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Temporal variation in the availability of Mediterranean food resources: do badgers *Meles meles* track them?

Filipa Loureiro, John A. Bissonette, David W. Macdonald & Margarida Santos-Reis

The Mediterranean landscape of Serra de Grândola, Portugal, is one of many habitats inhabited by Eurasian badgers *Meles meles*, and in this area, the onset of food availability is seasonally predictable, but abundance is often temporally unpredictable and ephemeral. In our study, we investigated the responses of badgers to the temporal pattern of resource availability. We predicted that they would respond both to the seasonal timing of resource availability and to occasional pulses when food items are superabundant. We hypothesised that badgers' diet would reflect the seasonal onset of specific food resources, closely tracking food abundance, and that this tracking would reflect a relationship between the energetic value and water content of each resource and badger requirements at the time. To evaluate our predictions, we assessed the availability of the primary foods of badgers in Serra de Grândola (i.e. insects and fruits) over four years, and we analysed 120 faecal samples over one year to test for any congruence that might suggest tracking. Fruits and insects showed temporal fluctuations in peaks of availability that occurred on an annual basis, suggesting a temporal pulsing dynamic. Comparison of diet results with phenology and availability of food resources showed a high degree of overlap for practically all main items consumed. Moreover, the consumption of Coleoptera, olives *Olea europaea* and pears *Pyrus bourgaeana* appeared to be associated, but only partially, with their availability ($r_{\text{Coleoptera}} = 0.21$, $P = 0.50$; $r_{\text{olives}} = 0.36$, $P = 0.24$; $r_{\text{pears}} = 0.20$, $P = 0.54$); whilst acorns *Quercus suber* were closely tracked ($r_{\text{acorns}} = 0.70$, $P = 0.01$). Orthoptera were the only exception, with a negative relation between consumption and availability ($r_{\text{Orthoptera}} = -0.31$, $P = 0.32$). This tracking by badgers of primary resources with temporally differing peaks of availability and abundance appeared to involve trade-offs with energy and water requirements. Acorns peaked simultaneously with olives which, although not as abundant, had a higher fat content. Other minor fruits (e.g. loquats *Eriobotrya japonica* and figs *Ficus carica*) also seemed to be tracked; they were important resources for badgers during summer when air temperatures were high. These results have implications for understanding badger ecology in areas with temporally unpredictable resources.

Key words: badger, food availability, Mediterranean habitats, *Meles meles*, pulsed resources, seasonality, unpredictable environments

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In Mediterranean and other arid environments, animals often depend on food resources that are unpredictable and ephemeral over time scales ranging

from a few weeks to months (Shettleworth et al. 1988). This creates seasonal as well as interseasonal and intraseasonal pulsed patterns of availability,

quality and abundance. Seasonal availability results from regular phenological events, while inter-seasonal and intraseasonal differences in resource pulses occur irregularly and discontinuously over time (Schmidt 2003, Ostfeld & Keesing 2000). Familiar examples include periodic irruptions of insects, short-term transport of organic nutrients in plants and oak masting (Ostfeld & Keesing 2000).

The successful exploitation of irregular and unpredictable interseasonal resource pulses requires plasticity in foraging behaviour, space-use patterns, and in social organisation (Patterson et al. 1998). For animals dependent on such resources, tracking changes in availability is of paramount importance (Shettleworth et al. 1988). A possible example of seasonal food tracking is the Eurasian badger *Meles meles* in Mediterranean habitats. In these landscapes, badgers are considered generalist feeders (Rosalino et al. 2005). In Portugal, fruits (mainly olives, acorns, pears and figs) and arthropods (mainly insects of the orders Coleoptera and Orthoptera) represented >90% of the consumed biomass and Rosalino et al. (2005) concluded that badgers behaved like opportunistic consumers which apparently exploited the most available food resources. Nevertheless, Rosalino et al.'s (2005) study focused mostly on a description of badger diet according to season.

In our study, we combined previously published data on badger diet (nine months of diet analysis and one year of food resources availability; Rosalino et al. 2005) with new diet data using a longer temporal scale. Our aim was to determine if there were temporal differences in badger food consumption of fruits and insects, consistent with tracking and trade-offs of food availability. We expected to see regularity in the timing of food availability related to season, coupled with occasional pulses when food items were superabundant. We predicted that badgers' diets would reflect the seasonal onset of specific food resources with some food tracking, but that tracking would reflect food composition trade-offs. We expected to see a deviation in strict tracking as a consequence of an assumed relationship between the energetic value and water content of each resource and badger requirements at the time. Thus, badgers would be expected to feed primarily on the most abundant food items, but to switch to other less abundant resources to fulfil their energetic and water needs. This concept differs significantly from, and refines, the more common view

of the opportunistic forager that consumes the most available and abundant resource(s).

Material and methods

Study area

Our study was conducted during April 2000 - March 2004 in Serra de Grândola, a hilly area of southwestern Portugal (38°07'N; 8°36'W), located in one of the largest and most continuous areas of cork oak *Quercus suber* woodland in the Iberian Peninsula (Costa & Pereira 2007), which is a key habitat of the Mediterranean landscape. The climate is Mediterranean with an Atlantic influence, characterised by temperate winters and hot and dry summers. The average annual temperature ranged within 15-16°C, and precipitation averaged ~600 mm/year (Santos & Miranda 2006).

Our study area of 66 km² was mainly covered by cork oak woodland, combined with patches of other oak e.g. *Quercus ilex* and *Q. faginea*, maritime pines *Pinus pinaster* and eucalyptus *Eucalyptus globules*. The understory consisted of pastures and shrubs (e.g. rock-roses *Cistus* spp., lavender *Lavandula lusitani*, strawberry tree *Arbutus unedo* and heath *Erica* spp.). Other important land-cover classes in this landscape included riparian corridors with typical vegetation (e.g. alder *Alnus glutinosa*, raywood ash *Fraxinus angustifolia*, grey willow *Salix atrocinerea* and blackberry-bush *Rubus ulmifolius*), orchards (e.g. figs *Ficus carica*, loquats *Eriobotrya japonica* and plums *Prunus* spp.) and olive *Olea europaea* yards. Human density was ~18.5 inhabitants/km² (INE 2001) with most of the population concentrated in small villages. Anthropogenic activities included cork and firewood extraction, traditional agriculture, livestock production (mainly sheep and pigs), and small game hunting. Badgers were distributed throughout the study area at low densities, ranging within 0.36-0.48 individuals/km² (Rosalino et al. 2004).

Temporal variation of resources

Indices of food availability were calculated as relative abundances of insects of the orders Coleoptera and Orthoptera, and of the following dominant fruits in the study area: acorns, pears *Pyrus bourgaeana* and olives. Sampling was conducted from April 2000 to March 2004, combining pitfall trapping for insects (Benest 1989) and fruit counts (adapted from Diaz et al. 1997).

To estimate relative abundances for Coleoptera and Orthoptera, we set pitfall traps (Ward et al. 2001) in the seven predominant land-cover classes within the study area: 1) cork oak woodland with shrubs, 2) cork oak woodland without shrubs, 3) pasture areas, 4) riparian vegetation, 5) orchards, 6) eucalyptus plantations, and 7) pine tree plantations, following the methodology described by Westerberg (1977). Three replicates of eight pitfall traps each were set for eight consecutive nights in the different land-cover units for each season (February, May, August and November) in each year. Seasons were defined according to the 'Observatório Astronómico de Lisboa' (Lisbon Astronomic Observatory) as: winter (January-March), spring (April-June), summer (July-September) and autumn (October-December). Insects of >2 cm were identified to species and counted. Since only insects this size were detected in the badgers' diet, we assumed that insects <2 cm were not important food items to badgers. Mean relative abundances of insect as well as standard errors were calculated from the different land-cover units and were used as the index of availability for each season. Monthly insect availability was extrapolated from season estimates.

To estimate relative abundances in the availability of fruits, we randomly selected 30 individuals each of cork, olive and pear trees dispersed throughout the study area and placed 1 m² quadrats beneath each tree (adapted from Diaz et al. 1997). We counted fallen fruits in each quadrat once a month, every month, and left them *in situ* to monitor the duration of their availability. Mean monthly values (and standard errors) were calculated for each tree species and were used as indices of availability. A literature review regarding the phenology of other non-major fruits known to be eaten by badgers, and occurring on the study site (e.g. blackberries, figs and loquats), was also conducted (Aas & Riedmiller 1994, González 1994, Romo & Sierra 1996, Cela et al. 1998) and was used to reveal the relationship between fruit availability and appearance in the diet.

Diet analyses

During April 2000 - March 2001, we collected 165 faecal samples from three different social groups fortnightly from badger latrines. Each month, we randomly selected ca 10 samples for analysis (7-13, average: 10) for a total of 30 samples per season. Since a different number of faecal samples were analysed per month, data were standardised to 10

samples per month. Each sample in this study represents the content of a pit latrine and not of an individualised scat, since it was often very difficult to distinguish different scats. Thus, our sample here represents analytical units of >2 scats.

Diet analyses followed standard procedures which included the separation, identification and quantification of all undigested food item remains (Rosalino et al. 2003, 2005). Seeds and skeletal remains of arthropods were used to identify the materials consumed (e.g. Barrientos 1988, our own collection) and to estimate the minimum number of fruits/insects consumed (e.g. number of insect legs and wings, and of seeds). Whenever needed, correction factors were also used (see Rosalino et al. 2003). Consumed biomass was estimated by multiplying the consumed number by the mean weight of the food item (see Rosalino et al. 2003).

Data analysis

We analysed differences in availability of food resources throughout the four years of study with a univariate repeated measure ANOVA in which responses to different years were considered as separate dependent variables (Tabanick & Fidell 1996). Differences between years were investigated by multiple mean comparisons of main effects with a Bonferroni confidence interval adjustment correction.

We used autocorrelation analyses, represented as correlograms (Case 2000), to determine both the cyclic pattern of primary food availability, as well as the time lag between availability and consumption of these resources. Correlograms for each studied food item were created by plotting the Spearman correlation coefficients value between food availability at time *t* and time *t* + 1 on the y-axis, and time on the x-axis. From the four years of data, we used monthly data for fruits and quarterly seasonal data for insects as the temporal resolution. We also created time lag correlograms between consumption at time *t* and availability at time *t*-1 of each food item over the time period (Case 2000). For this analysis, we used only the year with both availability and consumption data, and month was used as the temporal unit. Statistical analyses were performed in SPSS 13 for Windows (evaluation version, SPSS Inc., Illinois, USA) using a significance level of 0.05.

The University of Lisbon does not have an Institutional Animal Care and Use Committee, so during the course of our study, we conformed to best practices and followed ASM guidelines. Our pitfall

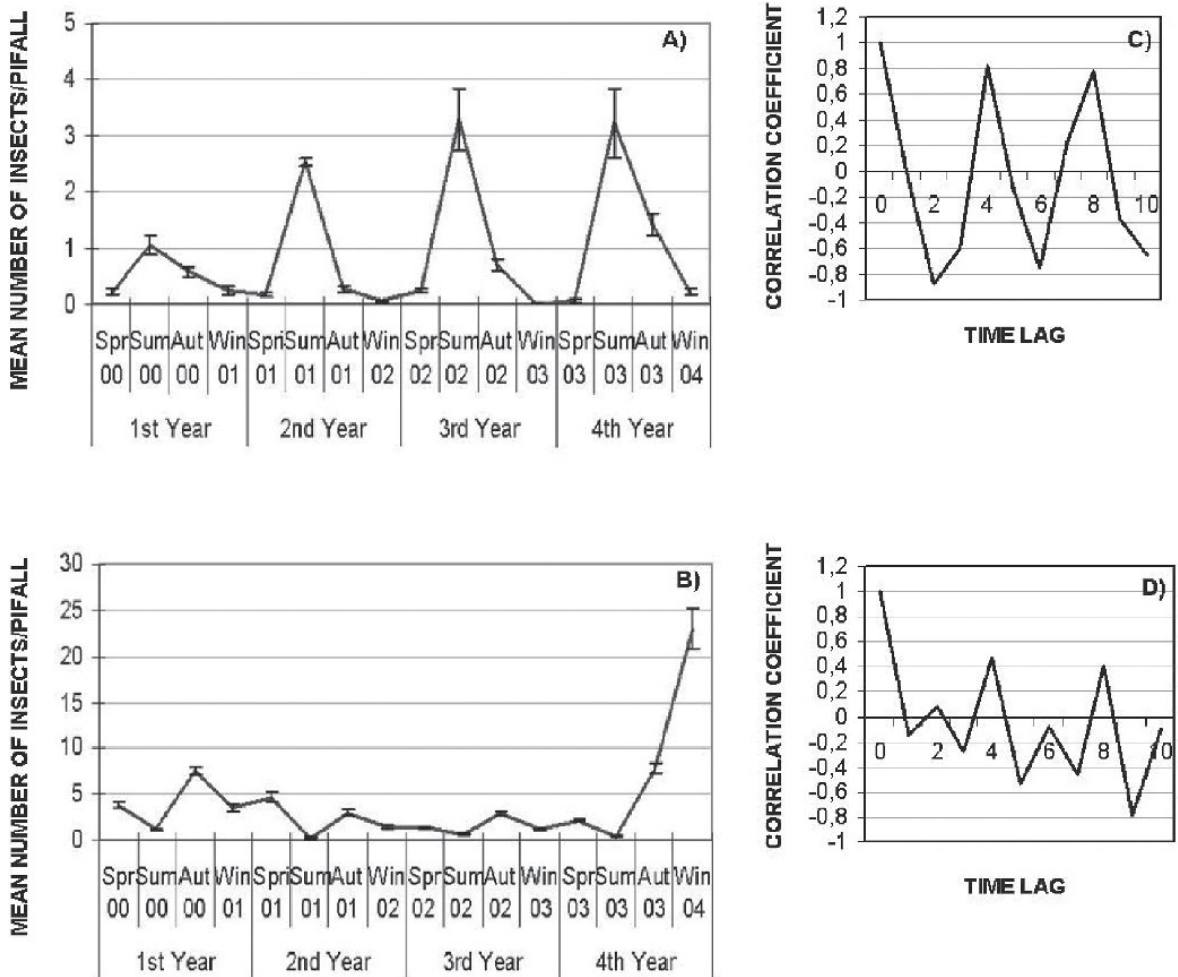


Figure 1. Temporal variation of insect availability in Serra de Grândola, measured as the mean number of insects/pitfall in a 4-year period where whiskers represent the standard error of the mean values (left) and correlograms indicating the length of availability cycles where each point represents correlation between availability at t and $t + 1$, where t is a season unit (right); A) and C) Orthoptera, B) and D) Coleoptera. Spr = spring, Sum = summer, Aut = autumn and Win = winter.

trapping was confined to capturing primarily insects and other than that, besides observation, we conducted no research on live animals.

Results

Temporal variation of resources

Insects

Availability of insects varied significantly among the four years of study for both Orthoptera ($F_{(1.35,14.89)} = 4.65$, $P = 0.04$) and Coleoptera ($F_{(1.08,11.93)} = 4.90$, $P = 0.04$). For Orthoptera, differences were detected between the second and fourth year ($M = -0.48$, $SD = 0.15$, $P = 0.04$), whereas for Coleoptera, differ-

ences were apparent between the first and third year ($M = 2.47$, $SD = 0.45$, $P < 0.001$).

A seasonal pattern of availability existed for insects. Orthoptera displayed a clear pattern with higher abundances in summer and lower abundances in spring and winter (Fig. 1A). Coleoptera showed two peaks of availability each year; one during spring and another in autumn (see Fig. 1B) with a very low abundance in summer. Coleoptera also had a very high peak of abundance in the autumn and winter of the fourth year of sampling.

The analyses of the correlograms (see Figs. 1C and 1D) confirmed the annual periodicity of availability for Orthoptera and the biannual availability for Coleoptera: both orders showed an annual peak of abundance. In Orthoptera, these cycles were clear

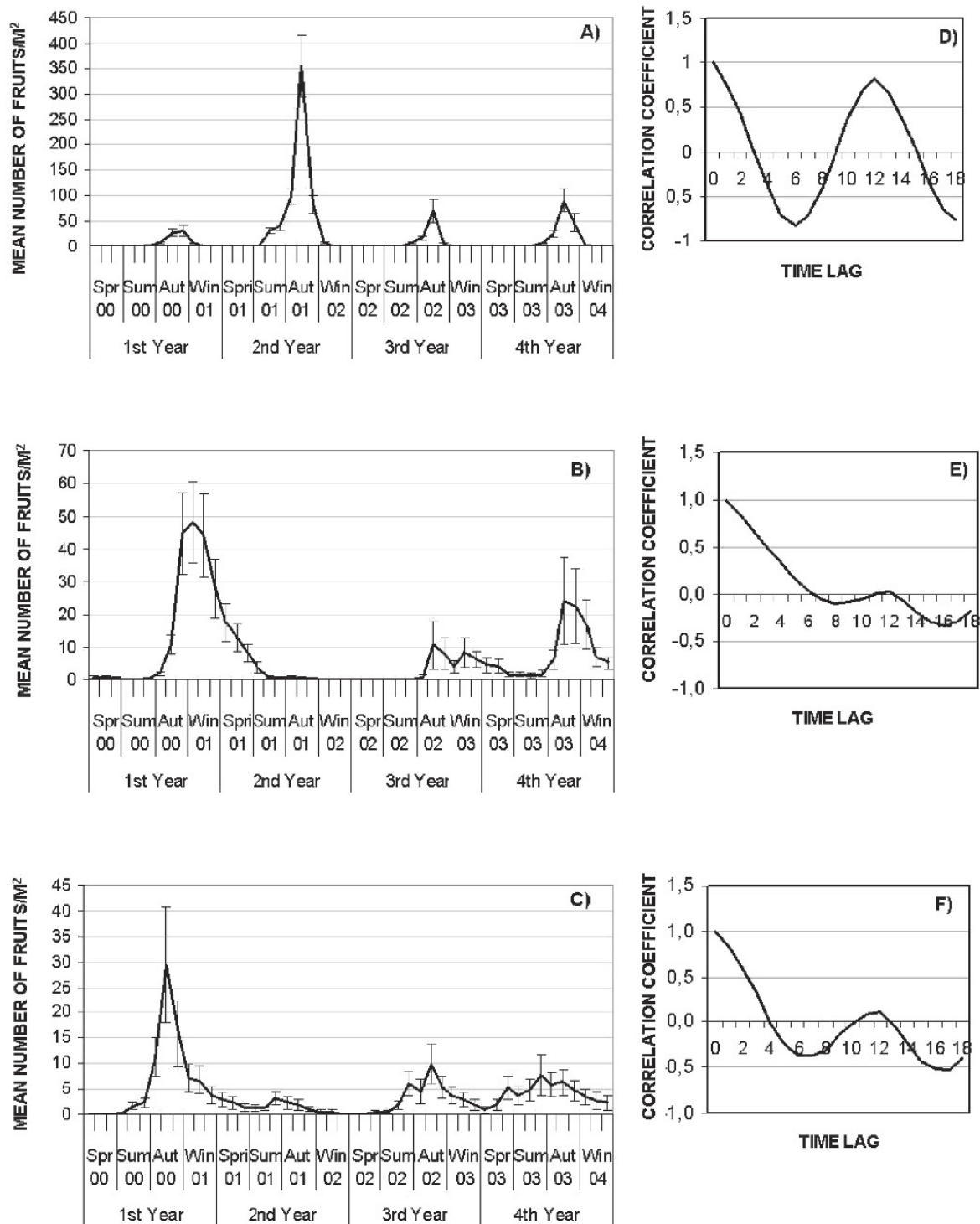


Figure 2. Temporal variation of fruit availability in Serra de Grândola, measured as the mean number of fruits/m² in a 4-year period where whiskers represent the standard error of the mean values (left) and correlograms indicating the length of availability cycles where each point represents correlation between availability at t and $t + 1$ and t is a month unit (right); A) and D) olives, B) and E) acorns, and C) and F) pears. Spr = spring, Sum = summer, Aut = autumn and Win = winter.

and their yearly occurrence was evident, as shown by the positive correlation peaks which occurred annually every fourth season. In Coleoptera, small intermediate cycles existed between cycles of higher availability.

Fruits

We also observed variation in fruit productivity among the four sampling years as well as a year-to-year fluctuation in availability (Fig. 2). Although, no statistical differences were detected between years (olives: $F_{(1.03,11.29)}=2.93$, $P=0.11$; acorns: $F_{(1.33, 14.64)}=3.13$, $P>0.09$; pears: $F_{(1.10,12.07)}=3.10$, $P=0.10$), a clear pattern of fruit availability was evident. Olives became available during the autumn months (October-December) and had a very high peak of productivity in the second year (see Fig. 2A). Acorns, in general, became available in autumn, but lasted through winter and remained available until spring (see Fig. 2B). A gap in acorn availability, probably due to a failure in mast crop, was detected during the second year of the study. Pears did not show as clear a pattern but were mostly available during summer and autumn, and less during spring (see Fig. 2C).

Pears were present practically all year round. Nevertheless, after a certain period on the ground they were dry, rotten and presumably much less edible. The first year of the study revealed high productivity for both acorns and pears, which appeared to exhibit more variation in temporal pattern than did olives. However, and importantly, the correlograms shown in figures 2D and 2F indicate that both pears and olives had cycles of high abundance every 12 months, i.e. on an annual basis, indicated by the highest positive correlation peak at the 12th month. For acorns, these cycles were not as clear, probably due to the gap in acorn availability during the second year (see Fig. 2E).

Tracking food availability

Comparison of diet results with phenology and availability of food resource showed a high degree of overlap for practically all main items consumed (Fig. 3). Arthropods (Coleoptera and Orthoptera) were present and consumed throughout the year. Of fruits, only acorns and pears were available the entire year, even though they were not consumed continuously. All other fruits were only seasonally available, being present for three (e.g. loquats and blackberries) to nine months (e.g. olives). Summer and autumn were the richest fruiting seasons with

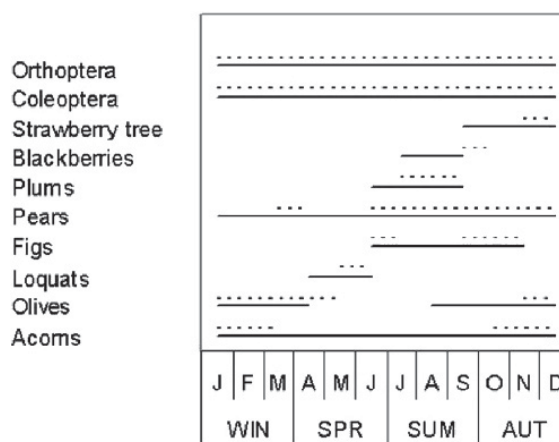


Figure 3. Overlap in consumption (---) and availability (—) of main food items consumed by badgers in Serra de Grândola. Consumption was measured between April 2000 and March 2001 in terms of presence of the food items in faecal samples in a certain month, and availability was obtained considering field availability and a literature review.

>5 different fruits available. On the other hand, winter and early spring were the poorest seasons with few fruits available. Interestingly, olives and blackberries occurred in the diet at low frequencies beyond the period of their apparent availability as a result of small scattered patches that escaped our routine sampling.

The consumption of acorn coincided with its peak of availability, as shown by the significant correlation result ($r_{\text{acorns}}=0.70$, $P=0.01$; Fig. 4B). On the other hand, consumption of olives, pears and Coleoptera appears to be only partially associated (Figs. 4A and C and 5B) and did not show a significant correlation ($r_{\text{olives}}=0.36$, $P=0.24$; $r_{\text{pears}}=0.20$, $P=0.54$; $r_{\text{Coleoptera}}=0.21$, $P=0.50$). Orthoptera were the only exception with a negative relation between consumption and availability ($r_{\text{Orthoptera}}=-0.31$, $P=0.32$; see Fig. 5A).

Badger response to higher availability of Coleoptera occurred twice (see Fig. 5D), at time zero ($r_{\text{Coleoptera}}=0.21$, $P=0.50$) and four months later ($r_{\text{Coleoptera}}=0.58$, $P=0.13$), which probably corresponds to a close tracking of the biannual nature on the availability of this food item (see Fig. 1B). Concerning Orthoptera, the maximum correlation coefficient only occurred after a three month lag ($r_{\text{Orthoptera}}=0.59$, $P=0.09$; see Fig. 5C). Contrary to this, badger response to high availability of acorns was immediate and highly significant ($r_{\text{acorns}}=0.70$, $P=0.01$; see Fig. 4E). The same happened to pears, which although not significant, also had the maximum correlation coefficient between consumption

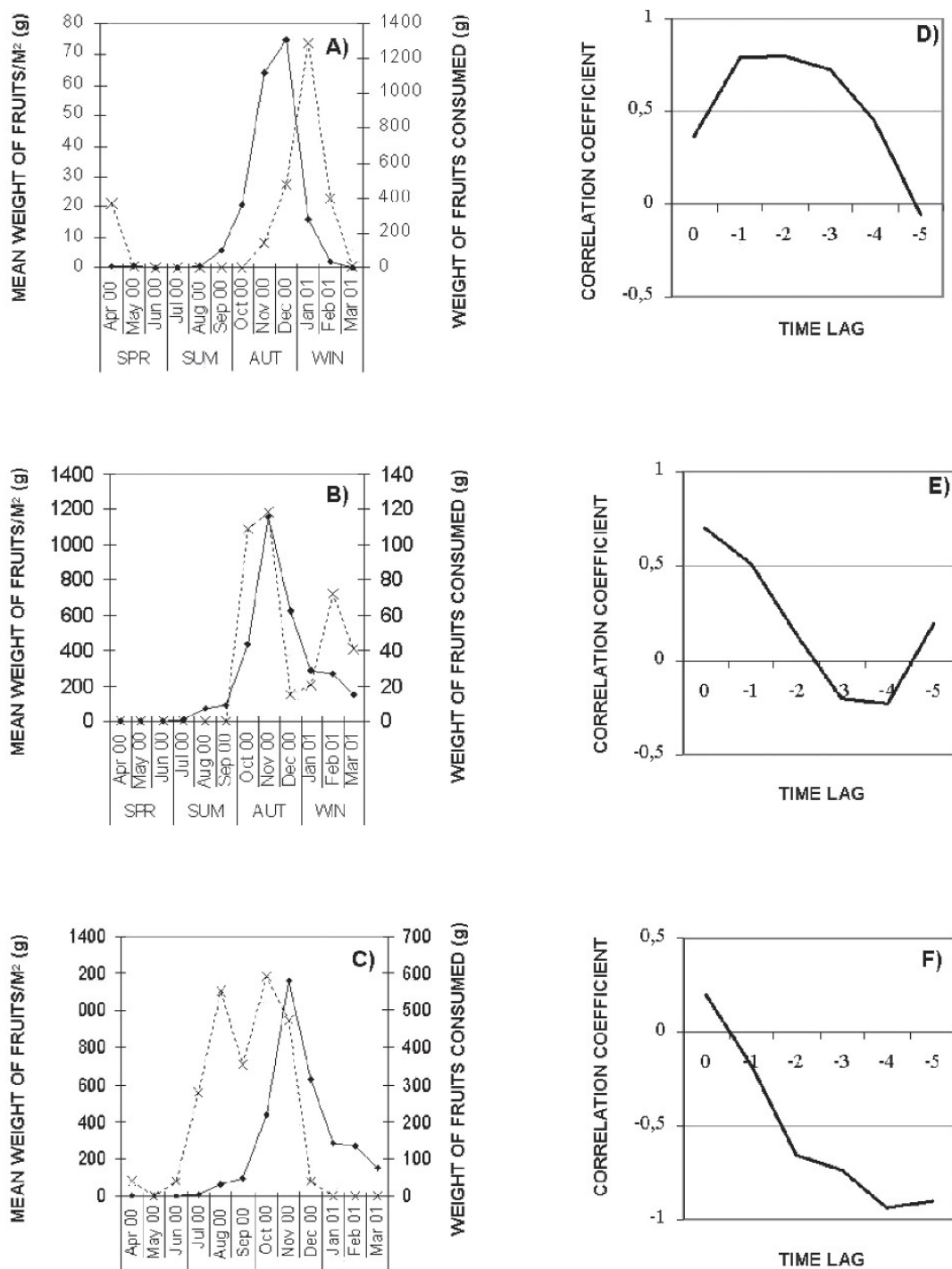


Figure 4. Consumption (---) and availability (—) of badgers' main food items in Serra de Grândola during one year, and correlograms indicating the lag between food availability and food consumption of olives (A and D), acorns (B and E) and pears (C and F). Consumption was measured as the total weight of a food item found in faecal samples in different months, and availability was measured as the average weight of fruits available for that month in m². Each point represents correlation between consumption at t and availability t-1 during one year, where t is a month unit.

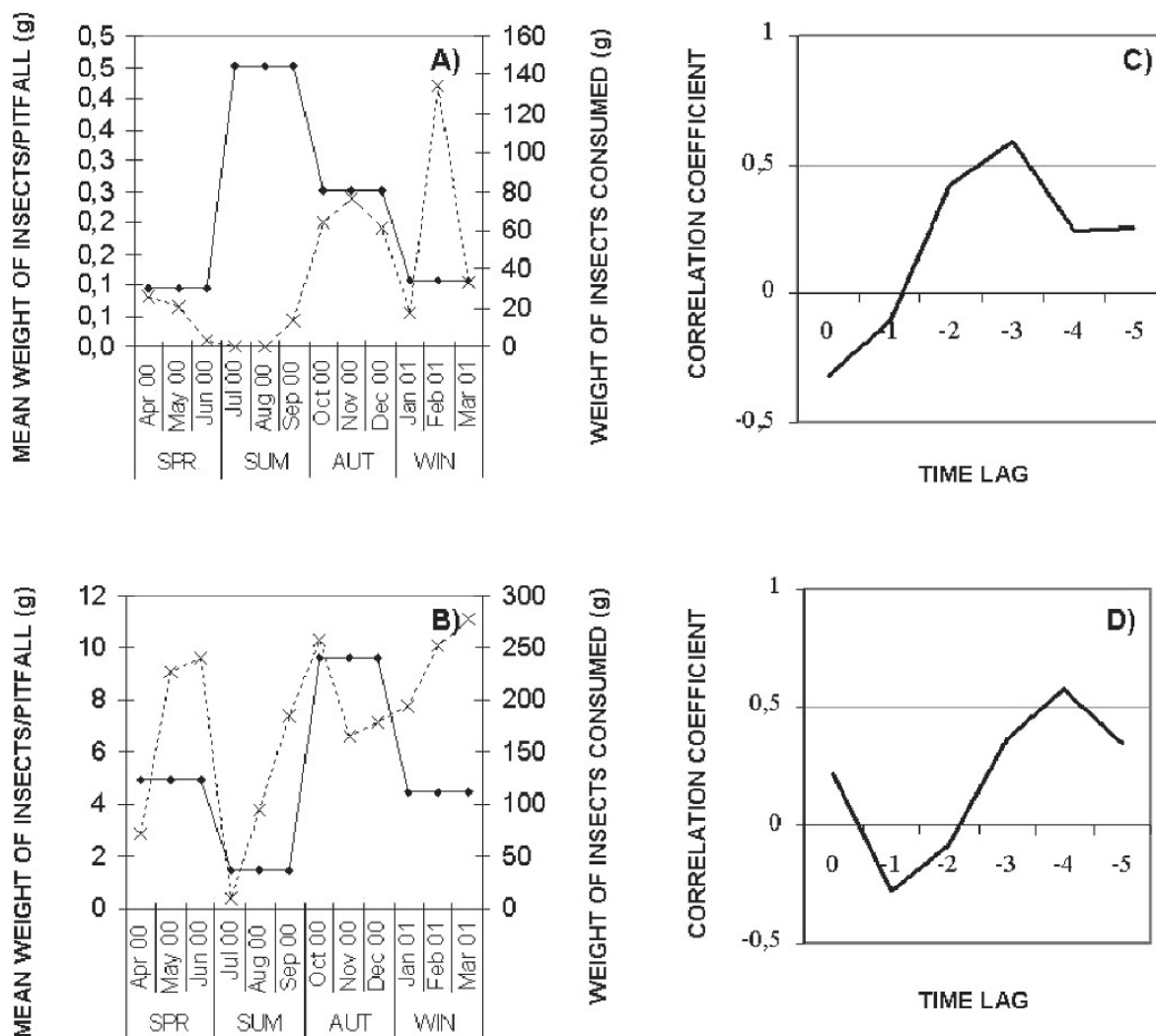


Figure 5. Consumption (---) and availability (—) of badgers' main food items in Serra de Grândola during one year, and correlograms indicating the lag between food availability and food consumption of Orthoptera (A and C) and Coleoptera (B and D). Consumption was measured as the total weight of a food item found in faecal samples in different months, and availability was measured as the average weight of insects available for that month in a pitfall. Each point represents correlation between consumption at t and availability $t-1$ during one year, where t is a month unit.

and availability at time zero ($r_{\text{pears}} = 0.20$, $P = 0.54$; see Fig. 4F). For olives, consumption lagged about one month behind the peak of availability ($r_{\text{olives}} = 0.79$, $P < 0.01$; see Fig. 4D). These results demonstrate that badgers tracked some of their main resources when they were most available.

Discussion

Our results showed that the availability of the primary foods of badgers in Serra de Grândola (Ro-

salino et al. 2005) showed seasonal regularity in the timing of their peaks of abundance coupled with occasional pulses of superabundance, characterised by longer inter-pulse intervals (Ostfeld & Keesing 2000). Although badger diets reflected the seasonal onset of the availability of specific food resources, tracking of diet on abundance was not exact for all foods items. Fruits that played a major role in the diet, i.e. olives, acorns and pears, were generally available for protracted periods. Other fruits had a much more restricted period of availability, during which they briefly occurred with some importance in

the badger's diet (e.g. blackberries 38.8% of occurrence in August and loquats 9.5% of occurrence in May). Peaks of availability in Orthoptera were not closely tracked. Instead, their pattern of occurrence in the diet suggested a trade-off between the energetic value of these and other resources available at the time and badger energetic requirements. Figs, loquats, plums and blackberries, for example, all seemed to be important resources, and badgers tracked their availability even during the peak of abundance of Orthoptera, demonstrating that fruits were more valuable to badgers at that time. Similarly, higher consumption of olives occurred at a time when acorns were still available, suggesting active tracking and selection.

Energy and nutritional demands of badgers vary according to season, reproductive status and availability of alternative food resources (Pigozzi 1992), in ways that affect diet selection. While fruits represent a poor source of protein, they have high energetic values (plant seeds range: 4.5-6.1 kcal/g; Robbins 1993). Insects usually have low caloric content (2.2 kcal/g; Robbins 1993). Nevertheless, Coleoptera and Orthoptera have relatively high energetic content, with 5.1 and 4.8 kcal/g of ash free dry mass, respectively (Chen et al. 2004). During spring, badgers need to replenish body resources depleted during winter, especially for lactating females, and the ingestion of protein becomes particularly important (Neal & Cheeseman 1996). In Serra de Grândola, sources of protein such as mammalian prey are scarce. Thus, Coleoptera, with peaks of abundance during spring and autumn, although with low biomass, emerge as an important source of protein, since specimens of this order are an abundant item. During summer, food is abundant. Coincidentally, air temperature and solar radiation are high, and badgers made a concerted effort to find water-rich fruits (e.g. pears, loquats, plums, figs and blackberries), rather than focusing on the peak availability of Orthoptera. Fruits often contain >70% water (Herrera 1987) constituting an important source of hydration (Robbins 1993), at a time when temperatures can exceed 40°C. During autumn, badgers accumulate fat reserves for winter and for reproduction (Woodroffe 1995) and once again the ingestion of proteins becomes important. These aspects of the badgers' natural history may explain the close tracking during autumn of the peaks in abundance of Coleoptera, Orthoptera, pears and acorns. In winter, the ingestion of foods with high caloric value becomes extremely im-

portant, since it allows the accumulation of fat reserve and contributes to the maintenance of body temperature (Kruuk & de Kock 1981). Olives, in particular, have a high caloric value (>40% lipid content; Herrera 1987) and this is probably the reason why they were preferred to acorns in this season.

The flexibility of badgers' social organisation (Kruuk 1978), their foraging efficiency (Pyke 1984) and their ability to move long distances (Ostfeld & Keesing 2000) enhances the ability of the animals to take advantage of resource fluctuations and certainly influences survival rates and reproductive strategy (Bekoff et al. 1984). Clearly, understanding animal responses to the temporal pattern of resource availability is an important component of foraging ecology theory, and it is likely that when availability of important resources is pulsed, population performance will be affected. Harsh, highly seasonal environments, such as at our Mediterranean study area, offer a promising test site for ideas that relate spatially and temporally patchy resources to associated guilds of species (e.g. predators and seed eating birds) which feed on resources with these characteristics.

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