



Original investigation

Dietary shifts of the badger (*Meles meles*) in Mediterranean woodlands: an opportunistic forager with seasonal specialisms

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Abstract

Accumulating publications on the feeding ecology of the Eurasian badger (*Meles meles* Linnaeus, 1758) in different habitats throughout Europe provide a basis for intra-specific comparisons, however, none has described their diet in cork oak “montado” woodlands, found in the southwestern extreme of the species’ distribution. This study aims to understand how badgers use the available trophic resources in “Serra de Grândola” (SW Portugal) and is based on 450 scat samples collected between 1999 and 2000. Nine food-items were identified, 3 of which comprise 89% of the biomass ingested by badgers in the cork oak woodland: fruits (mainly olives, pears and figs), and adult and larval arthropods. Food abundance was measured, and was shown to fluctuate seasonally; the comparison between availability and consumption suggests that food selection is affected by the pattern of olive availability. These findings reinforce the accumulating evidence that badger ecology in many parts of Europe is heavily affected by local patterns of agriculture and reveal that in this habitat the badger is a generalist forager with seasonal specialisms.

Key words: *Meles meles*, badger, diet, Mediterranean environments, cork oak woodlands

Introduction

Identifying the pattern of resource use by species is a fundamental step in unravelling community organization, the pattern of species coexistence, and niche structure (TOKESHII 1999). In this context, because food is a crucial niche dimension, describing feeding ecology is essential (KREBS 1989). Adaptations to trophic circumstances will be complicated where food types are diverse, patch-

ily distributed and unpredictably available, all of which are characteristics of “montado” (woodlands of cork oak *Quercus suber*), a semi-natural agro-forest system adapted to Mediterranean conditions (PINTO-CORREIA 2000). This is particularly important when considering carnivores because they tend to have the characteristics of umbrella species (SCHONEWALD-COX et al. 1991).

The badger, *Meles meles*, has an extensive Eurasian distribution (NEAL and CHEESEMAN 1996). In some parts of western Europe this carnivore is regarded as an extreme specialist, feeding on one species of earthworm, *Lumbricus terrestris* (KRUUK and PARISH 1981), a prey species whose great abundance can make it an influential component of lowland agricultural ecosystems (MACDONALD 1984). In Mediterranean areas previous studies have reached contradictory conclusions about the badger's trophic classification, with some authors labelling it as a generalist (e.g. CIAMPALINI and LOVARI 1985) whereas others regard it as a specialist (e.g. KRUUK and DE KOCK 1981; MARTÍN et al. 1995). REVILLA and PALOMARES (2002) may provide one, essentially methodological, explanation of these seemingly contradictory views: they suggest that short-term studies, underestimating temporal variability, can lead to a false impression of local specialization. Alternatively, badgers may not be constrained to a given classification, but may be specialists in some circumstances and generalists in others (see reviews by KRUUK 1989, and WOODROFFE and MACDONALD 1993). Indeed, GOSZCZYNSKI et al. (2000) identified trends in latitudinal variation of the badger's feeding habits, and extrapolating from these we might expect badgers in this western Mediterranean woodland habitat to be generalist feeders. Our aim, therefore, is to describe how Eurasian badgers exploit the available food resources in the Portuguese cork oak woodlands or "montado" systems. Although published data from the Iberian Peninsula already exists (e.g., FEDRIANI et al. 1998; MARTÍN et al. 1995), it regards Southwest Spain, in areas dominated mainly by extensive marshes, dunes systems, xerophytic scrubland and pine stands, being cork oaks just scattered throughout the landscape. The relevance of the "montado" is heightened because it is the major remaining wood-pasture system of Europe (GROVE and RACKHAM 2003). Indeed, this traditional landscape has mounting significance to conservation as its future is threatened by the exodus of rural populations.

Material and methods

Study area

The study area, with a size of 66 km², is located near the south-western coast of Portugal, 115 km south of Lisbon, in the eastern slope of "Serra de Grândola". The relief of the region is gently undulating, with 0–15% slopes and elevations of 150 to 270 m a.s.l., and the climate is semi-arid, with mild winters and hot, dry summers (Mediterranean). Mean annual temperature is 15.6 °C and mean precipitation is 500 mm/year (CORREIA and SANTOS-REIS 1999). This region is mostly covered by cork oaks – "montado" – with an understory of Mediterranean shrubs (*Cistus* spp., *Lavandula* spp., *Erica* spp., etc.) or pasture. A network of valleys with riparian vegetation (mainly *Populus* spp., *Fraxinus angustifolia* and *Rubus ulmifolius*) cross the area and many small orchards and olive groves (*Olea europaea*) can be found around farms, most of which are now abandoned (CORREIA and SANTOS-REIS 1999). These last patches are small sized and scattered. The orchards are composed of fruit trees, especially fig (*Ficus carica*), loquats (*Eriobotrya japonica*), plums (*Prunus* spp.), orange-trees (*Citrus sinensis*) and quinces (*Cydonia oblonga*). Patches of wild berry-bearing bushes and pear-trees (*Pyrus bourgaeana*) are scattered throughout the area; blackberries (*R. ulmifolius*) are restricted to valleys with riparian vegetation; and strawberry-trees (*Arbutus unedo*) are limited mainly to patches of original Mediterranean woodlands. Although the landscape was created by the local system of agro-forestry, human population density is now low and principal activities are cork extraction, cattle raising and hunting.

Diet analysis

Between January 1999 and December 2000 all badger latrines found in the study area were monitored, and faecal samples (n = 450) collected fortnightly. Scat samples were processed following standard analytical procedures (e.g. KRUUK and PARISH 1981; ROSALINO and SANTOS-REIS 2002) and the recommendations of REYNOLDS and AEBISCHER (1991). Skeletal remains of vertebrates and arthropods, hairs, feathers, scales and seeds were used to identify the materials consumed (SANTERO and ALVAREZ 1985; BROM 1986; BARRIENTOS 1988; TEERINK 1991; our own collection) and estimate the minimum number of individuals/fruits eaten (e.g. number of teeth, seeds, etc.), a parameter used to calculate percentage of occurrence. Earthworm's remains were detected

by microscopic examination for chaetae (see KRUK and PARISH 1981). Several samples (0.1 ml each) were examined, and the number of chaetae in each counted. Subsequently, this number was extrapolated for all the scat samples' volume. The number of earthworms was attained by dividing the number of chaetae in a scat by the mean number of chaetae in an earthworm (WROOT 1985). Undigested remains were categorised in 9 food-items: mammals, birds, reptiles, amphibians, annelids, molluscs, arthropods (adults and larvae) and fruit.

Diet composition was expressed as the percentage of occurrence [$PO = (\text{number of individuals or fruits of the same species or taxonomic group} \times 100) / (\text{total number of consumed items})$] and as the percentage of fresh weight biomass intake [$PB = (\text{ingested biomass of the same species or taxonomic group} \times 100) / (\text{total consumed biomass})$] (REYNOLDS and AEBISHER 1991; ROSALINO and SANTOS-REIS 2002).

To estimate biomass intake we calculated correction factors, also called digestibility coefficients (DC), derived from mean ratios of fresh mass eaten and dry weight in faeces obtained in the frame of a feeding trial during which representative local foods were fed to a captive adult male badger (ROSALINO et al. 2003). For untested resources we used DC values previously published (PALOMARES and DELIBES 1990; REVILLA 1998; GOSZCZYNSKI et al. 2000), or the mean weight of prey/fruits (pers. obs. for gastropods and plums; OMEDES et al. 1997 for Columbiformes; GOSZCZYNSKI et al. 2000 for Passeriformes; J. C. BRITO pers.comm. for reptiles).

Resource availability

Relative abundance of the key resources (adult arthropods and fruit) was analysed in order to investigate food preferences.

For ground dwelling arthropods, such as ground beetles, diversity and relative abundance were evaluated using pitfall trapping (BENEST 1989). Pit-fall traps were placed in the four dominant habitats (cork woodland without understory; cork woodland with understory; pasture; riparian vegetation) following WESTERBERG'S (1977) recommendations: 24 traps per habitat (3 sites \times 8 pitfalls) with traps separated by 1 m during 8 consecutive days per season. Each pit-fall consisted in a receptacle containing water, formalin (4%) and soap. The formalin acted as a preservative with no known repellent or attractant properties (WAAGE 1985); the soap breaks the surface tension of the water, making the insects drown more ra-

pidly (BASEDOW 1976). To facilitate the capture of badger's main insect prey (Coleoptera), all pitfalls were baited with herbivore droppings. The pitfall traps were active every three months (one trapping session per season), for 5 seasons. This methodology was designed to provide relative measures of the availability of arthropods between seasons.

Fruit production was estimated monthly from the number of ripe fruits on the ground within a pre-defined square meter under each sample tree. Tree species were sampled in proportion to their abundance in the field, determined by the degree of cover of the habitats containing those fruit-trees: cork oaks – 40 trees; olive-trees – 30; pear-trees – 20.

Data analysis

Results were analysed by year (1999–2000) and season (winter: January to March; spring: April to June; summer: July to September; and autumn: October to December). Representative sampling for temporal comparisons was tested, after randomisation, by plotting the cumulative frequency of resource items against increase in sample size (MASON and MACDONALD 1980). Sub-sample size homogeneity was tested using chi-square tests (ZAR 1999).

Absolute frequency of the food categories was compared between seasons and years using Yates' correction for continuity applied to a modified chi-square test (SIMPSON et al. 1960). Food diversity was evaluated using the Shannon-Wiener index (H'), ranging from 0 (specialists) to $H'_{\max} = \log_{2n} \text{ of categories}$ (generalists), and the Evenness index (J'), ranging from 0 (specialists) to 1 (generalists), (KREBS 1989). In order to compare our results with the feeding model of GOSZCZYNSKI et al. (2000), we also used the Levins index (B), which ranges from 1 (specialists) to n (generalists), where n is the number of food item categories.

H' values of sub-samples were compared with Hutcheson t-test (ZAR 1999), and trophic niche overlap was calculated on the basis of Morisita index (C), that ranges from 0 (null niche overlap) to 1 (full niche overlap) (KREBS 1989), a measure least biased under changing numbers of resources, sample size, and evenness of resource distribution (SMITH and ZARET 1982). In all indices formulas a base ten logarithms were used.

The contribution of resource-type, season and year variables to explain observed variability in diet composition (expressed as PB) was evaluated through a generalized linear model (GLM – Pois-

son model) (TABACHNICK and FIDELL 1996) performed using S-Plus 2000 (MathSoft, Inc.)

Correlations between availability and consumption of analysed food categories were calculated using the Pearson coefficient (r), and seasonal differences in food availability were tested using the Kruskal-Wallis test (k), having confirmed normality using Kolmogorov-Smirnov statistics, with a Lilliefors significance level (ZAR 1999). Food selection was quantified using Jacobs Index (D), ranging from -1 (negative selection) to 1 (positive selection) (JACOBS 1974).

Statistical significance was taken as $p < 0.05$ and analyses were carried out using the statistical package SPSS for Windows, Release 11.5, except where specified otherwise.

Results

Overall diet

Sample size was sufficient to characterize the badgers' diet once the cumulative frequency of resources items reached an asymptote at $n = 282$.

Badgers in "Serra de Grândola" cork oak woodland had a diverse diet ranging from vegetables to mammals (Tab. 1). Nonetheless, arthropods (adult and larvae) and fruits together account for 97.1% of PO and 89.3% of PB (Tab. 1). Fruits (PB = 44.9%) and adult arthropods (PB = 29.5%) constitute the bulk of the diet and secondary resources include arthropod larvae (PB = 14.9%), mammals (PB = 5.8%) and amphibians (PB = 3.9%).

Olives were the dominating fruits in the diet (PO = 21.7%; PB = 12.4%, Tab. 1), corresponding to almost 70% of the total number of fruits ingested and 30% of the fruit biomass. Other fruits were also important, especially if ingested biomass is considered: figs (PO = 1.2%; PB = 12.5%) and pears (PO = 1.5%; PB = 12.4%). Acorns (PO = 2.9%; PB = 3.5%) supplemented the fruit diet.

Adult insects predominated amongst arthropod prey, especially Coleoptera (PO = 24.2%; PB = 9.3%) and Orthoptera (PO = 22.4%; PB = 4.4%), that together account for 88% of the arthropod number and 46%

of its biomass. Arthropods larvae, mainly Scarabaeoidea, supplemented the diet (PO = 13.4%; PB = 14.9%) in terms of number of prey, but were as important for badgers as adult insects when the ingested biomass is considered.

From the remaining food categories only mammals and amphibians recorded noteworthy PB values (5.8% and 3.9%, respectively). Mammal remains were mainly of voles, probably the Mediterranean pine vole, *Microtus (Terricola) duodecimcostatus*, the most common species in the study area (MATHIAS and RAMALHINHO 1999). Most amphibian remains could not be identified, although 7 Anura species and 4 Caudata species occurred in the study area (REBELO and CRESPO 1999).

The diversity indices ($J' = 0.51$ and $H' = 0.48$) were intermediate on the generalist-specialist continuum.

Seasonal and annual dietary shifts

Proportions of prey categories in the diet varied significantly according to season and year (Tab. 2). The results of the generalized linear model indicated that all factors and their interactions were significant.

Corroborating this result some PB values for fruit and arthropods (adults and larvae) differed inter-annually ($\chi^2_{\text{art.adults}} = 356.117$, $P < 0.001$; $\chi^2_{\text{art.larvae}} = 111.028$, $P < 0.001$; $\chi^2_{\text{fruits}} = 776.277$, $P < 0.001$), although no sampling effect was detected in the two years, once sample sizes were equalised ($\chi^2 = 1.280$, $P > 0.05$). In 1999, diet was more balanced between fruits and adult arthropods (PB_{fruits} = 39.84%; PB_{art.adults} = 32.8#5%). In 2000, fruits predominated, accounting for more than 50% of the consumed biomass. This variation is reinforced by the observed annual difference in H' values ($t = -3.341$, $P < 0.001$), and the greater diversity index in 2000 ($J_{1999} = 0.48$; $J_{2000} = 0.50$). Nonetheless, the Morisita index indicates a high inter-annual overlap ($C = 0.93$). We repeated analyses treating the same seasons in different years as independent data (Fig. 1). Despite the resulting reduction in sample sizes, which differed significantly be-

Table 1. Food items in the diet of the Eurasian badger (*Meles meles* L.) in “Serra de Grândola”. Number of individual items (N); Percentage of Occurrence (PO); Percentage of Consumed Biomass (PB)

Food item	N	PO	PB	Food item	N	PO	PB
Mammals	238	1.348	5.802	Arthropods (adults)	9 271	52.515	29.523
Ord. Insectivora	12	0.068	0.233	Cl. Arachnida –Ord. Araneae	123	0.697	0.069
<i>Erinaceus europaeus</i>	6	0.034	0.136	Ord. Scorpionida	102	0.578	0.237
<i>Crocodyrus russula</i>	3	0.017	0.003	Cl. Malacostraca – Ord. Isopoda	1	0.006	0.001
<i>Talpa occidentalis</i>	3	0.017	0.094	Cl. Chilopoda – <i>Scolopendra</i> sp.	546	3.093	1.297
Ord. Lagomorpha	3	0.017	0.215	Cl. Diplopoda	26	0.147	0.053
Ord. Rodentia	223	1.263	5.310	Cl. Insecta	8 470	47.978	13.781
<i>Arvicola sapidus</i>	1	0.006	0.022	Ord. Orthoptera	3 948	22.363	4.392
<i>Microtus</i> sp.	63	0.357	1.267	• Fam. Gryllidae	3 107	17.866	a
<i>Microtus cabreræ</i>	7	0.040	0.379	• Fam. Gryllotalpidae	598	3.444	a
<i>Microtus duodecimcostatus</i>	69	0.391	2.793	• Fam. Acrididae	183	1.054	a
<i>Apodemus sylvaticus</i>	22	0.125	0.233	Ord. Dermaptera	4	0.023	0.001
<i>Rattus norvegicus</i>	2	0.011	0.014	Ord. Neuroptera	18	0.102	0.001
<i>Mus</i> sp.	45	0.255	0.602	Ord. Coleoptera	4 270	24.187	9.324
Mammals N.I.	14	0.079	0.044	• Fam. Carabidae	1 921	10.881	a
Birds	25	0.142	0.503	• Fam. Tenebrionidae	333	1.886	a
Ord. Columbiformes	1	0.006	0.264	• Fam. Cetoniidae	131	0.724	a
Ord. Passeriformes	16	0.091	0.212	• Fam. Dynastidae	187	1.059	a
Birds N.I.	5	0.028	0.014	• Fam. Geotrupidae	230	1.303	a
Eggs	3	0.017	0.013	• Fam. Melolonthidae	53	0.300	a
Reptiles	52	0.295	0.205	• Fam. Scarabaeidae	504	2.855	a
Ord. Sauria	5	0.028	0.112	• Fam. Trogidae	3	0.017	a
<i>Podarcis hispanica</i>	1	0.006	0.012	• Fam. Cerambycidae	26	0.147	a
<i>Psammmodromus algirus</i>	1	0.006	0.025	• Fam. Curculionidae	4	0.023	a
Fam. Lacertidae N.I.	3	0.017	0.076	• Fam. Chrysomelidae	8	0.045	a
Ord. Serpentes –				• Fam. Staphylinidae	9	0.051	a
Fam. Colubridae N.I.	3	0.017	0.014	• Fam. Hydrophilidae	2	0.011	a
Reptiles N.I.	44	0.249	0.079	Ord. Coleoptera N.I.	859	4.866	a
Amphibians	83	0.470	3.903	Ord. Diptera	3	0.017	0.001
Ord. Caudata	8	0.045	0.235	Ord. Hymenoptera	227	1.286	0.063
<i>Salamandra salamandra</i>	7	0.040	0.219	Arthropods (Larvae)	2 367	13.408	14.892
Ord. Caudata N.I.	1	0.006	0.016	Fruits	5 510	31.211	44.906
Ord. Anura	29	0.164	1.897	<i>Quercus suber</i>	505	2.861	3.521
<i>Alyctes cisternasii</i>	4	0.023	0.084	<i>Ficus carica</i>	207	1.173	12.493
<i>Pelobates cultripes</i>	4	0.023	0.294	<i>Eriobotrya japonica</i>	57	0.323	2.889
<i>Bufo</i> sp.	5	0.028	0.441	<i>Pyrus bourgaena</i>	259	1.467	12.423
<i>Rana perezi</i>	7	0.040	0.262	<i>Rubus ulmifolius</i>	572	3.240	1.133
Ord. Anura N.I.	9	0.051	0.815	<i>Arbutus unedo</i>	10	0.057	0.014
Amphibians N.I.	46	0.261	1.770	<i>Olea europaea</i>	3 931	21.700	12.349
Molluscs (Cl. Gastropoda)	100	0.566	0.232	<i>Prunus</i> sp.	45	0.255	0.064
Annelids (Cl. Oligochaeta)	8	0.045	0.033	<i>Solanum lycopersicum</i>	1	0.006	0.012
				Fruits N.I.	23	0.130	0.009
^a – PB was not calculated due to the impossibility of clearly identify every exoskeleton part of each group for weighting.							

Table 2. Results from the General Linear Model performed to assess differences in badger diet composition (PB) based on year, season and food category in "Serra de Grândola" (year: 1999 and 2000; season: winter, spring, summer and autumn; food category: mammals, birds, etc.).

	df	Deviance	Resid. df	Resid. Dev.	Pr (chi)
Null	47	31277.690			
Year	1	4.764	46	31272.920	0.029
Season	1	309.071	45	30963.850	<0.001
Food category	1	404.101	44	30559.750	<0.001
Season * Year	1	1414.490	43	29145.260	<0.001
Season * Food category	1	6.582	42	29138.680	0.010
Year * Food category	1	233.838	41	28904.840	<0.001
Year * Food category * season	1	136.315	40	28768.530	<0.001

(df – degrees of freedom; Resid. df – Residual degrees of freedom; Resid. Dev. – Residual deviance; Pr (chi) – p-value)

tween seasons (n = 40 to 91; $\chi^2 = 39.164$, $P < 0.001$), differences emerged. Due to some seasonal sampling constrains it was not possible to minimise the discrepancy between season sub-sample sizes.

With the exception of spring and winter 1999, fruits dominated the badgers' diet throughout the study, representing on average of 46.2% of PB and reaching more than 80% of the ingested biomass in summer 2000.

Although present throughout the year (see availability versus consumption), adult arthropods were most important in spring, whereas there was little seasonality in consumption of larvae (most were eaten in

spring 1999). Mammals assumed a higher importance in winter 1999 and autumn 2000 and amphibians were represented in two predation peaks in summer 1999 and winter 2000.

Variation in the diet is also expressed by J' index values, with all seasons reaching values near 0.50 (ranging from 0.45 in spring 1999 to 0.55 in spring 2000) and showing significant inter-seasonal differences (Tab. 3); the most diverse diet was consumed in spring 2000 and the least in spring 1999.

Dietary shifts emerge also from the variability of the results of Morisita index with diet overlap varying between 0.996 (near 1

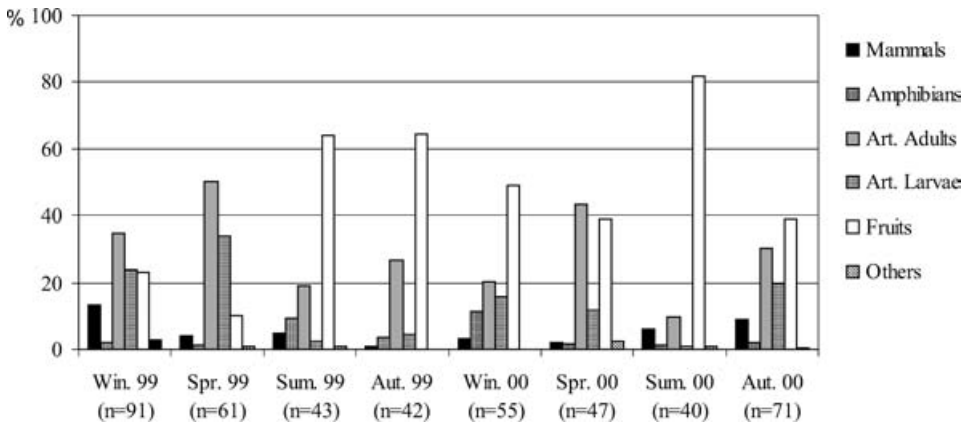


Fig. 1. Seasonal variation of badgers diet (using PB) in "Serra de Grândola" (n = number of scats; Art. – Arthropoda).

Table 3. Values of t-tests and p-values of inter-seasonal comparisons between H' values.

	t-test	p-value		t-test	p-value
winter 99 vs spring 99	2.341	P < 0.05	summer 99 vs winter 00	1.307	P > 0.05
winter 99 vs summer 99	-1.212	P > 0.05	summer 99 vs spring 00	-1.523	P > 0.05
winter 99 vs autumn 99	-0.922	P > 0.05	summer 99 vs summer 00	2.609	P < 0.01
winter 99 vs winter 00	0.227	P > 0.05	summer 99 vs autumn 00	0.435	P > 0.05
winter 99 vs spring 00	-3.366	P < 0.001	autumn 99 vs winter 00	1.052	P > 0.05
winter 99 vs summer 00	2.265	P < 0.05	autumn 99 vs spring 00	-2.445	P < 0.05
winter 99 vs autumn 00	-1.451	P > 0.05	autumn 99 vs summer 00	2.695	P < 0.01
spring 99 vs summer 99	-2.59	P < 0.01	autumn 99 vs autumn 00	-3.391	P < 0.001
spring 99 vs autumn 99	-2.774	P < 0.01	winter 00 vs spring 00	2.011	P < 0.05
spring 99 vs winter 00	-2.015	P < 0.05	winter 00 vs summer 00	-0.249	P > 0.05
spring 99 vs spring 00	-4.631	P < 0.001	winter 00 vs autumn 00	-1.544	P > 0.05
spring 99 vs summer 00	0.284	P > 0.05	spring 00 vs summer 00	4.46	P < 0.001
spring 99 vs autumn 00	-3.482	P < 0.001	spring 00 vs autumn 00	2.529	P < 0.05
summer 99 vs autumn 99	0.536	P > 0.05	summer 00 vs autumn 00	-3.212	P < 0.01

– maximum similarity; winter 1999/spring 2000) and 0.558 (medium similarity; spring 1999/winter 2000).

Availability versus consumption

A large number ($n = 8844$) and diversity (15 categories – Orders or Classes) of insects and other arthropods (e. g., scorpions) were caught in pit-fall traps, of which the most commonly eaten by badgers (Coleoptera) is depicted in Fig. 2, together with the monitored fruits (acorns, olives and pears). The availability of food resources varied among seasons ($k_{\text{pears}} = 50.952$, $P = < 0.001$; $k_{\text{olives}} = 110.766$, $P = < 0.001$; $k_{\text{acorns}} = 152.257$, $P = < 0.001$; $k_{\text{coleoptera}} = 117.842$, $P = < 0.001$). According to the Pearson correlation coefficients, no significant association was found between availability and use of the selected food resources ($r_{\text{olives}} = 0.270$, $P = 0.661$; $r_{\text{acorns}} = 0.238$, $P = 0.700$; $r_{\text{coleoptera}} = 0.005$, $P = 0.994$; $r_{\text{pears}} = -0.019$, $P = 0.975$). However, as depicted in Fig. 2 (a and b) olives are the most eaten item as long as they are available. Jacobs index confirms that olives are positively selected in winter and spring ($J_{\text{winter}} = 0.98$; $J_{\text{spring}} = 0.97$). Pears are also positively selected in summer ($J = 0.97$). The low importance of acorns in the diet is confirmed by the J values, which indicate that acorns are avoided ($J_{\text{winter}} = -0.96$; $J_{\text{spring}} = -1$; $J_{\text{summer}} = -1$; $J_{\text{autumn}} = -0.52$).

Although arthropods are a supplementary food resource, their consumption seems to track their availability (but not significantly).

Discussion

In “Serra de Grândola”, the Eurasian badger feeds mainly on fruits and arthropods (adults and larvae), especially olives, pears, figs, beetles (larvae and adults) and crickets. This is similar to results from other Mediterranean areas (e. g., RIVERA and REY 1983; PIGOZZI 1991). Fruits occur in predictable patches, and their consumption tracks their availability (see also RODRÍGUEZ and DELIBES 1992); indeed, 64% of badgers’ active radio-locations were within 300 m of olive groves or/and orchards (unpublished data). Fruits were available, and eaten, throughout the year, but were consumed least in spring, when their energetic value was least (HERRERA 1982; PLESNER-JENSEN 1993). The selection of olives, a high fat content fruit, seems to follow the same energetic rule. Arthropods are apparently consumed opportunistically, with no significant relation between measured abundance and consumption (see also RODRÍGUEZ and DELIBES 1992). The heightened consumption of ar-

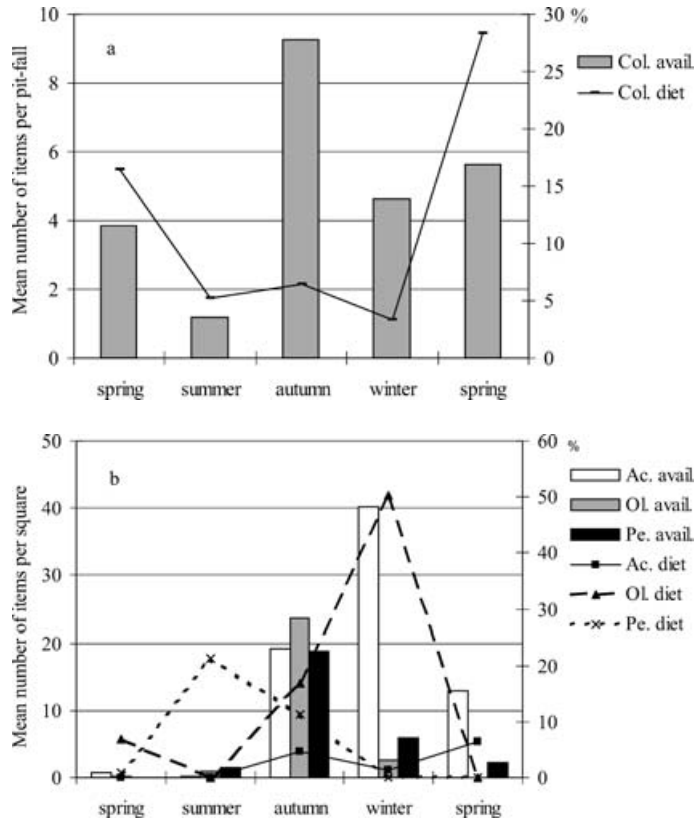


Fig. 2. Availability and consumption (PB) of coleopters (a) and main fruits (b) included in the badger diet at “Serra de Grândola” (Col. – Coleoptera; Ac. – acorn; OL. – olives; Pe. – pears; avail. – availability).

thropods in spring coincides not only with their abundance but also a trough in the availability of olives and pears. Although it was impossible to identify the species of larvae consumed (all Scarabaeoidea), the fact that these larvae live in the soil, in decaying parts of trees, in debris, etc. suggests that they were actively sought for (RICHARDS and DAVIES 1988). They may be most easily excavated in wet weather (PIGOZZI 1987), and indeed larval consumption was highest when precipitation was high (winter and spring 1999 and autumn 2000).

Fruits are rich in sugar contents but a poor source of proteins (HERRERA 1987), which may be compensated by the consumption of arthropods that are an important source of minerals and proteins (CAVANI 1991).

The badgers’ diet appeared to be governed by the availability of olives (although pears and figs revealed to be important) and sup-

plemented by arthropods, which were consumed regularly and were especially important when fruits are scarce. In seasons where olives were accessible they were preferred, as they were always the most consumed prey-item when available, even when they were not the most abundant food resource. This fact was not confirmed by any measurable correlation due, probably, to the fact that olives became buried after some time on the ground, thus being under-represented during the availability surveys. Olives fell from the trees mostly in autumn but, because they decay slowly, badgers can still find them buried on the ground until the following summer (KRUIK and DE KOCK 1981). Pears seemed to come next in the preference order, being the most important resource-category when available, except when olives were accessible. No association between figs availability

and consumption could be tested due to the lack of data.

Although acorns were very abundant (cork oak woodland represent 88.7% of the land-use in the study area), they were not preferred, perhaps because of their indigestibility (ROSALINO et al. 2003) due to tannins, secondary plant metabolites with deleterious effects on protein digestion (SMALLWOOD and PETERS 1986).

Our results, and the Evenness value ($J' = 0.51$), place badgers of the "montado" at an intermediate position along the opportunistic-specialist continuum. In short, they are seasonally specialist on olives, as this item is always the most consumed food when available, but otherwise generalists. This conclusion is compatible with the expectation that badgers would be generalists where resources are unpredictable and highly variable (PIANKA 1983). This corroborates the predictions of the feeding model of GOSZCZYNSKI et al. (2000), according to which, at latitude $\pm 39^\circ$, badgers diet would be mainly composed of vegetable material (including fruits) and insects. This is confirmed by the Levins index value ($B = 2.55$) that is graphically located on the predicted line of the proposed model for our latitude.

Our findings are in accordance with those of RIVERA and REY (1983), PIGOZZI (1991), CANOVA and ROSA (1994) and CIAMPALINI and LOVARI (1995) who have indicated that fruits and insects represent the bulk of the badgers' diet in Spain and Italy. In the cork oak woodland, earthworms were found in only 5 of 450 scat samples. In a similarly dry climate, RODRÍGUEZ and DELIBES (1992) also found few earthworms in the

diet. In Italy, KRUK and DE KOCK (1981) also found specialisation on olives, and attributed this to the energetic fat content of the fruit.

The majority of the fruits consumed by badgers were not wild, but characteristic of the traditional multi-use "montado" system. Fruit production (especially olives) is directly linked with traditional human activities, further emphasising the badger's dependence upon agricultural landscapes as highlighted in the UK (e.g., KRUK and PARISH 1985) and in Italy (e.g., KRUK and DE KOCK 1981) and the influence of local patterns of agriculture on the badgers' ecology. As human populations dwindle, through aging and a declining rural economy, this traditional land-use is degrading. Such changes in the agro-system affect not only badgers but also biodiversity in general.

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Zusammenfassung

Verschiebungen der Nahrungswahl beim Dachs (*Meles meles*) in Mittelmeer-Waldgebieten: eine opportunistische Art mit saisonaler Spezialisierung

Eine große Zahl von Publikationen widmete sich in den letzten zwei Jahrzehnten der Nahrungsökologie des eurasischen Dachses (*Meles meles* Linnaeus, 1758) in verschiedenen Habitaten Europas, was sich als Basis für innerartliche Vergleiche als sehr nützlich erweist. Bisher fehlten aber Angaben über die in Korkeichen-Waldgebieten („Montado“) der iberischen Halbinsel aufgenommene Nahrung, d. h. an der südwestlichen Grenze des Verbreitungsgebietes dieser Art. Ziel dieser

Studie war, die Nutzung der verfügbaren Nahrungsquellen in der „Serra de Grândola“ zu untersuchen. Dafür wurden 450 Kotproben zwischen 1999 und 2000 gesammelt. Es gelang, 9 Nahrungskategorien zu unterscheiden, von denen 3 für 89% der eingenommenen Biomasse verantwortlich sind: Früchte (hauptsächlich Oliven, Birnen und Feigen), adulte Arthropoden und Arthropoden-Larven. Das gemessene Nahrungsangebot wies starke saisonale Schwankungen auf. Der Vergleich zwischen Angebot und Nutzung zeigt, daß die Nahrungswahl stark vom Angebot an Oliven beeinflusst wurde. Diese Resultate verstärken die wachsende Überzeugung, daß die Ökologie des Dachses in zahlreichen Gebieten Europas stark durch die lokale Bewirtschaftung beeinflusst wird. Der Dachs ist im „Montado“ ein Generalist, der sich saisonal auf bestimmte Nahrungskategorien spezialisiert.

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