Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula

Francisco DÍAZ-RUIZ* *Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM), Ronda de Toledo, s/n, 13071 Ciudad Real, Spain. E-mail: pacodi1480@hotmail.com*
Miguel DELIBES-MATEOS *Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM), Ronda de Toledo, s/n, 13071 Ciudad Real, Spain. E-mail: miguel.delibes@uclm.es*
José Luis GARCÍA-MORENO *Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM), Ronda de Toledo, s/n, 13071 Ciudad Real, Spain. E-mail: joselgmm@hotmail.com*
José María LÓPEZ-MARTÍN *Dirección General del Medio Natural y Biodiversidad. Generalitat de Catalunya, Dr Roux 80, 08017 Barcelona, Spain. E-mail: josep.lopez@gencat.cat*
Catarina FERREIRA *Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM), Ronda de Toledo, s/n, 13071 Ciudad Real, Spain, and CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos (Universidade do Porto), Campus Agrário de Vairão, 4485-661 Vairão, Portugal. E-mail: catferreira@gmail.com*
Pablo FERRERAS *Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM), Ronda de Toledo, s/n, 13071 Ciudad Real, Spain. E-mail: Pablo.Ferreras@uclm.es*

Keywords
carnivore, feeding patterns, generalist predator, Portugal, Spain

*Correspondence author.

Submitted: 6 June 2011
Returned for revision: 4 August 2011
Revision accepted: 3 October 2011
Editor: KH

doi:10.1111/j.1365-2907.2011.00206.x

ABSTRACT

1. Biogeographical diversity is central to the trophic ecology of predators. Understanding the biogeographical trophic patterns of generalist predators, such as the red fox *Vulpes vulpes*, is particularly challenging because of their wide distributions, broad trophic spectra and high ecological plasticity, which often generate conflicts with humans.
2. We reviewed 55 studies from the Iberian Peninsula concerning the diet of the red fox to describe its trophic patterns from a biogeographical perspective.
3. We considered the frequency of occurrence of seven food groups and characterized each study site according to environmental variables. We tested relationships between geographical variables and each food group independently, and assessed the consumption of lagomorphs in relation to the other food groups. We also tested the relationships between trophic diversity, the main food groups, latitude and altitude, and finally investigated changes in the consumption of all food groups in relation to habitat type and seasonality.
4. We found a latitudinal pattern in the diet of the red fox, which was characterized by a greater consumption of lagomorphs and invertebrates in southern areas, and a higher intake of small mammals and fruits/seeds in northern regions. Additionally, the consumption of invertebrates increased from east to west, while fruit/seed consumption increased from west to east. Consumption of lagomorphs decreased, and of small mammals increased, with altitude. Trophic diversity was not associated with geographical variables. The intake of lagomorphs and small mammals was greatest in Mediterranean scrub and forest, respectively. Reptiles and invertebrates were consumed mostly during summer; fruits/seeds in autumn.
5. Iberian red foxes show variation in their feeding habits associated with environmental variables, which are in turn associated with the availability of their main prey. Foxes select rabbits where they are abundant, and feed on small mammals and fruits/seeds where lagomorphs are scarce.

INTRODUCTION

Feeding habits have been one of the most studied features of carnivore ecology. The traditional approach to studies of carnivore diets is to investigate the feeding habits of species (mainly in terms of diet composition) at local or regional scales (e.g. Brand et al. 1976, Zapata et al. 2007, Wang & Macdonald 2009). Comprehensive studies of carnivore trophic ecology at broader geographical scales have only recently been undertaken (e.g. Clavero et al. 2003, Lozano et al. 2006, Zhou et al. 2011). The study of trophic biogeographical patterns of predators is fundamental to understanding their ecology and life history strategies (Daan & Tinbergen 1997). For instance, defining a species as a trophic generalist or specialist is only relevant in the context of extensive ecological studies in which variation in feeding behaviour among populations over a broad range of environmental conditions is considered (Lozano et al. 2006). Investigations of the diet of medium-sized carnivores at large biogeographical scales have included studies of the Eurasian badger *Meles meles* (Roper & Mickevicius 1995, Goszczynski et al. 2000, Hounsome & Delahay 2005); the polecat *Mustela putorius* (Lodé 1997); the common genet *Genetta genetta* (Virgós et al. 1999); the Eurasian otter *Lutra lutra* (Clavero et al. 2003); the European wildcat *Felis silvestris* (Lozano et al. 2006); and the Holarctic martens, *Martes* sp. (Zhou et al. 2011). Surprisingly, this type of study is lacking for the red fox *Vulpes vulpes*, which is the world's most widespread member of the order Carnivora (Sillero-Zubiri et al. 2004) and one of the most abundant carnivore species in the Iberian Peninsula (Blanco 1998, Palomo et al. 2007) and elsewhere.

Environmental and climatic conditions affect food availability, and can have an impact on dietary composition and diversity (Hill & Dunbar 2002). Thus, variations in the distribution of potential prey species across biogeographical regions have been postulated to affect the feeding habits of medium-sized carnivores. For instance, dietary diversity in wildcats increases at lower latitudes (i.e. Mediterranean areas; Lozano et al. 2006), where potential prey richness is greater (Rosenzweig 1995). Latitudinal gradients have also been observed in relation to dietary diversity and in the consumption of particular prey. For example, the Eurasian otter's diet is more diverse in southern localities, while further north the species is more piscivorous, predating upon a large diversity of fish families (Clavero et al. 2003). Similarly, food availability can vary along altitudinal gradients, and this can affect the dietary composition of carnivores. For instance, small mammals (mice, voles and shrews) are the primary food of martens, but are less frequently consumed at lower altitudes, where other food resources are more abundant and are available throughout the year (Zhou et al. 2011).

Diet is one of the most studied aspects of the ecology of the red fox. Most studies indicate that the red fox is a generalist predator that uses resources according to their availability and hence is opportunistic in its behaviour (e.g. Webbon et al. 2006, Dell'Arte et al. 2007). However, most studies were undertaken at local or regional scales, and specific studies describing biogeographical patterns in the red fox diet are lacking. Although some studies have shown variations in the feeding habits of foxes based on environmental variables including habitat type (Fedriani 1996, Gortázar 1999), the effects of latitude, longitude and altitude on the composition of fox diets at a larger scale remain unknown. Similarly, there is a lack of information about how the consumption by foxes of some preferred prey, such as lagomorphs or small mammals, varies spatially at biogeographical scales.

The ecological features of red foxes can bring them into conflict with human activities where their prey is of economic or conservation concern (Baker & Harris 2003). For example, predation by foxes is often regarded as one of the factors preventing the recovery of small game (Reynolds & Tapper 1995, Smedshaug et al. 1999, Beja et al. 2009, Knauer et al. 2010), and farmers consider predation of livestock by foxes to cause economic losses (Moberly et al. 2004). Furthermore, several researchers have reported negative impacts of fox predation on species of conservation concern (Yanes & Suárez 1996, Ruiz-Olmo et al. 2003, Dickman 2010). However, predators, including generalists such as red foxes, play major roles in ecological processes by limiting populations of pest species (O'Mahony et al. 1999, Newsome et al. 2001), reducing the transmission of disease (Hudson et al. 1992, Millán et al. 2002) and acting as seed dispersers (Guitián & Munilla 2010, Rosalino et al. 2010). Our ability to understand biogeographical patterns is crucial for developing efficient management programs in the context of human usage (Whittaker et al. 2005). From this perspective, a large-scale study of the trophic ecology of the red fox could provide valuable knowledge concerning its ecosystem functions and improve management of this predator.

The Iberian Peninsula is included in the Mediterranean Basin hotspot (Myers et al. 2000) and is thereby an interesting site for the study of biogeographical patterns (e.g. Carvalho et al. 2011). It includes distinct Atlantic (Northern Iberia), Mediterranean (Central and Southern Iberia) and Alpine (Pyrenees mountains) biogeographical regions (Rivas-Martínez 1987; Fig. 1), and is characterized by high environmental heterogeneity because of its climatic and physiographical complexity (the altitude ranges from 0m at sea level to 3479m above sea level at Sierra Nevada, Granada, Spain). The variability in environmental conditions underpins the diversity in community composition and structure in this region (Blondel & Aronson 1999,

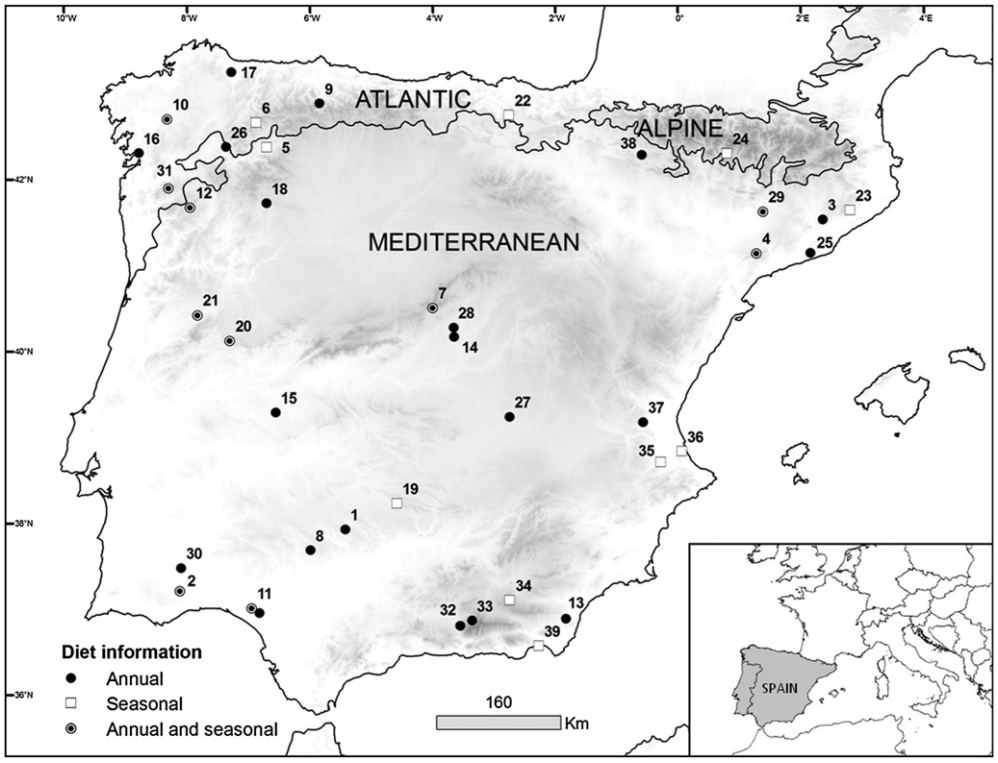

Fig. 1. Geographical distribution in the Iberian Peninsula of studies of the diet of the red fox *Vulpes vulpes* included in this review. Biogeographical regions are shown, and the numbers represent study site identifiers (ID; see Appendix S1).

Stefanescu et al. 2004). Several patterns in the distribution and abundance of the main prey species of Iberian predators have been described. For instance, wild rabbits *Oryctolagus cuniculus*, which are a key prey for red foxes and other Iberian predators (Delibes & Hiraldo 1981, Calzada 2000, Ferreras et al. 2011), are most abundant at central–southern latitudes (Villafuerte et al. 1998), and small mammals show a gradient in abundance and species richness from south to north (Soriguer et al. 2003). The theory of feeding specialization predicts an increase in dietary diversity when the preferred prey becomes scarce (Futuyma & Moreno 1988). In this study, we tested this prediction in relation to the red fox and rabbits as its preferred prey. Although the Iberian Peninsula is a relatively small biogeographical area, its high environmental variability and biodiversity justifies a biogeographical analysis of the diet of resident generalist carnivores such as the red fox.

Our main objective was to describe the trophic biogeographical patterns of the red fox in the Iberian Peninsula, based on a comprehensive literature review. Specifically, we: (i) evaluated changes in consumption by red foxes of main food groups in relation to geographical variables (latitude, longitude and altitude); (ii) analysed the relationships between red fox dietary diversity, consumption of its main prey and geographical variables; (iii) assessed the relationships between the consumption of different food groups and habitat type and season; and (iv) interpreted patterns in the diet of this generalist predator from a biogeographical perspective.

METHODS

Literature compilation and standardization of dietary data

Various sources of information were used to review the available literature comprehensively, as recommended by Pullin and Stewart (2006). Search engines (ISI Web of Science and Google Scholar) were used to identify relevant scientific studies containing information about the trophic ecology of the red fox in the Iberian Peninsula. We searched for terms that were identified using the following combinations of keywords: 'red fox' or '*Vulpes vulpes*' and 'diet' or 'feeding' and 'Iberian Peninsula', 'Spain' or 'Portugal'. We consulted several zoological bibliographical data bases including the Zoological Record (http://scientific.thomson.com/products/zr/) and the bibliographical data set of the Spanish Society for the Conservation and Study of Mammals (http://www.secem.es/Secem_la_biblioteca.htm). We also sought information on the topic from informal

contacts with expert researchers (colleagues working in different institutions – universities and environmental public administration – in Spain and Portugal). This provided us with less readily accessible sources of information, including unpublished or unedited studies (e.g. PhD theses, MSc and BSc dissertations, and public administration data bases).

We compiled a total of 55 published and unpublished studies concerning the diet of the red fox in Portugal and Spain, spanning the period 1971–2008. Some authors reported data pooled annually, others reported data pooled seasonally, and several provided both annual and seasonal data. To simplify the statistical procedures, two independent data bases were created for analysis: one comprising annual data and the other seasonal data. These data bases were analysed independently (see Statistical analyses).

To standardize data from different geographical areas (for later comparison and analysis), we excluded studies: (i) with small sample sizes (scat or stomachs; $n < 30$ for annual studies and $n < 15$ for seasonal studies); (ii) reporting data for only one prey group; (iii) containing duplicated information, e.g. academic dissertations later published as scientific articles; and (iv) reporting only relative frequency of occurrence (RF, expressed as the percentage of times one food item occurs in relation to the total times all food items occur) or percentage biomass. This last exclusion meant that we only considered studies reporting the frequency of occurrence (FO, expressed as the percentage of scats/stomachs containing a particular food item) for the various food groups. RF values are considered to be highly suitable for inter-population comparisons in diet studies (Clavero et al. 2003), and biomass is considered a direct measure of the energetic value of prey items consumed (Reynolds & Aebischer 1991), and therefore the best approximation to the true diet (Klare et al. 2011). However, only a small proportion of the reviewed studies presented RF or biomass information, while FO is widely used in carnivore diet studies and was used in most of the red fox studies considered in this review. Moreover, FO can be used to assess whether a predator behaves as an opportunist or as a specialist forager (Klare et al. 2011), and it is considered a valid parameter for comparative purposes (Reynolds & Aebischer 1991, Klare et al. 2011).

The application of the four exclusion criteria above resulted in a final set of 37 studies that were further analysed to describe red fox feeding patterns in the Iberian Peninsula. These studies were carried out in 39 locations distributed throughout the region (Fig. 1; for more detailed information, see Appendices S1, S2 and S3). The data were highly heterogeneous among the variables, which reflected the diversity of environmental conditions in the Iberian Peninsula. For example, a broad altitudinal range (20–1425m) was included, and various habitat types were represented, including several types of Mediterranean scrub, agricultural lands, *dehesas* (savannah-like formations that combine pastures with intermittent cereal cultivation in park-like oak woodlands; Blondel & Aronson 1999) and forests containing various tree species (e.g. *Pinus* sp. and *Quercus pyrenaica*).

Variable selection

From each study we derived the following parameters: respective geographical variables (latitude and longitude, in degrees; and altitude, in metres) either from the study itself or, if they were not provided in the study, from Google Earth (http://earth.google.com); the source of food materials analysed (scats or stomach contents); and the sample size, study duration, season, habitat, and FO of each food group (see Appendices S1 and S2). We categorized dietary items into the following main groups: lagomorphs (mainly European wild rabbits; see Results), small mammals (rodents and insectivores), birds, reptiles, invertebrates, fruits/seeds, and carrion/garbage (mainly large mammals and leftover food of anthropogenic origin). Four seasons were considered: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). The habitat type at each location was categorized as Mediterranean scrub, forest or agricultural–dehesa (agricultural land and dehesas), according to the descriptions given in each study. We calculated Herrera's trophic diversity index (D; Herrera 1976) from the FO data as an index of the trophic diversity for each diet. The index is computed according to the formula $D = -\sum_{i=1}^{s} \log p_i$, where p is the frequency of occurrence of the various prey categories (i). This index is recommended for presence–absence food data, because other diversity indices such as the Shannon index cannot be calculated from this type of data (Herrera 1976).

Statistical analyses

To test for bias caused by the study duration, sample size or source of analysed food material (scats or stomach contents; Putman 1984), we followed the approach of earlier authors (Lozano et al. 2006, Zhou et al. 2011) and used multivariate analysis of covariance with the study duration and sample size as covariates, food material as a fixed factor and the FO of each of the seven food groups as response variables.

To avoid temporal pseudo-replication, we considered only those studies in which annual information on the Iberian fox diet was provided: 30 studies and localities, including a total of 9459 samples (stomachs and scats; see Appendix S1 and S2). Therefore, analyses of the relationship of the consumption of various food groups to geographical variables and habitat type were performed using the annual data base. The testing of seasonal variation was based only on those studies in which seasonal data were reported: 18

studies and 20 localities, including a total of 5027 samples (stomachs and scats; see Appendices S1 and S2).

The relationships between geographical variables (latitude, longitude and altitude) and the FO of each food group were tested using simple regression analyses. In view of the potential importance of wild rabbits in the diet of red foxes, we used a simple regression analysis to investigate the relationships between the lagomorph FO (mainly wild rabbits; see Results) and the FO of other food groups. To evaluate whether trophic specialization occurred in Iberian red foxes, we tested the relationships between diet diversity (Herrera D index) and the FO of each of the four main food groups (lagomorphs, small mammals, invertebrates and fruits/seeds) using data from annual studies. We applied general linear models (GLMs) using a normal distribution for errors of the response variable (Herrera D index) and an identity link function. One-way analysis of variance was used to test the effect of habitat type on the FO of each food group. We assessed seasonal variations in the diet by performing separate one-way analyses of variance with the FO of each food group as a dependent variable. We conducted Tukey's post-hoc tests to assess differences between pairs of habitat types and seasons.

Prior to statistical analyses, the FO for each food group and the Herrera D index values (dependent variables) were arc sine and log transformed, respectively, to achieve normality (Zar 1984), which was assessed visually from normal probability plots. All statistical analyses were performed using Statistica 6.0 software (StatSoft 2001).

RESULTS

We found no significant effect of study duration ($F_{7,26} = 0.86$, $P = 0.55$), sample size ($F_{7,26} = 0.73$, $P = 0.64$), source of analysed food material (scats or stomach contents; $F_{7,26} = 0.43$, $P = 0.11$) or the interaction between sample size and food material ($F_{7,26} = 1.04$, $P = 0.42$) on the FO of food groups in the diet. Thus, for further analyses we pooled data from studies with differing durations, sample sizes and sources of analysed food material.

Overall diet

Iberian red foxes consume a wide range of food items. Invertebrates were the most frequent food group in their diet (mean FO ± SD, 40.1 ± 25.5%), followed by fruits/seeds (38.9 ± 22.0%), small mammals (34 ± 20.9%), lagomorphs (20.6 ± 22.0%), carrion/garbage (15.3 ± 14.2%), birds (13.4 ± 15.3%) and reptiles (1.8 ± 2.8%).

Coleoptera and Orthoptera species were the most common among the invertebrates, and both wild and cultivated fruits were included among the fruits/seeds consumed. The most common small mammal prey was *Apodemus sylvaticus*, followed by *Microtus* spp., *Crocidura* spp. and *Eliomys quercinus*. Wild rabbit was the dominant species among the lagomorphs, while hares *Lepus* spp. were rare in the red fox diet (only identified in 6 of the 27 studies that recorded lagomorphs; FO = 1.2 ± 0.43%). For this reason, we will use indistinctly 'rabbits' and 'lagomorphs' from now on in the text. The large mammals reported as fox food items included *Cervus elaphus*, *Dama dama*, *Sus scrofa*, *Bos taurus*, *Ovis aries* and *Capra hircus*, and were presumably consumed as carrion. Among birds in the fox diet, the most common species consumed were *Columba* spp., *Alectoris rufa*, *Galerida* spp. and *Anas* spp. Several reptile species were consumed, including *Psammodromus* spp., *Malpolon monspessulanus* and *Elaphe scalaris*.

Geographical patterns (latitude, longitude and altitude)

We found a negative and statistically significant relationship between latitude and the FO of lagomorphs ($R^2 = 0.19$, $F_{1,35} = 8.47$, $P = 0.006$; Fig. 2a) and invertebrates ($R^2 = 0.11$, $F_{1,35} = 4.37$, $P = 0.04$; Fig. 2b), and a positive and significant relationship between latitude and the FO of small mammals ($R^2 = 0.16$, $F_{1,35} = 6.78$, $P = 0.01$; Fig. 2c) and fruits/seeds ($R^2 = 0.12$, $F_{1,35} = 5.04$, $P = 0.03$; Fig. 2d). Therefore, at lower latitudes, lagomorphs and invertebrates were more frequently eaten, while at higher latitudes small mammals and fruits/seeds were more commonly consumed.

Only the FO of invertebrates and fruits/seeds were significantly related to longitude. The consumption of invertebrates increased towards the east ($R^2 = 0.12$, $F_{1,35} = 4.95$, $P = 0.03$), whereas that of fruits/seeds increased towards the west ($R^2 = 0.16$, $F_{1,35} = 6.99$, $P = 0.01$).

Altitude was significantly and negatively associated with the FO of lagomorphs ($R^2 = 0.29$, $F_{1,30} = 12.67$, $P = 0.001$; Fig. 3a), and positively associated with that of small mammals ($R^2 = 0.27$, $F_{1,30} = 11.31$, $P = 0.002$, Fig. 3b). Thus, the consumption of lagomorphs decreased with altitude, and that of small mammals increased.

Is the red fox specialized on rabbits in the Iberian Peninsula?

The consumption of wild rabbits (represented by lagomorphs) was significantly and negatively related to the consumption of both small mammals ($R^2 = 0.15$, $F_{1,35} = 6.23$, $P = 0.02$) and fruits/seeds ($R^2 = 0.17$, $F_{1,35} = 8.41$; $P = 0.006$). The GLM results suggest that diet diversity was not significantly associated with latitude ($F_{1,25} = 0.33$, $P > 0.5$), altitude ($F_{1,25} = 0.552$, $P > 0.4$) or the FO of the four main food groups (lagomorphs: $F_{1,25} = 0.126$, $P > 0.7$; small mammals: $F_{1,25} = 0.004$, $P > 0.9$; invertebrates: $F_{1,25} = 0.253$, $P > 0.6$; and fruits/seeds: $F_{1,25} = 0.196$, $P > 0.6$).

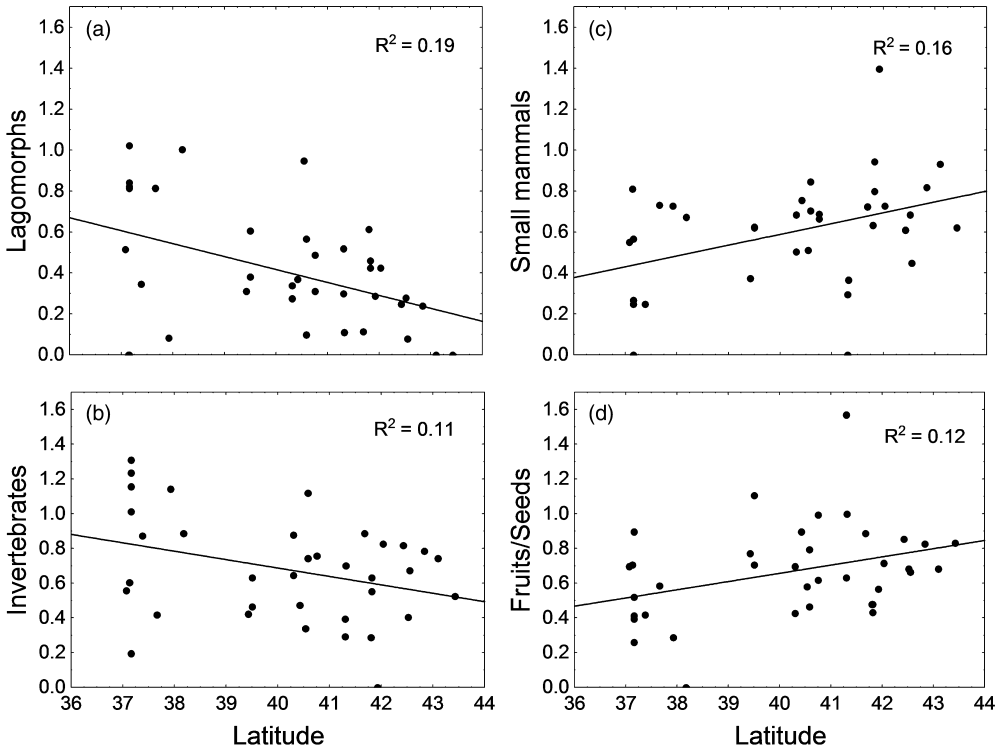

Fig. 2. Relationships between latitude and the frequency of occurrence (FO; arc sine transformed) of (a) lagomorphs (b) invertebrates (c) small mammals and (d) fruits/seeds in the diet of the red fox. Each point represents one study site (see Fig. 1).

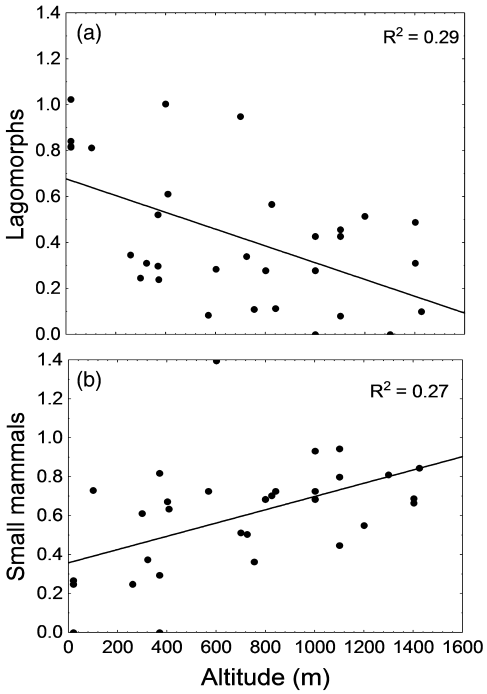

Fig. 3. Relationships between altitude (in metres) and the frequency of occurrence (FO; arc sine transformed) of (a) lagomorphs and (b) small mammals in the diet of the red fox. Each point represents one study site (see Fig. 1).

Habitat type and seasonality

We found a significant relationship between habitat type and the FO of lagomorphs ($F_{2,21} = 8.10$, $P = 0.002$) and small mammals ($F_{2,20} = 4.05$, $P = 0.03$) in red fox diet. The FO of lagomorphs was higher in Mediterranean scrub than in forest (Fig. 4a), but the opposite was observed for small mammals (Fig. 4b).

A significant seasonal relationship in the red fox diet was found for reptiles ($F_{3,53} = 3.34$, $P = 0.02$), invertebrates ($F_{3,53} = 9.45$, $P < 0.0001$) and fruits/seeds ($F_{3,53} = 11.49$, $P < 0.0001$). The FO of reptiles increased from winter to summer (Fig. 5a); invertebrates were mostly consumed in summer, and their occurrence in the diet was lowest in winter (Fig. 5b); and fruits/seeds were consumed most in autumn and least in spring (Fig. 5c). Marginally significant differences were found for lagomorphs ($F_{3,53} = 2.40$, $P = 0.07$), which were consumed most in summer (Fig. 5d).

DISCUSSION

Biogeographical variations in the diet of the red fox in Iberia

Generalist predators feed on different food resources according to their abundance and availability (Futuyma &

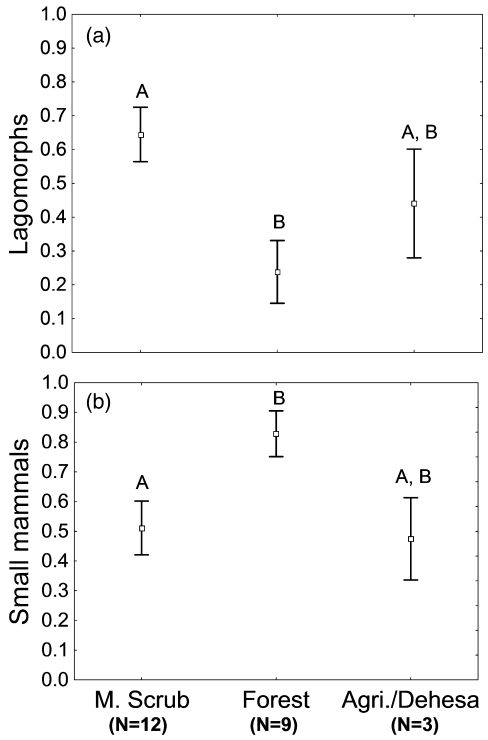

Fig. 4. Frequency of occurrence (FO; arc sine transformed; means ± SE) of (a) lagomorphs and (b) small mammals in the diet of the red fox as a function of habitat type. Means marked with the same letter are not significantly different from one another ($P < 0.05$; Tukey's post-hoc test). M. scrub, Mediterranean scrub; Agri., agricultural lands.

Moreno 1988). This study confirms that the red fox is a generalist predator; its trophic patterns can be explained by geographical variables, habitat type and seasonality. These factors determine directly the abundance and availability of its main foods [e.g. wild rabbits are more abundant at southern latitudes (Villafuerte et al. 1998) and in Mediterranean scrubland habitats (Calvete et al. 2004); small mammals are more abundant at northern latitudes (Soriguer et al. 2003) and in forest habitats (Torre et al. 2002)]. Latitude influences the feeding patterns of many medium-sized carnivores (Clavero et al. 2003, Hounsome & Delahay 2005, Lozano et al. 2006, Zhou et al. 2011). Some researchers relate dietary patterns in the abundance and diversity of prey species with the latitudinal gradient described in Eurasia, which increases towards the south (Pianka 1966, Blondel & Aronson 1999). Our results are consistent with these findings as we observed a latitudinal gradient in the consumption of lagomorphs, invertebrates, small mammals and fruits/seeds by red foxes.

The increase in the consumption of lagomorphs, mainly wild rabbits, towards southern Iberia is a consequence of the greater abundance of this prey at these latitudes (Villafuerte et al. 1998). The same pattern in rabbit intake has been shown for other medium-sized Iberian carnivores including the wildcat (Lozano et al. 2006), the badger (Virgós et al. 2005, Barea-Azcón et al. 2010) and the polecat (Santos et al. 2009). This feeding pattern could explain the negative latitudinal gradient found in the body size of Iberian red foxes, which contradicts Bergmann's Rule (Yom-Tov et al. 2007). The high occurrence of invertebrates in the red fox diet in southern regions may be explained by the greater availability of this food type at low latitudes (Chapman 1998, Blondel & Aronson 1999) and is in agreement with studies of the diet of other medium-sized Iberian generalist carnivores including the genet (Virgós et al. 1999).

The positive relationship between latitude and small mammal consumption by Iberian red foxes corresponds to a south–north gradient in the abundance and species richness of this prey group (Blanco 1998, Soriguer et al. 2003). The decrease in rabbit abundance in northern regions of the Iberian Peninsula also promotes the switch to small mammals as the main prey in these areas. This pattern was also observed by Zhou et al. (2011) in Holarctic marten species at a larger biogeographical scale.

The consumption of fruits/seeds by the red fox is greater in northern regions than in southern regions. However, this pattern is opposite to that described for other Eurasian generalist carnivores, which decrease their consumption of plant matter and increase carnivory with increasing latitude (Virgós et al. 1999, Goszczynski et al. 2000, Vulla et al. 2009, Zhou et al. 2011). In some of these studies, this pattern is explained by a reduction in primary production with increasing latitude, but the narrow latitudinal range covered in the present study leads us to believe that the higher consumption of fruits/seeds is likely to be due to the greater availability of this resource in the north of the Iberian Peninsula.

The FO of invertebrates in the fox diet increases from east to west, while that of fruits/seeds increases from west to east. Rosalino and Santos-Reis (2009) were not able to explain a similar longitudinal gradient found in fruit/seed consumption by medium-sized carnivores in Iberia because of the absence of data on the availability of plant species producing fruits and seeds. Invertebrates are an alternative food source for some omnivorous species, especially larger carnivorous mammals, where larger prey items are not available (Capinera 2010). However, as there is currently no information on the availability of invertebrates over a longitudinal gradient in Iberia, we have no data to enable us to interpret our results.

The decrease in consumption of lagomorphs by foxes with increasing altitude could be because of the reduced presence and abundance of rabbits above 1000m (Blanco 1998, Palomo et al. 2007), but the consumption of small mammals by foxes increased in high altitude areas. This is in contrast with previous findings that the species richness and

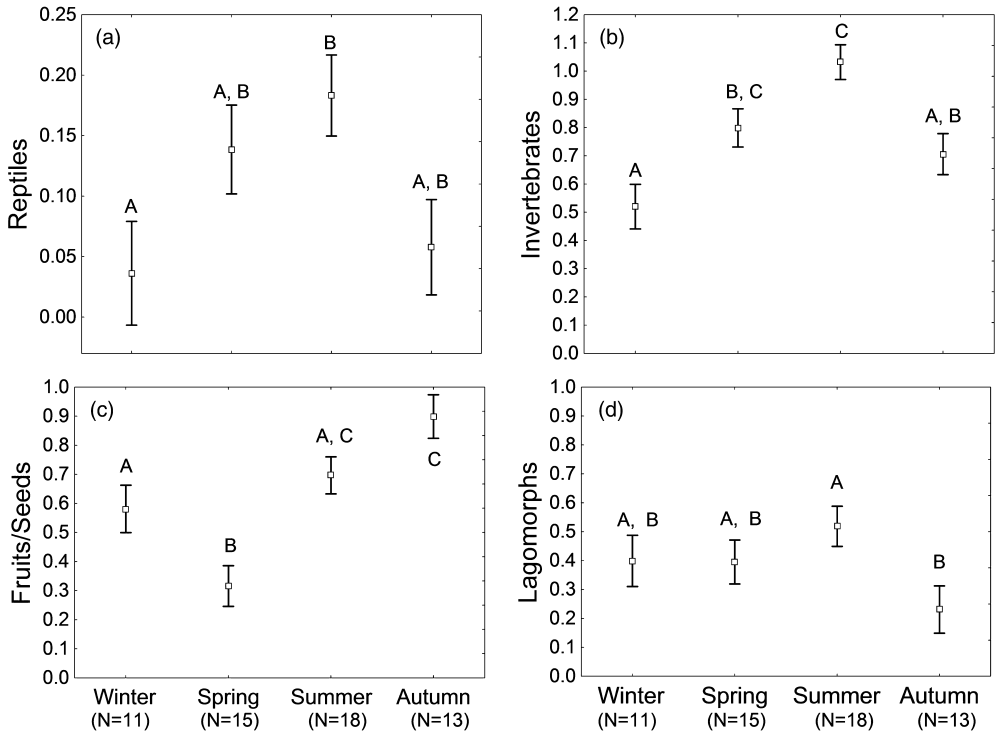

Fig. 5. Frequency of occurrence (FO; arc sine transformed; means ± SE) of (a) reptiles (b) invertebrates (c) fruits/seeds and (d) lagomorphs in the diet of the red fox, as a function of season (marginally non-significant for lagomorphs, $P = 0.07$). Means marked with the same letter are not significantly different from one another ($P < 0.05$; Tukey's post-hoc test).

abundance of small mammals decreases at higher altitudes (Torre 2004). However, the altitudinal range considered in this study (only three localities were higher than 1400m; see Appendix S1) did not include altitudes that may limit the presence of most small mammals consumed by the red fox (Palomo et al. 2007), which prevents us from confirming this trend in small mammal consumption. Thus, the increased intake of small mammals seems to be a functional response to the reduced availability of lagomorphs at higher altitudes, as Hartová-Nentvichová et al. (2010) found for red foxes in the mountains of the Czech Republic.

Is the red fox specialized on rabbits in the Iberian Peninsula?

A negative relationship between a given food group and dietary diversity is usually interpreted as indicating trophic specialization (Futuyma & Moreno 1988, Fedriani et al. 1998, Lozano et al. 2006). A negative relationship at a regional scale between lagomorph consumption and dietary diversity has been described for red foxes (Delibes-Mateos et al. 2008) and for other small and medium-sized Mediterranean carnivores (Sarmento 1996, Lozano et al. 2006, Santos et al. 2009). However, we did not find any significant relationship between dietary diversity and the consumption of lagomorphs or other prey, or geographical variables, perhaps because of the high trophic flexibility of the fox in the Iberian Peninsula. These results suggest that, at the scale of the peninsula, only small mammals and fruits/seeds are eaten by foxes as alternatives to lagomorphs. This confirms the opportunistic and generalist feeding behaviour of the red fox, as has consistently been reported for different geographical areas and at various scales (e.g. Kjellander & Nordstrom 2003, Dell'Arte et al. 2007).

Habitat type and seasonality

We observed a high intake of lagomorphs by red foxes in the Mediterranean scrubland, where wild rabbits reach higher densities (Fedriani 1996, Palomares 2001, Calvete et al. 2004). In contrast, Fedriani (1996) found no difference in consumption of wild rabbits by red foxes in adjacent areas of scrubland and dehesa habitat in Doñana (southwest Iberian Peninsula), despite higher rabbit density in the scrubland patches. This is probably a consequence of the larger scale considered in our review, where habitats were clearly differentiated between studies. The preference for forests shown by the small mammal species most frequently consumed by foxes (e.g. the wood mouse *Apodemus sylvaticus*; Torre et al. 2002), together with the low abundance of

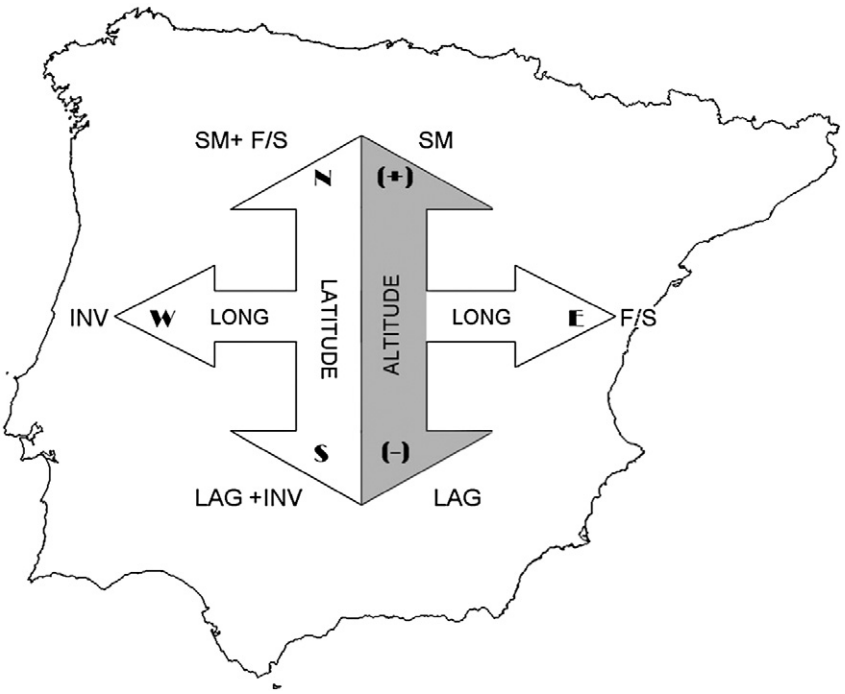

Fig. 6. Conceptual model illustrating the biogeographical patterns found in the consumption of the main food groups by the Iberian red fox, in relation to geographical variables (LAG, lagomorphs; SM, small mammals; F/S, fruits/seeds; INV, invertebrates). The white arrows represent latitudinal (LATITUDE) and longitudinal (LONG) gradients, and the grey arrow shows the altitudinal gradient (ALTITUDE).

rabbits in this type of habitat, explains why foxes include in their diet a greater proportion of small mammals in forests than in others habitats.

Several researchers have reported marked seasonality in the diet of the red fox (Dell'Arte et al. 2007, Hartová-Nentvichová et al. 2010). Mediterranean ecosystems have marked climatic seasonality, with hot dry summers and cold wet winters (Blondel & Aronson 1999); thus, some trophic resources for carnivores are only seasonally available (Virgós 2002). We also observed a marked seasonality in the diet of the red fox, which is a result of the seasonal availability of some food groups at the Iberian scale. Populations of Orthoptera and Coleoptera, the invertebrates most consumed in summer, increase dramatically during this season (Aranda et al. 1995, Loureiro et al. 2009). The availability of cultivated and wild fruits is greatest in summer and autumn (Loureiro et al. 2009), when they are most consumed by foxes. The annual abundance of wild rabbits in the Iberian Peninsula peaks in the spring–summer period (Soriguer 1981, Beltrán 1991). At this time the greater availability of juvenile rabbits and the susceptibility of the rabbit population to myxomatosis (Calvete et al. 2002) may make this prey more vulnerable to predation and consumption as carrion by foxes, so that rabbits may provide a valuable energy source for foxes during the highly critical breeding period. This explains the observed seasonal increase in the FO of lagomorphs from spring to summer (Fig. 5d). However, in areas where rabbits are very abundant, their availability is high throughout the year (Angulo & Villafuerte 2003), which could explain the lack of statistically significant differences between seasons in the FO of lagomorphs in the red fox diet.

CONCLUSIONS

Biogeographical variation in the feeding habits of Iberian red foxes are associated with geographical variables, habitat type and season, which affect the availability of alternative potential foods (Fig. 6). Our results confirm that the feeding habits of the red fox, a generalist predator, vary widely both spatially and temporally, even within a relatively small biogeographical area such as the Iberian Peninsula. Therefore, we demonstrate that the flexibility of this generalist predator really reflects the biogeographical patterns of distribution and abundance of its main food sources. Understanding these patterns in the feeding ecology of the red fox, the most abundant carnivore in the Iberian Peninsula, will facilitate the understanding of the geographical variations in its abundance and behaviour, and improve the management and conservation of this species.

ACKNOWLEDGEMENTS

We are especially grateful to Drs P. C. Alves and C. Gortázar for providing unpublished data to be included in this review. We thank also Drs. Jennings and Hackländer, and two anonymous referees whose comments greatly improved the manuscript. M. Delibes-Mateos currently holds a Juan de la Cierva research contract awarded by the Ministerio de Ciencia e Innovación and the European Social Fund. C.

Ferreira was supported by a PhD grant (Ref. SFRH/BD/22084/2005) funded by the Fundação para a Ciência e Tecnologia of the Ministério da Ciência, Tecnologia e Ensino Superior, Portuguese government. Financial support for the study was provided by the Spanish MICINN Project CGL2009-10741 from Spanish Plan Nacional de I+D and FEDER funds.

REFERENCES

Angulo E, Villafuerte R (2003) Modelling hunting strategies for the conservation of wild rabbit populations. *Biological Conservation* 115: 291–301.

Aranda Y, Isern-Valberdú J, Pedrochi C (1995) Dieta estival del zorro *Vulpes vulpes* L. en pastos del Pirineo Aragonés: Relación con la abundancia de artrópodos. *Lucas Mallada* 7: 9–20.

Baker PJ, Harris S (2003) A review of the diet of foxes in rural Britain and a preliminary assessment of their impact as a predator. In: Tattersall F, Manly WM (eds) *Conservation and Conflict – Mammals and Farming in Britain*, 120–140. Linnean Society Occasional Publication No. 4, Westbury Publishing, Otley, UK.

Barea-Azcón JM, Ballesteros-Duperón E, Gil-Sánchez JM, Virgós E (2010) Badger *Meles meles* feeding ecology in dry Mediterranean environments of the southwest edge of its distribution range. *Acta Theriologica* 55: 45–52.

Beja P, Gordinho L, Reino L, Loureiro F, Santos-Reis M, Borralho R (2009) Predator abundance in relation to small game management in southern Portugal: conservation implications. *European Journal of Wildlife Research* 55: 227–238.

Beltrán JF (1991) Temporal abundance pattern of the wild rabbit in Doñana, SW Spain. *Mammalia* 55: 591–599.

Blanco JC (1998) *Mamíferos De España*, vol. I & II. Ed. Planeta, Barcelona, Spain.

Blondel J, Aronson J (1999) *Biology and Wildlife of the Mediterranean Region*. Oxford University Press, Oxford, UK.

Brand CJ, Keith LB, Fisher CA (1976) Lynx responses to changing snowshoe hare densities in central Alberta. *Journal of Wildlife Management* 40: 416–428.

Calvete C, Estrada R, Villafuerte R, Osacar JJ, Lucientes J (2002) Epidemiology of viral haemorrhagic disease (VHD) and myxomatosis in free-living population of wild rabbits. *Veterinary Record* 150: 776–782.

Calvete C, Estrada R, Angulo E, Cabezas-Ruíz S (2004) Habitat factors related to wild rabbit conservation in an agricultural landscape. *Landscape Ecology* 19: 531–542.

Calzada J (2000) *Impacto de la Depredación y Selección de Presa del Lince y el Zorro Sobre el Conejo*. PhD thesis, University of León, Spain.

Capinera JL (2010) *Insects and Wildlife: Arthropods and their Relationships with Wild Vertebrate Animals*. Wiley-Blackwell, Oxford, UK.

Carvalho JC, Cardoso P, Crespo LC, Henriques S, Carvalho R, Gomes P (2011) Biogeographic patterns of spiders in coastal dunes along a gradient of mediterraneity. *Biodiversity and Conservation* 4: 873–894.

Chapman RF (1998) *The Insects: Structure and Function*. Cambridge University Press, Cambridge, UK.

Clavero M, Prenda J, Delibes M (2003) Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats. *Journal of Biogeography* 30: 761–769.

Daan S, Tinbergen JM (1997) Adaptation of life histories. In: Krebs JR, Davies NB (eds) *Behavioural Ecology: an Evolutionary Approach*, 311–333. Wiley-Blackwell, Oxford, UK.

Delibes M, Hiraldo F (1981) The rabbit as prey in the Iberian Mediterranean ecosystem. In: Myers K, MacInnes CD (eds) *Proceedings of the I World Lagomorph Conference*, 614–622. University of Guelph, Guelph, Ontario, Canada.

Delibes-Mateos M, Fernández de Simón J, Villafuerte R, Ferreras P (2008) Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. *European Journal of Wildlife Research* 54: 71–78.

Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimaki E (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecologica* 31: 276–281.

Dickman CR (2010) The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review* 40: 181–211.

Fedriani JM (1996) Dieta anual del zorro *Vulpes vulpes* en dos hábitats del Parque Nacional de Doñana. *Doñana Acta Vertebrata* 23: 143–152.

Fedriani JM, Ferreras P, Delibes M (1998) Dietary response of the Eurasian badger, *Meles meles*, to a decline of its main prey in the Doñana National Park. *Journal of Zoology* 245: 214–218.

Ferreras P, Travaini A, Zapata SC, Delibes M (2011) Short-term responses of mammalian carnivores to a sudden collapse of rabbits in Mediterranean Spain. *Basic and Applied Ecology* 12: 116–124.

Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics* 19: 207–233.

Gortázar C (1999) *Ecología y Patología del Zorro (*Vulpes vulpes, *L.) en el Valle Medio del Ebro*. Consejo de Protección de la Naturaleza de Aragón, Zaragoza, Spain.

Goszczynski J, Jedrzejewska B, Jedrzejewski W (2000) Diet composition of badgers (*Meles meles*) in a pristine forest and rural habitats of Poland compared to other European populations. *Journal of Zoology* 250: 495–505.

Guitián J, Munilla I (2010) Responses of mammal dispersers to fruit availability: rowan (*Sorbus aucuparia*) and carnivores in mountain habitats of northern Spain. *Acta Oecologica* 36: 242–247.

Hartová-Nentvichová M, Šálek M, Červený J, Koubek P (2010) Variation in the diet of the red fox (*Vulpes vulpes*) in mountain habitats: effects of altitude and season. *Mammalian Biology* 75: 334–340.

Herrera CM (1976) A trophic diversity index for presence–absence food data. *Oecologia* 25: 187–191.

Hill RA, Dunbar RIM (2002) Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology* 16: 579–593.

Hounsome T, Delahay R (2005) Birds in the diet of the Eurasian badger *Meles meles*: a review and meta-analysis. *Mammal Review* 35: 199–209.

Hudson P, Dobson AP, Newborn D (1992) Do parasites make prey vulnerable to predation? Red grouse and parasites. *Ecology* 61: 681–692.

Kjellander P, Nordstrom J (2003) Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. *Oikos* 101: 338–344.

Klare U, Kamler JF, Macdonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41: 294–312.

Knauer F, Küchenhoff H, Pilz S (2010) A statistical analysis of the relationship between red fox *Vulpes vulpes* and its prey species (grey partridge *Perdix perdix*, brown hare *Lepus europaeus* and rabbit *Oryctolagus cuniculus*) in Western Germany from 1958 to 1998. *Wildlife Biology* 16: 56–65.

Lodé T (1997) Trophic status and feeding habits of the European Polecat (*Mustela putorius* L. 1758). *Mammal Review* 27: 177–184.

Loureiro F, Bissonete JA, Macdonald DW, Santos-Reis M (2009) Temporal variation in the availability of Mediterranean food resources: do badgers *Meles meles* track them? *Wildlife Biology* 15: 197–206.

Lozano J, Moleón M, Virgós E (2006) Biogeographical patterns in the diet of the wildcat, *Felis sylvestris* Schreber, in Eurasia: factors affecting the trophic diversity. *Journal of Biogeography* 33: 1076–1085.

Millán J, Gortázar C, Tizzani P, Buenestado FJ (2002) Do helminths increase the vulnerability of released pheasants to fox predation? *Journal of Helminthology* 76: 225–229.

Moberly RL, White PCL, Webbon CC, Baker PJ, Harris S (2004) Modelling the costs of fox predation and preventive measures on sheep farms in Britain. *Journal of Environmental Management* 70: 129–143.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Newsome AE, Catling PC, Cooke BD, Smyth R (2001) Two ecological universes separated by the Dingo Barrier fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangeland Journal* 23: 71–98.

O'Mahony D, Lambin X, MacKinnon JL, Coles CF (1999) Fox predation on cyclic field vole populations in Britain. *Ecography* 22: 575–581.

Palomares F (2001) Comparison of 3 methods to estimate rabbit abundance in Mediterranean environment. *Wildlife Society Bulletin* 29: 578–585.

Palomo LJ, Gisbert J, Blanco JC (2007) *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Dirección General de Conservación de la Naturaleza – SECEM-SECEMU, Madrid, Spain.

Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100: 33–46.

Pullin AS, Stewart GB (2006) Guidelines for systematic review in conservation and environmental management. *Conservation Biology* 20: 1647–1656.

Putman RJ (1984) Facts from faeces. *Mammal Review* 14: 79–97.

Reynolds JC, Aebischer N (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review* 21: 97–122.

Reynolds JC, Tapper SC (1995) The ecology of the red fox *Vulpes vulpes* in relation to small game in rural southern England. *Wildlife Biology* 1: 105–119.

Rivas-Martínez S (1987) Nociones sobre Fitosociología, Biogeografía y Bioclimatología. In: Peinado M, Rivas-Martínez S (eds) *La Vegetación de España*, 15–57. University of Alcalá de Henares, Madrid, Spain.

Roper TJ, Mickevicius E (1995) Badger *Meles meles* diet: a review of literature from the former Soviet Union. *Mammal Review* 25: 117–129.

Rosalino LM, Santos-Reis M (2009) Fruit consumption by carnivores in Mediterranean Europe. *Mammal Review* 39: 67–78.

Rosalino LM, Rosa S, Santos-Reis M (2010) The role of carnivores as Mediterranean seed dispersers. *Annales Zoologici Fennici* 47: 195–205.

Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Ruiz-Olmo J, Blanch F, Vidal F (2003) Relationships between the red fox and waterbirds in Ebro Delta Natural Park, N.E. Spain. *Waterbirds* 26: 217–225.

Santos MJ, Matos HM, Baltazar C, Grilo C, Santos-Reis M (2009) Is polecat (*Mustela putorius*) affected by 'mediterraneity'? *Mammalian Biology* 74: 448–455.

Sarmento P (1996) Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. *Oikos* 26: 378–384.

Sillero-Zubiri C, Hoffmann M, Macdonald DW (2004) *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*. IUCN/SSC Canid Specialist Group. Gland, Switzerland and Cambridge, UK.

Smedshaug CA, Selas V, Lund SE, Sonerud GA (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biology* 5: 157–166.

Soriguer RC (1981) Biología y dinámica de una población de conejos (*Oryctolagus cuniculus*) en Andalucía occidental. *Doñana Acta Vertebrata* 8: 1–379.

Soriguer RC, Carro C, Fandos P, Márquez FJ (2003) La diversidad y abundancia de los micromamíferos ibéricos. In:

University of Jaen (ed.) *In Memorian al Prof. Dr. Isidoro Ruiz Martínez*, 439–478. University of Jaen, Jaen, Spain.
Statsoft (2001) *STATISTICA for Windows*. Ver. 6.0. Statsoft Inc., Tulsa, Oklahoma, USA.
Stefanescu C, Herrando S, Páramo F (2004) Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *Journal of Biogeography* 31: 905–915.
Torre I (2004) *Distribution, Population Dynamics and Habitat Selection of Small Mammals in Mediterranean Environments: the Role of Climate, Vegetation Structure, and Predation Risk*. PhD thesis, University of Barcelona, Barcelona, Spain.
Torre I, Arrizabalaga A, Díaz M (2002) Ratón de campo (*Apodemus sylvaticus*). *Galemys* 14: 1–26.
Villafuerte R, Viñuela J, Blanco JC (1998) Extensive predator persecution caused by population crash in a game species: the case of the red kite and rabbits in Spain. *Biological Conservation* 84: 181–188.
Virgós E (2002) Are habitat generalists affected by forest fragmentation? A test with Eurasian badgers (*Meles meles*) in coarse-grained fragmented landscapes of Central Spain. *Journal of Zoology* 258: 313–318.
Virgós E, Llorente M, Cortés Y (1999) Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. *Mammal Review* 29: 119–128.
Virgós E, Revilla E, Mangas G, Barea-Azcón JM, Rosalino LM, De Marinis AM (2005) Revisión de la dieta del tejón (*Meles meles*) en la Península Ibérica: comparación con otras localidades de su área de distribución natural. In: Virgós E, Revilla E, Mangas JG, Domingo-Roura X (eds) *Ecología y Conservación del Tejón en Ecosistemas Mediterráneos*, 67–80. Sociedad Española para la Conservación y Estudio de los Mamíferos, Málaga, Spain.
Vulla E, Hobson KA, Korsten M, Leht M, Martin AJ, Lind A, Männil P, Valdmann H, Saarma U (2009) Carnivory is positively correlated with latitude among omnivorous mammals: evidence from brown bears, badgers and pine martens. *Annales Zoologici Fennici* 46: 395–415.
Wang SW, Macdonald DW (2009) Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. *Journal of Zoology* 277: 275–283.
Webbon CC, Baker PJ, Cole NC, Harris S (2006) Macroscopic prey remains in the winter diet of foxes *Vulpes vulpes* in rural Britain. *Mammal Review* 36: 85–97.
Whittaker RJ, Araújo MA, Jepson P, Ladle RJ, Watson JEM, Willis KJ (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions* 11: 3–23.
Yanes M, Suárez F (1996) Incidental nest predation and lark conservation in an Iberian semiarid shrubsteppe. *Conservation Biology* 10: 881–887.
Yom-Tov Y, Yom-Tov S, Barreiro J, Blanco JC (2007) Body size of the red fox *Vulpes vulpes* in Spain: the effect of agriculture. *Biological Journal of the Linnean Society* 90: 729–734.
Zapata SC, Travaini A, Ferreras P, Delibes M (2007) Analysis of trophic structure of two carnivore assemblages by means of guild identification. *European Journal of Wildlife Research* 53: 276–286.
Zar JH (1984) *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
Zhou YB, Newman C, Xu WT, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie ZQ (2011) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *Journal of Biogeography* 38: 137–147.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Studies of the diet of the red fox in Iberia used in this review, with an indication of the latitude (Lat.), longitude (Long.) and altitude (Alt.) where the study took place, year, sample size, duration of the study, predominant habitat, season and type of material. The Map ID (see Fig. 1) is also shown.
Appendix S2. Fox diets as described in the reviewed studies (see Fig. 1 and Appendix S1). The information is presented as the frequency of occurrence (FO) of each prey group. We also indicate the values of trophic diversity (Herrera diversity index, D) recorded for each study.
Appendix S3. References used for the analyses in this review of the diet of the red fox in the Iberian Peninsula, and included in Fig. 1.