A change of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator?

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Abstract

The results of a study testing the hypothesis that wildcats *Felis silvestris* are rodent-specialist predators is reported. The diet of wildcats was studied in different habitats from central Spain where rabbits *Oryctolagus cuniculus* were either present or absent in order to explore whether the wildcat is a facultative or a rodent specialist. We predicted that if the wildcat was a rodent specialist there would be no differences in rodent composition in scats between areas with or without another profitable prey such as rabbits. To test this hypothesis, 239 scats were collected in two contrasting habitat types: Mediterranean vegetation areas, where rabbits were either present or absent, and Pyrenean oak forests, where there were no rabbits. All areas and habitat types were sampled in different seasons. The frequency of occurrence and biomass of different prey items and diet diversity were compared between habitats and areas with the presence/absence of rabbits. Wildcats consumed significantly fewer rodents in areas with rabbits than in areas where rabbits were absent, and diet diversity showed important seasonal variations. Values for diet diversity were lower in areas where rabbits were present. Thus it can be stated that wildcats do not specialize in rodents, and we suggest a facultative specialization on different prey items (rabbits or rodents) according to prey availability.

Key words: diet, facultative specialist, rodents, *Felis silvestris*, rabbit

INTRODUCTION

Diet composition is one of the best known subjects of the ecology of wildcats (e.g. see Condé *et al.*, 1972; Corbett, 1979; Schauenberg, 1981; Aymerich, 1982; Hewson, 1983; Sarmento, 1996). Most of these studies conclude that rodents (murids and microtines) constitute the staple prey of wildcats, although lagomorphs and birds can also be taken (Kolb, 1977; Corbett, 1979; Aymerich, 1982; Hewson, 1983; Sarmento, 1996).

In France, rodents account for 97% of diet composition (relative frequency of occurrence in stomach contents; Condé *et al.*, 1972), and in many other regions wildcats have a similar rodent-based diet: Carpathians (Sladek, 1973), Apenines (Ragni, 1978), western Scotland (Hewson, 1983), Portugal (Sarmento, 1996); high mountain areas of southern Spain (Moleón & Gil-Sánchez, 2003). Thus, the general conclusion that wildcats are rodent specialists could be drawn from these studies. Nevertheless, some studies have shown that rabbits may constitute the main item in the diet in regions where

they are present (Corbett, 1979; Aymerich, 1982; Gil-Sánchez, Valenzuela & Sánchez, 1999). In the Iberian Peninsula this shift towards rabbits has also been reported for other carnivores such as lynxes *Lynx pardinus*, badgers *Meles meles* and foxes *Vulpes vulpes* (Delibes & Hiraldo, 1981). All this descriptive literature does not resolve the uncertainty about the degree of specialization in wildcats on rodents or other potential alternative prey such as rabbits (Virgós, Llorente & Cortés, 1999).

In general, predators should generalize if the abundance of profitable prey is low and should specialize as its abundance increases (Pyke, Pulliam & Charnov, 1977; Lea, 1981; Stephens & Krebs, 1986). Discussions on whether a predator species is a generalist or specialist have been common in the ecological literature (Futuyma & Moreno, 1988). A species is considered a trophic specialist if it feeds almost entirely on one species, regardless of its abundance, or other alternative prey abundance or presence among areas or seasons. On the other hand, a facultative specialist may behave more opportunistically, in such a way that it may change a key food item when other profitable prey is available (Glasser, 1982).

The aim of this study was to test the hypothesis that the wildcat is a rodent specialist. Given that rabbits may

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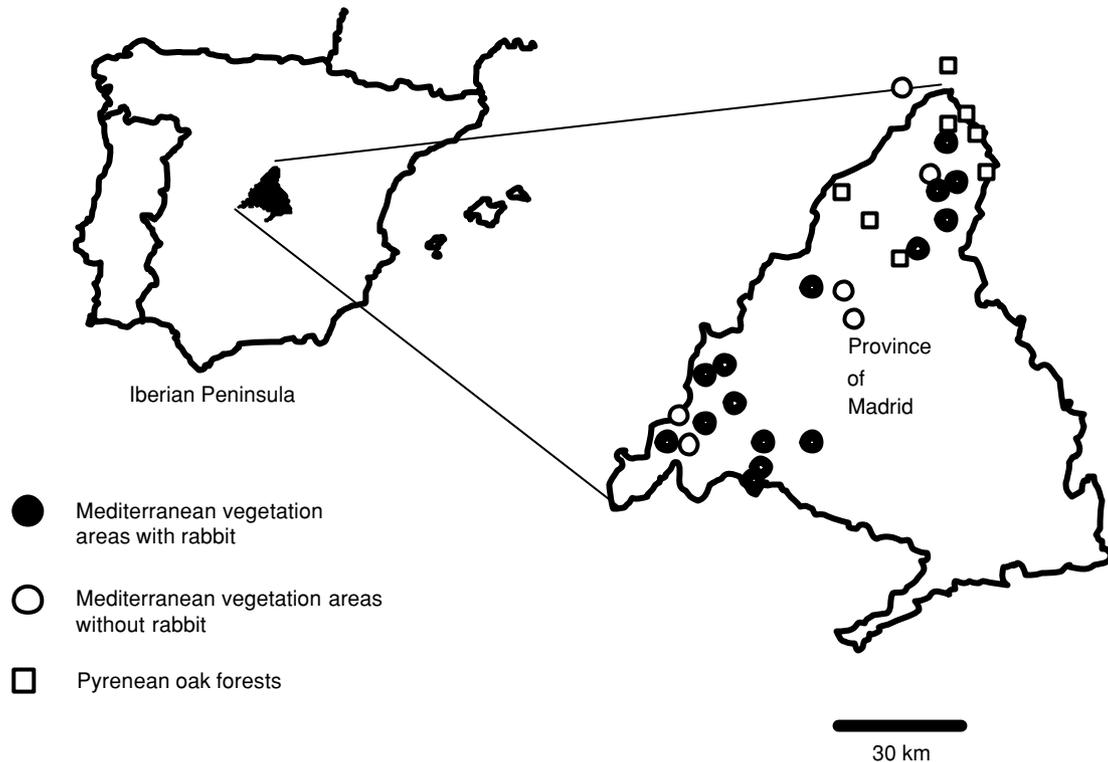E-mail: evirgos@escet.urjc.es

Fig. 1. Location of the study areas within the Iberian Peninsula and Madrid province.

be an alternative optimal prey to rodents, this hypothesis was tested by comparing rodent importance in the diet of wildcats across areas with and without rabbits and between seasons within central Spain, a particularly suitable region, because wildcats show a homogeneous distribution (Lozano *et al.*, 2003) while rabbit populations show a patchy one (Virgós, Cabezas-Díaz *et al.*, 2003).

If the wildcat is a rodent specialist, those living in areas with and without rabbits should have a high rodent intake and would show no significant differences in rodent consumption between areas. Conversely, if the wildcat is not a rodent specialist, but may change its preference to other profitable prey such as rabbits, a decrease of rodent intake in areas where rabbits are abundant would be expected.

METHODS

Fieldwork was carried out in a 2916 km^2 region in the centre of the Iberian Peninsula (Fig. 1). To confirm the presence of wildcats at the local level, trails distributed across different habitat types were surveyed for scats. Habitat type was defined as either Mediterranean vegetation areas (700–1250 m a.s.l.) or Pyrenean oak forests (1250–1700 m a.s.l.). Mediterranean vegetation was a mixture of forests dominated by holm oaks *Quercus ilex*, scrublands whose main understorey shrub species are *Cistus ladanifer* and *Retama sphaerocarpa*, and mosaics with pasturelands. Pyrenean oak forests *Q. pyrenaica* occasionally included other deciduous trees, with *Cistus laurifolius* and *Citysus scoparius* as the main understorey

shrub species (for details about vegetation see Rivas-Martínez, Fernández-González & Sánchez-Mata, 1987).

Once areas with wildcat occurrence were selected (21 with Mediterranean vegetation *vs* 8 with Pyrenean oak forest), every area was subsequently surveyed to determine the presence or absence of rabbits by searching for rabbit burrows and latrines. Rabbit presence was confirmed in 15 out of 21 Mediterranean vegetation areas and, as expected, in none of the 8 Pyrenean oak forests, given that rabbits show a strong preference for low elevation areas (Blanco & Villafuerte, 1993; Trout *et al.*, 2000). Overall, 15 areas with rabbit (all of them Mediterranean vegetation areas) and 14 areas without rabbit (6 Mediterranean vegetation areas, and 8 Pyrenean oak forest areas) were surveyed. We are confident about the absence of rabbits in these areas as they were extensively surveyed over several years.

During 1997–99 the areas studied were visited and trails surveyed every season. In each visit, the status of rabbit presence was checked and, in addition, a routine monitoring of the rabbit populations was undertaken in these areas from 1989. At least 1 km/area was surveyed and a total of 239 wildcat scats (558 prey items) collected: 132 in areas with rabbits and 107 in areas without rabbits. Wildcat scats were recognized using the methods of Lozano *et al.* (2003). Prey items were identified from bones and teeth using key references (Gállego & López, 1982; Gállego & Alemany, 1985; Blanco, 1998).

The frequency of occurrence (FO) was compared and the consumed biomass (CB) of the different prey items among areas was estimated. To estimate biomass the following mean weight data were used: *Microtus*

Table 1. Diet composition of wildcats *Felis silvestris* in areas with or without rabbits *Oryctolagus cuniculus* in central Spain. FO, frequency of occurrence in scats; CB, consumed biomass. Non-identified (n.i.) items are specified in parentheses. For clarity, remains of a non-identified ungulate and a cat are not shown

	Overall	Areas with rabbits (132 scats)			Areas without rabbits (107 scats)		
	No. of prey	No. of prey	FO(%)	CB(%)	No. of prey	FO(%)	CB(%)
Rodents (n.i.)	259 (11)	90 (8)	40.91	8.21	169 (3)	82.24	68.38
Muridae (n.i.)	248 (28)	82 (9)	34.85	7.46	166 (19)	75.70	65.33
Murinae (n.i.)	111 (23)	51 (13)	24.24	4.63	60 (10)	39.25	23.70
Apodemus sylvaticus	75	29	13.64	3.07	46	29.91	19.74
Mus sp.	13	9	6.06	0.55	4	2.8	0.99
Microtinae (n.i.)	109 (23)	22 (4)	12.88	1.88	87 (19)	49.53	33.48
Microtus arvalis	46	4	3.03	0.42	42	24.3	18.03
Pitymys sp.	40	14	8.33	1.14	26	14.95	8.58
Lagomorphs	85	83	61.36	90.11	2	1.87	10.56
Rabbit	83	83	61.36	90.11	0	–	–
Hares	2	0	–	–	2	1.87	10.56
Insectivores	41	6	4.55	0.18	35	15.89	14.79
Crocidura sp.	26	6	4.55	0.18	20	10.28	2.48
Sorex sp.	3	0	–	–	3	0.93	0.27
Talpa occidentalis	12	0	–	–	12	9.35	12.04
Birds	21	9	6.82	0.88	12	11.21	4.75
Reptiles (n.i.)	20 (5)	5 (2)	3.79	0.05	15 (3)	12.15	0.59
Psammodromus sp.	15	3	2.27	0.029	12	11.21	0.48
Arthropods	132	73	22.73	0.56	59	28.97	0.73
Insects	128 (46)	69 (45)	20.45	0.11	59 (1)	26.17	0.28
Myriapods	2	1	0.76	0.006	1	0.03	0.01
Coleoptera	53	19			34		
Gryllotalpa sp.	14	12	5.30	0.04	2	0.93	0.03
Other coleoptera	39	7	5.30	0.006	32	12.15	0.11
Orthopthera	26	4	3.03	0.01	22	10.28	0.29
Crustacea (freshwater crayfish)	4	4	3.03	0.39	0	–	–

(32.5 g), *Pitymys* (25 g), *Apodemus* (32.5 g), *Mus* (18.8 g), *Crocidura* (9.4 g), *Sorex* (6.7 g), *Talpa occidentalis* (76 g), bird (30 g), lacertid (3 g), cray-crab fish (39 g), *Gryllotalpa* (1 g) and other insects (0.5 g) (Castells & Mayo, 1993; Blanco, 1998). With these mean weights, non-identified Microtinae, Murinae and other rodents were calculated as 30 g, 23 g and 26 g, respectively. A maximum consumption of 400 g for hares *Lepus granatensis* was assumed.

Wildcats vary the age class of rabbits they prey on depending on the season (Gil-Sánchez *et al*., 1999). In spring and summer, the contribution to the wildcat diet of juvenile rabbits compared to adult rabbits is *c*. 50%, and in autumn and winter *c*. 20%. It is assumed that a wildcat consumes a maximum of 400 g from an adult or sub-adult rabbit (Aymerich, 1982) and 250 g from a juvenile (Gil-Sánchez *et al*., 1999). With this information and according to the following expression, the rabbit consumed biomass (RCB) for the two seasonal periods was calculated:

$$\text{RCB} = P(\text{ad-sub})^*(400\,\text{g}) + P(\text{juv})^*(250\,\text{g})$$

where $P(\text{ad-sub})$ and $P(\text{juv})$ are the probabilities of consumption of an adult or sub-adult and of a juvenile rabbit, respectively. Thus we used a value of 370 g for autumn–winter and of 325 g for spring–summer.

The seasonal fluctuations in the contribution of each prey item to the diet in areas with and without rabbits were also analysed. The Shannon–Weaver index (Shannon & Weaver, 1949) was used to calculate diet diversity from FO among seasons and areas using the following prey categories: rodents, lagomorphs, insectivores, birds, reptiles and arthropods.

G-tests were used to analyse the frequency of occurrence of each prey group as this test is robust and conservative and greatly diminishes the possibility of statistical type I errors. Yates' correction was applied where expected frequencies were < 10 (Mantel, 1974). Kruskal–Wallis tests were used to compare biomass across areas and seasons. All statistical analyses were conducted with the STATISTICA 6.0 computer package for Windows.

RESULTS

Diet comparison between areas with and without rabbits

Overall diet diversity for all areas and prey groups considered was maximum in summer (2.24) and minimum in winter (1.03), reaching intermediate values in autumn and spring (1.65 and 1.71, respectively). Comparison across areas showed that the diet of wildcats was slightly more diverse in areas without rabbits (Table 1, Fig. 2).

In areas where rabbits were present they were the most important prey type (Table 1). The contribution of
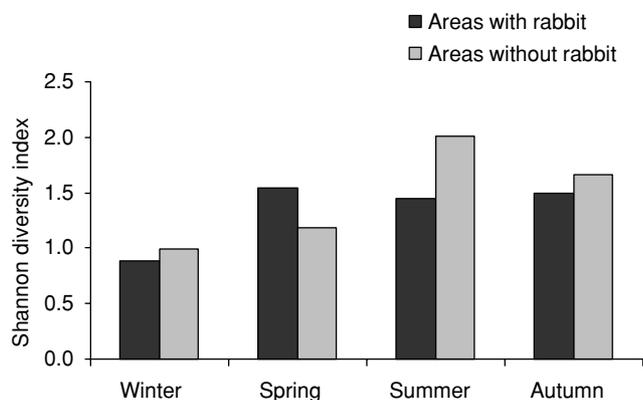
Fig. 2. Diet diversity of wildcats *Felis silvestris* in areas with and without rabbits *Oryctolagus cuniculus*.

rodents to the diet decreased where rabbits were present (FO: $\chi^2 = 42.2$, d.f. $= 1$, $P < 0.0001$; CB: $H_{1,233} = 24.46$, $P < 0.0001$).

This decrease was also significant in other prey types such as insectivores and reptiles (FO: $G = 9.8$, d.f. $= 1$, $P < 0.01$ and $\chi^2_{Yates} = 5.8$, d.f. $= 1$, $P < 0.05$, respectively, and for CB: $H_{1,233} = 11.205$, $P < 0.001$; $H_{1,233} = 5.95$, $P < 0.05$, respectively). Conversely, the contribution of birds and arthropods does not significantly differ between areas with and without rabbits (FO: $\chi^2_{Yates} = 0.897$, d.f. $= 1$, $P = 0.344$; and FO: $\chi^2_{Yates} = 0.495$, d.f. $= 1$, $P = 0.48$, respectively).

Comparison in Mediterranean vegetation areas with and without rabbits

To rule out the possibility that habitat effects were responsible for differences in diet and to be sure that the differences were the result of the presence or absence of rabbits, the frequency of occurrence of rodents and rabbits

in a data subset were compared only in Mediterranean vegetation areas. Non-significant results in this analysis would imply that differences observed in diet composition between areas with and without rabbits were the result of habitat effects rather than the presence of rabbits, but significant results would confirm that diet shift is solely owing to rabbit presence.

Rodents showed a significant decrease in their FO in the Mediterranean vegetation areas where rabbits are available (FO: $G = 48.2$, d.f. $= 1$, $P = 0.0001$; CB: $H_{1,171} = 24.69$, $P < 0.0001$; see Fig. 3), thus implying that habitat effects were not responsible for the shift in wildcat diet.

Likewise, other secondary species such as insectivores, birds, reptiles or arthropods did not show statistical differences between Mediterranean vegetation areas with and without rabbits (FO: $G = 0.33$, d.f. $= 1$, $P = 0.56$; $G = 0.15$, d.f. $= 1$, $P = 0.69$; $G = 2.63$, d.f. $= 1$, $P = 0.10$ and $G = 3.29$, d.f. $= 1$, $P = 0.07$, respectively).

The principal taxa responsible for the increase of rodents in the diet of wildcats in areas without rabbits were *Microtus arvalis* and *Apodemus sylvaticus* (FO: $G = 44.9$, d.f. $= 1$, $P < 0.0001$ and $G = 4.1$, d.f. $= 1$, $P < 0.05$, respectively).

Comparison between Mediterranean vegetation areas without rabbits and Pyrenean oak forest to test for habitat effects

In the absence of rabbits, wildcats eat more rodents in Mediterranean vegetation areas than in the Pyrenean oak forests (FO: 97% *vs* 77%, $G = 9.32$, d.f. $= 1$, $P < 0.01$; CB: $H_{1,99} = 1.81$, $P = 0.17$).

In the Pyrenean oak forests, there was an increase in the consumption of other secondary prey, such as reptiles (FO: $\chi^2_{Yates} = 6.40$, d.f. $= 1$, $P < 0.05$; CB: $H_{1,99} = 8.77$; $P < 0.01$), insectivores (FO: $\chi^2_{Yates} = 8.03$, d.f. $= 1$, $P < 0.01$; CB: $H_{1,99} = 7.14$; $P < 0.01$), and arthropods ($G = 10.34$,
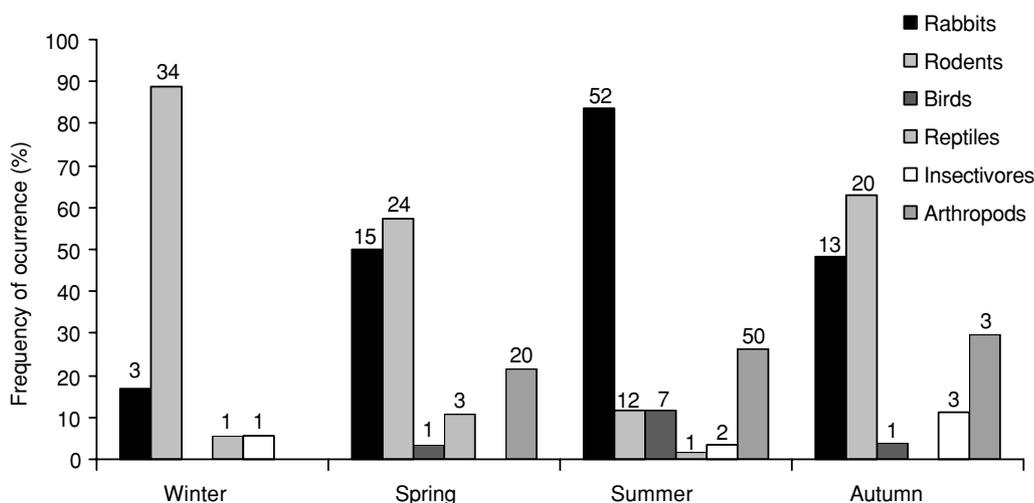

Fig. 3. Frequency of occurrence of wildcat *Felis silvestris* prey across seasons in areas with rabbits *Oryctolagus cuniculus*. Prey item number per group is shown.
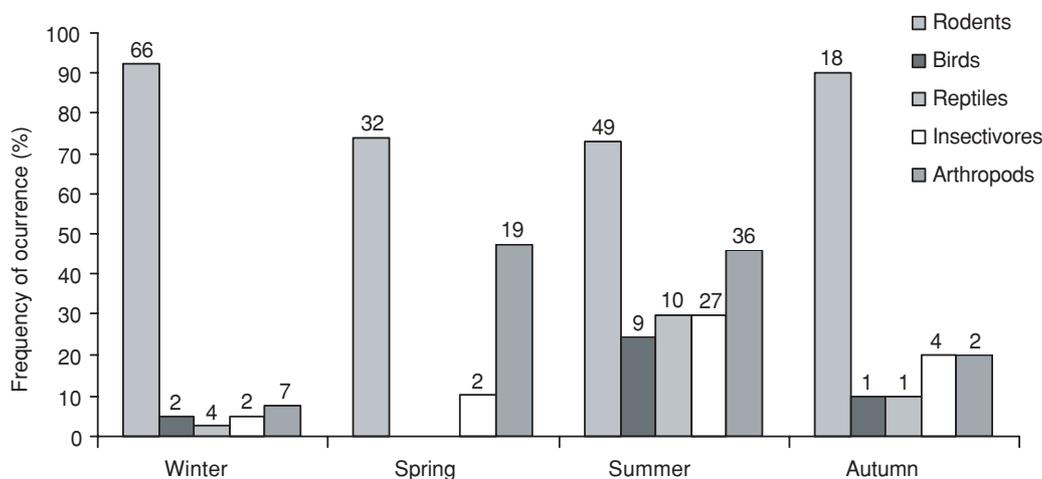
Fig. 4. Frequency of occurrence of wildcat *Felis silvestris* prey across seasons in areas without rabbits *Oryctolagus cuniculus*. Prey item number per group is shown.

d.f. $= 1$, $P < 0.01$). The increase in insectivores was the result of the greater consumption of white-toothed shrew *Crocidura russula* (16% in Pyrenean oak forest *vs* 4% in Mediterranean vegetation areas; $\chi^2_{Yates} = 8.10$, d.f. $= 1$, $P < 0.01$) and Iberian blind mole *Talpa occidentalis* (16% in Pyrenean oak forest *vs* 0% in Mediterranean vegetation areas; $\chi^2_{Yates} = 5.29$, d.f. $= 1$, $P < 0.05$).

Remains from two Iberian hares *Lepus granatensis*, a non-identified ungulate and a cat's claw were found in scats from the Pyrenean oak forest.

Diet seasonality in areas with and without rabbits

The consumption of rabbits showed seasonal variation (Fig. 3) in areas where it was present (FO: $G = 33.01$, d.f. $= 3$, $P < 0.0001$; CB: $H_{3,239} = 27.15$; $P < 0.0001$), with a maximum FO value in summer (83.61%) and minimum in winter (16.67%), showing the same value for autumn and spring (50%). In these areas, the consumption of rodents also showed seasonal differences (FO: $G = 52.27$, d.f. $= 3$, $P < 0.0001$) but following the inverse pattern, with a maximum in winter (88.89%) and a minimum in summer (11.48%). Nevertheless, in areas without rabbits, the consumption of rodents was constant throughout the year (FO: $G = 6.56$, d.f. $= 3$, $P = 0.087$; Fig. 4), with a FO value of *c*. 82%.

In areas with rabbits, there were also seasonal fluctuations in the consumption of arthropods (FO: $G = 10.39$, d.f. $= 3$, $P < 0.05$), being zero in winter and maximum in autumn and summer (FO: 29.63% and 26.23%, respectively). The other prey for areas with rabbits did not show seasonality in FO, which was under 12% in all cases; in insectivores (FO: $G = 4.83$, d.f. $= 3$, $P = 0.184$) mean consumption is equal to FO 4.98%; reptiles (FO: $G = 5.69$, d.f. $= 3$, $P = 0.127$) mean consumption of FO 4.48% and birds (FO: $G = 5.34$, d.f. $= 3$, $P = 0.148$) mean consumption of the FO 4.69%.

In areas without rabbits (Fig. 4), all prey groups except rodents showed significant differences in their FO across seasons. Insectivores were consumed more in summer (FO: 29.73%) and less in winter (FO: 5.13%, $G = 9.38$, d.f. $= 3$, $P < 0.05$). Reptiles also showed this pattern (FO: summer, 29.73% and winter 2.56%: $G = 17.79$, d.f. $= 3$, $P < 0.001$) but were not present in spring. Arthropod consumption was higher in spring (FO: 47.37%) and summer (FO: 45.95%) and lower in winter (FO: 7.69%, ($G = 18.92$, d.f. $= 3$, $P < 0.001$). Birds showed a similar pattern to reptiles, being consumed more in summer (FO: 24.32%, $G = 11.29$, d.f. $= 3$, $P < 0.05$).

DISCUSSION

General foraging theory considers a certain species to be a trophic specialist when it invariably exploits a certain resource regardless of its availability or the presence and/or availability of other potential resources (Glasser, 1982, Stephens & Krebs, 1986). Therefore, significant variations in diet composition among populations or seasons would not be expected from a trophic specialist species.

This study shows, that: (1) overall diet diversity of wildcats increases more than twofold in summer with respect to winter, which seriously challenges the view of wildcats as trophic specialists; (2) overall diet diversity decreases in areas where rabbits are present; (3) in areas where rabbits are available, wildcats shift their diet from rodents to rabbits; (4) in the absence of rabbits and where rodent richness and abundance is low, wildcats shift their diet towards other prey groups.

Therefore, these results dismiss the rodent specialist hypothesis showing that wildcats cannot be considered rodent specialized predators. Wildcats are more likely to be facultative specialists in rabbits where these are present or when both prey types present spatial overlapping (most frequently), and in rodents where there are no rabbits. A similar suggestion has been recently made by Moleón &

Gil-Sánchez (2003), who indicated that voles and mice, the main prey items in the high mountain of southern Spain, are less important in areas where rabbits are abundant (Gil-Sánchez *et al*., 1999). Moreover, in scenarios with low prey availability, such as Pyrenean oak forests (Castells & Mayo, 1993), wildcats behave like typical generalist species (Pyke *et al*., 1977; Lea, 1981; Glasser, 1984; Krebs & McCleery, 1984).

Rabbits could be considered an optimal prey type for wildcats in energetic terms. In theory, for a predator like a wildcat weighing 4–5 kg (Stahl & Leger, 1992), a daily food intake of *c*. 1000 g would be optimal (Carbone *et al*., 1999), thus two to three adult rabbits or four juveniles should be enough to fulfil its energetic needs. Alternatively, wildcats would need about 30 small rodents daily to fulfil their energetic requirements. Catchability is also a key parameter in prey selection (Stephens & Krebs, 1986). Although rodent capture may generally be less demanding than rabbit capture, the fact that rabbits are affected by myxomatosis or RHD viruses might facilitate the task for wildcats. The large consumption of rabbits made by wildcats and domestic cats around the world (Corbett, 1979; Sunquist & Sunquist, 2002) indicates that wildcats are behaviourally well able to catch rabbits. Under this scenario of high energetic profitability and low costs of catchability it is not surprising that rabbits may be considered as the key resource of wildcats when they are present.

Even though we have not controlled for rabbit abundance, only for its presence or absence, seasonal rabbit abundance in Mediterranean areas is well known (Blanco, 1998), and the diet of wildcats in our study shows the seasonal fluctuations in abundance of the different prey groups. In particular, in summer, rabbit availability is maximum for wildcats given the recruitment of inexperienced young rabbits and the increased vulnerability of adult ones affected by myxoma virus (Blanco, 1998), so in this season they are the staple prey. However, as the availability of rabbits decreases, wildcats consume more rodents, showing a maximum in winter, when chasing rabbits is more difficult. The seasonal variation in the feeding behaviour of wildcats is an alternative support to the facultative trophic characterization of the species (Glasser, 1982).

In our study area, ungulates do not have such an important contribution (one scat out of 239) to wildcat diet as in other regions from the south of Spain (Moleón & Gil-Sánchez, 2003). However, these results show that wildcats might be an exception to the fact that species from the order *Carnivora* with a weight < 21.5 kg can only hunt prey as large as 45% of their body weight (Carbone *et al*., 1999), as this would mean that the diet of a 'standard' wildcat weighing *c*. 4250 g would be restricted to small vertebrates with a maximum weight of 1900 g.

Surprisingly, in Pyrenean oak forests we also found cat remains. A case of genet and stone marten superpredation has already been reported (Moleón & Gil-Sánchez, 2003) but, to our knowledge, this is the first case of superpredation or cannibalism (depending on whether the remains were from a domestic or from a wildcat, respectively),

reported in literature (for a review see Palomares & Caro, 1999).

In conclusion, and overall, we have shown that wildcats do not behave like trophic specialists in rodents, but like opportunistic predators that feed upon small animals according to their availability, with a strong tendency to specialize facultatively in rabbits when these are present in the home range of wildcats. Thus, the diet variations reported at a regional scale in our study demonstrate the trophic generalist behaviour of a species which adapts to time–space variation in prey availability.

Acknowledgements

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