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Habitat effects on resource tracking ability: do wintering Blackcaps *Sylvia atricapilla* track fruit availability?

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If resource availability shapes population distribution, changes in resource abundance should cause parallel changes in population numbers. However, tracking ability may be disrupted by different environmental and behavioural factors that act at different spatial and temporal scales. Here we analyse the ability of wintering Blackcap *Sylvia atricapilla* populations to track spatio-temporal variation in fruit availability in southern Spain in two habitats (forests and shrublands) with different population structure. Former studies had shown that forests are equally used by both adult migrant and local Blackcaps, whereas shrublands are nearly monopolized by juvenile migrants. These differences might affect resource tracking: it should be disrupted in forests, as local birds remain over winter in their breeding territories, but not in shrublands where similarly competitive juvenile migrants can freely track the spatial distribution of fruits. We analysed the fruit-tracking ability of Blackcap populations among sites and years in both habitat types using a habitat-matching model, which predicts spatio-temporal changes in population abundance proportional to changes in resource availability. We counted Blackcaps and fruiting shrubs (dominated by Lentiscs *Pistacia lentiscus* and Wild Olives *Olea europaea sylvestris*) during four winters in forest and shrubland patches. The abundance of fruits was always higher in shrublands than in forests. In shrublands, Blackcaps seemed to move freely across fruit-rich habitat patches, tracking changes in fruiting-shrub abundance among sites and years. However, such tracking was not observed in forests. This supports the view that fruit-tracking ability may be constrained by local factors, such as the social structure of populations occurring in different habitat types, which introduces spatio-temporal variation in the way fruit availability shapes the abundance distribution of these birds in their Mediterranean wintering grounds.

Food availability is thought to be a major determinant of the abundance of birds at times when individuals are mainly constrained by self-maintenance. Consequently, an association between food abundance and population size is expected (e.g. Newton 2004). In principle, whether food determines the carrying capacity of a given habitat should depend on the balance between actual food abundance and the ability of birds to track its spatio-temporal distribution efficiently within that habitat (Shochat *et al.* 2002). This should be particularly so for species whose food resources are spatially and seasonally unpredictable, as is the case for frugivores (Jordano 1992, Levey & Stiles 1992, Herrera 1998). Stochastic fruit production among habitat patches and seasons, together with the fact that birds and fruits are generally easy to count in the field, has made fruits and frugivores a model system for the analysis of resource tracking by natural populations. However, we are still far from understanding the ability of bird populations to track fruit crops (Levey & Benkman 1999, García & Ortiz-Pulido 2004). Although some studies support the existence of an adaptive association between fruit and bird abundance (Rey 1995, Moegenburg & Levey 2003), others suggest a non-equilibrium system with little, if any, resource tracking (Herrera 1998). These differences can be explained because resource tracking is a complex process affected by factors other than the distribution of resources, such as climate or the social

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environment, which may disrupt the association between birds and resources acting at different spatial and temporal scales (García & Ortiz-Pulido 2004, Tellería *et al.* 2005). So, further investigations are needed to understand the way in which frugivorous birds respond to variation in food availability in different habitats and regions.

We studied the ability of a typical Mediterranean winter frugivore (the Blackcap *Sylvia atricapilla*) to track fruit abundance changes between habitat patches and years in southern Spain. We tested whether this tracking ability changes between two contiguous habitat types, differing in population structure because of the coexistence of local sedentary individuals and overwintering migrants. Local Blackcaps show winter site tenancy in forests, coinciding during winter with migrants (which account for around 50% of individuals in this habitat type). However, resident local birds (hereafter termed locals) largely avoid neighbouring shrublands, which act as a major wintering habitat for large populations of migrants (migrants make up 95% of individuals wintering in shrublands; Pérez-Tris & Tellería 2002). Differences between habitats in age structure, body size and body condition (shrublands are occupied by younger and smaller individuals) suggest that habitat segregation is due to the social dominance of migrants, and to the defence of breeding territories by locals, both in Blackcaps and in other species wintering in the area. In fact, forests might tend towards saturation each winter because both local and dominant migrant Blackcaps prefer to winter in this habitat (Tellería *et al.* 2001, Pérez-Tris & Tellería 2002, Tellería & Pérez-Tris 2004; for similar examples in other regions, see Sherry & Holmes 1996, Marra 2000). This suggests a scenario in which forests would present a more resilient habitat than shrublands for efficient spatio-temporal tracking of fruit resources by Blackcap populations.

In this paper, we study whether these socially influenced dynamics of habitat occupation affect spatial (inter-site) and temporal (inter-year) fruit-tracking ability of Blackcap populations. Our approach was based on the habitat matching rule (Pulliam & Caraco 1984), an ideal free distribution model (IFD; Fretwell & Lucas 1970) that predicts that any variation in resource abundance between two habitat patches or two different winters in a set of localities will be followed by a change in animal density according to the algorithm

$$\log\left(\frac{D_{1i}}{D_{2i}}\right) = a + b \times \log\left(\frac{R_{1i}}{R_{2i}}\right) \qquad (1)$$

where D_{1i} and D_{2i}, and R_{1i} and R_{2i}, are the abundances of animals and resources, respectively, in the two patches or years in the locality i. This model allows us to determine analytically whether populations match ($b = 1$), undermatch ($b < 1$) or overmatch ($b > 1$) the changes in resource availability (reviewed in Kennedy & Gray 1993). It should be noted that, if this model is applied to test matching ($b = 1$), animals are assumed to have information on the availability of resources, to move without significant travel-costs among localities, not to deplete resources and to have similar competitive abilities (see review in Shochat *et al.* 2002). Obviously, these assumptions, which require a proper evaluation of resource availability and bird behaviour, are hardly accomplished in many circumstances, making the habitat matching approach a helpful methodological tool for exploring the fit between the abundance of animals and abundance of resources, but not an explicit way of testing IFD (Tellería & Pérez-Tris 2003).

METHODS

Study area

We studied an area of about 200 km^2 on the northern side of the Strait of Gibraltar, in southern Spain (Campo de Gibraltar, 36°01′N, 5°36′W). In this area, forests are dominated by oaks (*Quercus suber* L. and *Q. canariensis* Willd.), mixed with fruit-producing shrubs among which Lentisc *Pistacia lentiscus* L. and Wild Olive *Olea europaea sylvestris* (Miller) are the most abundant. Shrublands are largely open environments, mainly covered by Lentisc and Wild Olive. During autumn, the area is occupied by large numbers of wintering birds, among which the Blackcap is one of the most abundant species (Tellería *et al.* 1999, 2005).

Bird and fruit counts

We sampled eight study sites, four located in forests and four in shrublands, during two pairs of two consecutive winters (period 1: winters 1998/99 and 1999/2000; and period 2: winters 2001/02 and 2002/03).

To obtain two different estimates of Blackcap density (D) and availability of resources (R) for each study site i (see Equation 1), we worked on two habitat patches in each locality during the four study winters (in January). Each habitat patch included 3–5 line transects, 500 m long and 50 m wide (25 m at either side of the progression line). In our analyses of year-to-year tracking of fruit resources, we used annual average abundances of Blackcaps and fruiting shrubs in each study site. The same transects were repeated in all years. We counted all Blackcaps observed within transects.

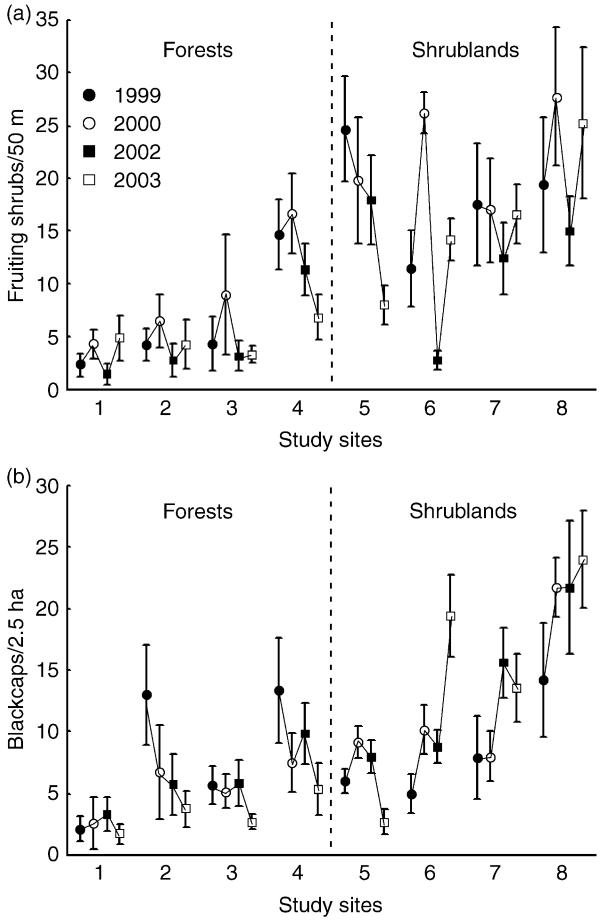

Figure 1. Year-to-year changes in abundance of fruiting shrubs (a) and Blackcaps (b) in the eight study sites. Means (± se) for each study site have been grouped by a line.

During bird counts, we measured fruit abundance by counting the number of bushes with ripe fruits in a 10-m wide belt, 5 m at either side of the progression line of the transects. Given that birds and fruits were counted on the same transects every year, we used repeated-measures models to test for variation between habitats (a between-subject factor) and winters (a repeated-measures factor) in these variables.

In addition, and for a proper evaluation of inter-habitat patterns of fruit availability, we counted the number of fruits during the winters 1998/99 and 1999/2000, differentiating between ripe and unripe, on four randomly selected racemes of individual Lentiscs, which were also randomly selected in each study site. Our aim was to estimate between-habitat differences in per-bush availability of edible fruits, as an index of food depletion (we assumed that Blackcaps prefer to consume ripe fruits only). To control for possible differences between habitats in the ability of shrubs to produce fruits, we also counted fruits on bushes in September 1999, when most fruits were unripe and migrants had not yet arrived in the area. We conducted these analyses using individual bush averages as dependent variables in mixed general linear models, using study sites as random factors (to avoid power inflation, as we sampled 15–20 bushes per site), and habitat type and winter as fixed factors. We used the Satterthwaite method of denominator synthesis (Satterthwaite 1946), implemented in the program Statistica 6.1 (StatSoft 2002), to obtain appropriate error terms for each effect. Given that this method uses fractions of sources of variation in synthesizing error terms for significance testing, the degrees of freedom for the denominator mean squares were sometimes fractional rather than integer values.

RESULTS

Patterns of bird and fruit abundance

Both fruiting shrubs and Blackcaps showed considerable variation in abundance during the study period, and the abundance of fruits was, on average, greater in shrublands than in forests (Fig. 1, Table 1).

Table 1. Results of repeated-measures general linear models of the effects of year (a repeated measures factor) and habitat type (forests vs. shrublands, a between-subject factor) on abundance of Blackcaps and fruits (both log-transformed). Repeated measures of fruit abundance in each year were included as a changing covariate of Blackcap abundance (StatSoft 2002).

	Blackcap abundance			Abundance of fruiting shrubs		
	F	*df*	*P*	*F*	*df*	*P*
Winter	2.72	3,120	0.048	6.57	3,123	< 0.001
Habitat	0.06	1,40	0.804	28.32	1,41	< 0.001
Winter × habitat	7.76	3,120	< 0.001	0.54	3,123	0.658
Abundance of fruiting shrubs	6.64	4,37	< 0.001			

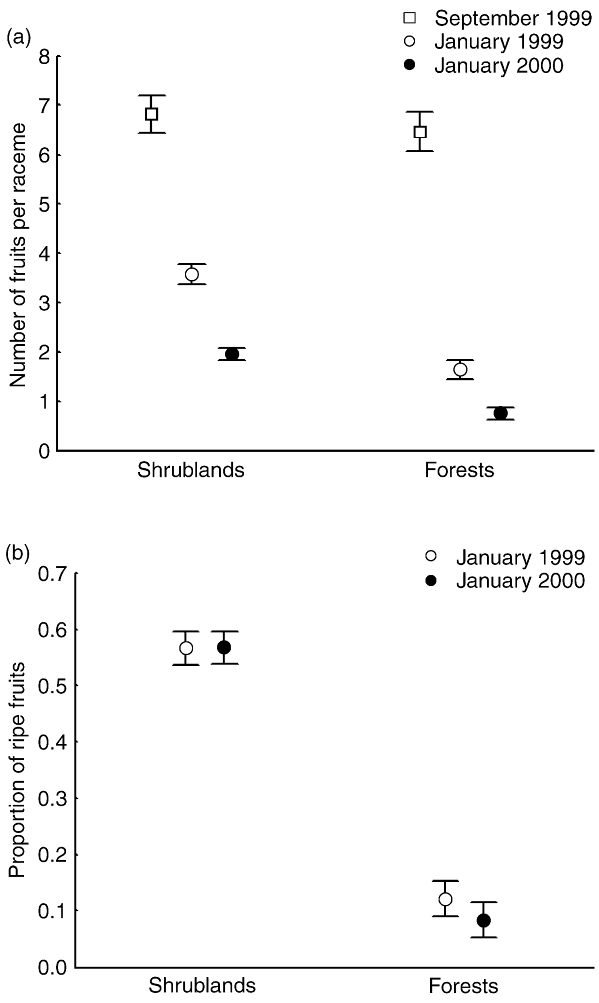

Figure 2. Variation between habitat types and years in the total number of fruits per raceme (a) and percentage of ripe fruits per raceme (b) on Lentiscs (*Pistacia lentiscus*) as two complementary indices of fruit availability in shrublands and forests (means ± se).

Blackcap abundance was strongly correlated with fruiting shrub abundance, but after controlling for this effect, it was independent of habitat type (Table 1). There was a significant interaction between habitat and year (Table 1), owing to stronger inter-annual changes in bird abundance in shrublands (winter $F_{3,54} = 6.33$, $P < 0.001$; fruit abundance Wilks' lambda = 0.012, Rao's $R_{16,37} = 7.89$, $P < 0.001$) than in forests (winter $F_{3,63} = 3.23$, $P = 0.028$; fruit abundance Wilks' lambda = 0.160, Rao's $R_{16,46} = 2.39$, $P = 0.011$; Fig. 2).

The higher abundance of fruiting shrubs in shrublands was coupled with a higher proportion of ripe fruits on individual Lentisc bushes (Fig. 2, Table 2). This probably resulted from a higher fruit-consumption rate in forests than in shrublands, and not from a lower production of fruits in forests, as the number of fruits per raceme was similar in both habitat types in September 1999, before the arrival of migrants (mixed model with log-transformed abundances: habitat type (fixed effect) $F_{1,6} = 0.09$, $P = 0.77$; site (random effect) $F_{6,152} = 7.14$, $P < 0.001$; Fig. 2), and no difference was found either in the proportion of ripe fruits at that moment (mixed model with arcsine-transformed ratios: habitat type (fixed effect) $F_{1,6} = 0.10$, $P = 0.758$; site (random effect) $F_{6,152} = 1.49$, $P = 0.185$).

A lower realized availability of food resources in forests than in shrublands was also revealed by differences between habitats in the ratio between number of fruiting shrubs and number of birds per transect (measured in January), which averaged (± se) 1.37 ± 0.20 in forests and 1.97 ± 0.19 in shrublands (ANOVA with arcsine-transformed ratios: habitat type $F_{1,150} = 14.16$, $P < 0.001$; winter $F_{3,150} = 5.17$, $P = 0.002$; habitat × winter $F_{3,150} = 3.01$, $P = 0.032$).

Table 2. Result of mixed general linear models of the number of fruits per raceme (log-transformed) and the percentage of ripe fruits per raceme (arcsine-transformed) on individual lentisc bushes sampled in both habitat types (shrublands and forests) during two winters (January 1999 and 2000). Study site has been used as a random factor, and winter and habitat type as fixed factors. Appropriate error terms and degrees of freedom have been computed using Satterthwaite's (1946) method.

	Fruits per raceme			Percentage of ripe fruits		
	F	*df*	*P*	*F*	*df*	*P*
Winter	42.70	1,6.02	< 0.001	1.43	1,5.84	0.279
Habitat	32.16	1,5.98	0.0013	71.54	1,5.98	< 0.001
Winter × habitat	0.08	1,5.96	0.783	0.86	1,5.87	0.390
Study site (random)	2.28	6,5.91	0.170	6.56	6,5.81	0.020
Winter × site (random)	1.78	6,289	0.103	0.53	6,271	0.782

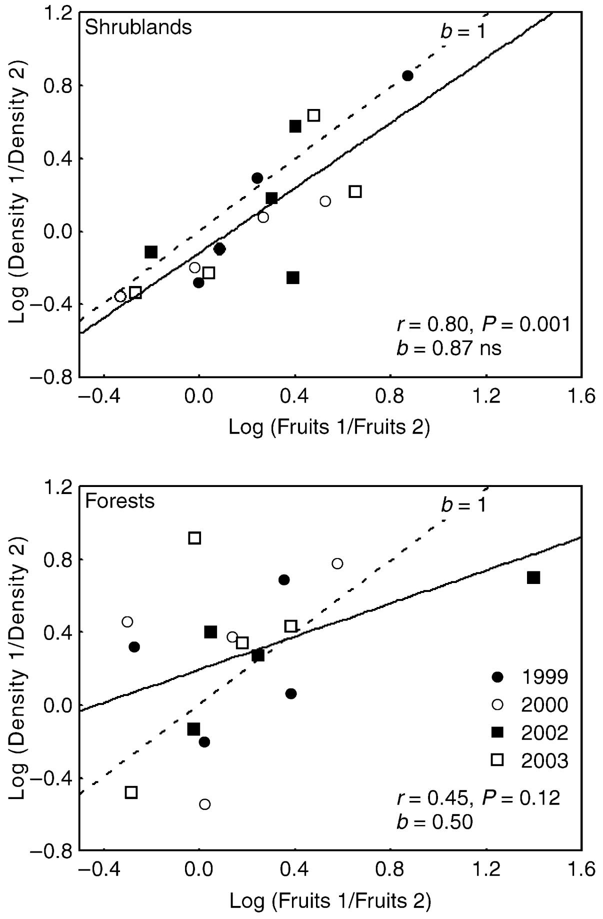

Figure 3. Relationships between changes in abundance of fruiting shrubs and changes in abundance of Blackcaps between habitat patches, controlling for year effects in an ANCOVA (not significant). Each dot represents a different locality including two habitat patches (one of the *i* sites in Equation 1), and different symbols identify study years. When correlations were significant, deviations of the slope (*b*) from *b* = 1 were tested using Student *t*-tests.

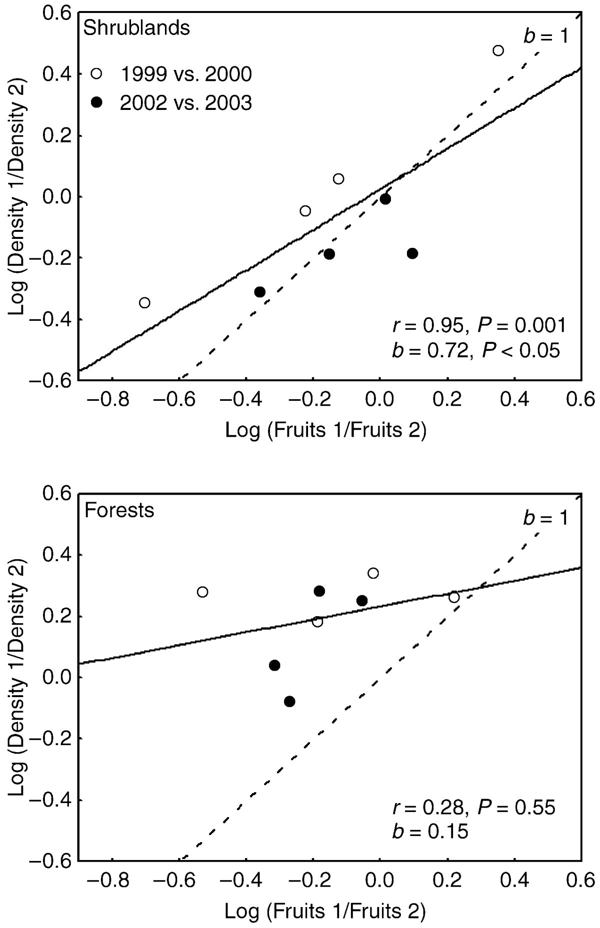

Figure 4. Relationships between year-to-year changes in abundance of fruiting shrubs and year-to-year changes in abundance of Blackcaps in forests and shrublands. Each dot represents a different locality including two annual average values (one of the *i* sites in Equation 1), and different symbols identify study years. When correlations were significant, deviations of the slope (*b*) from *b* = 1 were tested using Student *t*-tests.

Spatial and temporal tracking of fruit resources

We found different associations between changes in Blackcap abundance and spatial changes in fruit abundance in forests and shrublands (Fig. 3). In forests, the abundance of Blackcaps did not match with spatial changes in fruit abundance, supporting the idea that a substantial part of the population wintering in this habitat (i.e. the territorial local Blackcaps) did not track spatial variation in fruit abundance. However, the abundance of Blackcaps in shrublands matched spatial changes in fruiting shrub abundance. In fact, the average pattern of such a relationship during the four study winters did not deviate from *b* = 1 (Fig. 3).

The association between changes among years in Blackcap abundance and changes among years in fruit availability also differed between forests and shrublands. In forests, Blackcap abundance did not track the temporal variation of fruit availability. However, inter-annual changes in Blackcap abundance in shrublands were strongly correlated with year-to-year changes in fruit availability. In this case, the slope of such a relationship was significantly lower than *b* = 1 (Fig. 4), revealing temporal resource undermatching of fruiting shrub abundance by Blackcaps wintering in shrublands.

DISCUSSION

Spatial tracking of fruit resources

It is generally accepted that animal abundance is influenced by several interacting factors, and therefore it is difficult to anticipate abundance distributions using information on just one such factor (Brown *et al.* 1996). However, on some occasions a single type of resource may play a key role as a determinant of population abundance. Fruit availability largely determined the abundance distribution of wintering Blackcaps in the Campo de Gibraltar area (see also Tellería & Pérez-Tris 2003), which agrees with the patterns obtained in other lowland areas in southern Spain (Rey 1995). Lentiscs and Wild Olives, the dominant fruiting shrubs in the region, produce two of the most nutritious fruit types in southern Spain, and they are actively selected by Blackcaps (Herrera 1984, 1998, our unpubl. data for the area). Therefore, the functional relationship between fruit and bird abundance reported here seems to be straightforward.

In shrublands, but not in forests, changes in the spatial distribution of Blackcap abundance fitted the spatial variation in fruiting shrub abundance according to a habitat matching-rule model (*b* in Equation 1 equal to 1; Fig. 3). This is not surprising, as migrant Blackcaps wintering in seasonal habitats of the Mediterranean could meet the conditions of such a distribution model particularly well. Mediterranean shrublands are occupied seasonally by Blackcap populations in which juveniles represent around 80% of individuals (Pérez-Tris & Tellería 2002), which wander in search of fruit in areas with a high availability of fruit resources. In addition to the greater abundance of fruiting shrubs in shrublands (compared with forests, Fig. 1, Table 1), the ratio between the abundance of fruiting shrubs and Blackcaps was also higher in shrublands than in forests. Moreover, our analysis of the proportion of ripe Lentisc fruits per raceme revealed that around 60% of fruits remained uneaten in shrublands, while fruit production of forests had been more intensively consumed (Fig. 2, Table 2). Therefore, populations of transient Blackcaps moving across fruit-rich habitat patches might be included among the few natural systems that meet the assumption of similarly competitive individuals (juvenile birds) moving freely in a scenario of ‘continuous resource input’ where resource matching tends to occur (Tregenza 1994, Shochat *et al.* 2002).

Temporal tracking of fruit resources

Year-to-year changes in fruit abundance in forests were not associated with changes in Blackcap abundance (Fig. 3). Again, this disruption of resource tracking in forests could be explained by the presence of locals, whose between-winter abundance distribution depends on factors other than fruit availability. However, we found a significant annual coupling of changes in fruit and bird abundance in shrublands. It has been argued that bird–fruit abundance correlations among years are difficult to obtain because they require that the effects of large-scale, independent, processes regulating annual fluctuations of both birds and fruits be overridden (Herrera 1998). We are aware that the abundance of migratory Blackcaps in the wintering grounds of southern Spain depends on the breeding success of populations from all over Western Europe, while fruit abundance in wintering areas represents the culmination of local processes affected by the success of flowering and pollination. As a consequence, the productive outcomes of birds and fruits are uncoupled and largely unpredictable from one year to the next (Herrera 1998). Therefore, given that the abundance of fruits in southern Spain shows dramatic fluctuations between years (Jordano 1985, 1992, Herrera 1998, this study), the most plausible explanation for the inter-annual fruit tracking found in this study is the existence of regional-scale movements of transient Blackcaps that redistribute abundance according to fruit availability (Rey 1995, Tellería *et al.* 2005).

Large-scale movements seem to be a common behaviour among Mediterranean wintering frugivores (Santos 1982, Jordano 1993, Guitián *et al.* 2000). This might overcome, at least partially, the stochasticity expected from the asynchronous reproductive cycles of migratory birds and the fruits upon which they rely. These movements have been documented by ringing recoveries of Blackcaps that shifted wintering areas between years, sometimes between places located more than 300 km apart (Cuadrado *et al.* 1995, our unpubl. data). However, large-scale movements of Blackcaps did not match population abundance to inter-year actual fruit abundance in shrublands (Fig. 4) as in the case of intra-year spatial distribution of birds and fruiting shrubs. This view is supported by the greater availability of uneaten ripe fruits per raceme on Lentiscs in this habitat during January (Fig. 2), an atypical pattern in the Mediterranean, where seed-dispersing plants tend to be consumed at higher rates, particularly in the case of lowland habitats where birds consume around 90% of fruit crops (Herrera 2001). This rate tends to decrease, however, in disturbed habitats, where frugivorous birds can be scarce (Alcántara *et al.* 1997), or in years and habitats in which fruits are exceptionally abundant (Herrera 1995). This suggests that wintering Blackcap numbers do not always approach the carrying capacity of shrublands in our study area. Given that habitats with a seasonally high abundance of fruits make up the largest part of Blackcap wintering grounds in the Iberian Peninsula (Mediterranean shrublands, olive groves, etc.; Tellería *et al.* 1999), the patterns obtained in this study are likely to be general to many wintering populations of this species. Thus, the annual decoupling between bird numbers and fruit production in winter should impose a constraint on the overall population limitation of migratory Blackcaps (Newton 2004).

Do populations of frugivorous birds track fruit availability?

According to our results and previous studies, the answer to this question should be 'sometimes'. The patterns of fruit tracking by birds seem to be shaped by factors affecting behavioural responses to resource heterogeneity (García & Ortiz-Pulido 2004). These can form a hierarchical system of interactions, with factors acting at the larger spatial and temporal scales hampering the innate ability of birds to track fruit resources at smaller scales (Kottiar & Wiens 1990, Sallabanks 1993, Burns 2004). For example, the annual productivity of breeding and wintering areas, or unpredictable climatic events (frosts, snowfalls, cold waves in northern areas, etc.), can decouple the pattern of association between the abundance of fruits and abundance of frugivorous birds in wintering grounds of the Mediterranean (Jordano 1993, Herrera 1998), thereby hampering any behavioural optimization of food resources. In addition, adaptive fruit tracking can be disrupted by less evident factors, such as the different social environments of forests and shrublands in our study area and other factors that are difficult to control for (predation risk, human disturbances, etc.). However, this situation can change at smaller scales, particularly in mild regions such as the large areas of coastal Mediterranean shrublands, which are less frequently affected by climatic disturbances (Tellería *et al.* 2005). In these less constraining environments, our results show that Blackcap populations are able closely to track the spatial distribution of fruiting shrub abundance every winter, and adjust their numbers less efficiently to annual oscillations in this resource.

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