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

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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.

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

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 and 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. 2006b; Zhou et al. 2011). The study of trophic biogeographical patterns of predators is fundamental to understanding their ecology and life history strategies (Daan and 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. 2006b). Investigations of the diet of medium-sized carnivores at large biogeographical scales have included studies of the Eurasian badger (*Meles meles*) (Roper and Mickevicius 1995; Goszczynski et al. 2000; Hounsome and 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. 2006b), 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 and Dunbar 2002). Thus, variations in the distribution of potential prey species across biogeographical regions have been

81 postulated to affect the feeding habits of medium-sized carnivores. For instance, dietary
82 diversity in wildcats increases at lower latitudes (i.e. Mediterranean areas; Lozano et al.
83 2006b), where potential prey richness is greater (Rosenzweig 1995). Latitudinal
84 gradients have also been observed in relation to dietary diversity and in the consumption
85 of particular prey. For example, the Eurasian otter's diet is more diverse in southern
86 localities, while further north the species is more piscivorous, predating upon a large
87 diversity of fish families (Clavero et al. 2003). Similarly, food availability can vary
88 along altitudinal gradients, and this can affect the dietary composition of carnivores. For
89 instance, small mammals (mice, voles and shrews) are the primary food of martens, but
90 are less frequently consumed at lower altitudes, where other food resources are more
91 abundant and are available throughout the year (Zhou et al. 2011).
92 Diet is one of the most studied aspects of the ecology of the red fox. Most studies
93 indicate that the red fox is a generalist predator that uses resources according to their
94 availability and hence is opportunistic in its behaviour (e.g. Webbon et al. 2006;
95 Dell'Arte et al. 2007). However, most studies were undertaken at local or regional
96 scales, and specific studies describing biogeographical patterns in the red fox diet are
97 lacking. Although some studies have shown variations in the feeding habits of foxes
98 based on environmental variables including habitat type (Fedriani 1996; Gortázar 1999),
99 the effects of latitude, longitude and altitude on the composition of fox diets at a larger
100 scale remain unknown. Similarly, there is a lack of information about how the
101 consumption by foxes of some preferred prey, such as lagomorphs or small mammals,
102 varies spatially at biogeographical scales.
103 The ecological features of red foxes can bring them into conflict with human activities
104 where their prey is of economic or conservation concern (Baker and Harris 2003). For
105 example, predation by foxes is often regarded as one of the factors preventing the

106 recovery of small game (Reynolds and Tapper 1995; Smedshaug et al. 1999; Beja et al.
107 2009; Knauer et al. 2010), and farmers consider predation of livestock by foxes to cause
108 economic losses (Moberly et al. 2004). Furthermore, several researchers have reported
109 negative impacts of fox predation on species of conservation concern (Yanes and Suárez
110 1996; Ruiz-Olmo et al. 2003; Dickman 2010). However, predators, including
111 generalists such as red foxes, play major roles in ecological processes by limiting
112 populations of pest species (O'Mahony et al. 1999; Newsome et al. 2001), reducing the
113 transmission of disease (Hudson et al. 1992; Millán et al. 2002) and acting as seed
114 dispersers (Guitián and Munilla 2010; Rosalino et al. 2010). Our ability to understand
115 biogeographical patterns is crucial for developing efficient management programs in the
116 context of human usage (Whittaker et al. 2005). From this perspective, a large-scale
117 study of the trophic ecology of the red fox could provide valuable knowledge
118 concerning its ecosystem functions and improve management of this predator.
119 The Iberian Peninsula is included in the Mediterranean Basin hotspot (Myers et al.
120 2000) and is thereby an interesting site for the study of biogeographical patterns (e.g.
121 Carvalho et al. 2011). It includes distinct Atlantic (Northern Iberia), Mediterranean
122 (Central and Southern Iberia) and Alpine (Pyrenees mountains) biogeographical regions
123 (Rivas-Martínez 1987; Figure 1.1), and is characterized by high environmental
124 heterogeneity because of its climatic and physiographical complexity (the altitude
125 ranges from 0 m at sea level to 3479 m above sea level at Sierra Nevada, Granada,
126 Spain). The variability in environmental conditions underpins the diversity in
127 community composition and structure in this region (Blondel and Aronson 1999;
128 Stefanescu et al. 2004). Several patterns in the distribution and abundance of the main
129 prey species of Iberian predators have been described. For instance, wild rabbits
130 (*Oryctolagus cuniculus*), which are a key prey for red foxes and other Iberian predators

131 (Delibes and Hiraldo 1981; Calzada 2000; Ferreras et al. 2011), are most abundant at
132 central–southern latitudes (Villafuerte et al. 1998), and small mammals show a gradient
133 in abundance and species richness from south to north (Soriguer et al. 2003). The theory
134 of feeding specialization predicts an increase in dietary diversity when the preferred
135 prey becomes scarce (Futuyma and Moreno 1988). In this study, we tested this
136 prediction in relation to the red fox and rabbits as its preferred prey. Although the
137 Iberian Peninsula is a relatively small biogeographical area, its high environmental
138 variability and biodiversity justifies a biogeographical analysis of the diet of resident
139 generalist carnivores such as the red fox.
140 Our main objective was to describe the trophic biogeographical patterns of the red fox
141 in the Iberian Peninsula, based on a comprehensive literature review. Specifically, we:
142 (i) evaluated changes in consumption by red foxes of main food groups in relation to
143 geographical variables (latitude, longitude and altitude); (ii) analysed the relationships
144 between red fox dietary diversity, consumption of its main prey and geographical
145 variables; (iii) assessed the relationships between the consumption of different food
146 groups and habitat type and season; and (iv) interpreted patterns in the diet of this
147 generalist predator from a biogeographical perspective.

148 ## Material and Methods

149 **Literature compilation and standardization of dietary data**
150 Various sources of information were used to review the available literature
151 comprehensively, as recommended by Pullin and Stewart (2006). Search engines (ISI
152 Web of Science and Google Scholar) were used to identify relevant scientific studies
153 containing information about the trophic ecology of the red fox in the Iberian Peninsula.
154 We searched for terms that were identified using the following combinations of
155 keywords: ‘red fox’ or ‘Vulpes vulpes’ and ‘diet’ or ‘feeding’ and ‘Iberian Peninsula’,

156 ‘Spain’ or ‘Portugal’. We consulted several zoological bibliographical data bases
157 including the Zoological Record (http://scientific.thomson.com/products/zr/) and the
158 bibliographical data set of the Spanish Society for the Conservation and Study of
159 Mammals (http://www.secem.es/Secem_la_biblioteca.htm). We also sought information
160 on the topic from informal contacts with expert researchers (colleagues working in
161 different institutions – universities and environmental public administration – in Spain
162 and Portugal). This provided us with less readily accessible sources of information,
163 including unpublished or unedited studies (e.g. PhD theses, MSc and BSc dissertations,
164 and public administration data bases).
165 We compiled a total of 55 published and unpublished studies concerning the diet of the
166 red fox in Portugal and Spain, spanning the period 1971–2008. Some authors reported
167 data pooled annually, others reported data pooled seasonally, and several provided both
168 annual and seasonal data. To simplify the statistical procedures, two independent data
169 bases were created for analysis: one comprising annual data and the other seasonal data.
170 These data bases were analysed independently (see Statistical analyses).
171 To standardize data from different geographical areas (for later comparison and
172 analysis), we excluded studies: (i) with small sample sizes (scat or stomachs; $n < 30$ for
173 anual studies and $n < 15$ for seasonal studies); (ii) reporting data for only one prey
174 group; (iii) containing duplicated information, e.g. academic dissertations later
175 published as scientific articles; and (iv) reporting only relative frequency of occurrence
176 (RF, expressed as the percentage of times one food ítem occurs in relation to the total
177 times all food items occur) or percentage biomass. This last exclusion meant that we
178 only considered studies reporting the frequency of occurrence (FO, expressed as the
179 percentage of scats/stomachs containing a particular food item) for the various food
180 groups. RF values are considered to be highly suitable for interpopulation comparisons

181 in diet studies (Clavero et al. 2003), and biomass is considered a direct measure of the
182 energetic value of prey items consumed (Reynolds and Aebischer 1991), and therefore
183 the best approximation to the true diet (Klare et al. 2011). However, only a small
184 proportion of the reviewed studies presented RF or biomass information, while FO is
185 widely used in carnivore diet studies and was used in most of the red fox studies
186 considered in this review. Moreover, FO can be used to assess whether a predator
187 behaves as an opportunist or as a specialist forager (Klare et al. 2011), and it is
188 considered a valid parameter for comparative purposes (Reynolds and Aebischer 1991;
189 Klare et al. 2011).
190 The application of the four exclusion criteria above resulted in a final set of 37 studies
191 that were further analysed to describe red fox feeding patterns in the Iberian Peninsula.
192 These studies were carried out in 39 locations distributed throughout the region (Figure
193 1.1; for more detailed information, see Appendices 1.1 and 1.2). The data were highly
194 heterogeneous among the variables, which reflected the diversity of environmental
195 conditions in the Iberian Peninsula. For example, a broad altitudinal range (20–1425m)
196 was included, and various habitat types were represented, including several types of
197 Mediterranean scrub, agricultural lands, dehesas (savannah-like formations that
198 combine pastures with intermittent cereal cultivation in park-like oak woodlands;
199 Blondel and Aronson 1999) and forests containing various tree species (e.g. *Pinus* sp.
200 and *Quercus pyrenaica*).
201 **Variable selection**
202 From each study we derived the following parameters: respective geographical variables
203 (latitude and longitude, in degrees; and altitude, in metres) either from the study itself
204 or, if they were not provided in the study, from Google Earth (http://earth.google.com);
205 the source of food materials analysed (scats or stomach contents); and the sample size,

206 study duration, season, habitat, and FO of each food group (see Appendices 1.1 and
207 1.2). We categorized dietary items into the following main groups: lagomorphs (mainly
208 European wild rabbits; see Results), small mammals (rodents and insectivores), birds,
209 reptiles, invertebrates, fruits/seeds, and carrion/garbage (mainly large mammals and
210 leftover food of anthropogenic origin). Four seasons were considered: spring (March–
211 May), summer (June–August), autumn (September–November) and winter (December–
212 February). The habitat type at each location was categorized as Mediterranean scrub,
213 forest or agricultural–dehesa (agricultural land and dehesas), according to the
214 descriptions given in each study. We calculated Herrera's trophic diversity index (D;
215 Herrera 1976) from the FO data as an index of the trophic diversity for each diet. The
216 index is computed according to the formula $D = -\sum_{i=1}^{s} \log \mathrm{pi}$, where p is the
217 frequency of occurrence of the various prey categories (i). This index is recommended
218 for presence–absence food data, because other diversity indices such as the Shannon
219 index cannot be calculated from this type of data (Herrera 1976).

220 **Statistical analyses**

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

226 To avoid temporal pseudo-replication, we considered only those studies in which annual
227 information on the Iberian fox diet was provided: 30 studies and localities, including a
228 total of 9459 samples (stomachs and scats; see Appendices 1.1 and 1.2). Therefore,
229 analyses of the relationship of the consumption of various food groups to geographical
230 variables and habitat type were performed using the anual 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 1.1 and 1.2).

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;

256 $F_{7,26}$ = 0.43, P = 0.11) or the interaction between sample size and food material ($F_{7,26}$ =
257 1.04, P = 0.42) on the FO of food groups in the diet. Thus, for further analyses we
258 pooled data from studies with differing durations, sample sizes and sources of analysed
259 food material.

260 **Overall diet**

261 Iberian red foxes consumed a wide range of food items. Invertebrates were the most
262 frequent food group in their diet (mean FO±SD, 40.1±25.5%), followed by fruits/ seeds
263 (38.9±22.0%), small mammals (34±20.9%), lagomorphs (20.6±22.0%), carrion/garbage
264 (15.3±14.2%), birds (13.4±15.3%) and reptiles (1.8±2.8%).

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

278 **Geographical patterns (latitude, longitude and altitude)**

279 We found a negative and statistically significant relationship between latitude and the
280 FO of lagomorphs (R^2 = 0.19, $F_{1,35}$ = 8.47, P = 0.006; Figure 1.2a) and invertebrates (R^2

281 = 0.11, $F_{1,35}$ = 4.37, P = 0.04; Figure 1.2b), and a positive and significant relationship
282 between latitude and the FO of small mammals (R^2 = 0.16, $F_{1,35}$ = 6.78, P = 0.01; Figure
283 1.2c) and fruits/seeds (R^2 = 0.12, $F_{1,35}$ = 5.04, P = 0.03; Figure 1.2d). Therefore, at lower
284 latitudes, lagomorphs and invertebrates were more frequently eaten, while at higher
285 latitudes small mammals and fruits/seeds were more commonly consumed.
286 Only the FO of invertebrates and fruits/seeds were significantly related to longitude.
287 The consumption of invertebrates increased towards the east (R^2 = 0.12, $F_{1,35}$ = 4.95, P =
288 0.03), whereas that of fruits/seeds increased towards the west (R^2 = 0.16, $F_{1,35}$ = 6.99, P
289 = 0.01).
290 Altitude was significantly and negatively associated with the FO of lagomorphs (R^2 =
291 0.29, $F_{1,30}$ = 12.67, P = 0.001; Figure 1.3a), and positively associated with that of small
292 mammals (R^2 = 0.27, $F_{1,30}$ = 11.31, P = 0.002, Figure 1.3b). Thus, the consumption of
293 lagomorphs decreased with altitude, and that of small mammals increased.
294
295 **Is the red fox specialized on rabbits in the Iberian Peninsula?**
296 The consumption of wild rabbits (represented by lagomorphs) was significantly and
297 negatively related to the consumption of both small mammals (R^2 = 0.15, $F_{1,35}$ = 6.23, P
298 = 0.02) and fruits/seeds (R^2 = 0.17, $F_{1,35}$ = 8.41, P = 0.006). The GLM results suggest
299 that diet diversity was not significantly associated with latitude ($F_{1,25}$ = 0.33, P > 0.5),
300 altitude ($F_{1,25}$ = 0.552, P > 0.4) or the FO of the four main food groups (lagomorphs:
301 $F_{1,25}$ = 0.126, P > 0.7; small mammals: $F_{1,25}$ = 0.004, P > 0.9; invertebrates: $F_{1,25}$ = 0.253,
302 P > 0.6; and fruits/seeds: $F_{1,25}$ = 0.196, P > 0.6).
303 **Habitat type and seasonality**
304 We found a significant relationship between habitat type and the FO of lagomorphs
305 ($F_{2,21}$ = 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 (Figure 1.4a), but the opposite was observed for small mammals (Figure 1.4b).

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 (Figure 1.5a); invertebrates were mostly consumed in summer, and their occurrence in the diet was lowest in winter (Figure 1.5b); and fruits/seeds were consumed most in autumn and least in spring (Figure 1.5c). Marginally significant differences were found for lagomorphs ($F_{3,53}$ = 2.40, P = 0.07), which were consumed most in summer (Figure 1.5d).

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 and 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 and Delahay 2005; Lozano et al. 2006b; 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 and 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. 2006b), 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 and 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

355 range covered in the present study leads us to believe that the higher consumption of
356 fruits/seeds is likely to be due to the greater availability of this resource in the north of
357 the Iberian Peninsula.
358 The FO of invertebrates in the fox diet increases from east to west, while that of
359 fruits/seeds increases from west to east. Rosalino and Santos-Reis (2009) were not able
360 to explain a similar longitudinal gradient found in fruit/seed consumption by medium-
361 sized carnivores in Iberia because of the absence of data on the availability of plant
362 species producing fruits and seeds. Invertebrates are an alternative food source for some
363 omnivorous species, especially larger carnivorous mammals, where larger prey items
364 are not available (Capinera 2010). However, as there is currently no information on the
365 availability of invertebrates over a longitudinal gradient in Iberia, we have no data to
366 enable us to interpret our results.
367 The decrease in consumption of lagomorphs by foxes with increasing altitude could be
368 because of the reduced presence and abundance of rabbits above 1000m (Blanco 1998;
369 Palomo et al. 2007), but the consumption of small mammals by foxes increased in high
370 altitude areas. This is in contrast with previous findings that the species richness and
371 abundance of small mammals decreases at higher altitudes (Torre 2004). However, the
372 altitudinal range considered in this study (only three localities were higher than 1400m;
373 see Appendix 1.1) did not include altitudes that may limit the presence of most small
374 mammals consumed by the red fox (Palomo et al. 2007), which prevents us from
375 confirming this trend in small mammal consumption. Thus, the increased intake of
376 small mammals seems to be a functional response to the reduced availability of
377 lagomorphs at higher altitudes, as Hartová-Nentvichová et al. (2010) found for red
378 foxes in the mountains of the Czech Republic.
379 **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 and Moreno 1988; Fedriani et al. 1998; Lozano et al. 2006b). A negative relationship at a regional scale between lagomorph consumption and dietary diversity has been described for red foxes (Delibes-Mateos et al. 2008b) and for other small and medium-sized Mediterranean carnivores (Sarmento 1996; Lozano et al. 2006b; 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 and 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 áreas 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. *Apodemus sylvaticus*; Torre et al. 2002), together with the low abundance of 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 and 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 (Figure 1.5d). However, in areas where rabbits are very abundant, their availability is high throughout the year (Angulo and 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, hábitat type and season, which affect the availability of alternative potential foods (Figure 1.6). 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

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655

656 **SUPPORTING INFORMATION**

657 Additional Supporting Information may be found in the online version of this article:
658 **Appendix S1**. Studies of the diet of the red fox in Iberia used in this review, with an
659 indication of the latitude (Lat.), longitude (Long.) and altitude (Alt.) where the study
660 took place, year, sample size, duration of the study, predominant habitat, season and
661 type of material. The Map ID (see Fig. 1) is also shown.
662 **Appendix S2.** Fox diets as described in the reviewed studies (see Fig. 1 and Appendix
663 S1). The information is presented as the frequency of occurrence (FO) of each prey
664 group.We also indicate the values of trophic diversity (Herrera diversity index, D)
665 recorded for each study.
666 **Appendix S3.** References used for the analyses in this review of the diet of the red fox
667 in the Iberian Peninsula, and included in Fig. 1.
668

669 **FIGURE LEGENDS**

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

673

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

677

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

681

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

687

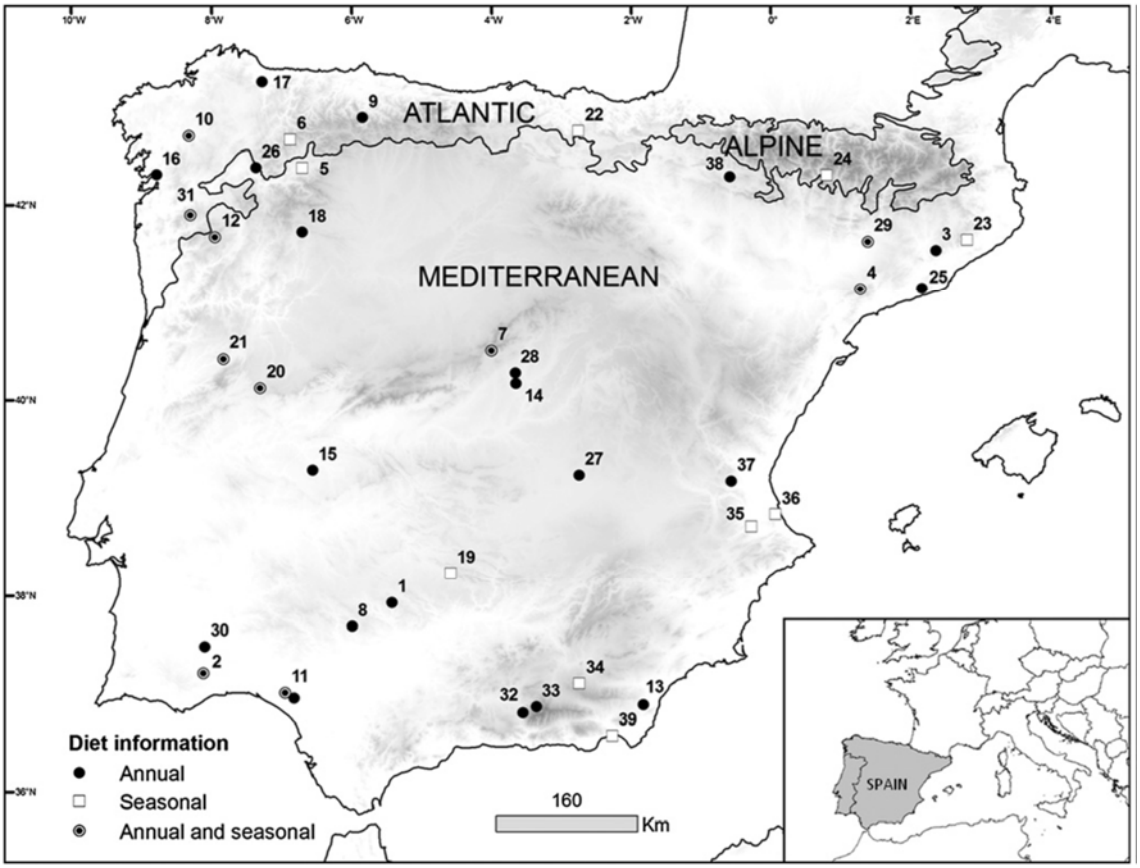
688 **Fig. 5.** Frequency of occurrence (FO; arc sine transformed; means ± SE) of (a) reptiles
689 (b) invertebrates (c) fruits/seeds and (d) lagomorphs in the diet of the red fox, as a
690 function of season (marginally non-significant for lagomorphs, $P = 0.07$). Means
691 marked with the same letter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

693

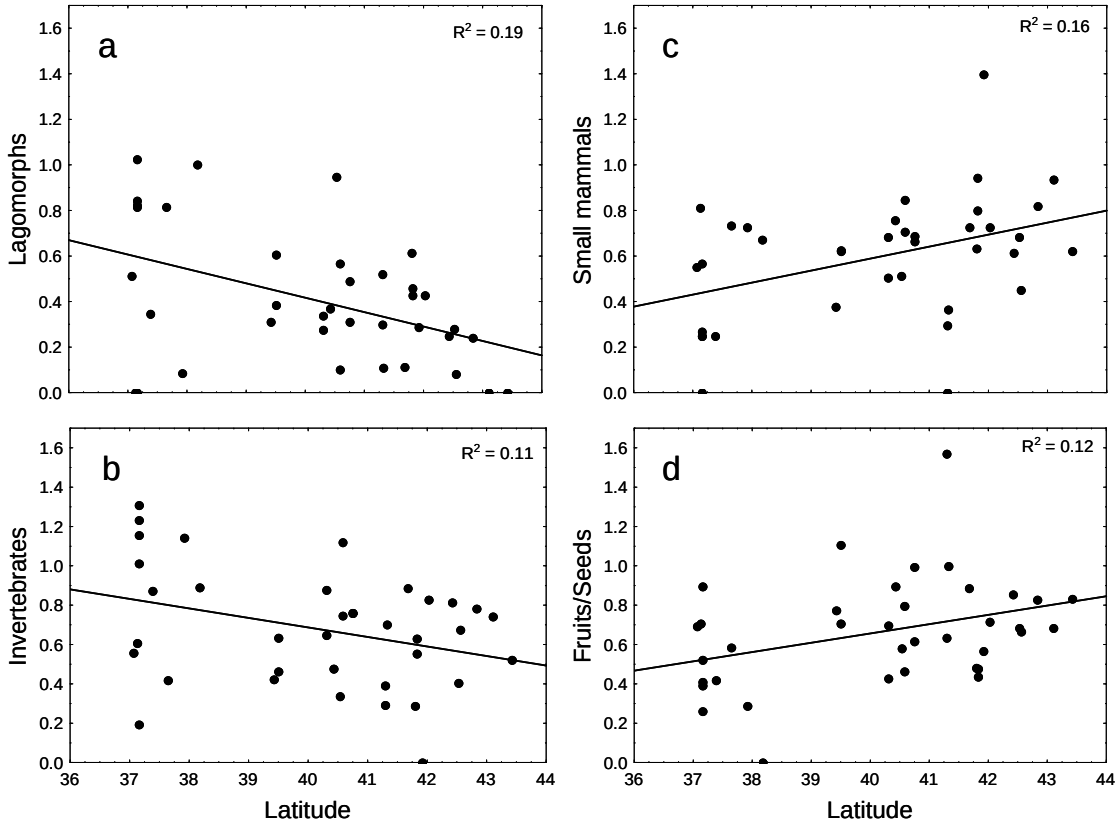
694 **Fig. 6.** Conceptual model illustrating the biogeographical patterns found in the
695 consumption of the main food groups by the Iberian red fox, in relation to geographical
696 variables (LAG, lagomorphs; SM, small mammals; F/S, fruits/ seeds; INV,
697 invertebrates). The white arrows represent latitudinal (LATITUDE) and longitudinal
698 (LONG) gradients, and the grey arrow shows the altitudinal gradient (ALTITUDE).
699

FIGURES

FIG.1



703 **FIG.2**



704

705

FIG.3

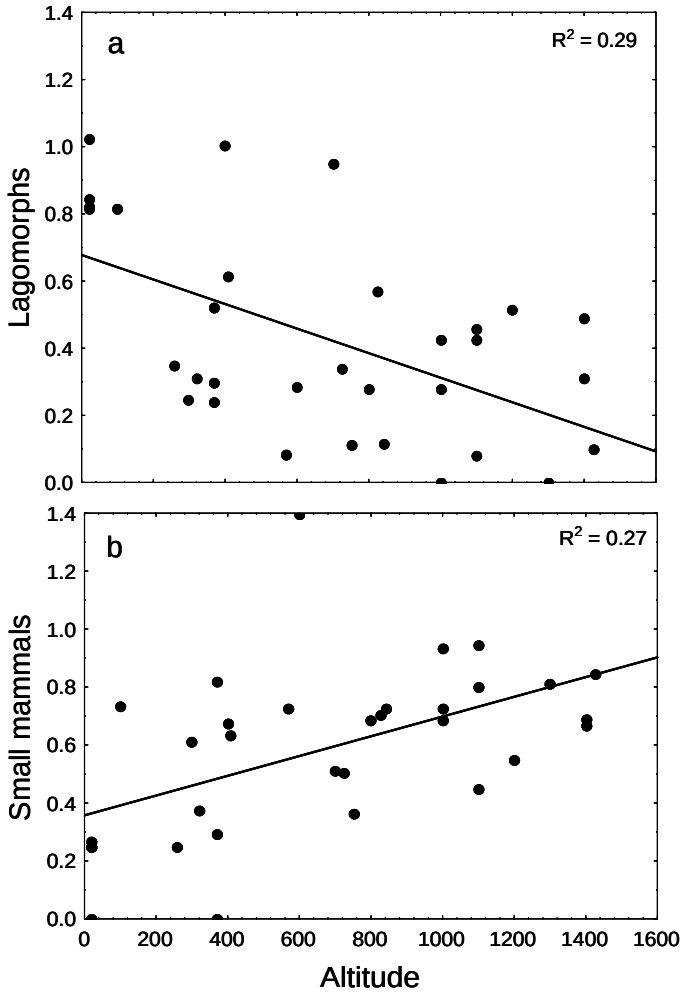

a
R^2 = 0.29
Lagomorphs
b
R^2 = 0.27
Small mammals
Altitude
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0
200
400
600
800
1000
1200
1400
1600

FIG.4

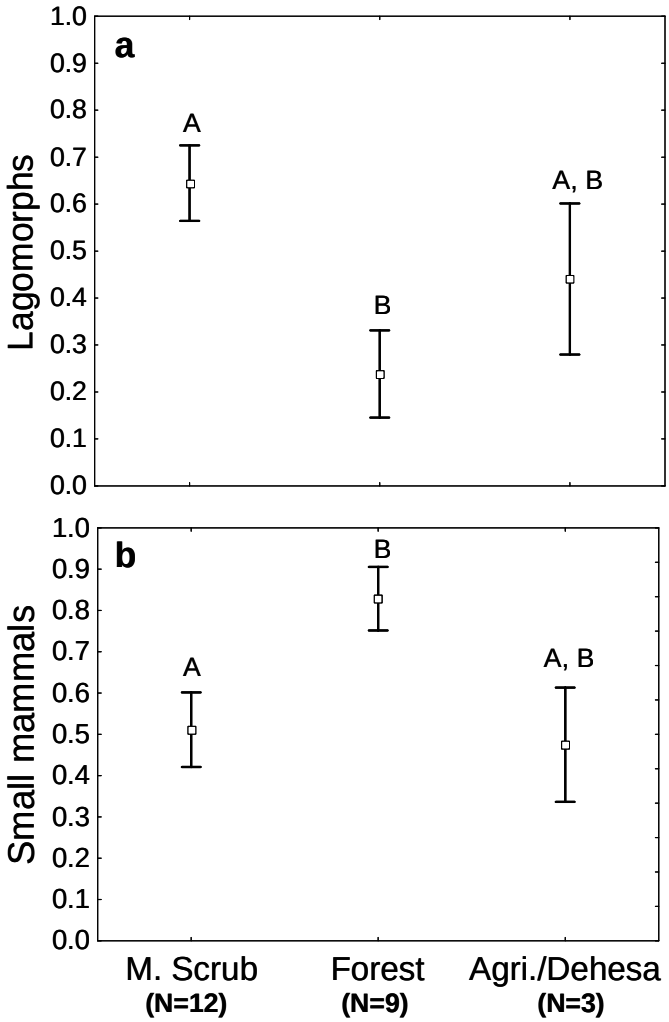
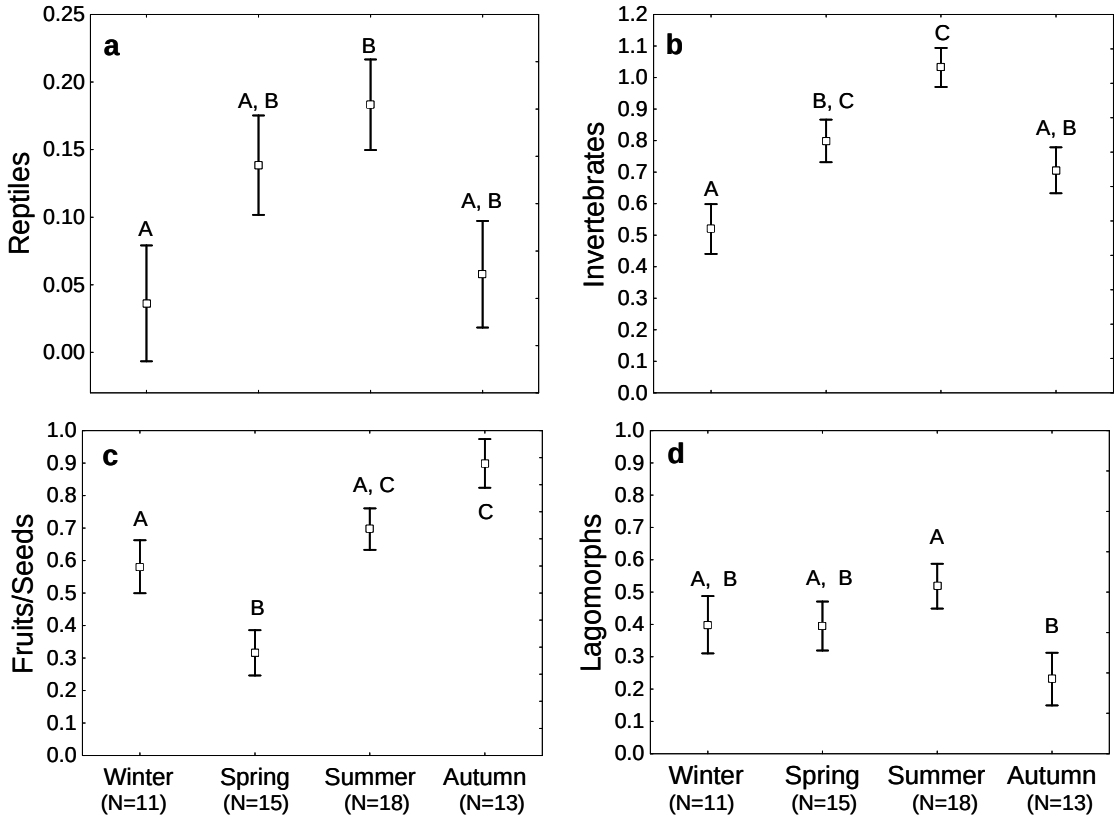

a
b
Lagomorphs
Small mammals
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
A
B
A, B
A
B
A, B
M. Scrub
(N=12)
Forest
(N=9)
Agri./Dehesa
(N=3)

FIG.5


a
Reptiles
0.25
0.20
0.15
0.10
0.05
0.00
A
A, B
B
A, B
b
Invertebrates
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
A
B, C
C
A, B
c
Fruits/Seeds
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
A
B
A, C
C
d
Lagomorphs
A, B
A, B
A
B
Winter
(N=11)
Spring
(N=15)
Summer
(N=18)
Autumn
(N=13)

774 **FIG.6**
775