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

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23 **Iberia**

24

25 **Abstract**

26 1. Biogeographical diversity is central to the trophic ecology of predators.  
27 Understanding the biogeographical trophic patterns of generalist predators, such as the  
28 red fox (*Vulpes vulpes*), is particularly challenging because of their wide distributions,  
29 broad trophic spectra and high ecological plasticity, which often generate conflicts with  
30 humans.

31 2. We reviewed 55 studies from the Iberian Peninsula concerning the diet of the red fox  
32 to describe its trophic patterns from a biogeographical perspective.

33 3. We considered the frequency of occurrence of seven food groups and characterized  
34 each study site according to environmental variables. We tested relationships between  
35 geographical variables and each food group independently, and assessed the  
36 consumption of lagomorphs in relation to the other food groups. We also tested the  
37 relationships between trophic diversity, the main food groups, latitude and altitude, and  
38 finally investigated changes in the consumption of all food groups in relation to habitat  
39 type and seasonality.

40 4. We found a latitudinal pattern in the diet of the red fox, which was characterized by a  
41 greater consumption of lagomorphs and invertebrates in southern areas, and a higher  
42 intake of small mammals and fruits/seeds in northern regions. Additionally, the  
43 consumption of invertebrates increased from east to west, while fruit/seed consumption  
44 increased from west to east. Consumption of lagomorphs decreased, and of small  
45 mammals increased, with altitude. Trophic diversity was not associated with  
46 geographical variables. The intake of lagomorphs and small mammals was greatest in  
47 Mediterranean scrub and forest, respectively. Reptiles and invertebrates were consumed  
48 mostly during summer; fruits/seeds in autumn.

49 5.Iberian red foxes show variation in their feeding habits associated with environmental  
50 variables, which are in turn associated with the availability of their main prey. Foxes  
51 select rabbits where they are abundant, and feed on small mammals and fruits/seeds  
52 where lagomorphs are scarce.

53

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

55

## 56 **Introduction**

57 Feeding habits have been one of the most studied features of carnivore ecology. The  
58 traditional approach to studies of carnivore diets is to investigate the feeding habits of  
59 species (mainly in terms of diet composition) at local or regional scales (e.g. Brand et  
60 al. 1976; Zapata et al. 2007; Wang and Macdonald 2009). Comprehensive studies of  
61 carnivore trophic ecology at broader geographical scales have only recently been  
62 undertaken (e.g. Clavero et al. 2003; Lozano et al. 2006b; Zhou et al. 2011). The study  
63 of trophic biogeographical patterns of predators is fundamental to understanding their  
64 ecology and life history strategies (Daan and Tinbergen 1997). For instance, defining a  
65 species as a trophic generalist or specialist is only relevant in the context of extensive  
66 ecological studies in which variation in feeding behaviour among populations over a  
67 broad range of environmental conditions is considered (Lozano et al. 2006b).  
68 Investigations of the diet of medium-sized carnivores at large biogeographical scales  
69 have included studies of the Eurasian badger (*Meles meles*) (Roper and Mickevicius  
70 1995; Goszczynski et al. 2000; Hounsome and Delahay 2005); the polecat (*Mustela*  
71 *putorius*) (Lodé 1997); the common genet (*Genetta genetta*) (Virgós et al. 1999), the  
72 Eurasian otter (*Lutra lutra*) (Clavero et al. 2003), the European wildcat (*Felis silvestris*)  
73 (Lozano et al. 2006b), and the Holarctic martens (*Martes* sp.) (Zhou et al. 2011).  
74 Surprisingly, this type of study is lacking for the red fox (*Vulpes vulpes*), which is the  
75 world's most widespread member of the order Carnivora (Sillero- Zubiri et al. 2004)  
76 and one of the most abundant carnivore species in the Iberian Peninsula (Blanco 1998;  
77 Palomo et al. 2007) and elsewhere.

78 Environmental and climatic conditions affect food availability, and can have an impact  
79 on dietary composition and diversity (Hill and Dunbar 2002). Thus, variations in the  
80 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, preying 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 (Gutián 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](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  $D = -\sum_{i=1}^s \log p_i$ , 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 annual data base. The testing of

231 seasonal variation was based only on those studies in which seasonal data were  
232 reported: 18 studies and 20 localities, including a total of 5027 samples (stomachs and  
233 scats; see Appendices 1.1 and 1.2).

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

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

## 253 **Results**

254 We found no significant effect of study duration ( $F_{7,26} = 0.86$ ,  $P = 0.55$ ), sample size  
255 ( $F_{7,26} = 0.73$ ,  $P = 0.64$ ), 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  $FO \pm SD$ ,  $40.1 \pm 25.5\%$ ), followed by fruits/ seeds  
263 ( $38.9 \pm 22.0\%$ ), small mammals ( $34 \pm 20.9\%$ ), lagomorphs ( $20.6 \pm 22.0\%$ ), carrion/garbage  
264 ( $15.3 \pm 14.2\%$ ), birds ( $13.4 \pm 15.3\%$ ) and reptiles ( $1.8 \pm 2.8\%$ ).

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;  $FO = 1.2 \pm 0.43\%$ ). 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

306 FO of lagomorphs was higher in Mediterranean scrub than in forest (Figure 1.4a), but  
307 the opposite was observed for small mammals (Figure 1.4b).

308 A significant seasonal relationship in the red fox diet was found for reptiles ( $F_{3,53} =$   
309  $3.34$ ,  $P = 0.02$ ), invertebrates ( $F_{3,53} = 9.45$ ,  $P < 0.0001$ ) and fruits/seeds ( $F_{3,53} = 11.49$ ,  $P$   
310  $< 0.0001$ ). The FO of reptiles increased from winter to summer (Figure 1.5a);  
311 invertebrates were mostly consumed in summer, and their occurrence in the diet was  
312 lowest in winter (Figure 1.5b); and fruits/seeds were consumed most in autumn and  
313 least in spring (Figure 1.5c). Marginally significant differences were found for  
314 lagomorphs ( $F_{3,53} = 2.40$ ,  $P = 0.07$ ), which were consumed most in summer (Figure  
315 1.5d).

## 316 **Discussion**

### 317 **Biogeographical variations in the diet of the red fox in Iberia**

318 Generalist predators feed on different food resources according to their abundance and  
319 availability (Futuyma and Moreno 1988). This study confirms that the red fox is a  
320 generalist predator; its trophic patterns can be explained by geographical variables,  
321 habitat type and seasonality. These factors determine directly the abundance and  
322 availability of its main foods [e.g. wild rabbits are more abundant at southern latitudes  
323 (Villafuerte et al. 1998) and in Mediterranean scrubland habitats (Calvete et al. 2004);  
324 small mammals are more abundant at northern latitudes (Soriguer et al. 2003) and in  
325 forest habitats (Torre et al. 2002)]. Latitude influences the feeding patterns of many  
326 medium-sized carnivores (Clavero et al. 2003; Hounsome and Delahay 2005; Lozano et  
327 al. 2006b; Zhou et al. 2011). Some researchers relate dietary patterns in the abundance  
328 and diversity of prey species with the latitudinal gradient described in Eurasia, which  
329 increases towards the south (Pianka 1966; Blondel and Aronson 1999). Our results are

330 consistent with these findings as we observed a latitudinal gradient in the consumption  
331 of lagomorphs, invertebrates, small mammals and fruits/seeds by red foxes.

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

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

349 The consumption of fruits/seeds by the red fox is greater in northern regions than in  
350 southern regions. However, this pattern is opposite to that described for other Eurasian  
351 generalist carnivores, which decrease their consumption of plant matter and increase  
352 carnivory with increasing latitude (Virgós et al. 1999; Goszczynski et al. 2000; Vulla et  
353 al. 2009; Zhou et al. 2011). In some of these studies, this pattern is explained by a  
354 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?**



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

### 393 **Habitat type and seasonality**

394 We observed a high intake of lagomorphs by red foxes in the Mediterranean scrubland,  
395 where wild rabbits reach higher densities (Fedriani 1996; Palomares 2001; Calvete et al.  
396 2004). In contrast, Fedriani (1996) found no difference in consumption of wild rabbits  
397 by red foxes in adjacent areas of scrubland and dehesa habitat in Doñana (southwest  
398 Iberian Peninsula), despite higher rabbit density in the scrubland patches. This is  
399 probably a consequence of the larger scale considered in our review, where habitats  
400 were clearly differentiated between studies. The preference for forests shown by the  
401 small mammal species most frequently consumed by foxes (e.g. *Apodemus sylvaticus*;  
402 Torre et al. 2002), together with the low abundance of rabbits in this type of habitat,  
403 explains why foxes include in their diet a greater proportion of small mammals in  
404 forests than in others habitats.

405 Several researchers have reported marked seasonality in the diet of the red fox  
406 (Dell'Arte et al. 2007; Hartová-Nentvichová et al. 2010). Mediterranean ecosystems  
407 have marked climatic seasonality, with hot dry summers and cold wet winters (Blondel  
408 and Aronson 1999); thus, some trophic resources for carnivores are only seasonally  
409 available (Virgós 2002). We also observed a marked seasonality in the diet of the red  
410 fox, which is a result of the seasonal availability of some food groups at the Iberian  
411 scale. Populations of Orthoptera and Coleoptera, the invertebrates most consumed in  
412 summer, increase dramatically during this season (Aranda et al. 1995; Loureiro et al.  
413 2009). The availability of cultivated and wild fruits is greatest in summer and autumn  
414 (Loureiro et al. 2009), when they are most consumed by foxes. The annual abundance  
415 of wild rabbits in the Iberian Peninsula peaks in the spring–summer period (Soriguer  
416 1981; Beltrán 1991). At this time the greater availability of juvenile rabbits and the  
417 susceptibility of the rabbit population to myxomatosis (Calvete et al. 2002) may make  
418 this prey more vulnerable to predation and consumption as carrion by foxes, so that  
419 rabbits may provide a valuable energy source for foxes during the highly critical  
420 breeding period. This explains the observed seasonal increase in the FO of lagomorphs  
421 from spring to summer (Figure 1.5d). However, in areas where rabbits are very  
422 abundant, their availability is high throughout the year (Angulo and Villafuerte 2003),  
423 which could explain the lack of statistically significant differences between seasons in  
424 the FO of lagomorphs in the red fox diet.

## 425 **Conclusions**

426 Biogeographical variation in the feeding habits of Iberian red foxes are associated with  
427 geographical variables, hábitat type and season, which affect the availability of  
428 alternative potential foods (Figure 1.6). Our results confirm that the feeding habits of  
429 the red fox, a generalist predator, vary widely both spatially and temporally, even within

430 a relatively small biogeographical area such as the Iberian Peninsula. Therefore, we  
431 demonstrate that the flexibility of this generalist predator really reflects the  
432 biogeographical patterns of distribution and abundance of its main food sources.  
433 Understanding these patterns in the feeding ecology of the red fox, the most abundant  
434 carnivore in the Iberian Peninsula, will facilitate the understanding of the geographical  
435 variations in its abundance and behaviour, and improve the management and  
436 conservation of this species

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## 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  $\pm$  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

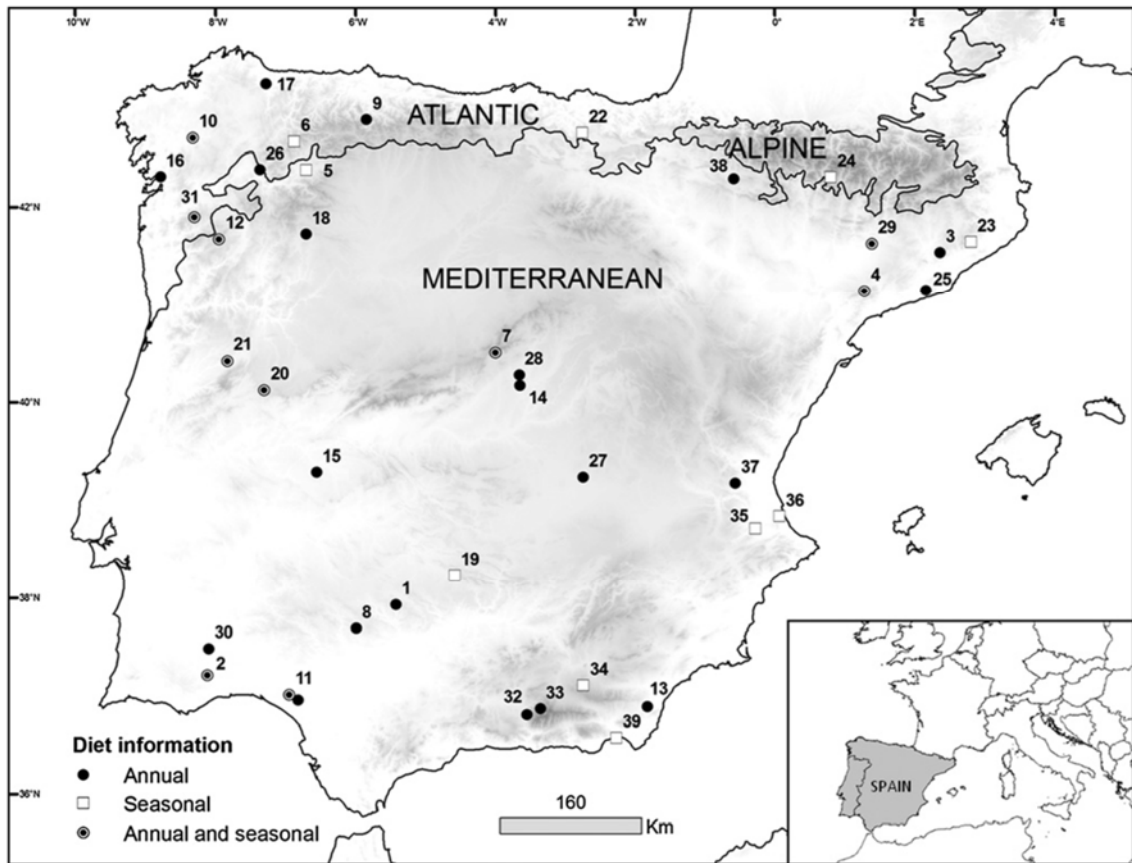
688 **Fig. 5.** Frequency of occurrence (FO; arc sine transformed; means  $\pm$  SE) of (a) reptiles  
689 (b) invertebrates (c) fruits/seeds and (d) lagomorphs in the diet of the red fox, as a  
690 function of season (marginally non-significant for lagomorphs,  $P = 0.07$ ). Means  
691 marked with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

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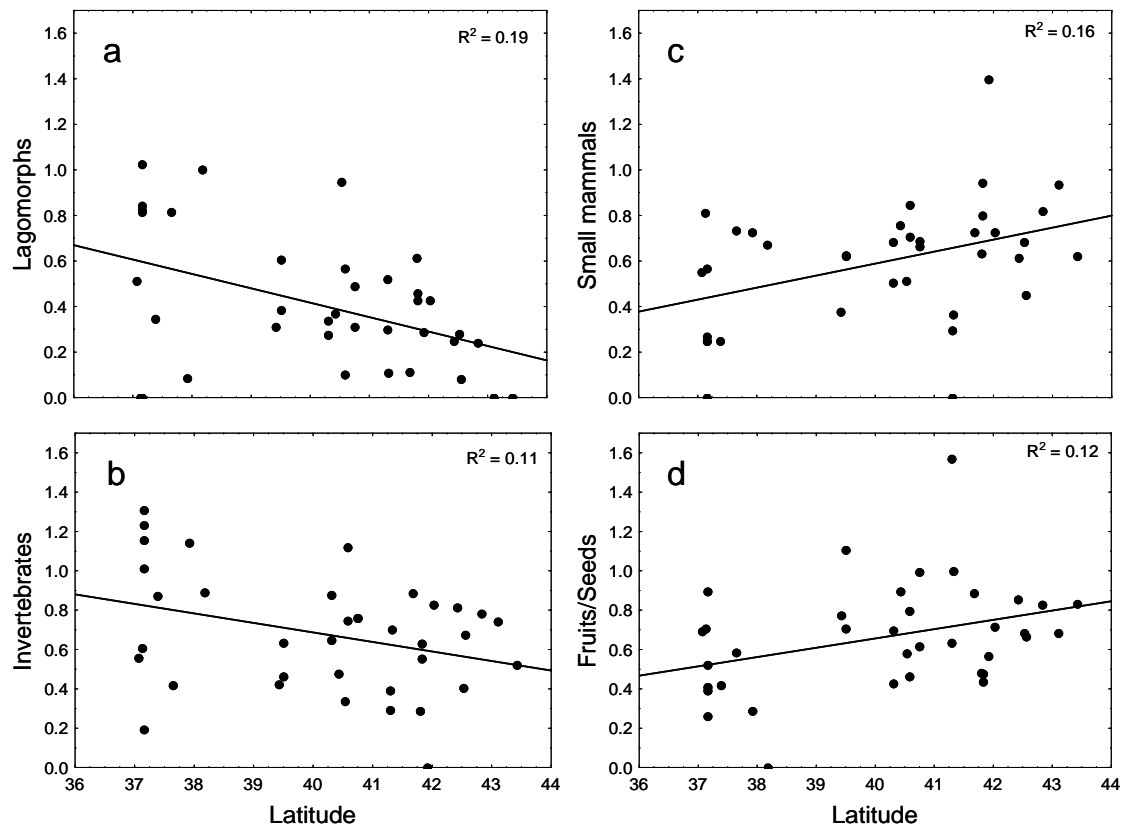
694 **Fig. 6.** Conceptual model illustrating the biogeographical patterns found in the  
695 consumption of the main food groups by the Iberian red fox, in relation to geographical  
696 variables (LAG, lagomorphs; SM, small mammals; F/S, fruits/ seeds; INV,  
697 invertebrates). The white arrows represent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

700 FIGURES

701 FIG.1



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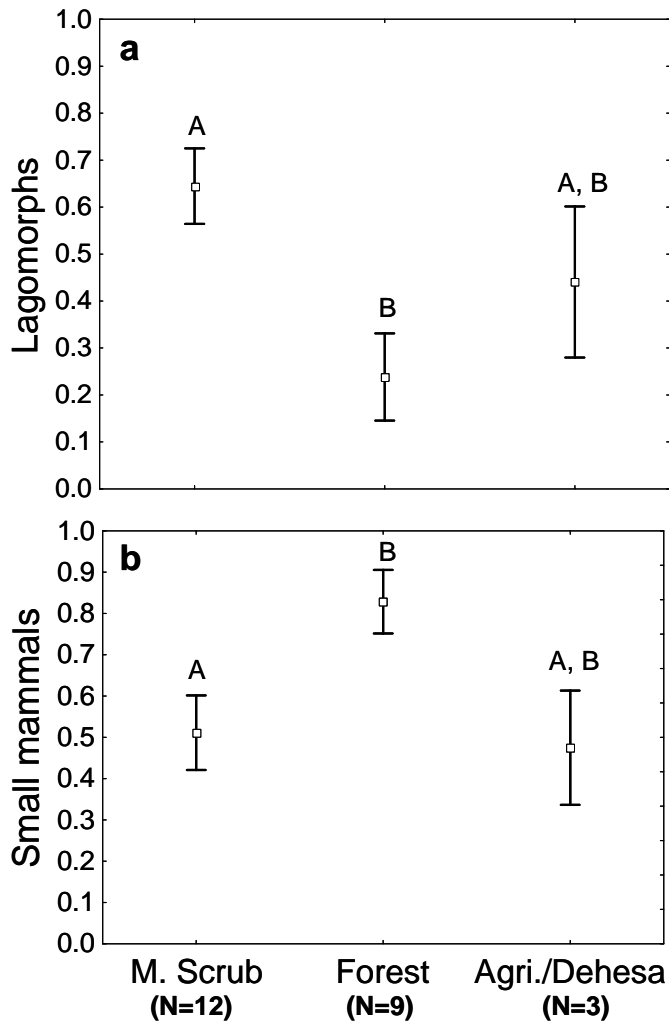
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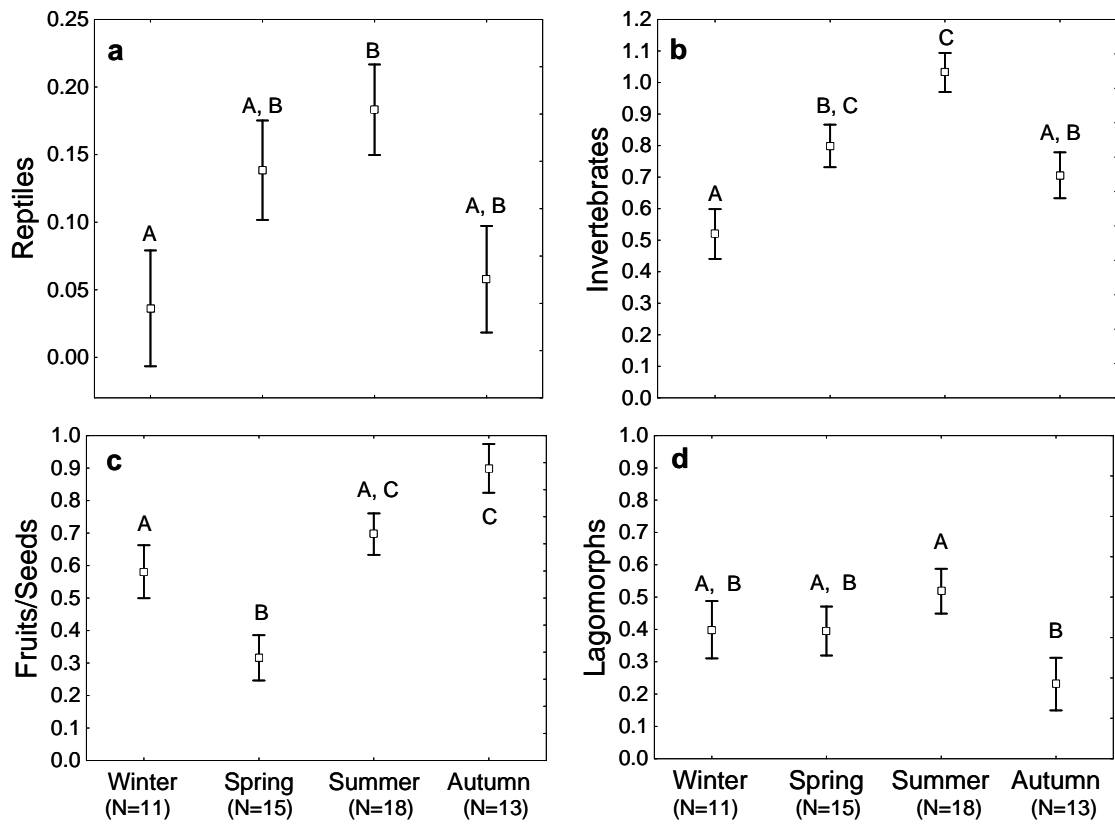


735 **FIG.4**

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768 **FIG.5**  
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774 **FIG.6**  
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