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TEMPORAL VARIATION IN FOOD AVAILABILITY AND DIET OF BLACKCAPS IN OLIVE ORCHARDS

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Abstract.—We examined temporal variation in the diet of Blackcaps (*Sylvia atricapilla*) in relation to food availability in four olive orchards in southern Spain. Four components of the diet were considered: olive fruits, non-olive fruits, animal matter, and non-fruit plant matter. The pattern of temporal variation in diet differed among olive orchards. The temporal pattern of olive availability, which differed among olive orchards as a consequence of different crops, ripening phenologies, and harvesting processes, was the main factor determining temporal variation in diet. This emphasizes the strong dependence of Blackcaps on olive fruits in this habitat. Arthropods and non-fruit plant material (the latter including leaves, flowers, and seeds of weed species) were also frequently included in the diet. Other fruits were eaten infrequently. However, the number of fruit species per diet sample increased wherever other fruits were available (e.g., near hedges), suggesting that such sites contribute to diet diversification.

VARIACIÓN TEMPORAL EN LA DISPONIBILIDAD DE ALIMENTO Y EN LA DIETA DE LA CURRUCA CAPIROTADA (*SYLVIA ATRICAPILLA*) EN OLIVARES

Sinopsis.—Se examina el patrón temporal de variación en la dieta de la Curruca capirotada (*Sylvia atricapilla*) y su relación con el patrón temporal de variación de sus principales recursos alimenticios en cuatro olivares del Sur de España. Se consideraron cuatro componentes en la dieta: aceitunas, otros frutos, materia animal (artrópodos fundamentalmente) y materia vegetal "no fruto." El patrón temporal de aparición de estos componentes en la dieta fue diferente entre olivares, de modo que la dieta fue temporalmente distinta en cada uno de ellos. El patrón temporal de disponibilidad de aceituna, variable entre olivares debido a diferencias en los tamaños de cosecha, en fenologia de maduración y en el proceso de cosechado, fue determinante en la variación temporal de la dieta del ave. Esto pone de manifiesto que la Curruca capirotada tiene una fuerte dependencia de las aceitunas en este hábitat. Los artrópodos y la materia vegetal "no fruto" (hojas, flores y semillas de plantas herbáceas) fueron también importantes en la dieta ya que aparecen en esta con frecuencia. La inclusión de otros frutos fue poco importante y muy infrecuente; sin embargo, el número de especies de fruto por muestra se incrementó en aquellos lugares que presentaban mayor diversidad de frutos (por ejemplo cerca de setos), lo que sugiere que tales lugares juegan un importante papel para la diversificación de la dieta en esta especie.

Abundance of different types of foods is one of the major determinants of the diet and abundance of birds (Elton and Greenwood 1987, Nilsson 1984, Schluter 1982a). Food abundance is spatially and temporally variable, and birds usually respond to this by consuming different foods or moving to other places (Loiselle and Blake 1991, Rey 1995, Schluter 1982b). In particular, the diet of frugivorous-omnivorous birds is temporally variable because food availability changes between and within seasons (Berthold 1976; Debussche and Isenmann 1985a,b; Herrera 1981; Jordano 1988, 1989; Wheelwright 1986). However, even though the availability of resources presumably determines the diet of frugivorous species, few studies have directly and simultaneously analyzed both frugivore diet and fruit availability (but see Fuentes 1994; Jordano 1988, 1989; Loiselle and Blake 1990). Temporal and spatial availability of fruit in olive (*Olea europaea* var. *europaea*) orchards of southern Spain vary because olive cultivars found in the area differ in crop size, ripening phenology, and temporal pattern of harvesting by humans (Rey 1995). This makes olive orchards particularly suitable for examining how birds adjust their diets to temporal availability of food. Some birds are able to track the large spatio-temporal variation in olive availability in the orchards and this ability is likely responsible for their ability to inhabit this disturbed habitat (Rey 1995).

Due to the rarity of natural habitats, olive orchards in southern Spain are currently one of the main winter habitats for many small frugivorous birds (Rey 1993). Thus, knowledge of the processes that allow these birds to inhabit the olive orchards is important for understanding the factors limiting their wintering populations. At least three sources of information are useful to explain birds' ability to inhabit the orchards: (1) diet data, which have received some attention for several frugivorous species in this habitat (Jordano and Herrera 1981; Muñoz-Cobo 1987; Soler et al. 1988; Tejero et al. 1983, 1984), (2) food-tracking ability (Rey 1995), and (3) ability to adjust diet to food availability. This study examines this last point in the case of Blackcaps in several olive orchards (the most abundant frugivore species in this habitat; Muñoz-Cobo and Purroy 1980; Muñoz-Cobo 1987; Rey 1993, 1995; Rodriguez et al. 1986).

STUDY AREA AND METHODS

This study was conducted in the autumn and winter (October–March) of 1989–1990 and 1990–1991 in four olive orchards (hereafter plots A, B, C, and D) corresponding to four different olive cultivars (picual, picudo, lechin, and hojiblanca; see Barranco and Rallo 1984 for details about olive cultivars). The four plots, all of them located in the Guadalquivir Valley (Andalusia, southern Spain), were 6–9 km^2 each and were located in extensive olive cultivation areas (see Rey 1995 for details). We obtained diet samples fortnightly from mist-netted birds. A set of four nets (12-m long each) were placed at the same sites in which crop size, ripening phenology, and availability of fruits and arthropods were monitored. In 1989–1990 we placed nets within each plot at sites where other fruit species were extremely rare (far away from hedges). In 1990–1991 nets were placed through hedges within plots C and D, whereas in plots A and B nets were located at the same sites as the year before. It must be noted that hedges are immersed in the orchards and, from a landscape perspective, they are scarce and of small length and width. Captured birds were held individually in cloth bags until defecation or regurgitation. To increase the volume of each diet sample, we flushed the birds' guts with a 1% NaCl solution using a fine probe connected to a syringe (Brensing 1977, Herrera and Jordano 1981, Moody 1970). We placed the total sample for each bird in a small filter paper envelope, and its origin and date were noted. We analyzed the samples in the laboratory following Herrera and Jordano (1981) (see also Jordano 1988), separating the animal fraction, the non-fruit plant fraction (NFPF hereafter), the olive fruit fraction and the non-olive fruit fraction. Overall, 485 diet samples, all from different individuals, were analyzed.

Olive fruit availability.—Several parameters were combined to estimate olive availability. We obtained the following expression of fortnightly availability for each plot:

$$O = WXYZ + EF$$

where O = olive availability (number of ripe olives per ha in each orchard each fortnight), W = crop size (initial total amount of olives per ha in each orchard), X = proportion of ripe olives each fortnight in each orchard, Y = proportion of ripe undamaged olives, Z = proportion of olive orchard unharvested, E = proportion of olive orchard harvested, and F = number of fruit that remains in the harvested zones of each orchard each fortnight. Methodology used to estimate olive crops, amount of damaged fruits, ripening phenology, and progress of the harvesting has been provided elsewhere (Rey 1995). Briefly, crops were estimated through interviews with 10–20 harvester groups per plot. Ripening phenology and fruit damage were monitored fortnightly from four tagged branches in 10–20 randomly selected trees per plot. Harvesting progress was evaluated fortnightly from transects that estimated the percentage of trees already harvested. Finally, fruits remaining beneath the trees after harvesting were quantified from transects. Here, we use olive availability solely to illustrate correlations with its volume in the diet.

Arthropod availability.—Arthropods were censused fortnightly on 12 randomly selected trees in each study plot. Two substrates frequently used by Blackcaps to forage, primary and peripheral branches (including leaves), were selected for sampling. On each substrate, 5-min counts were done around one half of the tree at eye level. Only arthropods larger than 1 mm in length were counted (Carrascal and Tellería 1989). Arthropods too large for manipulation by Blackcaps were not considered in the counts. The upper size limit of arthropods considered in the counts was determined on the basis of our previous experience analyzing many diet samples. As a rule, arthropods considered in the counts were frequently found in diet samples of Blackcaps. Here, we use these field counts solely to illustrate correlations with the percentage of diet constituted by arthropods, not for description of diet content.

Data analysis.—To examine similarity among orchards in the temporal pattern of occurrence of each diet component, we used Kendall's coefficient of concordance. Because the number of diet samples obtained each fortnight in each plot was frequently too low to represent adequately the diet, we averaged data from the two study seasons for this analysis. We believe this is appropriate because no significant differences were found between seasons in the percent volume of each fraction in each plot (*t*-test, P's > 0.05 for each plot and diet fraction; all the samples for each season and plot were considered together in the analyses).

We examined the relationship between olive availability and percentage of olive in the diet using correlation analysis. Correlations were analyzed only in those plots in which there were at least eight diet samples for each fortnight, because diet diversity (calculated from the four diet components) stabilized at sample sizes between 7 and 12 in all cases (see Hurtubia 1973 for details on the determination of minimum sample sizes in diet analysis).

We used two approaches to examine the correlation between olive availability and volume of olive in the diet. First, a within-plot analysis explored the relationship between temporal availability of olives and olive inclusion in the diet. Given the low number of cases in each analysis (low number of fortnights), we used Spearman rank correlations. Second, we used an analysis pooling data from all plots. In this approach, we used Pearson correlations (with olive availability log transformed, and percentage in the diet arcsin transformed for normality) because sample sizes were higher. Cases in this last analysis were those plot-fortnights for which we had at least eight diet samples. The same analyses were done to examine relationships between arthropod availability and percentage of arthropods in diet.

RESULTS

Olive fruit constituted, in most cases, the largest fraction of the diet of Blackcaps in the olive orchards (Fig. 1), and it occurred in most of the diet samples in all plots (Table 1). Non-olive fruit occurred rarely in the diet. For the 485 diet samples collected, the number of samples containing non-olive fruit species was: 1 with *Jasminum fruticans* (Oleaceae), 22 with *Pistacia lentiscus* (Anacardiaceae), 1 with *P. terebinthus,* 3 with *Rosa* sp. (Rosaceae), 3 with *Crataegus monogyna* (Rosaceae), 2 with *Smilax aspera* (Smilaceae), 8 with *Vitis vinifera* (Vitaceae), 13 with *Viscum cruciatum* (Viscaceae), 1 with *Asparagus albus* (Liliaceae), and 4 with *A. acutifolius.*

Temporal pattern of the diet.—There was no significant concordance among the four plots in the temporal pattern of consumption of arthropods ($W = 0.30$, $P = 0.09$), NFPF ($W = 0.11$, $P = 0.47$), non-olive fruits ($W = 0.09$, $P = 0.54$) and olives ($W = 0.22$, $P = 0.14$). This lack of concordance in the diet among olive orchards is probably due to among-plot variation in the temporal pattern of olive consumption (largest fraction of the diet).

Food availability and diet.—Within-plot correlations between food availability and diet were only possible in plot A during 1989–1990 and in plot B during 1990–1991 (see methods), but the results are suggestive (Fig. 2). In both cases there was a significant correlation ($r_s = 0.90$, $P = 0.01$, $n = 9$ fortnights for plot A; $r_s = 0.81$, $P = 0.032$, $n = 8$ fortnights for plot B). The analysis was repeated after pooling data from all the fortnights and from all plots (Fig. 3). Again, there was a significant relationship between percentage of olive in the diet and olive availability ($r = 0.79$, $P < 0.001$, $n = 15$ for 1989–1990; $r = 0.62$, $P = 0.014$, $n = 15$ for

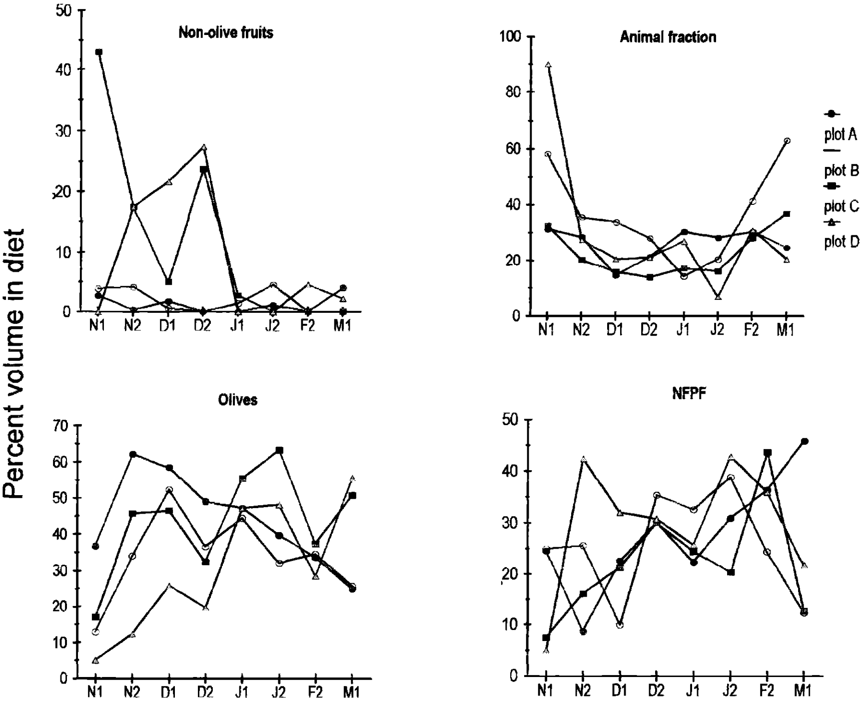


FIGURE 1. Temporal variation in the volume of different foods in Blackcap's diet in the four plots. Labels on x-axis indicate fortnights (e.g., N1 = first fortnight of November).

1990–1991). These results strongly suggest that Blackcaps included olives in their diet as a function of their availability.

There was no significant within-plot correlation between the volume of arthropods in the diet and arthropod abundance on primary or periphery branches in plot A during 1989–1990 ($r_s = 0.32$, $P = 0.44$, $n = 8$ fortnights for primary branches; $r_s = 0.35$, $P = 0.36$, $n = 9$ fortnights for

TABLE 1. Frequency of occurrence (shown as proportion of diet samples) of animals (ANIM), non-fruit plants (NFPF), olives (OLIVE) and non-olive fruits (NON-OLIVE) in diet samples of Blackcaps in olive orchards in southern Spain. n = number of diet samples analyzed.

	1989–1990					1990–1991				
	ANIM	NFPF	OLIVE	NON-OLIVE	n	ANIM	NFPF	OLIVE	NON-OLIVE	n
PLOT A	0.92	0.76	0.85	0.08	129	0.98	0.68	0.98	0.05	41
PLOT B	0.94	0.55	0.91	0.06	33	0.96	0.77	0.90	0.11	109
PLOT C	0.86	0.55	0.82	0.14	22	0.93	0.82	0.98	0.34	44
PLOT D	0.93	0.93	0.76	0.05	59	0.96	0.89	0.90	0.25	89

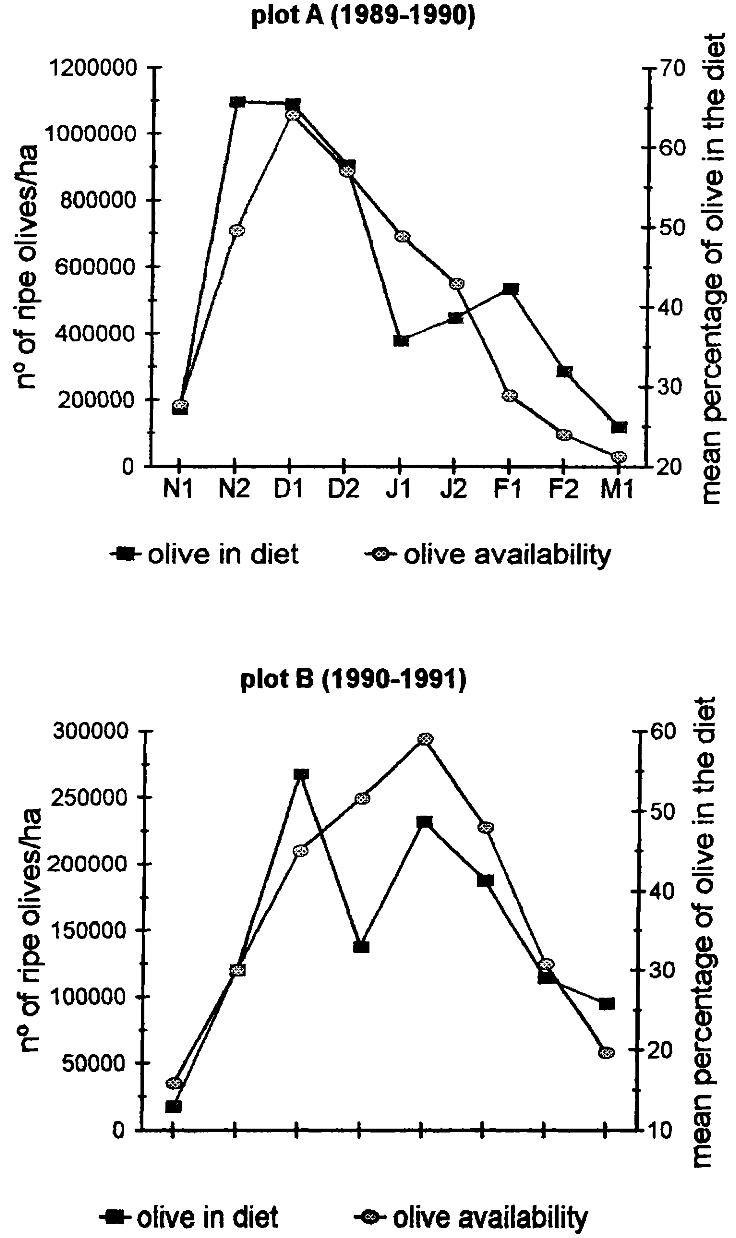
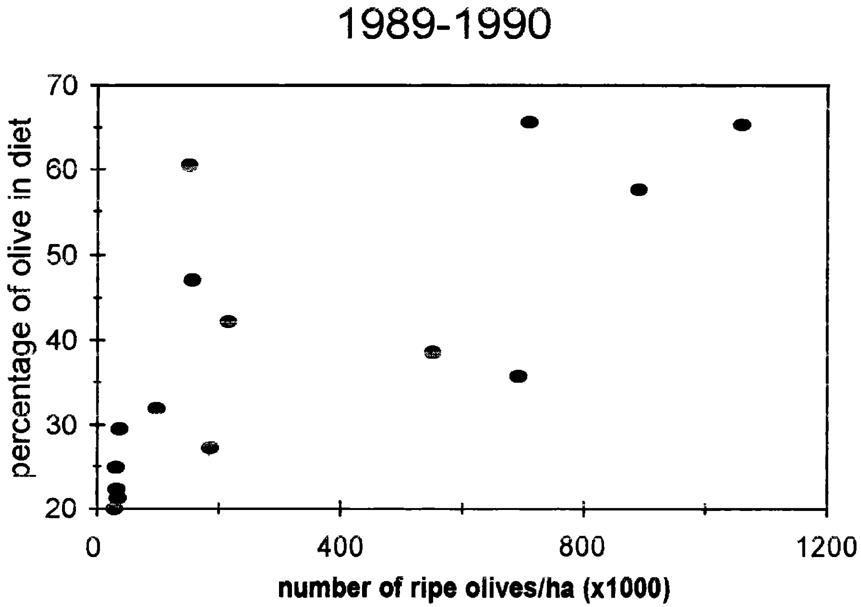


FIGURE 2. Temporal variation in olive availability and in volume of olive in the diet of Blackcaps. Only those plots and years in which enough data were available are shown (see text). Labels on x-axis as in Figure 1.



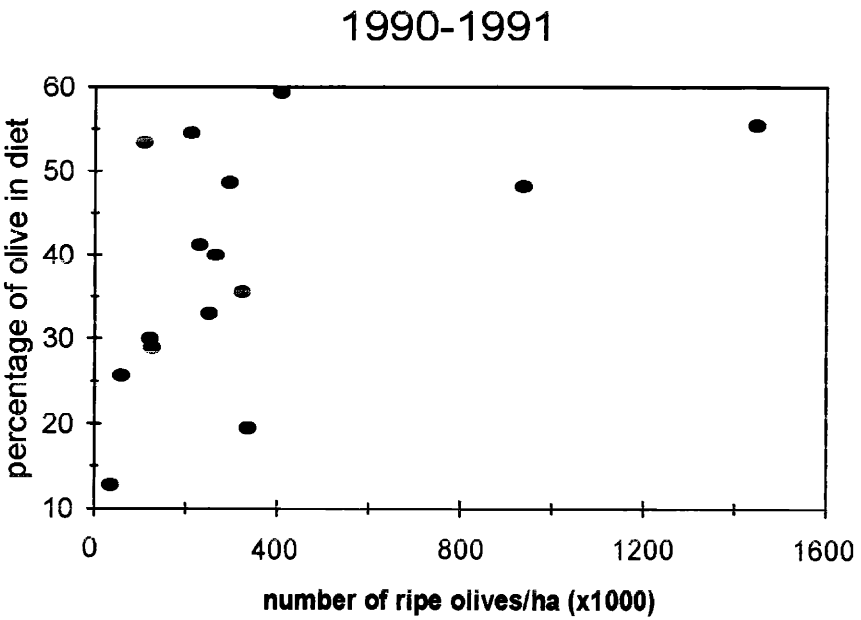


FIGURE 3. Among-plot relationship between olive availability and volume of olive in Blackcap's diet.

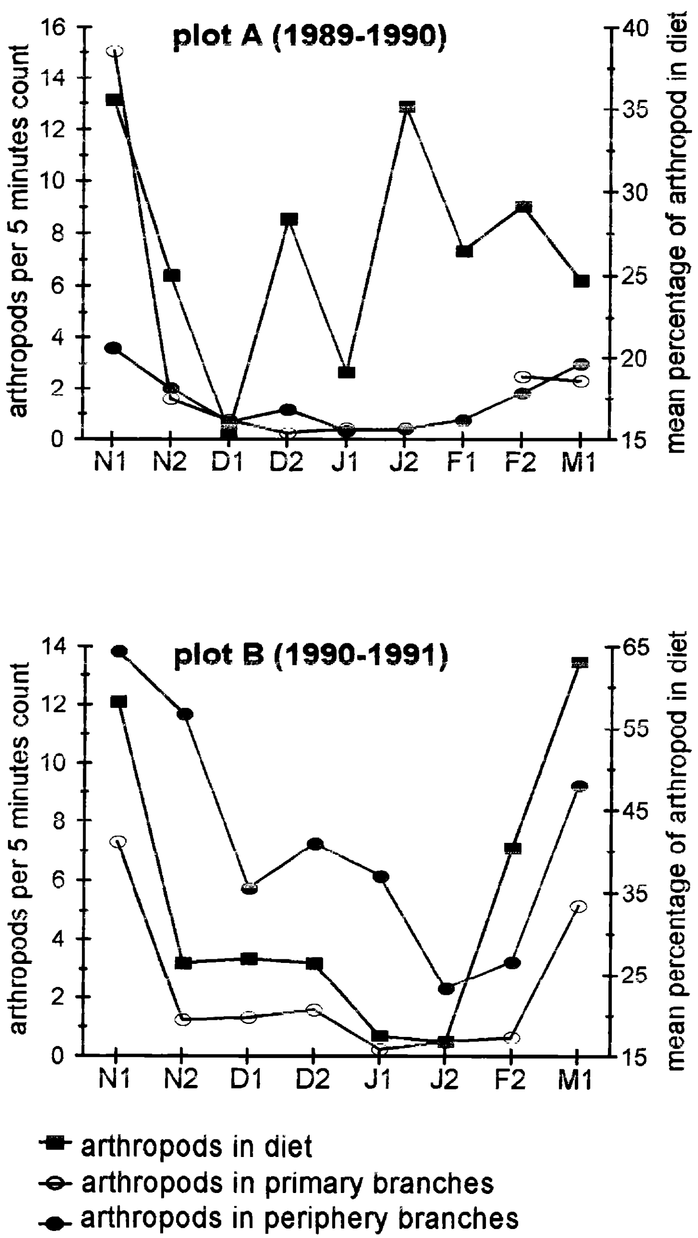


FIGURE 4. Relationship between arthropod abundance and their volume in the diet of Blackcaps. Only those plots and years in which enough data were available are shown (see text). Labels on x-axis as in Figure 1.

periphery branches; Fig. 4). During 1990–1991 (plot B), there was no significant correlation with arthropod abundance on periphery branches ($r_s = 0.45$, $P = 0.26$, $n = 8$ fortnights), but a significant correlation was found with the abundance of arthropods on primary branches ($r_s = 0.79$, $P = 0.021$, $n = 8$ fortnights; Fig. 4).

By grouping data from all the fortnights and plots we found a significant correlation between arthropod consumption and arthropod abundance on primary ($r = 0.78$, $P = 0.001$, $n = 15$) and periphery branches ($r = 0.53$, $P = 0.042$; $n = 15$) in 1990–1991, but not the year before.

Non-olive fruits were present in olive orchards almost exclusively in hedges (pers. observ.) and the diversity of fruits in the diet was higher in birds captured in hedges. For example, when nets in plots C and D were placed through hedges (season 1990–1991), the number of fruit species per sample increased significantly in both plots compared to the previous year (plot C: from 0.95 to 1.33; plot D: from 0.83 to 1.16; Mann-Whitney, P's < 0.01 in both cases). During 1990–1991, Blackcaps included a higher number of fruit species per sample in plot C and D than in the other plots (plot A = 1.00; plot B = 1.03 fruit species/sample) where nets were not placed through hedges. A significant difference among the four plots was found in this variable during 1990–1991 (Kruskal-Wallis, $H = 22.27$, $P < 0.01$), whereas there was not a significant difference the year before ($H = 4.79$, $P = 0.19$) when no nets were placed through hedges.

DISCUSSION

The number of fruiting species, volume of fruit in the diet, and diet diversity of Blackcaps is lower in olive orchards than in natural shrublands in southern Spain. However, arthropods are consumed more frequently in olive orchards than in natural shrublands (see Jordano 1988, Jordano and Herrera 1981 for comparison with shrublands). The high frequency of arthropods consumed in olive orchards may be related to the orchards lower diversity of fruits (Rey 1992), because the diversity of available fruits may influence the amount of insects ingested. Thus, Jordano and Herrera (1981) found that wintering Blackcaps in impoverished plant communities and/or during periods of low fruit availability consumed insects more frequently.

Although olives constitute the major fraction of the diet of Blackcaps in olive orchards, arthropods and non-fruit vegetable fractions were also important. The occurrence of non-fruit vegetable matter (NFPF), was surprising, because this fraction is generally not found in the diet of frugivores in other habitats (Debussche and Isenmann 1983, 1985a,b; Fuentes 1994; Herrera 1984; Jordano 1987a,b, 1988, 1989; Jordano and Herrera 1981; Loiselle and Blake 1990; Wheelwright 1986; White and Stiles 1990; Zamora 1990). Both components constitute alternative and complementary foods to olives in this habitat. In fact, significant correlations were found between arthropod availability and volume of arthropods in the diet suggesting that Blackcaps may compose their diet as a function of the seasonality of foods alternative to fruits (i.e., arthropods, see Debussche and Isenmann 1985b; Jordano 1988, 1989, for similar conclusions with other Mediterranean frugivorous birds). Likewise, ingestion of non-olive fruits in the orchards was low and infrequent. However the number of fruit species per diet sample increased wherever other non-olive fruits were available (e.g., near hedges), suggesting that such places have an important role for diet diversification. Although herbaceous cover beneath olive trees increases throughout the winter season (Valera 1992), this is not reflected in the non-fruit plant component of the diet (Spearman, $P > 0.1$ in all the plots).

In spite of these considerations, olive availability seems the major determinant of the composition of the diet of Blackcaps in olive orchards. Both within plots and among plots, the temporal pattern of olive consumption and olive availability were significantly correlated. Furthermore, diet varied among olive orchards, on the same dates, due to different ripening phenologies and crop sizes (Rey 1995). Thus, our data show that some frugivores are able to adjust their diet to temporal variation in their main food resources. We stress, however, a key limitation to extrapolating this result to natural systems. In natural systems, there are many fruiting species simultaneously or sequentially available and the most abundant food will not be temporally the same. Nevertheless, other studies in natural systems have shown that fruit availability is the principal variable affecting fruit consumption by frugivorous birds (Fuentes 1994; Jordano 1984, 1988, 1989; Wheelwright et al. 1984; Worthington 1982, 1983) and other frugivorous vertebrates (Fleming 1986; Janson et al. 1986; Sourd and Gautier-Hion 1986; Terborgh 1983). Our study demonstrates the potential capability of some birds to adjust their diet to the temporal pattern of availability of their main food resource. Frugivore dependence on olives as their main food source is probably possible because of the high energy content of olives (50–60% of dry mass is lipid, Rey 1992). But, when olive availability becomes too low, frugivores move to places with higher abundance of olives (Rey 1995). The combination of diet adjustment and tracking capability probably explains the ability of these birds to winter successfully in olive orchards.

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