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Fruit tracking between sites and years by birds in Mediterranean wintering grounds

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Knowledge of the ability of birds to track spatiotemporal variation in fruit distribution is essential for understanding plant-frugivore interactions. Arguably, although total fruit availability sets an upper limit to the number of birds that can exploit a habitat patch, not all species can equally distribute abundance according to variation in fruit resources. To explore this, we studied bird and fruit abundance in 1999–2005 in Mediterranean scrublands and woodlands of southern Spain. We analysed whether changes of fruit abundance in eight different sites during six winters could predict numerical changes of a set of frugivorous passerines of the area (blackcap *Sylvia atricapilla*, Sardinian warbler *S. melanocephala*, robin *Erithacus rubecula*, song thrush *Turdus philomelos* and blackbird *T. merula*). We also investigated if all frugivores together tracked fruits better than individual species, thereby supporting a shared use of resources. Results showed strong inter-specific differences. Only the most abundant species (blackcaps and robins) tracked the spatial patterning of food despite strong differences in the use of space (vagrant and territorial, respectively). This suggests plastic behaviour of territorial robins, with individuals changing from strictly territorial to wandering, a flexibility that would favour between-site numerical arrangements according to food resources. Annual changes in bird numbers were independent of the availability of fruits, except for blackcaps, an abundant vagrant bird that tracked inter-winter changes in fruit abundance. The abundance of blackcaps fitted the spatiotemporal patterning of fruit resources better than the whole guild of frugivorous birds, inconsistent with the idea that these species track together the changing availability of fruit resources.

Variable food distribution makes different species of migratory birds spend different periods of time each winter in each area, reaching in some years areas that remain vacant in other years (Newton 2004). To efficiently cope with spatiotemporal dynamics of food availability, birds need to have information on food distribution, for which they need to move among suitable sites (Fretwell 1972, Sutherland 1996). However, the circumstances required for efficient food tracking may change among regions, habitats and trophic groups, which makes it difficult to extrapolate the conclusions derived from case studies to other bird species or geographic regions.

We studied how the abundance of frugivorous birds tracks between-site and between-winter changes of fruit abundance in southern Spain, an important wintering area for migratory birds in the western Palaearctic. In the context of increasing awareness of the functional role of birds as ecosystem engineers (Sekercioglu 2006), frugivorous species are of particular conservation concern because they disperse the seeds of many plants in different regions connected by migratory routes. In the Mediterranean, mutualistic bird–plant relationships have been intensively studied (Herrera 2002), but whether bird numbers track fruit abundance is not understood. Some studies have shown aggregative responses of birds to fruit abundance (Jordano 1985, Rey 1995, Tellería et al. 2005), but others found weak relationships (Jordano 1995, Alcántara et al. 1997, Herrera 1998). In addition, there have been few specific approaches to test birds' adjustment of numbers to the extant availability of fruits. Previous studies showed that spatiotemporal changes in fruit abundance were followed by concomitant changes in blackcap abundance (Tellería and Pérez-Tris 2003, 2007). Whether other species similarly adjust numbers to the changing availability of fruits in the same region, and if these patterns are associated with particular spatial behaviours (vagrant or territorial), remains unknown. In addition, an important open question is whether species that are particularly well suited to tracking fruit abundance (such as the aforementioned blackcap) can track fruit resources better than the whole guild of frugivores that jointly exploit the habitat. To fill these gaps we studied fruit-tracking in five frugivorous birds (blackcap *Sylvia atricapilla*, Sardinian warbler *S. melanocephala*, European robin *Erithacus rubecula*, song thrush *Turdus philomelos* and European blackbird *T. merula*) wintering in southern Spain according to the following scheme.

1) First, we evaluated the strength of bird–fruit abundance relationships, which is important because a lack of aggregative response would preclude any evaluation of fruit tracking by birds (Sutherland 1996). We approached this by testing the role of fruit abundance on bird numbers, while controlling for the effect of protective vegetation cover (Hutto 1985) and altitude, a surrogate for variation in climate harshness (Carrascal and Díaz 2006).

2) If birds show significant aggregative responses to fruit abundance, then it is interesting to know whether they track between-site and between-winter changes in fruit abundance. We approached this using the habitat matching rule (Pulliam and Caraco 1984), an ideal free distribution (IFD) model which predicts that, if both resource abundance and population abundance have been measured in two habitat patches or two periods (e.g. two winters), any change in resource abundance between habitat patches or periods of time will be followed by a concomitant change in population density according to the following algorithm:

$$\log(D_{1i}/D_{2i}) = a + [b \times \log(R_{1i}/R_{2i})] \qquad (1)$$

where D_{1i} and D_{2i}, and R_{1i} and R_{2i} are the abundance of animals and resources, respectively, in the two patches or the two periods of time in the locality i. This model was used to explore whether abundance matched ($b = 1$), under-matched ($b < 1$) or overmatched ($b > 1$) changes in availability of resources (Kennedy and Gray 1993). Although some studies have used the matching rule to specifically test for IFD in fruit–frugivore interactions (Shochat et al. 2002), such a test is outside of our scope. Therefore, we used this method as a helpful model to explore food tracking, but not to explicitly test IFD (Tellería and Pérez-Tris 2003, 2007).

3) We predicted different fruit-tracking patterns in species with different behaviour. More specifically, relative to territorial birds, we expected vagrant birds to better track food resources because they should be free to move among sites in search of fruits (Levey and Stiles 1992). Thus, vagrant birds will more easily gather information on the distribution of resources, allowing ready response to changing patterns of fruit abundance (Shochat et al. 2002). However, Johnson and Sherry (2001) have shown that some territorial species adjust numbers to the spatial patterning of scarce food resources in wintering grounds.

4) Finally, we investigated whether frugivorous birds had a shared track of resources. Birds seem to rely on a variety of cues to find fruits. For instance, large fruit abundance or conspicuously-coloured fruits may be detected from great distances. However, the costs of this active searching may be reduced by tracking the behaviour of other frugivores. Under such conditions, birds feeding on fruits will act less as competitors than as facilitators enabling the co-occurrence of other individuals and species, particularly in circumstances where the shared resources are ephemeral and unevenly distributed (Saracco et al. 2004). This could favour strategies of multi-specific tracking of resources (Saracco et al. 2004) and perhaps improved matching of food changes by the whole guild (Shochat et al. 2002).

Materials and methods

The bird species

We selected five species (blackcap, Sardinian warbler, song thrush, European blackbird and European robin), which rely on fruits as the most important element of their diet in southern Spain (Herrera 1984, 1998, Jordano 1985, Telleria et al. unpubl.). These five species are the bulk of the community of birds in the area (Tellería et al. 2005). The two *Sylvia* spp. have breeding populations in the area, but differ in winter vagrancy. Blackcaps increase in numbers during winter due to the arrival of northern migratory individuals, which spread across the region showing a vagrant behaviour (Cramp 1992, Pérez-Tris and Tellería 2002). However, Sardinian warblers make restricted dispersive movements and show little seasonal change in abundance (Tellería et al. 1999). The two *Turdus* spp. also differ in vagrancy; the song thrush is exclusively migratory with great changes in abundance between winters (Jordano 1995), however, blackbirds have a local sedentary population that slightly increases in winter with small numbers of migratory conspecifics (Tellería et al. 1999). Finally, similarly to the blackcap, the European robin has a sedentary population that is greatly enlarged by migratory conspecifics during winter (Tellería et al. 1999). Unlike blackcaps, however, robins are territorial and often philopatric in wintering grounds (Cramp 1988, Tellería and Pérez-Tris 2004), a behaviour which could hamper their efficient between-site and between-winter tracking of food distribution.

Study area

We studied four woodlands and four scrublands ranging from 0 to 240 m a.s.l., scattered along a SW–NE 25 km-long stretch on the northern side of the Strait of Gibraltar (Campo de Gibraltar area, 36°07′N, 5°39′W; see Tellería et al. 2005 for details). The area of about 1500 km^2 is crossed from north to south by hill ranges covered by cork-oak forests *Quercus suber* mixed with patches of African oaks *Q. canariensis*. The surrounding lowlands are covered by scrublands, grasslands and croplands. Both forests and scrublands have abundant fruit-producing shrubs, dominated by lentiscs *Pistacia lentiscus* and wild olives *Olea europaea sylvestris*, two plants whose fruits are intensely used by birds (Herrera 1984) and account for $>80\%$ of all fruiting plants in the area (Tellería et al. 2005).

Fruit and bird counts

We studied spatiotemporal fruit tracking by birds during six winters (January 1999–January 2005, excluding 2001). In each study site we established 4–7 500-m long transects, on which each winter were counted the number of fruiting shrubs on a 10-m wide belt, 5 m either side of the progression line. We assumed that crop variation between shrubs was similar between transects and years, so the number of fruiting shrubs was a surrogate of fruit availability (Shochat et al. 2002). We counted birds along the same transects in a 50-m wide band (25 m either side of the progression line). In these transects we studied vegetation structure in two circles of radius 25 m distributed at intervals of 200 m. There, we measured cover of shrubs (vegetation <2 m high), cover of trees (vegetation >2 m high), density of trees (number of trunks with 10, 10–30 and 30 cm diameter at breast height) and number of tree and shrub species. We also measured the mean elevation of each transect. To reduce the number of variables, we conducted a principal component analysis of vegetation variables from where we extracted a principal component (PC) that depicted a gradient of increasing cover and diversity of shrubs (factor loading: tree cover: 0.118, trunks <10 cm: -0.062, trunks 10–30 cm: -0.030, trunks >30 cm: 0.073, shrub cover: 0.876, shrub species: 0.836; eigenvalue: 1.49, explained variance: 24.83%). Factor scores were used to characterise the vegetation structure of the study transects.

Analyses

Factors affecting bird abundance

We explored between-site and between-winter changes in the abundance of fruiting shrubs using repeated-measures ANOVA. To study the factors affecting the aggregative response of birds, we included altitude, shrub cover (PC) and number of fruiting shrubs per site (8 sites measured during 6 winters) as covariates in a mixed general linear model (GLM; StatSoft 2002) with the number of birds per transect as the dependent variable and year and site as random factors.

Fruit tracking

To obtain two different estimates of bird density (D) and fruit abundance (R) for each study site i (eq. (1)), we worked on two habitat patches in each study site during the six study winters. Each habitat patch included two to four line transects 500 m long (see above). In our analyses of year-to-year tracking of fruits, we compared three sets of annual mean abundances of birds and fruiting shrubs in each study site (1999–2000, 2002–2003 and 2004–2005). To test spatiotemporal tracking with eq. (1), we analysed all data of the six winters, using year as a random factor. We assumed that these data represented independent situations in which birds responded to the spatiotemporal heterogeneity of fruit resources (for a similar approach see García and Ortiz-Pulido 2004).

Results

Factors affecting bird abundance

The abundance of frugivorous birds changed from winter to winter, parallel with variation in the abundance of fruiting shrubs, particularly in 2004, the year with the highest fruit abundance (Fig. 1). Blackcaps and robins were most abundant, while Sardinian warblers and blackbirds were the least. We did not find temporal trends for any species other than the association with fruit abundance; except perhaps for the robin with steadily decreased abundance during the study period and, less clearly, the song thrush, which was scarce in the first half of the study and suddenly increased abundance in 2005 (Fig. 1).

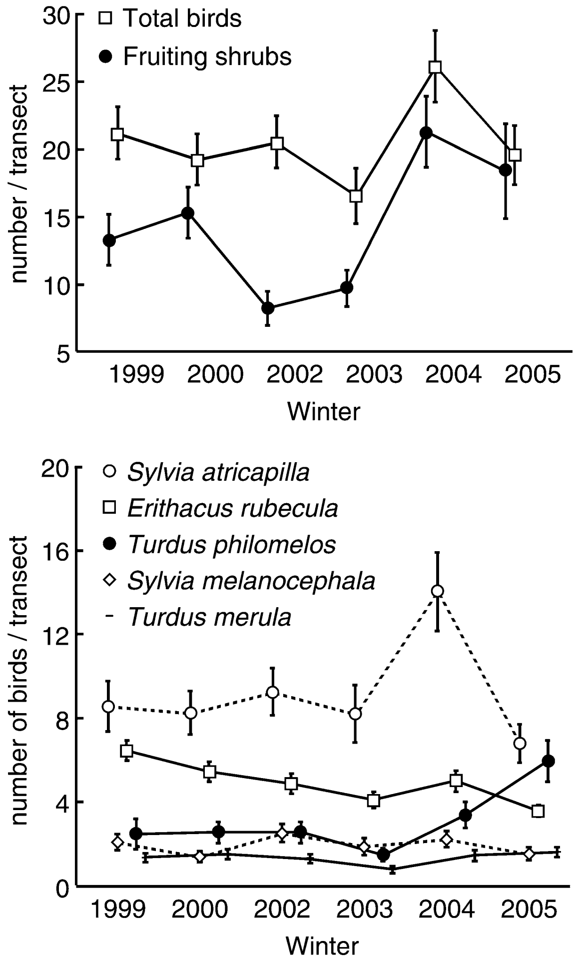

Figure 1. Between-winter changes in mean numbers (±SE, n = 43) of birds and fruit-producing shrubs counted in 500-m long transects. Above: variation in total number of birds and fruit-producing shrubs. Below: variation in numbers of each species considered in the study.

Fruit abundance changed both between sites and between years (ANOVA; site: $F_{7,34} = 10.48$, $p < 0.001$; year: $F_{5,170} = 13.03$, $p < 0.001$), leading to dynamic spatiotemporal patterning of fruit availability during the study (site × year interaction: $F_{37,170} = 2.87$, $p < 0.001$). Variation in fruit abundance best explained variation in bird numbers between sites and years (Table 1), supporting the distribution of food resources largely determining spatiotemporal variation in bird abundance. Altitude was also an important correlate of bird abundance, as birds tended to be more abundant in the lowest sectors of the area after controlling for the effect of food.

Spatiotemporal fruit tracking by birds

Spatiotemporal changes in the abundance of the whole set of frugivorous birds were positively correlated with spatiotemporal changes in fruit abundance, although variation in

Table 1. Results of mixed general linear model (GLM) analysing abundance of frugivorous birds in function of altitude, habitat structure (shrub cover) and fruit availability. Years and sites were random factors.

	DF	beta	F	p	beta	F	p
		Frugivorous bird guild ($R^2 = 0.748$)			*Sylvia atricapilla* ($R^2 = 0.708$)		
Altitude	1	−0.666	9.66	0.002	−0.803	11.90	<0.001
Shrub cover	1	0.007	0.04	0.851	−0.028	0.41	0.520
Fruit abundance	1	0.508	74.61	<0.001	0.514	66.72	<0.001
Site	7		6.33	<0.001	–	3.06	0.010
Year	5		2.97	0.023	–	2.60	0.041
Year × site	35		1.54	0.035	–	2.28	<0.001
Error	207				207		
		Sylvia melanocephala ($R^2 = 0.777$)			*Erithacus rubecula* ($R^2 = 0.\ 532$)		
Altitude	1	0.635	9.75	0.002	−0.757	6.62	0.010
Shrub cover	1	0.022	0.34	0.558	0.052	0.88	0.350
Fruit abundance	1	0.205	13.87	<0.001	0.464	33.99	<0.001
Site	7	–	22.83	<0.001	–	5.17	<0.001
Year	5	–	4.30	0.001	–	3.76	0.007
Year × site	35	–	1.57	<0.001	–	2.01	0.001
Error	207						
		Turdus philomelos ($R^2 = 0.573$)			*Turdus merula* ($R^2 = 0.380$)		
Altitude	1	0.129	0.21	0.644	−0.067	0.04	0.842
Shrub cover	1	−0.030	0.33	0.567	0.056	0.76	0.382
Fruit abundance	1	0.123	2.59	0.109	0.353	14.95	<0.001
Site	7	–	4.47	<0.001	–	2.07	0.048
Year	5	–	3.42	0.012	–	1.99	0.081
Year × site	35	–	2.60	<0.001	–	1.66	0.016
Error	207						

bird numbers under-matched ($b < 1$) the changes in food resources (Fig. 2).

Blackcaps and robins, the two most abundant species, tracked spatial changes in fruit abundance, a pattern not observed in the other species (Fig. 3). In both blackcaps and robins, variation in bird numbers under-matched ($b < 1$) the changes in fruit abundance. To further dissect the possible role of bird abundance on fruit tracking, we repeated the analyses with the song thrush in 2005, when this species became abundant in the area (Fig. 3). Although the sample was small, the analysis showed a strong positive correlation between fruit availability and abundance of song thrushes during 2005 (GLM, fruit abundance: $F_{1,31} = 14.46$, $p < 0.001$), as well as a spatial over-matching of fruit abundance by the species ($y = 0.043 + 2.054x$, $r = 0.79$, $p = 0.064$, $n = 6$). Blackcap was the only species that tracked (under-matched $b < 1$) between-winter changes in fruit abundance (Fig. 4). In fact, blackcaps tracked the spatiotemporal patterning of fruit abundance better than the whole guild of frugivorous birds (Fig. 2).

Discussion

General patterns

Fruits are often abundant but patchily distributed in space and time (Levey 1988). As a consequence, the interaction between fruit-producing plants and frugivores will depend on the spatiotemporal pattern of fruit abundance between sites or years. In addition, such interaction should also depend on the ability of different species of frugivores to track the spatiotemporal variation in fruit availability. We found evidence of fruit tracking by some, but not all frugivorous birds wintering in southern Spain, which was stronger in space within winters than between years. Great variation between years is a central characteristic of fruit–frugivore interactions (Jordano 1985, 1994, Loiselle and Blake 1994, Herrera 1998), which makes the patterns observed in a given year hardly generalisable to all years. In turn, there is general agreement that studies on the ecological consequences of fruit tracking in only one year will likely produce incorrect conclusions (Herrera 1998, Guitian and Bermejo 2006). Our study was based on repeated study of the same eight sites during six near consecutive winters, exploring how bird numbers reacted to changing fruit abundance in the Campo de Gibraltar area, a typical habitat of wintering Palaearctic frugivorous birds in the Mediterranean region.

Wintering birds were able to track fruit abundance (Fig. 2), despite great spatiotemporal shifts in fruit abundance in the Campo de Gibraltar area (significant site × year interaction). However, the abundance of the guild of frugivorous birds (all five species together) did not fit as well to changing fruit abundance as abundance of blackcaps (Fig. 3 and 4). This result suggests that the response by the whole guild was a mere combination of the patterns of fruit tracking of individual species, weighted by the relative abundance of each species. Therefore, hypothetical joint-tracking of food by frugivorous birds (Shochat et al. 2002) is not supported by our results, which indicate independent use of fruit abundance by each bird species.

Spatial tracking of fruit resources

The abundance of three out of five species studied (Sardinian warbler, blackbird and song thrush) did not match spatial changes in fruit resources. Considering the

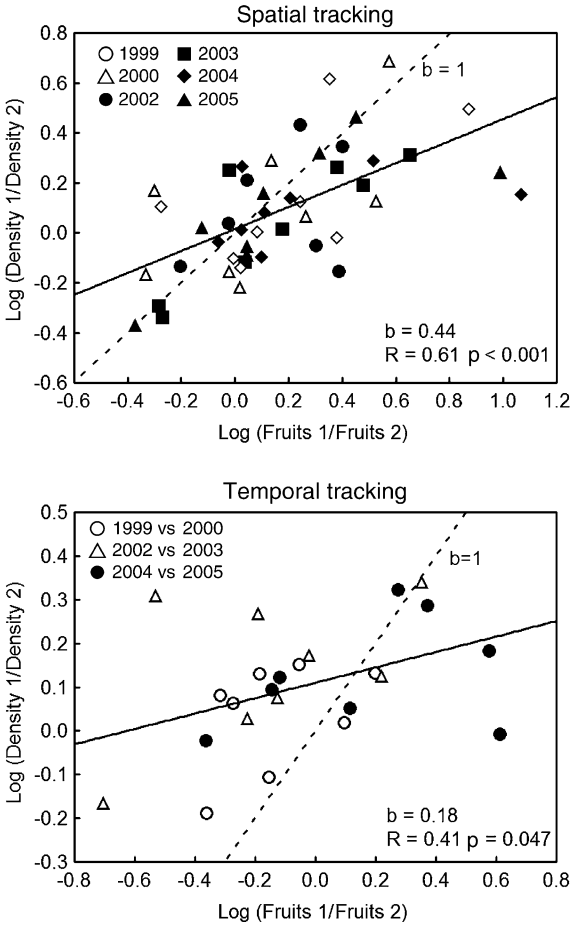

Figure 2. Above: relationships between changes in the abundance of fruiting shrubs and changes in the abundance of the frugivorous guild between two habitat patches. Each dot represents a different study site including two habitat patches. Different symbols identify the study winters. Below: relationships between year-to-year changes in abundance of fruiting shrubs and year-to-year changes in abundance of the frugivorous guild for the study sites. Different symbols identify the study winters. Discontinuous lines represent perfect matching (b = 1), and continuous lines fit to the data.

different use of space by each species (the song thrush is a good fruit tracker in Mediterranean wintering grounds; Jordano 1995, Rey 1995) this result seems to be related to the low regional abundances of these species. This interpretation is supported by clearer patterns of spatial fruit tracking by song thrushes during 2005, when the species reached its highest population density. That great regional population abundance was required for spatial fruit tracking to emerge was also supported by the two most abundant species (blackcaps and robins) having the closest spatial tracking of fruits, despite having the most dissimilar pattern of use of space (blackcaps are vagrant while robins are territorial).

Blackcaps adjusted their numbers to spatial variation in fruit abundance, but under-matched the spatial patterning of fruit resources. Under-matching of fruits has been related to imperfect knowledge of the distribution of food sources by vagrant birds (Shochat et al. 2002), but could also be affected by specific biological traits of blackcaps. This may be particularly important in our study area, where migratory and sedentary blackcaps exploit shrublands and forests, which are structurally very different habitat types (Pérez-Tris and Tellería 2002). In winter, shrubland patches show the highest fruit abundance, and are occupied by migratory blackcaps – mostly juveniles – that freely move in the search of food, matching the instantaneous availability of food resources (Tellería and Pérez-Tris 2007). In contrast, forests produce less fruits, yet they are the preferred habitat of local sedentary blackcaps, which have reproductive interests in shrubby forest sectors (Pérez-Tris and Tellería 2002). Such circumstances, which increase abundance in sites with scarce fruits, disguises the general pattern of fruit tracking by the whole population of blackcaps wintering in the Campo de Gibraltar area (Tellería and Pérez-Tris 2007).

Robin abundance also tracked spatial changes in fruit abundance, seemingly counterintuitive given the territorial and often philopatric behaviour of the species during winter (Cramp 1988). Thus, territoriality should favour a pre-emptive distribution of individuals, which should set an upper limit to the number of birds that can occur within a given habitat patch, and consequently limit any fit of bird numbers to fruit abundance at the scale of our study. Although a pre-emptive distribution of territorial robins could produce the observed spatial under-matching of fruit-abundance (Fretwell 1972), our results suggest that robins' spatial arrangements were also affected by the distribution of fruit abundance. For instance, fruit distribution may be important in determining the distribution of robins if birds with different competitive abilities occupy different habitats. In fact, in the Campo de Gibraltar area first-year robins and individuals in poor body condition tend to occupy fruit-rich shrublands (Tellería and Pérez-Tris 2004), and might be responsible for the pattern of fruit tracking that we observed. Similar adjustments to food resources have been recorded in territorial American redstarts *Setophaga ruticilla* wintering in Jamaica, which move in search of better sites when food is scarce. This species shows plastic behaviour in winter grounds, with individuals changing from strictly territorial to wandering, a flexibility that favours the spatial arrangement of abundance according to food resources (Johnson and Sherry 2001).

Fruit tracking between winters

It has been argued that consistently positive relationships between changes in fruit abundance and changes in bird abundance between years are difficult to obtain because they depend on independent processes that regulate annual fluctuations of birds and fruits (Herrera 1998). For example, between-year variation in bird abundance in southern Spanish wintering grounds largely depends on the annual breeding success of broadly distributed western European populations of the species, while between-year variation in fruit abundance depends on the local success of flowering, pollination and fruit-ripening. As a consequence, it can be assumed that abundance of migratory birds and fruits in wintering grounds will be frequently uncoupled and largely unpredictable from one year to the next.

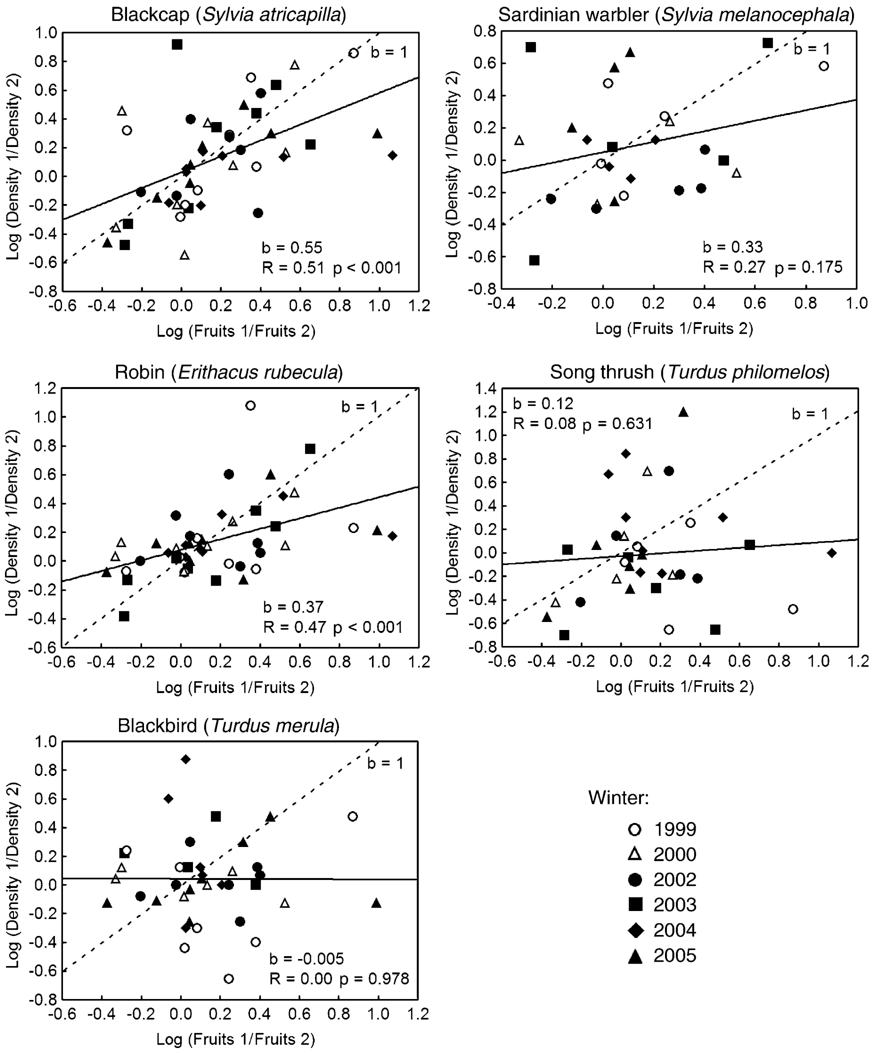

Figure 3. Relationships between changes in abundance of fruiting shrubs and changes in abundance of individual species between habitat patches. Each dot represents a different study site including two habitat patches. Different symbols identify the study winters. Discontinuous lines represent perfect matching (b = 1), and continuous lines fit to the data.

Although large-scale processes may affect regional population trends, some species may still track annual changes in the abundance of fruit resources at regional scales. Such effect may be created because some sites have low fruit abundance in winters when regional fruit abundance is highest, and vice versa. This pattern can be observed in the matching rule models (Fig. 2 and 4), in which between-winter variation in fruit abundance is near zero. In this scenario, birds can distribute themselves among sites to track regional changes in fruit resources each winter. Because of their vagrant behaviour, blackcaps seem well adapted to such dynamics of between-winter variation in fruit abundance, although they under-match the changing availability of resources. Conversely, robins did not distribute themselves according to the fruit pattern of each winter (Fig. 4). Given that territorial behaviour of robins has some plasticity (such that robins distribute each winter according to intra-site changes in fruit availability; Fig. 3), we cannot explain why they are apparently unable to adjust their numbers to changing fruit abundance between years.

Concluding remarks

The patterns of fruit tracking by birds seem to be shaped by a hierarchical system of interactions, with factors acting at greater spatial and temporal scales hampering the ability of birds to adjust their numbers to food abundance at smaller scales (Kottiar and Wiens 1990, Sallabanks 1993, Rey 1995, Burns 2004, García and Ortiz-Pulido 2004). According to our results, the regional abundance of individual species (largely dependent on the particular biology and history of each species) is a major determinant of the emergence of fruit-tracking patterns in the Campo de Gibraltar area. For scarce species, this effect is probably a consequence of the difficulties in adjusting the IFD model to scarce data (Tellería and Pérez-Tris 2003). However, in the case of abundant birds it supports a

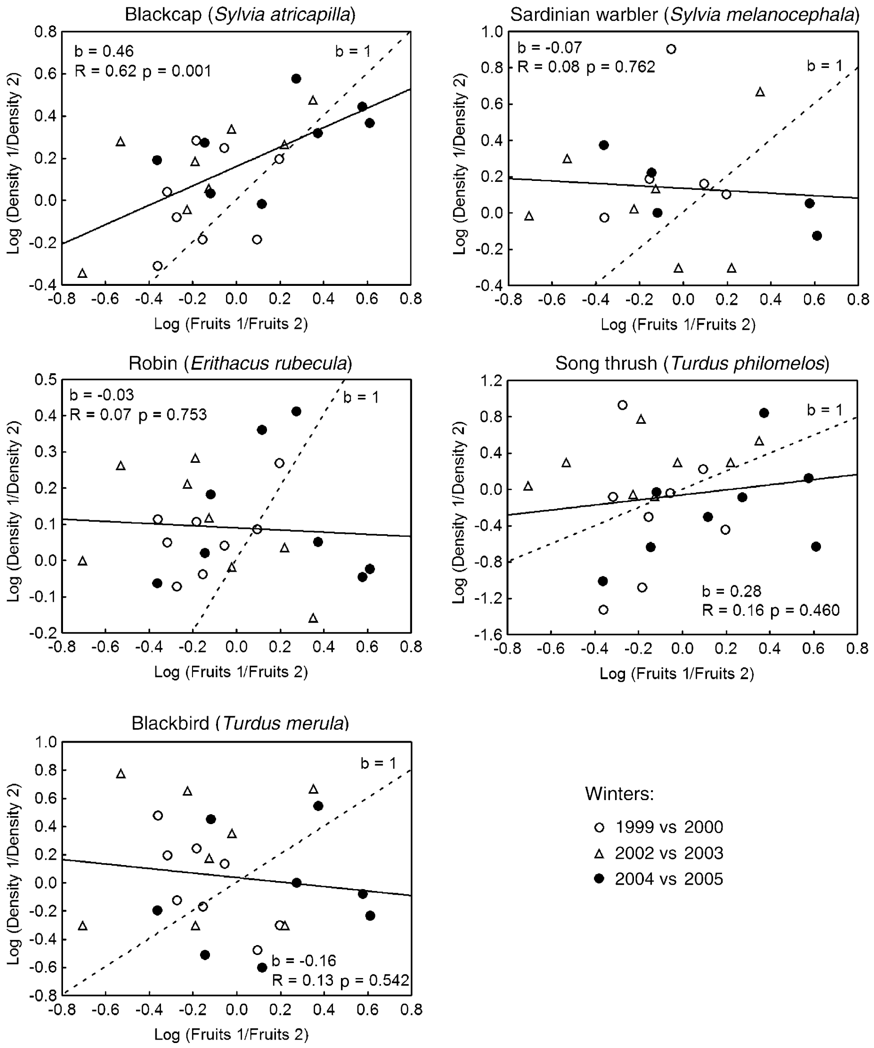

Figure 4. Relationships between year-to-year changes in abundance of fruiting shrubs and year-to-year changes in abundance of individual species. Different symbols identify the study winters. Discontinuous lines represent perfect matching (b = 1), and continuous lines fit to the data.

density-dependent process of habitat occupancy, in which the most abundant species adjust their numbers according to food resources (Fretwell 1972). In any case, this paper shows that the most abundant birds in the Campo de Gibraltar area (the species that have large populations of migratory conspecifics wintering in the area) occupy the habitat each winter according to the spatial distribution of fruit abundance and, in the case of blackcaps, according to between-winter changes in fruit availability. If food tracking is interpreted as a behavioural reaction to prevent starvation and guarantee an optimal body condition for migration and breeding (Goss-Custard et al. 2002), the observed patterns suggest that these species are under pressure each winter to select the most suitable sites, although they cannot thoroughly track changes in fruit abundance (recall the under-matching generally observed in our fruit-tracking models). Such a functional reaction of some species to changes in fruit abundance is a key issue for conservation, because it opens the possibility of sustaining bird numbers by managing the regional availability of fruiting plants.

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