

# Sexual dimorphism and trophic constraints: Prey selection in the European polecat (*Mustela putorius*)<sup>1</sup>

Thierry LODÉ, Laboratoire d'écologie animale, Université d'Angers, Faculté des Sciences, Belle Beille,  
49045 Angers cedex, France, e-mail: thierry.lode@univ-angers.fr

**Abstract:** Although widespread among mammals, sexual dimorphism raises several evolutionary and ecological issues. Despite strong sexual dimorphism (reaching the ratio 1.81), a study of diet and prey selection in polecats (*Mustela putorius*) revealed only minor differences in their feeding habits. There was a greater frequency of large-sized prey (mainly lagomorphs) in the summer diet of females than in that of males. The frequency of anurans (*Rana dalmatina* and *Bufo bufo*) in the diet did not differ significantly between the two sexes. Male prey predominated in the diet of both sexes. Although prey availability, as indicated by the trapping of small rodents and anurans, showed a predominance of males in populations, Ivlev's index for selectivity demonstrated selective predation on male prey exceeding availability both by male and female polecats. This selective predation by polecats may affect both population structure and population exchanges. My results suggest that sexual dimorphism of polecats was not linked to a different prey choice but results from independent intrasexual selective pressures, thus refuting the predictions of the trophic niche differentiation hypothesis. The wide size dimorphism reflects selection both for mating access in males and for food in females, illustrating the complementary influence of sexual selection and environmental constraints on sex divergence in growth.

**Keywords:** *Mustela putorius*, predation, trophic niche, sexual dimorphism.

**Résumé :** Bien qu'il soit très répandu chez les mammifères, le dimorphisme sexuel soulève plusieurs problèmes de nature évolutive et écologique. En dépit d'un grand dimorphisme sexuel atteignant un rapport de 1,81, une étude de l'alimentation et de la sélection des proies chez le putois (*Mustela putorius*) n'a permis de montrer qu'une différence partielle des habitudes alimentaires entre les sexes. Les femelles de putois consomment plus de grosses proies (principalement des Lagomorphes) que les mâles. La fréquence des Anoures (*Rana dalmatina* et *Bufo bufo*) dans le régime ne diffère pas considérablement en fonction du sexe. Les proies mâles prédominent dans le régime des deux sexes. Bien que la disponibilité des proies montre une prédominance de mâles dans les populations, l'indice de sélectivité d'Ivlev indique une prédation sélective s'exerçant sur les proies mâles et excédant cette disponibilité autant chez les putois mâles que femelles. Cette prédation sélective du putois peut affecter autant la structure des populations que les échanges de population. Ces résultats suggèrent que le dimorphisme sexuel des putois n'est pas lié à un choix de proies différentiel mais résulte de pressions sélectives intrasexuelles indépendantes, réfutant ainsi les prédictions de l'hypothèse de la différenciation de niche trophique. L'importance du dimorphisme sexuel reflète à la fois la sélection pour l'accès à la copulation chez les mâles et l'accès aux ressources alimentaires chez les femelles, illustrant l'influence complémentaire de la sélection sexuelle et des contraintes de l'environnement sur la divergence de croissance des sexes.

**Mots-clés :** dimorphisme sexuel, *Mustela putorius*, niche trophique, prédation.

**Nomenclature:** Arnold & Burton, 1978; Saint-Girons, 1973.

## Introduction

Sexual dimorphism results mainly from divergent selective pressures on male and female strategies. Widespread among vertebrates, sexual dimorphism in size is generally in favour of males in mammals, through rapid growth (Andersson, 1994; Short & Balaban, 1994). The significance of this phenomenon has often been discussed with emphasis on sex response to environmental variations (Downhower, 1976; Leberg & Smith, 1993; Reeve & Fairbairn, 2001; Blondel *et al.*, 2002), but the complexity of factors influencing sexual dimorphism has promoted numerous contradictory debates. Evolutionary theory predicts that the sexual size dimorphism in polygynous mammals derives from sexual selection (Ralls, 1977; Andersson, 1994), arguing that sex dimorphism chiefly results from

mate competition among males. A correlation between level of polygyny and dimorphism has been noted (Jarman, 1974; Clutton-Brock, 1985).

Because sexual dimorphism reflects a divergent mode of growth in relation to reproduction (Badyaev & Martin, 2000), it has also been hypothesized that trophic niche differentiation influences the process. This hypothesis, known as the "intersexual niche differentiation hypothesis", emphasizes the role of ecological and mainly trophic factors in influencing the use of distinct resources by the sexes (Van Valen, 1965; Shine, 1989; 1990). The variety in size of predators and their use of different hunting strategies favour the coexistence of carnivores in nature (Powell & Zielinski, 1983; Jaksic & Delibes, 1987; Jedrzejewski & Jedzejewska, 1993; Marti *et al.*, 1993). Consequently, the divergent sizes of males and females is expected to be affected by the exploitation of distinct resources, the smaller size of

<sup>1</sup>Rec. 2002-05-06; acc. 2002-09-30.

females facilitating the catching of smaller prey. Thus, divergent growth of males and females at age of maturity should be an adaptive response to resource availability. Although the niche differentiation hypothesis has received equivocal support, sexual dimorphism could also be considered from an energetic point of view. Thus, the "ecological cause hypothesis" (Shine, 1989) pointed out that different roles in parental investment could result in size dimorphism.

However, the studies that have been carried out concern few predators and sometimes have resulted in contradictory conclusions (Shine, 1989). Thus, Erlinge (1979), followed by Moors (1980), suggested an alternative hypothesis, reasoning that large-sized males could gain an adaptive advantage concerning reproduction, whereas the small size of females would favour less metabolic expenditure. Ralls (1976) and Mills (1990) proposed that larger females might improve their reproductive success, arguing that sexual dimorphism is directly linked to reproduction. Another hypothesis is that sexual dimorphism is mainly associated with reproductive mechanisms (Weckerly, 1998), but as it results from divergent evolutionary pressures, dimorphism also may be linked to foraging.

Numerous carnivores show a pronounced dimorphism, but the European polecat (*Mustela putorius*) is probably one of the species that exhibits the greatest difference, the male body mass often reaching twice that of the female body mass. In western France, the polecat shows a diversified diet mainly based on amphibians and rodents (Lodé, 1994; 1997), and it may exhibit prey storing behaviour (Lodé, 2000). Because growth and reproduction strategies should display competitive interactions related to foraging, it might be predicted that predator sexual dimorphism will result in a difference in hunting strategies concerning the size of the eaten prey and the sex of individuals caught.

Through a sample of scats and prey remains from animals followed by radiotracking during an eight-year period, this paper aims to check 1) whether male polecats select prey species of greater size than those selected by females, 2) whether there is selective predation upon one or the other sex of the prey considered, and 3) whether selective choice differs between male and female surveyed polecats.

## Methods

### STUDY AREA

The study was carried out in the wetlands of western France from 1989 to 1997. These wetlands fill in subsidence basins of an eroded Hercynian relief, the Armorican Massif. The Grande-Brière (47° 20' N, 2° 10' W), which covers 67 km<sup>2</sup>, is a marsh drained by a complex network of canals. Peat bogs, increasingly invaded by reeds and willows, give way progressively to drier natural meadows edged with ashes and oaks. Grand-Lieu (47° 05' N, 1° 39' W) is a naturally eutrophic lake with marshy meadows and reeds that covers 60 km<sup>2</sup>. Woods liable to flooding and dominated by willows cover marshes that were replaced by natural meadows edged with oaks and ashes. Many rivers supply the lake, whose surplus flows out to the river Loire through the Acheneau. The climate is mild and humid (mean temperature: 20°C in July to 5°C in February). Precipitation, evenly distributed during the year, reaches 750 mm per year.

### DIET ANALYSIS

During the radiotracking of five female and six male European polecats in the wetlands of western France, we obtained an important sample set of feces (Lodé, 1994). I collected recent feces by following the animal's path the morning after the radiotracking. Feces were analyzed by microscopic observation of hair and feather and by examination of bones and teeth. The remains, which were not digested, were identified by comparison with a collection of references and published works (Day, 1966; Debrot *et al.*, 1982). The data, expressed in frequency of relative occurrences (*i.e.*, the number of identified items for one prey category divided by the total number of identified items, see Lodé, 1994; 2000), were separated into seasons (winter: December, January, February; spring: March, April, May; summer: June, July, August; autumn: September, October, November) and into different food categories according to the precision of the determination or the relative importance of the food. The category named "other" corresponds to rare items (Reptile *Natrix natrix*, Osteichthyen fish *Tinca tinca*) or items exploited as carrion (Coypu *Myocastor coypus*, Cat *Felis catus*, Carrion Crow *Corvus corone*). I divided food categories into three size classes: prey with a body mass less than 50 g (shrews *Sorex coronatus*, *Sorex minutus*, Bank voles *Clethrionomys glareolus*, Meadow voles *Microtus arvalis*, Agile frogs *Rana dalmatina*, Invertebrates), prey with a body mass between 50 g and 200 g (Brown rats *Rattus norvegicus*, Water voles *Arvicola sapidus*, moles *Talpa europaea*, Common toads *Bufo bufo*), and prey with a body mass greater than 200 g (rabbits *Oryctolagus cuniculus*, muskrats *Ondatra zibethicus*), birds and carrion not being taken into account. Differences were tested with the  $\chi^2$  test considering comparable zoological groups (mammals, birds, amphibians, other) according to the level of required precision (mammals: shrews, Bank voles, Meadow voles, Brown rats, rabbits). The trophic niche overlap index (Schoener, 1974)  $C_{jk} = 1 - \sum |P_{ij} - P_{ik}|$  was calculated between male and female polecats, varying from 0 (avoidance) to 1 (complete overlap).

Boonstra, Gilbert, and Krebs (1993) proposed that dimorphism should be measured by body-weight rather than length. Therefore, we used body weight to assess the sexual dimorphism (mean weight of males/mean weight of females) of road-killed adult polecats (161 males and 103 females).

### PREY CHOICE

I tried to obtain a sample of prey of which the individual characteristics remained identifiable. Through the radiotracking, we were able to collect some prey remains in areas exploited by the polecats. Diurnal dens were located, and as soon as the polecats had left them, we collected available remains. In addition, 24 food caches hidden by polecats were examined. Most previous studies about prey selection were conducted through the study of remains found in caches or dens (Sargeant, Swanson & Doty, 1973; Boonstra, 1977). Finally, analysis of 276 stomachs from 348 road-killed animals provided complementary data ( $N = 57$  small rodent prey). The identification of prey was done through the observation of external characteristics and bones. The sex of prey was determined by the precise study of external sexual features (anogenital zone and callosity on

the male anuran's thumb) or dissecting the animal's genital tract. In the case of Brown rats, the male's skull has parasagittal crests that are more developed than those on the female's (Saint-Girons, 1973); this criterion, associated with skull measurements, appeared to be sufficient to distinguish the sex in this species. The sample of collected prey remains totalled 642 items, including 201 mammals, 412 anurans, 3 reptiles, and 26 birds, but this analysis was restricted to the more common prey in the polecat diet and concerned 65 Bank voles, 22 Meadow voles, 77 Brown rats, 327 Agile frogs, and 60 Common toads.

#### PREY AVAILABILITY

Changes of rodent availability (Bank and Meadow voles, Brown rats) were assessed by trap-line. Monthly, twelve lines of 32 baited live traps (25 cm × 8 cm × 8 cm) were set in the three main habitats used by polecats: marshes, dry meadows, and woods (Lodé, 1994). Wire-mesh traps were spaced every 3 m in straight lines for 3 consecutive nights. Caught animals were weighed, sexed, and marked, then released alive. The sex ratio is expressed by the male proportion in the trapped populations. The structure of Agile frog and Common toad populations was studied on seven referential sites and was restricted to the reproductive period, *i.e.*, from the end of February to the end of April. Anurans, which were found at night with the aid of a lamp, were counted by hand between 8 p.m. and 11 p.m. every fortnight, marked on the forelimb, and released. Results were confirmed by counting the laying number. The sex ratio is expressed by the percentage of males in populations (Lodé, 2000).

Data were divided into seasons. Ivlev's Electivity index, modified by Jacobs (1974), was calculated by seasonal rate for the five species as follows:  $D = (n - p)/(n + p - 2np)$ , in which  $n$  and  $p$  are the respective proportions of male prey in the polecat diet and in the available populations. Index  $D$  varies from -1 to +1 according to a selectivity pressure gradient.

## Results

#### SEXUAL DIMORPHISM OF POLECATS

The mean weight of adult males was heavier (1,550 g, SD ± 130 g) than that of adult females (854 g, SD ± 69 g), *i.e.*, sexual size dimorphism was 1.81 ( $N = 264$ ).

#### DIET ANALYSIS

In western France, the diet of male and female polecats did not really differ ( $\chi^2 = 4$ ,  $df = 3$ ,  $P > 0.05$ ) (Table I). Their food consisted mostly of mammals (71.5%) and anurans (21.3%). Birds (passeriforms, gruiforms, and anseriforms) and invertebrates were of minor importance. Mammals were essentially small microtines such as Bank and meadow voles and murids such as brown rats. In this hydromorph habitat, rabbits were just a secondary resource.

Within the mammal prey, however, the proportions of different species significantly differed between male and female polecats ( $\chi^2 = 10.65$ ,  $df = 5$ ,  $P < 0.03$ ), males eating more small rodents and females eating more rabbits. Caught anurans were mostly terrestrial anurans such as agile frogs and common toads; there was no difference in their distribution in the male and female diets ( $\chi^2 = 0.16$ ,  $df = 1$ ,  $P > 0.05$ ).

TABLE I. Composition of the diets (%) of female and male polecats in western France (revealed by fecal analysis). In bold, subtotals for each prey group.

	Total	
	M	F
<i>Sorex</i> sp. and <i>Crocidura</i> sp.	3.5	3.1
<i>Talpa europaeus</i>	0.3	0.3
<i>Clethrionomys glareolus</i>	28.1	29.9
<i>Microtus arvalis</i>	22.5	18.0
<i>Arvicola sapidus</i>	0.5	0.8
<i>Rattus norvegicus</i>	12.0	10.4
<i>Oryctolagus cuniculus</i>	4.4	9.0
<i>Ondatra zibethicus</i>	0.5	0.3
<b>Mammals</b>	<b>71.9</b>	<b>71.8</b>
Passeriforms	1.2	3.1
Anseriforms	0.2	0.6
Gruiforms	0.3	0.8
<b>Birds</b>	<b>1.8</b>	<b>4.5</b>
<i>Rana dalmatina</i>	15.5	13.8
<i>Bufo bufo</i>	5.8	4.5
<i>Rana esculenta</i>	0.9	0.6
Undetermined Anurans	0.5	0.3
<b>Anurans</b>	<b>22.7</b>	<b>19.2</b>
<b>Invertebrates</b>	<b>2.1</b>	<b>3.1</b>
<b>Carrion</b>	<b>1.6</b>	<b>1.4</b>
<i>N</i>	573	355

The diet showed seasonal variations that were significant both for male polecats ( $\chi^2 = 118.36$ ,  $df = 6$ ,  $P < 0.001$ ) and for female polecats ( $\chi^2 = 89.61$ ,  $df = 6$ ,  $P < 0.001$ , Figure 1). These changes mainly resulted from the preponderance of small mammals in winter and the exploitation of amphibians in spring. But during summer, males ate more anurans than females did ( $\chi^2 = 7.75$ ,  $df = 1$ ,  $P < 0.02$ ). Mammal prey also revealed seasonal variations in their proportions. Female polecats consumed more rabbits in autumn and more rats in winter ( $\chi^2 = 47.87$ ,  $df = 12$ ,  $P < 0.001$ ), whereas males ingested more shrews and brown rats in winter ( $\chi^2 = 76.25$ ,  $df = 12$ ,  $P < 0.001$ ).

Thus, there was a significant difference in the size of the prey caught by polecats: females ingested bigger prey than the males did ( $\chi^2 = 7.79$ ,  $df = 2$ ,  $P < 0.02$ ) (Table II). This difference seemed essentially to arise from a much greater consumption of rabbits by females ( $\chi^2 = 7.22$ ,  $df = 2$ ,  $P < 0.03$ ). On the other hand, male and female polecats did not seem to select anurans differently ( $\chi^2 = 0.31$ ,  $df = 1$ ,  $P > 0.05$ ).

Nevertheless, the male and female diet greatly overlapped and varied from  $C_{jk} = 0.793$  in summer to 0.991 in spring, with the autumn and winter values (respectively 0.894 and 0.955) being intermediate.

#### PREY SELECTION

The sample of collected remains totalled 551 prey (353 from male polecats, 198 from female polecats). Whatever the species, male prey predominated in remains ( $t_{Welch} = 17.6$ ,  $df = 8$ ,  $P < 0.008$ , Table III), with no significant difference between male and female polecats ( $\chi^2 = 2.21$ ,  $df = 4$ ,  $P > 0.05$ , Table III).

The capture rate was low on the trap-lines established to collect data on rodent availability, averaging 21.8% (range: spring: 9.4%; autumn: 34.4%). Study of the structure of rodent populations by trapping showed that males predominated in the populations of bank voles (56.9%) and meadow voles (55.7%), as well as brown rats (58.2%). But traps may be selective in regard to the animals captured, and

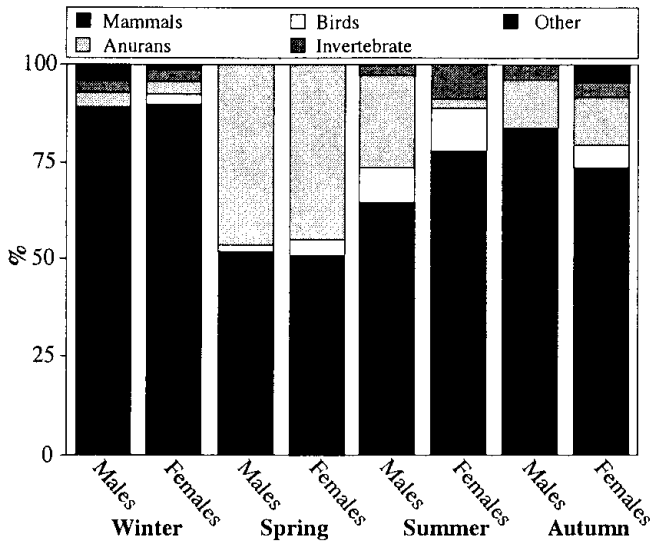


FIGURE 1. Seasonal changes of male and female polecats (*Mustela putorius*).

TABLE II. Distribution of different-sized prey in the diet of male and female polecats (revealed by fecal analysis).

	Polecat		
	Male	Female	
MAMMAL PREY			$\chi^2 = 7.22, df = 2, P < 0.03$
< 50 g	75.2	71.0	
50 g to 200 g	18.0	16.1	
> 200 g	6.8	12.9	
N	412	255	
ANURAN PREY			$\chi^2 = 0.31, df = 1, P > 0.05$
<i>Rana</i> sp.	73.8	76.1	
<i>Bufo bufo</i>	26.2	23.9	
N	126	67	
TOTAL PREY			$\chi^2 = 7.79, df = 2, P < 0.02$
< 50 g	75.6	73.0	
50 g to 200 g	19.3	17.1	
> 200 g	5.1	9.9	
N	553	334	

TABLE III. Proportion of male prey in remains from male and female polecats in western France (pooled data from data found in dens, in caches, and in stomachs).

	Male polecats	Female polecats	Total
<i>Clethrionomys glareolus</i> males	83.7	86.4	84.6
N	43	22	65
<i>Microtus arvalis</i> males	85.7	80.0	81.8
N	12	10	22
<i>Rattus norvegicus</i> males	72.7	72.7	72.7
N	44	33	77
<i>Rana dalmatina</i> males	74.6	73.7	74.3
N	213	114	327
<i>Bufo bufo</i> males	80.5	84.2	81.7
N	41	19	60

the most active individuals (e.g., dominant males) are the ones most often captured. Nonetheless, the proportion of microtine females exceeded that of males in summer, although it remained lower in the other seasons and was at its lowest in autumn (Table IV).

During spring, the sex ratio on spawning sites was also unbalanced in favour of males in anuran populations, both in agile frogs (64.1%) and in common toads (63.0%).

Nevertheless, polecats selected male prey, as shown by Ivlev's Electivity index (Table IV). Although it was less clear in the case of brown rats, this selective predation did not significantly vary according to either the prey species (Kruskal-Wallis  $H = 6.66, df = 4, P > 0.05$ ) or the season ( $H = 4.09, df = 4, P > 0.05$ ).

### Discussion

The sexual size dimorphism in the polecat reached the ratio 1.81, which clearly exceeded the mean ratio (1.31) obtained in mustelids by Weckerly (1998), thus showing that the polecat is one of the most dimorphic carnivores. The results of the present study emphasized both a preference for male prey and a dietary difference not linked to selection of bigger prey by male polecats.

### PREY CHOICE

According to niche differentiation hypothesis, food niche partitioning should be found as a consequence of distinct preying. However, in this investigation of the contribution of trophic constraints to the divergence in growth between sexes, only a few differences were detected. In female and male polecats, the overall structure of their diet showed a predominance of mammal prey alternating with a regular exploitation of anurans in spring. Moreover, polecats clearly exhibited selective predation on male prey, strongly exceeding the proportions of available males. In practice, all traps are selective in respect to different prey categories. Most small mammal traps select mobile and/or dominant individuals. The selectivity of traps may bias results if the capture of the most active individuals reduces the probability of catching the others (Koivunen *et al.*, 1996). Males often predominate among trapped individuals (Körpimäki, 1985; Koivunen *et al.*, 1996), but the predominance of males was significantly higher in polecat prey, making the estimate conservative enough.

The existence of selective choice of male prey has been noted in some raptors (Southern & Lowe, 1968; Korpimäki, 1985) and in brown bears (Quinn & Kinnison, 1999). In Alaska, the weasel mainly consumed female lemmings caught in their winter nests (Maclean, Fitzgerald & Pitelka, 1974). But because of the selective predation by polecats, Korpimäki's (1985) hypothesis of a possible preference of mammalian predators for female prey while avian predators prefer males may be debated. Besides, Longland and Jenkins (1987), and Dickman, Predavec, and Lyman (1991) concluded that owls mainly selected female mice. And underground hunting by the weasel, which was both diurnal and nocturnal, favoured the catching of female prey in their nests (Cushing, 1985). In contrast, the polecat sought small, nocturnal prey above ground (Weber, 1989) and synchronized its activity to the activity rhythm of its main prey (Lodé, 1995). This synchronization also has been noticed in other mustelids (Larivière & Messier, 1997). The polecat selective predation did not differ according to the predator's sex and mainly depended upon trophic availability reflecting a niche variation.

Nevertheless, this selection was not necessarily directed and might have resulted only from a greater vulnerability of male rodents (Mappes *et al.*, 1993) or anurans. Prey

TABLE IV. Selective predation in male and female polecats as revealed by seasonal variations of the Electivity index ( $D$ ) based on differences between percentage of males in prey remains and in available prey populations.

	Males					Females				
	Winter	Spring	Summer	Autumn	Total	Winter	Spring	Summer	Autumn	Total
<i>Clethrionomys glareolus</i>										
remains	77.8	100.0	100.0	85.7	83.7	83.3	100.0	75.0	90.9	86.4
availability	57.1	56.2	48.5	59.7	56.9	57.1	56.2	48.5	59.7	56.9
$D$	0.449	1.000	1.000	0.599	0.592	0.578	1.000	0.522	0.741	0.656
<i>Microtus arvalis</i>										
remains	100.0	0.0	50.0	85.7	83.3	100.0	0.0	100.0	66.7	80.0
availability	56.1	54.5	42.9	62.7	55.7	56.1	54.5	42.9	62.7	55.7
$D$	1.000	-1.00	-0.142	0.562	0.597	1.000	-1.000	1.000	0.087	0.521
<i>Rattus norvegicus</i>										
remains	73.9	50.0	0.0	81.2	72.7	82.4	33.3	100.0	66.7	72.7
availability	55.2	58.3	57.1	61.8	58.2	55.2	58.3	57.1	61.8	58.2
$D$	0.394	-0.166	-1.000	0.455	0.313	0.582	-0.473	1.000	0.106	0.313
<i>Rana dalmatina</i>										
remains		73.1			74.6		72.7			73.7
availability		64.1			64.1		64.1			64.1
$D$		0.207			0.245		0.197			0.222
<i>Bufo bufo</i>										
remains		81.5			80.5		80.0			84.2
availability		63.0			63.0		63.0			63.0
$D$		0.443			0.416		0.403			0.516

selectivity remains an unclear ecological term because it supposes an active choice among available different prey (Stephen & Krebs, 1986). Males may be more easily detectable because of their active behaviour, their aggressive interactions, and, in the case of anurans, by their territorial courtship calls. Predation upon male anurans is related to an area-restricted search (Lodé, 2000), and anuran males were more preyed upon than females (Licht, 1974). In rodents, Jedrzejewska (1989) and Bollinger, Harper, and Barrett (1993) underlined the greater vulnerability of transients, and there was a significant association of prey mobility with predation risk (Norrdahl & Korpimäki, 1998).

#### SEXUAL DIMORPHISM

The sexual size divergence raises numerous evolutionary issues: chiefly, the role of the respective influences of environmental variations and sexual selection. The question that arises is why was there such a wide dimorphism in the polecat since it did not reflect divergence in the diet structure and in the selective predation pattern. Food habits of male and female European polecats partially diverged. The difference between the male and the female diet only resulted from proportions of lagomorphs, and, paradoxically, the female ate more rabbits than the male did. Therefore, it was not possible to conclude that the sexual dimorphism of the European polecat leads to the catching of smaller prey by the female.

The difference between the diet of male and female American mink (*Mustela vison*) has been mainly attributed to their sexual dimorphism, the females eating a lower proportion of lagomorphs than did males (Birks & Dunstone, 1985). By contrast, Weber (1989) noted that female polecats caught bigger prey than males did. In fact, polecat diets largely overlapped between sexes, and the diet structure varied from one area to another (Lodé, 1997). The frequency of lagomorphs in the polecat diet remained very low and generally varied with their availability in the environment

(Weber, 1989; Lodé, 1994; 1997), a pattern also noted by Birks and Dunstone (1985) with respect to American mink. In western France, the catching of lagomorphs by females was closely linked to the breeding of young polecats (Lodé, 1989). The polecat's predation upon the rabbit seemed to be concentrated on young individuals or individuals suffering from myxomatosis. Errington (1954; 1956) proposed that substandard animals are more exposed to predation than others. In polecats, the capture of prey as large as rabbits was probably favoured by the prey's inexperience and weakness.

The potential association between predator size and prey size resulted in consideration of sexes as particular morphotypes (Dayan & Simberloff, 1994). This implies that the consumption of small prey by female polecats enhances their fitness, thus leading to a dimorphism. Such enhancement is only possible if the capture of small prey is easier than that of big prey. My results did not support this hypothesis, despite the fact that the sexual dimorphism of the polecat is one of the greatest among mustelids. There is no evidence for sexual size dimorphism enhancing the niche partitioning between the sexes, and trophic factors are likely to act only as a weak selection pressure, thus disproving (insofar as polecats are concerned) the intersexual niche differentiation hypothesis proposed by Van Valen (1965) and Shine (1989; 1990).

Polecats have a very solitary life (Lodé, 1996; 2000) and show sexual segregation in the use of space and habitats (Lodé, 1996), suggesting strong competition. Competing for mates, males may be mostly aggressive, while polygyny increases the mobility of dominant males searching for territorial females (Bekoff, Daniels & Gittleman, 1984; Sandell, 1986; Lodé, 2001). In polecats, the strong sexual competition among males and the fact that conflicts are resolved by the tenacity of the male contenders could lead to selection of large individuals (Poole, 1974). During the breeding season, mustelid females spend less time travelling and remain in their nest for a longer period (Wynne &

Sherburne, 1984; Robitaille & Raymond, 1995; Lodé, 1999). This sexual factor is expected to be more determinant than trophic ecology because it is fitness related. Natural selection should favour a precocious maturity both in males and females, but the large size of males confers a selective advantage because larger males are more likely to mate than small males. By contrast, breeding success of females relates strongly to their maternal investment (Clutton-Brock, 1988) and results in a decrease of dietary overlap with their cubs (Lodé, 1989). Alternatively, Powell and Leonard (1983), Raymond, Bergeron, and Plante (1984) and Raymond *et al.* (1990) suggested that the sexual dimorphism in body size of mustelids could be related to energy budgets. More studies are required to understand the role of parental care in sex differences.

In conclusion, males and females did not exhibit divergent responses to environmental features, suggesting that the dimorphism in polecats did not support the trophic niche differentiation hypothesis. The sexual dimorphism was not linked to different prey choice but should result from independent selective pressures on mustelids' size. Only a strong selection for a heritable morphological trait could result in a sexual size dimorphism (Slatkin, 1984; Reeve & Fairbairn, 2001). The spatial pattern and the polygynous organization, associated with the sexual dimorphism (Lodé, 2001) suggests that sexual selection plays the main role. It could be suspected that the larger body size of male polecats stems from sexual selection while the smaller size of females reduces food competition with cubs (Andersson, 1994), the size dimorphism reflects both selection for mating access in males by conferring an advantage in mate contests and for trophic resources in females, illustrating the ultimate and complementary influence of sexual selection and environmental constraints on sex divergence in growth.

### Acknowledgements

I thank J. Blondel (University of Montpellier) and K. Norrdahl (University of Turku) for their helpful comments on the first draft. My thanks to N. C. Stenseth for his help. Thanks are also due to D. Le Jacques and A. M. O'Donovan for English corrections.

### Literature cited

- Andersson, M. (ed.), 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.
- Arnold, E. N., & J. A. Burton, 1978. A Field Guide to Reptiles and Amphibians of Britain and Europe. Collins, London.
- Badyaev, A. V. & T. E. Martin, 2000. Sexual dimorphism in relation to current selection in the house finch. *Evolution*, 54: 987-997.
- Bekoff, M., T. J. Daniels & J. L. Gittleman, 1984. Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics*, 15: 191-282.
- Birks, J. D. S. & N. Dunstone, 1985. Sex-related differences in the diet of the mink *Mustela vison*. *Holarctic Ecology*, 8: 245-252.
- Blondel, J., P. Perret, M. C. Anstett & C. Thébaud, 2002. Evolution of sexual size dimorphism in birds: Test of hypotheses using blue tits in contrasted Mediterranean habitats. *Journal of Evolutionary Biology*, 15: 440-450.
- Bollinger, E. K., J. J. Harper & G. W. Barrett, 1993. Interbreeding avoidance increases dispersal movements of the meadow vole. *Ecology*, 74: 1153-1156.
- Boonstra, R., 1977. Predation on *Microtus townsendii* populations: Impact and vulnerability. *Canadian Journal of Zoology*, 55: 1631-1643.
- Boonstra, R., B. S. Gilbert & C. J. Krebs, 1993. Mating systems and sexual dimorphism in mass in microtines. *Journal of Mammalogy*, 74: 224-229.
- Clutton-Brock, T. H., 1985. Size, sexual dimorphism, and polygyny in primates. Pages 51-60 in C. M. Wemmer, (ed.). *Biology and Management of the Cervidae*. Plenum Press, London.
- Clutton-Brock, T. H., 1988. *Reproductive Success*. University of Chicago Press, Chicago, Illinois.
- Cushing, B., 1985. Oestrous mice and vulnerability to weasel predation. *Ecology*, 66: 1976-1978.
- Day, M. G., 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Journal of Zoology*, 148: 201-217.
- Dayan, T. & D. Simberloff, 1994. Character displacement, sexual dimorphism and morphological variations among British and Irish mustelids. *Ecology*, 75: 1063-1073.
- Debrot, S., G. Fivaz, C. Mermod & J. M. Weber, 1982. *Atlas des Poils des Mammifères d'Europe*. Institut Zoologique, Neuchâtel.
- Dickman, C. R., M. Predavec & A. J. Lyman, 1991. Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. *Oikos*, 62: 67-75.
- Downhower, J. F., 1976. Darwin's finches and the evolution of social dimorphism in body size. *Nature*, 263: 558-563.
- Erlinge, S., 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos*, 33: 233-245.
- Errington, P. L., 1954. The special responsiveness of minks to epizootics in muskrat populations. *Ecological Monographs*, 24: 377-393.
- Errington, P. L., 1956. Factors limiting higher vertebrate populations. *Science*, 124: 304-307.
- Jacobs, J., 1974. Quantitative measurement of food selection: A modification of the Forage Ratio and Ivlev's Electivity Index. *Oecologia*, 14: 413-417.
- Jaksic, F. M. & M. Delibes, 1987. A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: Causes, correlations, and consequences. *Oecologia*, 71: 461-472.
- Jarman, P. J., 1974. The social organisation of antelope in relation to their ecology. *Behaviour*, 4: 215-266.
- Jedrzejewska, B., 1989. Variation in weasels' response to transient and resident bank voles, enclosure experiments. *Acta Oecologica*, 10: 149-154.
- Jedrzejewski, W. & B. Jedrzejewska, 1993. Predation on rodents in Białowieża primeval forest, Poland. *Ecography*, 16: 47-64.
- Koivunen, V., E. Korpimäki, H. Hakkarainen & K. Norrdahl, 1996. Prey choice of Tengmalm's owls (*Aegolius funereus funereus*): Preference for substandard individuals? *Canadian Journal of Zoology*, 74: 816-823.
- Korpimäki, E., 1985. Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. *Annales Zoologici Fennici*, 22: 91-104.
- Larivière, S. & F. Messier, 1997. Characteristics of waterfowl nest depredation by the striped skunk, *Mephitis mephitis*: Can predators be identified from nest remains? *American Midland Naturalist*, 137: 393-396.
- Leberg, P. L. & M. H. Smith, 1993. Influence of density on growth of white-tailed deer. *Mammalia*, 74: 723-731.
- Licht, L. E., 1974. Survival of embryos, tadpoles, and adults of the frog *Rana aurora* and *Rana pretiosa* in southern British Columbia. *Canadian Journal of Zoology*, 52: 613-627.

- Lodé, T., 1989. Ontogenèse des comportements de prédation et rôle de l'expérience alimentaire précoce chez *Mustela putorius*. *Mammalia*, 53: 497-509.
- Lodé, T., 1994. Environmental factors influencing habitat exploitation by the polecat *Mustela putorius* in western France. *Journal of Zoology*, 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. Conspecific tolerance and sexual segregation in European polecat. *Acta Theriologica*, 41: 171-176.
- Lodé, T., 1997. Trophic status and feeding habits of the European polecat *Mustela putorius* L. 1758. *Mammal Review*, 27: 177-184.
- Lodé, T., 1999. Time budget as related to feeding tactics of European polecat *Mustela putorius*. *Behavioural Process*, 47: 11-18.
- Lodé, T., 2000. Functional response and area-restricted search in a predator: Seasonal exploitation of anurans by European polecat *Mustela putorius*. *Austral Ecology*, 25: 223-231.
- Lodé, T., 2001. Mating system and genetic variance in a polygynous mustelid, the European polecat. *Genes and Genetic Systems*, 76: 221-227.
- Longland, W. S. & S. H. Jenkins, 1987. Sex and age affect vulnerability of desert rodents to owl predation. *Journal of Mammalogy*, 68: 746-754.
- Maclean, S. F., B. M. Fitzgerald & F. A. Pitelka, 1974. Population cycles in arctic lemmings: Winter reproduction and predation by weasels. *Arctic and Alpine Research*, 6: 1-12.
- Mappes, T., M. Halonen, J. Suhonen & H. Ylonen, 1993. Selective avian predation on a population of the field vole *Microtus agrestis*: Greater vulnerability of males and subordinates. *Ethology, Ecology & Evolution*, 5: 519-527.
- Marti, C. D., K. Steenhof, M. N. Kochert & J. S. Marks, 1993. Community trophic structure: The roles of diet, body size, and activity time in vertebrate predators. *Oikos*, 67: 6-18.
- Mills, M. G. L., 1990. Kalahari Hyenas: Comparative Behavioural Ecology of Two Species. Unwin Hyman, London.
- 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.
- Norrdahl, K. & E. Korpimäki, 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology*, 79: 226-232.
- Poole, T. B., 1974. Detailed analysis of fighting in polecats (Mustelidae) using cine film. *Journal of Zoology*, 173: 393-396.
- Powell, R. A. & R. D. Leonard, 1983. Sexual dimorphism and energy expenditure for reproduction in female fisher *Martes pennanti*. *Oikos*, 40: 166-174.
- Powell, R. A. & W. J. Zielinski, 1983. Competition and coexistence in mustelid communities. *Acta Zoologica Fennica*, 174: 223-227.
- Quinn, T. P. & M. T. Kinnison, 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia*, 121: 273-282.
- Ralls, K., 1976. Mammals in which females are larger than males. *Quarterly Review of Biology*, 51: 245-276.
- Ralls, K., 1977. Sexual dimorphism in mammals: Avian models and unanswered questions. *American Naturalist*, 111: 917-938.
- Raymond, M., J. M. Bergeron & Y. Plante, 1984. Dimorphisme sexuel et régime alimentaire de l'hermine dans un agrosystème du Québec. *Canadian Journal of Zoology*, 62: 594-600.
- Raymond, M., J. F. Robitaille, P. Lauzon & R. Vaudry, 1990. Prey-dependent profitability of foraging behaviour of male and female ermine, *Mustela erminea*. *Oikos*, 58: 323-328.
- Reeve, J. P. & D. J. Fairbairn, 2001. Predicting the evolution of sexual size dimorphism. *Journal of Evolutionary Biology*, 14: 244-254.
- Robitaille, J. F. & M. Raymond, 1995. Spacing patterns of ermine, *Mustela erminea* L., in a Québec agrosystem. *Canadian Journal of Zoology*, 73: 1827-1834.
- Saint-Girons, M.-C., 1973. Les Mammifères de France et du Bénélux. Doin, Paris.
- 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., A. Swanson & H. A. Doty, 1973. Selective predation by mink, *Mustela vison*, on waterfowl. *American Naturalist*, 89: 208-214.
- Schoener, T. W., 1974. Resource partitioning in ecological communities. *Science*, 185: 27-39.
- Shine, R., 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *Quaternary Review of Biology*, 64: 419-461.
- Shine, R., 1990. Proximate mechanisms of sexual differences in adult body size. *American Naturalist*, 135: 278-283.
- Short, R. V. & E. Balaban, 1994. The Differences Between the Sexes. Cambridge University Press, Cambridge.
- Slatkin, M. K., 1984. Ecological causes of sexual dimorphism. *Evolution*, 38: 622-630.
- Stephen, D. W. & J. R. Krebs, 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey.
- Southern, H. N. & V. P. Lowe, 1968. The pattern of distribution of prey and predation in Tawny owl territories. *Journal of Animal Ecology*, 37: 75-97.
- Van Valen, L., 1965. Morphological variation and width of the ecological niche. *American Naturalist*, 99: 377-390.
- Weber, D., 1989. Foraging in polecats *Mustela putorius* L. of Switzerland: The case of a specialist anuran predator. *Zeitschrift für Säugetierkunde*, 54: 377-392.
- Weckerly, F. W., 1998. Sexual-size dimorphism: Influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy*, 79: 33-52.
- Wynne, K. M. & J. A. Sherburne, 1984. Summer home range use by adult marten in northwestern Maine. *Canadian Journal of Zoology*, 62: 941-943.