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Landscape influence on the feeding habits of European badger (*Meles meles*) in arid Spain

J. M. Requena-Mullor[1] · E. López[1,2] · A. J. Castro[1,4] · E. Virgós[5] · H. Castro[1,3]

Abstract This study evaluates the influence of landscape on the feeding habits of the European badger (*Meles meles*) in the southern Iberian Peninsula and discusses some potential implications that the scenarios of climate change and land use and land cover changes proposed for this region could have on the diet of badgers. We particularly explore whether different vegetation types and land uses affect its feeding habits across three arid landscapes: *maquia*, *xeric shrubland*, and *forestry*. Although badger diet in Mediterranean environments has been described as frugivorous, in which the key food resources are wild or cultivated fruit (e.g., olives or figs), this species' diet may vary in response to landscape composition, with individuals locally consuming different key items in an arid Mediterranean context. Based on the analysis of 252 scats collected monthly from June 2011 to May 2012, we found that diet significantly varied among the landscapes studied: Insects, carob, and small mammals were the key items in the *maquia*, figs, and oranges in the *xeric shrubland*, and earthworms and insects in the *forestry*. This shows that in an arid context, badgers adapt their diet to particular landscape conditions. Thus, our results support the important role of human activities, specifically the fruit orchards, in shaping badger diet and highlight the contrasting dietary differences of badgers, i.e., from an animal-based diet to one dominated by cultivated fruits when this type of crops are relevant in the landscape. In these circumstances and based on the proven effect of precipitation and land management practices on the food items identified here, we suggest that crop abandonment

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✉ J. M. Requena-Mullor
juanmir@ual.es

E. López
emlopez@ual.es

A. J. Castro
castanto@isu.edu

E. Virgós
emilio.virgos@urjc.es

H. Castro
hcn068@ual.es

[1] Andalusian Center for the Assessment and Monitoring of Global Change (CAESCG), University of Almería, Almería 04120, Spain

[2] Didactics of Experimental Sciences Area, Department of Education, University of Almería, La Cañada de San Urbano, 04120 Almería, Spain

[3] Department of Biology and Geology, University of Almería, La Cañada de San Urbano, 04120 Almería, Spain

[4] Department of Biological Sciences, Idaho State University, Gale Life Sciences Bldg. Rm 207, 921 S. 8th Avenue, Mail Stop 8007, Pocatello, ID 83209, USA

[5] Biodiversity and Conservation Area, College of Experimental Science and Technology, University Rey Juan Carlos, Department 1, Office 216, C/ Tulipán s/n, E-28933 Móstoles, Madrid, Spain

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and less precipitation could reduce the availability of the badger's key food resources, locally affecting its fitness and including local extinction where the habitats are extremely arid or crop abandonment is dominant.

Introduction

Feeding habits of the European badger (*Meles meles*) have been extensively studied and are one of its best-known ecological features (Goszczynski et al. 2000; Virgós et al. 2005a). The diet of this mustelid varies over its distribution range, with a wide assortment of trophic strategies (Melis et al. 2002). The European badger is considered an earthworm specialist forager in Britain and other areas of northwest Europe (Kruuk and Parish 1981; Kruuk 1989; but see Roper 1994), while in the middle latitudes of its distribution range, this specialization is not as strong (Virgós et al. 2005a). In the Mediterranean region, earthworms are less available than in northern Europe due to low precipitation and different landscape composition (Virgós et al. 2004). In these environments, the species is a trophic generalist (Roper 1994), consuming fruits, insects, and vertebrates (Pigozzi 1991; Rodríguez and Delibes 1992; Barea-Azcón et al. 2010). However, badgers also specialize in earthworm consumption in rainy mountainous Mediterranean areas, so it may be considered a locally facultative specialist, taking advantage of the most profitable resource depending on supply and availability (Martín et al. 1995; Virgós et al. 2004).

Apart from the above discussion about the feeding specialization of badgers, it has been suggested that the consumption of earthworms has a more important effect than other trophic resources on life-history traits of the species, such as population density or reproductive success (da Silva et al. 1993; Woodroffe and Macdonald 1993; Virgós et al. 2005a). However, badgers can survive at low densities in extremely arid landscapes, e.g., southeastern of the Iberian Peninsula (Lara-Romero et al. 2012; Requena-Mullor et al. 2014), where earthworms are absent or very scarce. Despite the importance of these regions to obtain a deeper understanding of badger feeding strategies, so far, only two studies investigated badger diet in such arid environments (Rodríguez and Delibes 1992; Barea-Azcón et al. 2010). Rodríguez and Delibes (1992) described the diet only during summer in a landscape with xerophytic vegetation and crops. Barea-Azcón et al. (2010) analyzed the annual diet in a region with a continental climate (14 °C/year and 620 mm/year) but during an especially dry year (250 mm), and in a landscape dominated by olive tree plantations (*Olea europaea*), dense pine reforestation (*Pinus halepensis*), and some holm oak patches (*Quercus ilex*). Both studies emphasized the importance of cultivated fruit and rabbits (*Oryctolagus cuniculus*) in the diet of badgers living in these environments.

Fruit is heavily consumed by badgers in some regions. Rosalino and Santos-Reis (2009) detected an increase in fruit consumption along a west-to-east Mediterranean gradient in a diversified guild of frugivorous mammals including the European badger. These authors argued that fruit consumption depends on several factors, such as characteristics of the fruit (e.g., pulp content), availability of wild and cultivated fruit, and abundance of other food resources (see also Herrera 1989), which vary throughout the Mediterranean basin. In fact, some authors have highlighted cultivated fruit as a key food resource for badgers in Mediterranean arid environments (Pigozzi 1991; Rodríguez and Delibes 1992; Barea-Azcón et al. 2010), making orchards important habitats for the species in these environments (Lara-Romero et al. 2012; Requena-Mullor et al. 2014). Thus, in arid habitats, cultivated fruit could replace earthworms as the key food affecting badger life-history traits, enabling this mustelid to have higher densities.

Badger feeding strategy is very flexible, and they can modify tactics in use if environmental conditions change. The Mediterranean region is especially vulnerable to drivers of global change (Giorgi and Lionello 2008). Aridity is expected to increase in the Iberian Peninsula, especially in already arid zones (Giorgi and Lionello 2008) due to rising temperatures and decreasing rainfall, particularly during summer (De Luis et al. 2001). Furthermore, over half of the area of the Mediterranean region is agricultural (Olesen and Bindi 2002). The 2014–2020 Common Agricultural Policy (CAP) reform outlines steps to promote crop diversification, establish and maintain permanent pastures, and leave some land fallow to restore natural ecological processes (Martínez and Palacios 2012). These measures would benefit the conservation of badger populations in Mediterranean environments (Virgós et al. 2005b). Although the conservation status of this mustelid is now considered of Least Concern (LC) in Spain (Palomo et al. 2007), two major changes could modify Mediterranean regions in the near future. First, most areas of the Mediterranean may become arid habitats (Giorgi and Lionello 2008), and second, much of the current agricultural areas may be abandoned (Castro et al. 2011). Badgers are very closely associated with traditional human activities and agricultural practices, especially in arid environments (Kruuk 1989; Virgós et al. 2005b; Lara-Romero et al. 2012), and consume food items derived directly or indirectly from these agricultural practices. Therefore, the diet of badgers in arid regions of the Mediterranean could be an indicator of what resources would be essentials for badgers in the new scenario of increasing aridity in most of the Mediterranean region, elucidating how changes in agricultural practices can impact on badger diet first and then on other important species traits (Macdonald et al. 2010).

This study explored European badger's diet in different vegetation types and land uses in three landscapes (*maquia*, *xeric shrubland*, and *forestry*) in the southern Iberia Peninsula, which is the arid limit of this species' distribution range, to find out whether they affect its feeding habits.

Materials and methods

Localization and description of landscapes

This study was conducted in the southeastern Iberian Peninsula (36° 06′ N, 2° 17′ E) (Fig. 1), the most arid area in Europe (Armas et al. 2011), with some of the most extremely arid conditions inhabited by badgers. It contains a wide variety of mixed arid environments with rural Mediterranean landscapes. The aridity of target landscapes was characterized based on the Martonne aridity index (Martonne 1926) (I_a), which considers a climate with an I_a of 5 to 15 arid (Requena-Mullor et al. 2014).
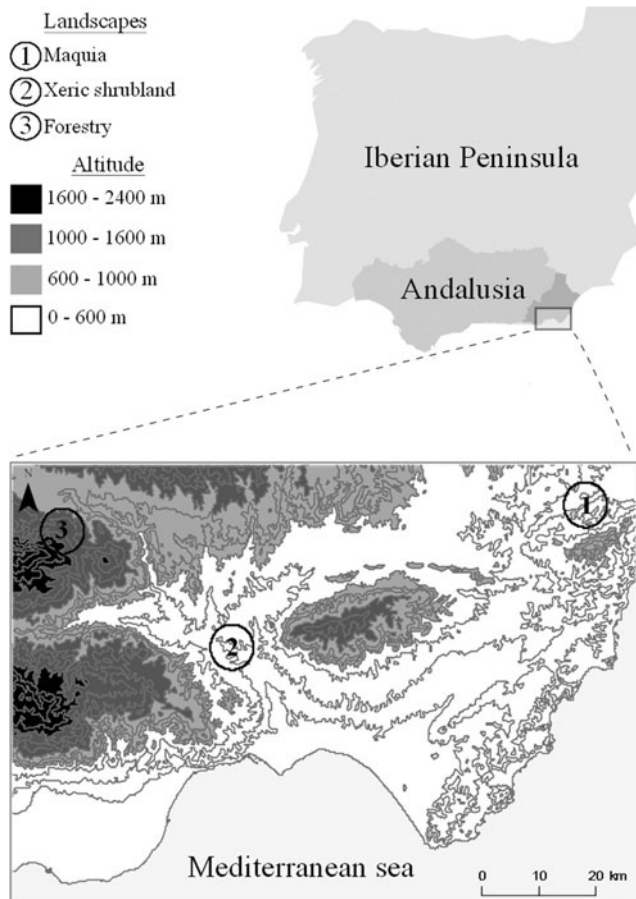

Fig. 1 Location of the three landscapes within the study area in Almería Province, Andalusia, Spain. In each landscape, we identified a zone with latrines frequently used by European badger (*Meles meles*). Then, we drew a 3-km radius buffer zone using the latrines as centroid

On a local scale, the composition of European badger's diet depends primarily on human land use and management (Kruuk 1989; Fischer et al. 2005). Therefore, to compare the diet among landscapes, we selected three landscapes with different land cover and use (*maquia*, *xeric shrubland*, and *forestry*). In each landscape, we first identified a zone with frequently used latrines. Then, we drew a 3-km radius buffer zone around the latrines as the centroids (Fig. 1). This method ensured inclusion of the potential home range size estimated for European badgers living in these poor environments (9 km²) (Lara-Romero et al. 2012). Finally, we characterized the type of land cover and use within the buffers based on GIS cartography acquired from the Land Use and Land Cover Map of Andalusia (scale 1:25,000; 2007).

Regarding potential badger food resources in the study area, the abundance of vertebrates, such as rabbits, is not especially relevant (personal observation based on the low abundance and scattered distribution of burrows and latrines). However, the abundance and richness of insect fauna in the Mediterranean region, which has been described as an important hotspot of this group, are potentially higher (Caterino 2007). In addition, as pesticides are used less in traditional agricultural practices, which are still frequent in the study area, the abundance of arthropods may be greater (Bengtsson et al. 2005). In contrast, in arid Mediterranean landscapes, the availability of earthworms is scarce (Virgós et al. 2005a). The variety of wild and cultivated fruit trees in the three landscapes studied is described below.

Landscape 1: Maquia

Maquia (37° 08′ N, 1° 55′ E) has the lowest altitude (102 m) and an I_a of 11.72 (±0.004). The mean annual rainfall is 340 mm/year and mean annual temperature is 19 °C (rainfall and temperature were calculated for 1971–2000). The area is mainly dominated by nonforested natural vegetation (65 % of the total area) including dense shrubland (e.g., *Macrochola tenacissima*, *Pistacia lentiscus*) and sparse shrubland (*Rhamnus lycioides*, *Anthyllis cytisoides*). Agricultural uses comprise 22 % of the area, in which homogeneous (i.e., no natural vegetation) irrigated and rainfed herbaceous crops in similar proportions are predominant. It is important to highlight the abundance of wild vegetation with fleshy fruits (e.g., *Ceratonia siliqua*, *Ficus carica*, *Chamaerops humilis*, *Vitis* spp., *O. europaea var. silvestris*) in watercourses.

Landscape 2: Xeric shrubland

Xeric shrubland (36° 58′ N, 2° 29′ E) is located at 228 m altitude and has an I_a of 6.98 (±0.012). The mean annual rainfall is 200 mm/year and the mean annual temperature is 18 °C. Seventy percent of the area is covered by sparse xeric shrubland (*M. tenacissima*, *Salsola genistoides*, *Anthyllis*

terniflora). Crops occupy only 12 % of the landscape, of which 44 % are irrigated woody crops (e.g., *Citrus* sp.) and the rest are greenhouse crops. The remaining 18 % of the area is occupied by minority uses (e.g., rural residential areas, herbaceous crops and watercourses).

Landscape 3: Forestry

Forestry (37° 06′ N, 2° 46′ E) is located at 1320-m altitude and has an I_a of 12.54 (±0.028). The mean annual rainfall is 310 mm/year and mean annual temperature is 12 °C. Natural vegetation covers 84 % of the area, with forest (e.g., *Pinus* spp.) and shrublands (e.g., *Genista* spp., *Adenocarpus decorticans*) in similar proportions. Agricultural uses represent 16 % of the total area, in which mosaics of natural vegetation with rainfed crops (*O. europaea*, *Prunus dulcis*) are predominant.

Diet analysis

For the analysis of the diet, scats were collected from badger latrines and their composition was examined in the laboratory. All latrines were emptied at the end of May 2011 before the start of the collection period. Sampling was conducted from June 2011 to May 2012, collecting feces from the latrines in all three target landscapes once a month. In each visit, the number of latrines and scats contained in them was recorded. Individual scats were classified based on their water content, shape, and color. If this was impossible, the entire latrine content was taken as a single scat (Pigozzi 1991). Washing and sieving were carried out according to Kruuk and Parish's (1981) protocol. The total number of items was counted or extrapolated from the remains of each scat, following the methods described by Kruuk and Parish (1981) and Pigozzi (1991). For earthworms in particular, three subsamples of 1.5 mL of the rinse water, after washing and sieving, were taken and washed again into a petri dish, stained with picric acid, and then examined under a ×40 binocular microscope for evidence of the presence of earthworm chaetae. From each 1.5-mL subsample, the volume of earthworms ingested was assessed by counting the number of chaetae in ten 1-cm^2 areas in the petri dish and calculating the mean. Then, the mean number of chaetae was found for the three subsamples of each scat sample and scored as described in Kruuk and Parish (1981). Their proposed correlation equation was used to estimate the number of earthworm gizzards from the chaetae score. Finally, the number of gizzards estimated was used as surrogate of the number of earthworms with the aim to calculate the volume ingested.

Items collected were classified in three broad categories: fruit, vertebrates, and invertebrates. Then, to identify what food resources were dominant within each landscape, a finer classification was made of the food remains to the lowest taxonomic level in each case (i.e., species). The food remains were compared with reference collections to ensure correct taxonomic determination. Lastly, data collected were grouped by season, i.e., summer (June, July, August), autumn (September, October, November), winter (December, January, February), and spring (March, April, May). For all categories (in both the broad and fine classifications), we estimated the percentage of occurrence PO (%) and relative volume RV when present (%), i.e., using the number of scats in which the food category was present. The RV was assessed visually based on Kruuk and Parish's (1981) method. Here, it is important to highlight that both indexes, i.e., PO and RV, should be interpreted together for a proper assessing of the importance of food items. In addition, Shannon's diversity index was calculated for each landscape and season (Shannon 1948):

$$H = -\sum_i P_i * log\,P_i \qquad (1)$$

where P_i = percentage of occurrence for each broad food category. The diversity is minimum when $H = 0$ and is maximum when $H = log\,n$ (n = number of categories). As we had three broad categories, $H\,maximum = 0.47$. To improve the interpretation of H and make comparisons with other studies, we also estimated the Evenness index ($J' = H/H\,maximum$), ranging from 0 (specialist) to 1 (generalist) (Krebs 1989).

Data analyses

Landscape type and seasonal differences in the relative volume of broad categories (i.e., fruits, vertebrates, and invertebrates) were analyzed by a two-way ANOVA with the relative volume of each category calculated by scat as a response variable and the landscape type and season as fixed factors (Virgós et al. 2004). When the effects of landscape or season were significant, a Duncan's test was performed to show in which landscape or season; there were wide differences in the relative volume of each item. All residuals were checked for normality (Shapiro–Wilk normality test) (Shapiro and Wilk 1965) and homogeneity of variances (Bartlett test) (Snedecor and Cochran 1989). In general, the residuals showed nonnormality and heteroscedasticity, so the data were resampled by bootstrapping (10,000 replicates) to estimate F distribution and the critical value for significance (0.05) was recalculated (see Online Resource 1). The partial eta-squared (η^2_p) (Cohen 1973) was also used to estimate the effect size in the ANOVA analysis.

Due to the importance of earthworms to badgers in other areas of its geographic range (Kruuk 1989; Virgós et al. 2004), consumption of this item was analyzed separately so that our data could be compared to other studies.

To find out whether badgers showed preference for a particular food item, the correlations between diet diversity

(measured by the monthly estimate of Shannon's index) and the relative volume of broad categories, diet diversity and main fine categories consumed, and of all broad categories were analyzed using Spearman's *rho* (Best and Roberts 1975).

Finally, similarities in the diet were explored by nonparametric multidimensional scaling (NMDS) based on both spatial (landscapes) and temporal (seasonal) variations. For this, the seasons for each landscape were arranged on a Cartesian axis based on clustering of fruits, vertebrates, and invertebrates (in RV) consumed. A shorter distance between seasons would mean greater similarity and vice versa. The Bray–Curtis distance (d_{jk}) was used to compute the NMDS.

$$d_{jk} = \sum_i |x_{ij} - x_{ik}| / \sum_i (x_{ij} + x_{ik}) \qquad (2)$$

where x is the RV (%) of food category i (i.e., fruits, vertebrates, invertebrates) in j and k seasons. To check the goodness of NMDS, we measured the agreement in the rank order of the inter-season distances observed and those predicted from the similarities. One measure of fit is Kruskal's stress (Kruskal 1964). According to Clarke's (1993) guidelines for stress values, a value over 0.3 would indicate that the configuration found is no better than random.

All statistical analyses were carried out using R software version 2.14.2 (R Development Core Team 2014).

Results

Diet composition

A total of 252 feces were collected, 54 in *maquia*, 140 in *xeric shrubland*, and 58 in *forestry* (Table 1) from 31, 64, and 27 latrines, respectively. In *maquia*, fruits were consumed throughout the year (annual PO = 81 %) (Fig. 2), although the mean RV was greatly reduced in summer (RV = 29.3 % ± 4.7 SE). Carobs were the most frequent fruits in excrements (Table 1). Grapes (summer), carobs (autumn and winter), and oranges (spring) were the fruits with the highest mean relative volume. Vertebrates were more frequent in spring (PO = 72.7 %). Small mammals (e.g., rodents) were the main prey with an important mean volume in spring and winter. Invertebrates were very frequent in summer (PO = 100 %) (mainly Coleoptera), but with a low mean volume.

In *xeric shrubland*, fruits were the key food resource for badgers both in terms of percentage of occurrence (annual PO = 95.0 %) and relative volume (mean annual RV = 73.4 % ± 2.5 SE) (Fig. 2). The two main types of fruits consumed were figs (from summer to autumn) and oranges (from winter to spring) (Table 1). Vertebrates were not very relevant throughout the year and only appeared in any considerable volume in summer (mean RV = 73.8 % ± 18.2 SE), when rabbits (RV = 87.5 % ± 2.5 SE) were the predominant food

resource. Invertebrates were more frequent in spring (PO = 70.9 %) and winter (PO = 54.5 %), although with no important volume in any season (mean annual RV = 17.6 % ± 2.0 SE). Orthoptera was the invertebrate prey eaten most frequently year round (annual PO = 34.0 %).

In *forestry*, there was high consumption of invertebrates throughout the year (annual PO = 86.0 %), although relative volume was low (mean annual RV = 36.0 % ± 3.0 SE) (Fig. 2). Scorpions (PO = 50.0 %; mean RV = 35.8 % ± 5.8 SE) (summer), Hymenoptera (PO = 60.0 %; mean RV = 54.0 % ± 11.6 SE) (autumn), earthworms (PO = 53.3 %; mean RV = 81.8 % ± 5.0 SE) (winter), and caterpillars (PO = 66.6 %; mean RV = 44.1 % ± 8.4 SE) (spring) were the most relevant invertebrates (Table 1). Fruits were consumed mainly in autumn (PO = 70.0 %), when figs (mean RV = 60.0 % ± 5.8 SE), wild blackberries (mean RV = 90.0 % ± 10.0 SE), and almonds (mean RV = 50.0 % ± 20.0) (fleshy pericarp) were most abundant. The relative volume of fruits was considerable throughout the year (mean annual RV = 62.0 % ± 6.6 SE). Vertebrates were consumed more frequently in spring (PO = 57.1 %). Spring and winter were the seasons with the highest volume of vertebrate remains in the feces (mean RV = 53.4 % ± 11.1 SE and mean RV = 61.3 % ± 12.3 SE, respectively), mainly reptiles and rabbits.

Effects of landscape and season on diet

Fruit consumption was statistically significantly different for landscape and season when the two factors were taken separately; however, there was no significant interaction between them (Table 2). Relative volume was higher in *xeric shrubland* than in *maquia* (Duncan's test, $p < 0.01$). Moreover, more fruit was consumed in winter than in summer (Duncan's test, $p < 0.01$).

We also observed significant differences in the consumption of vertebrates among landscapes, but not among seasons (Table 2). A significantly higher relative volume of vertebrates was consumed in the *maquia* than in *xeric shrubland* (Duncan's test, $p < 0.01$).

Differences in invertebrate consumption were observed between landscape and season even though the interaction was nonsignificant (Table 2). More invertebrates were consumed by badgers in *forestry* than those in *maquia* or *xeric shrubland* (Duncan's test, $p < 0.01$). Invertebrates were consumed in larger quantities in spring than in autumn (Duncan's test, $p < 0.05$). Due to the small number of scats collected in some seasons (mainly summer and autumn in *maquia* and *forestry*) (Table 1), seasonal variation in the diet should be interpreted with caution.

Earthworms were consumed in the three landscapes but always infrequently (mean annual PO = 3.7 %, 2.8 and 17.2 % for *maquia*, x*eric shrubland*, and *forestry*, respectively) (Table 1). However, the relative volume was high (mean annual RV = 90.0 % ± 10.0 SE, 50.0 % ± 12.2 SE, and

Table 1 Percentage of occurrence (%) and mean relative volume (%) values for the different fine food categories considered in each landscape and season. We reported values of percentage of occurrence for comparative purposes with other studies using these categories. In parentheses count of scats collected in each season and landscape

	Maquia								Xeric shrubland								Forestry							
	Summer (6)		Autumn (12)		Winter (25)		Spring (11)		Summer (26)		Autumn (15)		Winter (44)		Spring (55)		Summer (12)		Autumn (10)		Winter (15)		Spring (21)	
	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV
Fruits																								
Olea europaea	50.0	18.3	25.0	10.0	16.0	47.5	18.1	57.5	0.0	0.0	6.6	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chamaerops humilis	33.3	5.0	33.3	34.5	28.0	52.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceratonia siliqua	66.6	30.0	58.3	81.7	28.0	96.4	63.6	31.7	7.6	5.0	6.6	96.0	4.5	97.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vitis sp.	33.3	47.5	16.6	37.5	0.0	0.0	0.0	0.0	11.5	46.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ficus carica	33.3	35.0	33.3	52.0	0.0	0.0	0.0	0.0	73.0	78.4	93.3	94.2	84.0	80.0	0.0	0.0	0.0	0.0	30.0	60.0	0.0	0.0	0.0	0.0
Citrus sinensis	0.0	0.0	0.0	0.0	8.0	60.0	18.1	62.5	0.0	0.0	0.0	0.0	0.0	0.0	67.2	83.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Opuntia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.4	45.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Malus domestica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	26.9	51.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phoenix dactylifera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	15.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Annona cherimola	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prunus armeniaca	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.8	44.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eriobotrya japonica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Juglans regia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Morus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	33.3	70.0	20.0	90.0	0.0	0.0	0.0	0.0
Prunus dulcis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	20.0	50.0	0.0	0.0	4.7	50.0
Castanea sativa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.6	5.0	0.0	0.0
Others	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.3	27.2	0.0	0.0	11.3	57.0	3.6	95.0	0.0	0.0	30.0	20.0	33.3	80.0	0.0	0.0
Vertebrates																								
Birds	16.6	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.6	10.0	4.5	20.0	5.4	31.6	0.0	0.0	0.0	0.0	0.0	0.0	4.7	10.0
Eggs	33.0	15.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	30.0	0.0	0.0	0.0	0.0	0.0	0.0
Rodents	0.0	0.0	16.6	45.0	40.0	82.5	54.5	70.1	3.8	20.0	6.6	30.0	15.9	49.2	9.0	22.0	8.3	30.0	20.0	30.0	20.0	53.3	14.2	46.6
Rabbits	0.0	0.0	0.0	0.0	8.0	42.5	0.0	0.0	7.6	87.5	0.0	0.0	0.0	0.0	1.8	35.0	0.0	0.0	0.0	0.0	0.0	0.0	9.5	100.0
Reptiles	0.0	0.0	0.0	0.0	0.0	0.0	18.1	45.0	0.0	0.0	0.0	0.0	2.2	10.0	5.4	13.3	0.0	0.0	10.0	20.0	6.6	85.0	28.5	46.6
Anuran	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Invertebrates																								
Orthoptera	33.3	4.0	16.6	19.0	4.0	10.0	18.1	12.5	15.4	6.2	20.0	8.3	25.0	18.1	54.5	38.0	25.0	28.3	10.0	10.0	53.3	11.8	0.0	0.0
Coleoptera	100.0	25.3	25.0	10.0	12.0	11.6	0.0	0.0	15.4	8.0	20.0	5.0	18.1	8.1	32.7	19.4	58.3	52.8	10.0	5.0	13.3	17.5	28.5	25.8
Buthus occitanus	16.6	10.0	16.6	5.5	4.0	10.0	0.0	0.0	7.6	7.5	0.0	0.0	0.0	0.0	0.0	0.0	50.0	35.8	10.0	50.0	0.0	0.0	4.7	5.0
Isopoda	50.0	4.3	25.0	7.0	0.0	0.0	0.0	0.0	3.8	5.0	0.0	0.0	0.0	0.0	0.0	0.0	16.6	5.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	0.0	0.0	16.6	4.0	0.0	0.0	27.2	6.0	0.0	0.0	6.6	2.0	0.0	0.0	1.8	30.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 1 (continued)

	Maquia								Xeric shrubland								Forestry							
	Summer (6)		Autumn (12)		Winter (25)		Spring (11)		Summer (26)		Autumn (15)		Winter (44)		Spring (55)		Summer (12)		Autumn (10)		Winter (15)		Spring (21)	
	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV	PO	RV
Lumbricus sp.	0.0	0.0	0.0	0.0	8.0	90.0	0.0	0.0	0.0	0.0	0.0	0.0	6.8	30.0	1.8	60.0	0.0	0.0	0.0	0.0	53.3	81.8	9.5	61.0
Hymenoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.6	4.0	0.0	0.0	4.5	30.0	3.6	7.5	41.6	27.8	60.0	54.2	20.0	16.6	57.1	33.3
Arachnida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Odonata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	15.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.6	0.0	0.0	0.0	0.0	0.0	0.0
Caterpillars	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	10.0	0.0	0.0	66.6	44.1
Others	0.0	0.0	0.0	0.0	0.0	0.0	9.0	84.0	0.0	0.0	0.0	0.0	4.5	10.0	1.8	10.0	0.0	0.0	0.0	0.0	6.6	15.0	0.0	0.0

77.7 %±4.8 SE for *maquia*, *xeric shrubland*, and *forestry*). Relative volume only differed among seasons (ANOVA, $F = 59.2$, $p < 0.0001$) and was higher in winter than in spring (Duncan's test, $p < 0.0001$).

Diet diversity

Diet diversity was similar in the three landscapes, and according to the Evenness index, badger diet was gradually more generalist, from *xeric shrubland* ($H = 0.30$; $J' = 0.64$) to *forestry* ($H = 0.37$; $J' = 0.79$) and finally *maquia* ($H = 0.39$; $J' = 0.83$). Diet diversity was positively correlated with fruit and vertebrate consumption ($rho = 0.44$, $p = <0.001$, $n = 36$; $rho = 0.58$, $p < 0.001$, $n = 36$) and not correlated with invertebrate consumption ($rho = -0.17$, $p = 0.30$, $n = 36$). Highly consumed food resources (e.g., carobs, figs, oranges, coleopteran, and earthworms; see Table 1) showed no correlation with diet diversity, except rodents which were positively correlated ($rho = 0.41$, $p < 0.05$, $n = 36$). Relative volumes of fruits and invertebrates in broad categories were negatively correlated ($rho = -0.41$, $p < 0.05$, $n = 36$), indicating higher consumption of fruits in landscapes where, or during seasons when, invertebrates are not very important in the badger diet. There was no correlation between fruits and vertebrates ($rho = -0.03$, $p = 0.84$, $n = 36$) or vertebrates and invertebrates ($rho = -0.10$, $p = 0.53$, $n = 36$).

Nonparametric multidimensional scaling

The spatial configuration found by NMDS (Fig. 3) was better than random (Kruskal's stress < 0.2). By season, summer in the *maquia* (mean $d_{jk} = 0.37$) and autumn in the *xeric shrubland* (mean $d_{jk} = 0.31$) were the farthest apart (Fig. 3 and Table 4 in Online Resource 2).

Distance between seasons in diet was greatest in the *maquia* (mean $d_{jk} = 0.34$), while in the *xeric shrubland*, the distances were intermediate (mean $d_{jk} = 0.26$) and, in the *forestry*, the seasons were the closest (mean $d_{jk} = 0.15$) (Table 4 in Online Resource 2). Summer in the *maquia* and autumn in the *xeric shrubland* showed the lowest Shannon's diversity index (0.26 and 0.27, respectively) (Fig. 3).

Discussion

Despite the arid environmental features common to all three locations, badger diet varied significantly across the three landscapes and one or two dominant food resources were identified in each. This supports Virgós et al.'s (2004) findings in other Mediterranean areas, where badger feeding behavior varied even in locations which were close to each other but were characterized by different habitat types, rainfall regimens, or human land uses.

Fig. 2 Mean relative volume (%) for each broad food category whenever it was eaten vs. percentage of occurrence. Isopleths connect points of equal relative volume in the overall diet of the badger. Landscapes showed: *Maquia* (*black*), *xeric shrubland* (*gray*), and *forestry* (*white*)
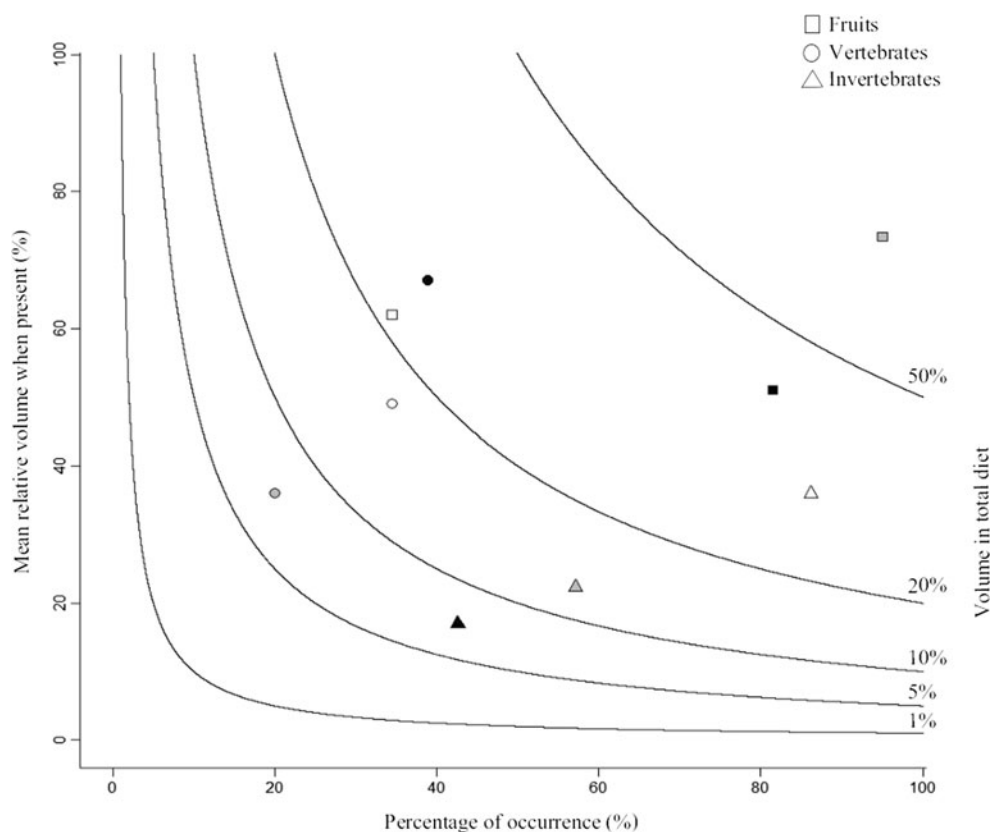
We found that in *maquia*, badgers were mainly frugivores, although vertebrates were also important in winter and spring. This feeding pattern has also been described in other Mediterranean areas (Pigozzi 1991; Rosalino et al. 2004). Carobs were the fruit most consumed throughout the year. This is the first time that this food resource is described in this type of landscape. Carobs were available and abundant all year long (personal observation), highlighting the generalist-opportunist character of the European badger (Kruuk 1989;

Table 2 Results of the two-way ANOVA with season and landscape type as fixed factors and the relative volume of the broad food categories as the response variable. No effect varied its significance by applying the bootstrap resampling (see Table 3 in Online Resource 1)

Relative volume	Effect	df	F	p value	η^2_p [(*)]
Fruits	Season	3	4.04	<0.01	0.06
	Landscape	2	13.3	<0.001	0.11
	Season × landscape	6	1.22	0.29	0.03
Vertebrates	Season	3	2.07	0.11	0.09
	Landscape	2	5.56	<0.01	0.16
	Season × landscape	6	1.36	0.24	0.12
Invertebrates	Season	3	2.85	<0.05	0.04
	Landscape	2	11.61	<0.001	0.09
	Season × landscape	6	1.96	0.07	0.05

[(*)] η^2_p partial eta-squared

Pigozzi 1991). However, fruit consumption was lower than in the *xeric shrubland*, and fruit consumed was mainly wild, so the direct dependence of badgers on orchards would be less decisive. Small mammals were the second most important item, probably providing the necessary proteins in a vegetarian diet (Ciampalini and Lovari 1985).
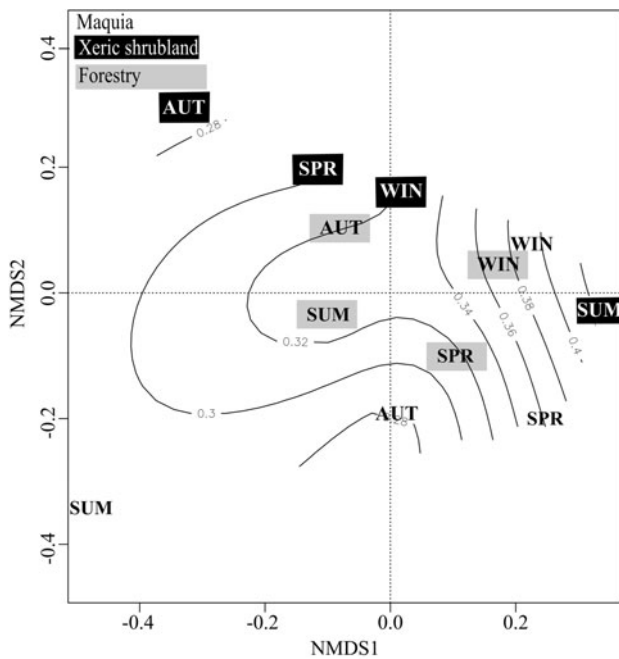
In *xeric shrubland*, fruits, especially cultivated, were the most important food resource. Oranges from winter to spring and figs from summer to autumn were the items most consumed. While figs have been described in dry Mediterranean landscapes as a usual food resource for badgers (Barea-Azcón et al. 2010), this is the first time that oranges are described in these environments. The *xeric shrubland* is the most arid of the case studies and, therefore, reinforces the importance of orchards for the survival of badgers in these environments (Lara-Romero et al. 2012).

In *forestry*, badger diet was dominated by insects in terms of percentage of occurrence, but fruits prevailed again when relative volume was taken into account. Heavy consumption of insects supports findings by Virgós et al. (2004) in some of the habitats sampled in the mountainous areas of central Spain. However, the relevance of fruit in this habitat as well highlights the key importance of this food resource for badgers in all three arid landscapes. When badgers preferentially consume the same type of food resource, such as fruits in *xeric shrubland* or invertebrates in *forest*, all year long, the similarity

SUM: summer; AUT: autumn; WIN: winter; SPR: spring. NMDS: estimated distances
Isopleths connect points with the same value of Shannon´s diversity index.

Fig. 3 Nonparametric multidimensional scaling (*NMDS*). The axes NMDS1 and NMDS2 show the range of distances reached between seasons in the three landscapes. Seasons are arranged so that the distances between them are as close to the real differences between the mean relative volume (%) of fruit, vertebrates, and invertebrates consumed in each landscape. A lower distance between seasons means greater similarity between them, whereas a longer distance corresponds to a greater dissimilarity. Isopleths are based on Shannon's diversity index

in diet among the seasons is closer. On the other hand, *maquia* showed the greatest distances between seasons (e.g., summer vs. winter) and the most diversified diet, suggesting that the availability of the food resources was not constant between seasons. Under these circumstances, i.e., marked seasonal fluctuations in the availability of the most important food resources, badgers change their food choice so as to maximize their intake from available food resources (Pigozzi 1991).

Olives were not relevant in any of the three landscapes. This disagrees with findings in other Mediterranean areas (Kruuk and de Kock 1981; Rosalino et al. 2004; Barea-Azcón et al. 2010). This may be due to their low availability in the sampled localities (personal observation) and could be expected of a generalist (or facultative specialist) species such as European badger (Pigozzi 1991).

In arid Mediterranean landscapes, the availability of earthworms is scarce (Virgós et al. 2005a). Our results show that badgers consumed this item in *maquia* and *xeric shrubland*, supporting observations made by Barea-Azcón et al. (2010) in another Mediterranean area. In *forestry*, the consumption of earthworms was even higher than in the other landscapes. This difference may be due to greater availability of earthworms in mid-mountain areas with the heavier rainfall at higher altitudes

(Virgós et al. 2005a). However, the consumption of earthworms was not uniform over the year, appearing only in winter and spring, because this prey is mainly available in the rainy and mild conditions of spring and autumn-winter (Edwards and Lofty 1977; Kruuk and Parish 1981). All these results combined reinforce the usefulness of this trophic resource for badgers when available and its strong importance even in the extremely arid conditions of the southern edge of its distribution range, contradicting previous ideas about the lack of importance of earthworms in most of the European badger's southern range (Ciampalini and Lovari 1985; Pigozzi 1991; Roper 1994; Martín et al. 1995; but see Virgós et al. 2004).

Our results show that diet diversity did not decrease with the consumption of the main food items consumed (e.g., carobs, figs, oranges, coleopteran, earthworms, or rodents). This supports the generalist character of badgers in the arid Mediterranean environments described by Rodríguez and Delibes (1992) and Barea-Azcón et al. (2010). Despite the strong importance of fruit, this cannot be viewed as of equal importance to earthworms or rabbits in other areas, where diversity is strongly associated with the consumption of these resources (Kruuk 1989; Martín et al. 1995). On the other hand, fruits and invertebrates showed a negative correlation. An explanation for this could be that badgers compensate for the shortage of fruits with invertebrates (mainly insects which are abundant and their availability predictable). This aligns with a similar feeding strategy exhibited by badgers in the mountains of central Spain where earthworms are scarce (Virgós et al. 2004).

Regarding the potential bias derived from the small sample size in some seasons surveyed (mainly in summer and autumn in *maquia* and *forestry*), we have also provided the effect sizes of the seasonal ANOVA analysis which support the interpretation of p values (potentially affected by sample size) (Nakagawa and Cuthill 2007). Regarding the possible number of individuals in our study, in landscapes where habitat is not very suitable, as in much of arid southeast Spain, badgers are not abundant (Lara-Romero et al. 2012) and the densities do not usually exceed 1 badger/km^2 (Revilla et al. 2001). In these environments, badgers live alone or in pairs (male and female) (Revilla et al. 2005). Therefore, the latrines are expected to have been used by at most two individuals in each landscape surveyed, especially in the breeding season. This assumption is supported by camera trap data (personal observation). Thus, due to the potential number of badgers represented in the study, our data may not be fully representative of badger feeding habits in Mediterranean arid environments and there may be individuals with different feeding habits. However, the overall results were consistent with previous knowledge of badger diet in these environments (see for example Rodríguez and Delibes 1992; Virgós et al. 2004; Barea-Azcón et al. 2010). These authors studied badger diet in landscapes with similar expected abundance for the badger; likewise, our results can be also consistent, although the reader should be aware of its limitations.

Climate change and land use change have been described as two of the main direct drivers of global change in Mediterranean environments (Vitousek 1994; Giorgi and Lionello 2008). On one hand, it has been proven that the abundance of European badgers is related to climatic characteristics (Virgós and Casanovas 1999) and seasonality (Johnson et al. 2002). On the other hand, the composition of badger diet depends on the land management and use (Fischer et al. 2005), particularly in agricultural areas (Rosalino et al. 2004; Barea-Azcón et al. 2010). In this sense, a reduction in key food resources from crop abandonment or intensification and less precipitation could affect the regional occurrence and abundance of the badger and locally reduce their fitness (Kruuk and Parish 1985; Virgós et al. 2005b), including local extinction where habitats are extremely arid. Many of the items consumed by badgers across the three landscapes (e.g., carobs, figs, blackberries, fan palm fruits, earthworms) depend directly or indirectly (e.g., insects, small mammals, rabbits) on precipitation. Traditional Mediterranean agricultural practices provide the badgers with food resources such as oranges or olives which depend directly on irrigation and others such as figs, loquats, apples, and apricots that depend indirectly on irrigation. In addition, because of a lower use of pesticides, traditional agricultural practices also offer a wide diversity and abundance of arthropods (Bengtsson et al. 2005).

In conclusion, this study shows that in an arid context, badgers adapt their feeding behavior to the particular landscape conditions, and specifically, they shift from an animal-based diet to one dominated by cultivated fruits. This result supports the important role of human activities in shaping badger behavior and diet and highlights the contrasting dietary habits of badgers living in more pristine habitats versus those inhabiting human-made habitats. We also found that two food resources (i.e., oranges and carobs) are very important to the diet and are described here for the first time as key food resources to the European badger in Mediterranean arid landscapes.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

For this type of study, formal consent is not required.

This article does not contain any studies with human participants or animals performed by any of the authors.

Finally, this manuscript is original work which has not been submitted elsewhere. All authors agree with the content and to the submission, and any research in the paper not carried out by the authors is fully acknowledged.

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