand-Lieu $Id = 53.5$, $SD = 14.6$ and Brière $Id = 54.2$, $SD = 10.3$, $U = 13.0$; for females, Grand-Lieu $Id = 28.8$, $SD = 24.6$ and Brière $Id = 18.1$, $SD = 11.9$, $U = 12.0$, $P > 0.05$).

Frog availability

Rana dalmatina returned to their laying site in late February. Spring density reached a mean of 13.5/ha ($SD = 3.9$) but the frog density fell significantly in winter (Kruskal-Wallis $H = 16.1$, $P < 0.001$, Fig. 2). There was no significant difference in frog density between Grand-Lieu ($d = 7.84$ individuals per ha, $SD = 5.8$) and Brière ($d = 7.3$ individuals per ha, $SD = 6.9$; $U = 47.5$, $P > 0.05$). However, frogs were not evenly distributed in the environment and gathered in spring to form breeding aggregations. The dispersion index (Ad) varied seasonally and was highest in spring ($H = 16.2$, $P < 0.001$, Fig. 2). The dispersion index averaged $Ad = 5.29$ ($SD = 6.97$) and did not differ between Brière and Grand-Lieu ($t = 0.31$, d.f. 19, $P > 0.05$).

Polecat responses

Seasonal variations of *Rana dalmatina* in the polecat diet were directly correlated with the abundance of frogs in the environment ($r = 0.821$, $P < 0.001$, $n = 21$, $KS > 0.05$). The regression slopes did not significantly differ between Brière ($r = 0.925$) and Grand Lieu ($r = 0.804$) and the lines may be considered as parallel ($F_{1,19} = 0.012$, $P > 0.05$). However, the regression was not linear (non-linearity = 0.325, $F_{1,16} = 1407.3$, $P < 0.001$) and a polynomial curvilinear function (3 degrees) was the most likely to explain the relation (multiple regression $r_{mult.} = 0.828$, 68.5% of variance, $F_{3,20} = 12.33$, $P < 0.001$) (Fig. 3a). The exploitation of frogs increased with their abundance but this increase then reduced and stabilized. The dietary functional response of polecats to frog density is of type 3 (sigmoid).

Frog occurrences in the polecat diet were correlated with *Rana dalmatina* dispersion index Ad ($r = 0.758$, $P < 0.001$, $n = 21$, $KS > 0.05$) and the regression slopes did not differ between Brière ($r = 0.735$) and Grand-Lieu ($r = 0.791$) (parallel lines, $F_{1,19} = 0.04$, $P > 0.05$). The regression was not linear (non-linearity = 0.422, $F_{1,16} = 27.67$, $P < 0.001$). A polynomial curvilinear function (three degrees) explained 80.7% of variance (multiple regression $r = 0.898$, $F_{3,20} = 23.66$, $P < 0.001$; Fig. 3b). The dietary occurrences of frogs began to increase only when the anuran dispersion index reached a high value. Polecats mainly exploited anurans when frogs gathered at laying sites.

The variations of the dispersion index of movements in polecats (Id) were correlated with anuran dispersion ($r = 0.845$, $P < 0.001$, $n = 21$, $KS > 0.05$). The regression slopes did not differ between Brière ($r = 0.896$) and Grand-Lieu ($r = 0.859$) (parallel lines, $F_{1,19} = 1.10$, $P > 0.05$). The measure of non-linearity (non-linearity = 0.285, $F_{1,16} = 224.47$, $P < 0.001$) showed that the regression was not linear. The dispersion index of polecats and anuran dispersion index were best related by a polynomial function (two degrees, 86.1% of variance, multiple regression $r = 0.928$, $F_{2,20} = 52.9$, $P < 0.001$; Fig. 3c). Thus polecats exhibited an area-restricted search in response to the patchy distribution of frogs by changing their movements and by increasing their exploitation of anurans.

DISCUSSION

The seasonal exploitation of agile frogs by polecats is clearly influenced both by the availability of anurans and their distribution in the environment. In fact, the polecats' consumption is directly associated with the beginning of the activity period of frogs and coincided in western France with anuran breeding (Lodé 1994). Although predation may concentrate on different

species from region to region (Lodé 1997), the anuran taken are mainly nocturnal and terrestrial. In temperate Europe, these species form characteristic breeding congregations which are often temporary (Arnold & Burton 1978). For instance, groups of 15–85 adult agile frogs generally gather (Lodé 1996), although group size can reach several hundred individuals in common frogs (*Rana temporaria*) (Savage 1961; Blab 1986). It is probably the size and the number of these aggregations which has led to the prevalence of anurans in the polecats' diet in Karely (Danilov & Rusakov 1969), in Switzerland (Weber 1989) or in Poland (Jedrzejewski *et al.* 1993). On the other hand, polecats exploit more modestly aggregations of the common toad, *Bufo bufo*, and the painted frog, *Discoglossus pictus*, in Spain (Ballarin *et al.* 1980), the common toad (Blandford 1987) in Wales and of the agile frog (Lodé 1994) in France. However, even in those cases a link exists between the variation of anuran abundance in the environment and their occurrences in the diet. This shows that predation by polecats responds to the sudden accessibility of anurans. The presence of anurans is not very detectable by smell (Weber 1989) but polecats capture the most active and noisy individuals, mainly males (Lodé 1996) which remain for a longer time and chorus at the laying site. Predation on anurans also influences changes in the predator activity rhythm (Lodé 1995).

Here, functional response of polecats to frog density is sigmoidal shaped and corresponds to the type 3 functional response of Holling (1959a). In the type 3 response, few if any prey are taken at low density but then prey are actively removed at higher density. The predicted rate of polecat predation on frogs initially increases more slowly than prey density but shows an accelerating phase once a threshold of density has been reached. Typically, a predator exhibits a type 3 functional response when an increase in prey density results in an increase in the searching efficiency of the predator (Hassel *et al.* 1977; Begon *et al.* 1996). This intensive exploitation of frogs during their breeding would have a considerable impact on their reproductive success and their long-term survival. Frogs at higher densities in large spawning congregations have a higher probability of predation by polecats than individuals at lower densities in small congregations. Thus frog populations are moderately affected by polecat predation and this density dependent effect tends to stabilize the population dynamics.

Functional responses of mammalian predators are rarely linear (Murdoch & Oaten 1975) and depend broadly on the abundance of alternate prey (Krebs *et al.* 1978). Here the polecat concentrated its predation on anurans as the availability of small rodents declined (Lodé 1994). The changes in rodent and anuran relative abundance lead to a change in the structure of the diet, comparable to the 'switching' that Murdoch

(1969) and Lawton *et al.* (1974) revealed. Jedrzejewski *et al.* (1996) also found that Tawny owl hunting rate on anurans was shaped by temperature and availability of rodents.

However, prey dispersion also influences predation upon anurans. The spawning aggregations result in a patchy distribution of frogs in spring. The distribution of anuran populations is also influenced by certain factors in the environment, such as humidity or temperature (Bellis 1962; Blab 1986). Polecat predation on anurans is clearly associated with the spawning aggregations. Nevertheless, anuran occurrences in the polecat diet do not only increase at a steady rate but suddenly increase to increase the prey dispersion index as revealed by the curvilinear regression. This response illustrates that the predator tends to concentrate on profitable patches and this assiduous prey exploitation may induce temporary local feeding specializations.

Changes in polecat movements are also associated with anuran dispersion. The polecat responded to this resource unevenness by a more contrasted distribution of its movements, concentrating its efforts on the most profitable areas. This response is sigmoidal shaped. The dispersion index of polecat localizations increased with greater anuran dispersion index but increased more slowly with further increase of prey dispersion. This selective utilization of space corresponds to an optimization of the predatory choices (MacArthur & Pianka 1966; Connell 1970; Krebs *et al.* 1978). Hassel & May (1974) and Hassel *et al.* (1976) reported an aggregative response to describe a similar reaction among parasitoid insects. Polecat dispersion index is indirectly related to time spent in patches. This area-restricted search may hence be regarded as an 'aggregative' response according to the definition of Begon *et al.* (1996), 'predators spending more time in high-prey-density patches'. In strict ecological terms, the polecat response only supports the first part of the definition because an aggregative response should also 'lead to higher densities of predators with higher densities of prey' (Begon *et al.* 1996). Resident polecats defended an exclusive territory against any intruders (Poole 1973; Weber 1989; Brzezinski *et al.* 1992; Lodé 1993, 1994) and their density varied from 0.5 to 08/km² in western France (Lodé 1993). The home range size may reflect the availability of resources both in terms of density and prey dispersion as suggested by Carr & MacDonald (1986) in the Red fox, *Vulpes vulpes*. In polecats, predator density may not rapidly increase because of their territorial behaviour, their pronounced intolerance towards conspecifics, and the briefness of anuran spawning aggregations.

The characteristic of this area-restricted search response is both its regularity and the fact that a typically individualistic predator is concerned. Limiting the concurrence of patches, the individualistic habits

of polecats may favour intensive exploitation until depletion of resources, which are unevenly distributed. Functional and area-restricted search responses of polecats to the changes in frog availability constitute an original example in the strategies of coexistence of predators and prey among the vertebrates.

ACKNOWLEDGEMENTS

This work was funded by the Singer-Polignac Foundation.

I am very grateful to Dr T. P. Hodgman, University of Maine, Professor J. Y. Gautier, University of Rennes, Professor S. Erlinge, University of Lund and Professor M. Bull, Flinders University of South Australia, for their helpful criticisms on the manuscript. F. Cupertino, R. Dagault, F. Ibanez, D. Le Jacques, M. Pondaven and J. Y. Robert provided assistance in the field.

REFERENCES

- Andersson M. & Erlinge S. (1977) Influence of predation on rodent populations. *Oikos* **29**, 591–7.
- Arnold E. N. & Burton J. A. (1978) *Tous les Reptiles et Amphibiens d'Europe*. Elsevier séquoia, Paris.
- Ballarin I., Garzon J., Palacios P., Cuesta L. & Castroviejo J. (1980) On the diet of polecats (*Mustela putorius* L. (1758)) in Spain. *Reunion Iberoamer. Zool. Vertebrata* **1**, 625–7.
- Barbault R. (1981) *Ecologie Des Populations et Des Peuplements*. Masson, Paris.
- Barbault R. (1984) Strategies de reproduction et démographie de quelques amphibiens Anoures tropicaux. *Oikos* **43**, 77–87.
- Begon M. & Mortimer M. (1986) *Population Ecology, a Unified Study of Animals and Plants*. Blackwell Scientific Publications, Oxford.
- Begon M., Harper J. L. & Townsend C. R. (1996) *Ecology: Individuals, Populations, and Communities*. Blackwell Scientific Publications, Oxford.
- Bellis E. D. (1962) The influence of humidity on wood frog activity. *Amer. Midl. Nat.* **68**, 139–48.
- Berven K. A. (1990) Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* **71**, 1599–608.
- Blab J. (1986) *Biologie, Ökologie und Schutz Von Amphibien*. Kilda-Verlag, Bonn.
- Blandford P. R. S. (1987) Biology of the Polecat *Mustela putorius*: a literature review. *Mammal Rev.* **17**, 155–98.
- Böhme G. (1977) Zur Bestimmung quatarer Anuran Europas an Hand von Skelettelementen. *Wiss. Humboldt-Berlin* **26**, 289–98.
- Brzezinski M., Jedrzejewski W. & Jedrzejewska B. (1992) Winter home ranges and movements of polecats *Mustela putorius* in Bialowieza Primeval Forest, Poland. *Acta Theriol.* **37**, 181–91.
- Butet A. & Leroux A. (1993) Effect of prey on a predator's breeding success. A 7-year study on common vole (*Microtus arvalis*) and Montagu's harrier (*Circus pyrgargus*) in a West France marsh. *Acta Oecol.* **14**, 857–65.
- Calef G. W. (1973) Natural mortality of tadpoles in a population of *Rana Aurora*. *Ecology* **54**, 741–58.
- Carr G. M. & MacDonald D. W. (1986) The sociality of solitary

- foragers: a model based on resource dispersion. *Anim. Behav.* **34**, 1540–49.
- Chaline J., Baudvin H., Jammot P. & Saint-Girons M. C. (1974) *Les Proies Des Rapaces*. Doin, Paris.
- Connell J. H. (1970) A predator-prey system in the marine intertidal region. I. *Ballanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* **40**, 49–78.
- Danilov P. I. & Rusakov O. S. (1969) [Peculiarities of the ecology of *Mustela putorius* in North West districts of the european part of the USSR.]. *Zool. Zhur.* **48**, 1383–94. [In Russian with English abstract.]
- Day M. G. (1966) Identification of hair and feather remains in the gut and faeces of stoats and weasels. *J. Zool. Lond.* **148**, 201–17.
- Debrot S., Fivaz G., Mermod C. & Weber J. M. (1982) *Atlas Des Poils Des Mammifères d'Europe*. Institut de Zoologie, Neuchâtel, Neuchâtel.
- Erlinge S. (1986) Specialists and generalists among the mustelids. *Lutra* **29**, 5–11.
- Erlinge S., Göransson G., Högstedt G. *et al.* (1988) More thoughts on vertebrate predator regulation of prey. *Am. Nat.* **132**, 148–54.
- Erlinge S., Agrell J., Nelson J. & Sandell M. (1991) Why are some microtine populations cyclic while others are not? *Acta Ther.* **36**, 63–71.
- Erlinge S., Göransson G., Hansson L. *et al.* (1983) Predation as regulating factor on small rodent populations in southern Sweden. *Oikos* **40**, 36–52.
- Feunteun E. & Marion L. (1994) Assessment of Grey Heron predation on fish communities: the case of the largest European colony. *Hydrobiologia* **279/280**, 327–44.
- Frontier S. & Pichot-Viale D. (1993) *Ecosystèmes, Structures–Fonctionnement–Évolution*. Masson, Paris.
- Gerell R. (1967) Food selection in relation to habitat in mink *Mustela vison* in Sweden. *Oikos* **18**, 233–46.
- Hanski I., Hansson L. & Henttonen H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60**, 353–67.
- Hansson L. & Henttonen H. (1985) Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* **67**, 394–402.
- Hansson L. & Henttonen H. (1988) Rodent dynamics as community processes. *TREE* **3**, 195–200.
- Hassel M. P., Lawton J. H. & Beddington J. R. (1977) Sigmoid functional responses by invertebrate predators and parasitoids. *J. Anim. Ecol.* **46**, 249–62.
- Hassel M. P., Lawton J. H. & May R. M. (1976) Patterns of dynamical behaviour in single species populations. *J. Anim. Ecol.* **45**, 471–86.
- Hassel M. P. & May R. M. (1974) Aggregation in predators and insect parasites and its effects on stability. *J. Anim. Ecol.* **43**, 567–94.
- Henry C. (1984) Adaptation comportementale du blaireau européen (*Meles meles* L.) à la prédation d'une espèce-proie venimeuse: le crapaud commun (*Bufo bufo* L.). *Rev. Ecol. (Terre Vie)* **39**, 291–6.
- Hero J. M., Gascon C. & Magnusson W. E. (1998) Direct and indirect effects of predation on tadpole community structure in the Amazon rainforest. *Aust. J. Ecol.* **23**, 474–82.
- Holling C. S. (1959a) Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385–98.
- Holling C. S. (1959b) The components of predation as revealed by a study of a small mammal predation of the european pine sawfly. *Can. Entomol.* **91**, 293–320.
- Jedrzejewski W. & Jedrzejewska B. (1996) Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta Theriol.* **41**, 1–34.
- Jedrzejewski W., Jedrzejewska B. & Brzezinski M. (1993) Winter habitat selection and feeding habits of polecats (*Mustela putorius*) in the Bialowieza National Park, Poland. *Z. Säugetierk.* **58**, 75–83.
- Jedrzejewski W., Jedrzejewska B. & Szymura A. (1995) Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. *Ecology* **76**, 179–95.
- Jedrzejewski W., Jedrzejewska B., Szymura A. & Zub K. (1996) Tawny owl (*Strix aluco*) in a pristine deciduous forest (Bialowieza National Park, Poland). *J. Anim. Ecol.* **65**, 105–20.
- Korpimäki E. (1986) Predation causing synchronous decline phases in Microtine and Shrew populations in western Finland. *Oikos* **46**, 124–7.
- Korpimäki E. (1987) Dietary shifts, niche relationships and reproductive output of coexisting Kestrels and Long-eared owls. *Oecologia* **74**, 277–85.
- Korpimäki E., Norrdahl K. & Rinta-Jaskari T. (1991) Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to a mustelid predation? *Oecologia (Berlin)* **88**, 552–61.
- Krebs C. J. (1996) Population cycles revisited. *J. Mammal.* **77**, 8–24.
- Krebs J. R., Kacelnik A. & Taylor P. J. (1978) Test of optimal sampling by foraging great tits. *Nature* **275**, 27–31.
- Krebs C. J. & Myers J. H. (1974) Population cycles in small mammals. *Adv. Ecol. Res.* **8**, 267–399.
- Lawton J. H., Beddington J. R. & Bonser R. (1974) Switching in invertebrate predators. In: *Ecological Stability* (Eds M. B. Usher & M. H. Williamson) pp. 141–58. Chapman & Hall, London.
- Licht L. E. (1974) Survival of embryos, tadpoles, and adults of the frogs *Rana aurora* and *Rana pretiosa* in Southern British Columbia. *Can. J. Zool.* **52**, 613–27.
- 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**, 305–22.
- 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. (1996) Polecat predation on frogs and toads at breeding sites in western France. *Ethol. Ecol. Evol.* **8**, 115–24.
- Lodé T. (1997) Trophic status and feeding habits of the European Polecat *Mustela putorius* L. 1758. *Mammal Rev.* **27**, 177–84.
- MacArthur R. H. & Pianka E. R. (1966) On optimal use of a patchy environment. *Am. Nat.* **100**, 603–9.
- Mellgren R. L. & Roper T. J. (1986) Spatial learning and discrimination of food patches in the European badger.
- Mohr C. O. (1947) Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37**, 223–49.
- Murdoch W. W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* **39**, 335–54.
- Murdoch W. W. & Oaten A. (1975) Predation and population stability. *Adv. Ecol. Res.* **9**, 2–131.
- Poole T. B. (1973) The aggressive behaviour of individual male polecats (*Mustela putorius*, *M. furo* and hybrids) towards

- familiar and unfamiliar opponents. *J. Zool. Lond.* **170**, 395–414.
- Rage J. C. (1974) Batraciens fossiles du quaternaire. *Bull. Soc. Linn. Lyon* **43**, 276–89.
- Savage R. (1961) *The Ecology and Life History of the Common Frog Rana temporaria*. Pitman, London.
- Smith D. C. (1983) Factors controlling tadpole populations of the chorus frog (*Pseudocris triseriata*) on Isle Royale, Michigan. *Ecology* **64**, 501–10.
- Snedecor G. W. & Cochran W. G. (1967) *Statistical Methods*. State University of Press. Ames, Iowa.
- Southwood T. R. E. (1966) *Ecological Methods*. Chapman & Hall, London.
- Spitz F. (1963) Etude des densités de populations de *Microtus arvalis* Pall. à St-Michel-en-l'Hern, Vendée. *Mammalia* **27**, 497–531.
- Spitz F. (1964) Etude des densités de populations de *Microtus arvalis* Pall. à St-Michel-en-l'Hern, Vendée (suite et fin). *Mammalia* **28**, 40–75.
- Stenseth N. C., Bjornstad O. N. & Falck W. (1996) Is pacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern oriented studies. *Proc. R. Soc. Lond. B.* **263**, 1423–35.
- Walters B. (1975) Studies of interspecific predation within an amphibian community. *J. Herpetol.* **9**, 267–79.
- Weber D. (1989) Foraging in polecats (*Mustela putorius* L.) of Switzerland: the case of a specialist anuran predator. *Z. Säugetierk.* **54**, 377–92.
- Weber J. M. (1990) Seasonal exploitation of amphibians by otters (*Lutra lutra*) in north-east Scotland. *J. Zool. Lond.* **220**, 641–51.
- White G. C. & Garrott R. A. (1990) *Analysis of Wildlife Radio-Tracking Data*. Academic Press, New York.