Post-fire dynamics in Mediterranean shrublands: are bird communities structured by arthropod availability?

Sergi Herrando, Lluís Brotons & Santiago Llacuna

The relationship between arthropod availability and bird energy requirements was studied in Mediterranean shrublands. Specifically, we tested the hypothesis that food availability is a possible constraint in the recovery of bird communities in post-fire dynamics. We used the sweep-net sampling method to collect arthropods, and the point-census method to assess bird abundance. The censuses were carried out during the breeding and wintering seasons in a fire-free zone and in two burned zones (one burned four years before the fieldwork, the other 16 years before it). During the breeding season, we found a positive association between arthropod availability and bird requirements in all three zones. However, compared with the other two zones, the recently burned zone contained fewer birds than expected, based on arthropod availability. Thus, it seems that birds exerted significantly lower predation pressure on arthropod populations in this zone than in the other two zones, which resembled each other in this parameter. These results suggest that arthropod availability does not constrain breeding-bird numbers soon after fire; however, it could do so in later successional stages. During winter, when the studied bird species also feed on fleshy-fruits, there were no conclusive associations between arthropods and birds.

Key words: arthropod availability, bird community, predation pressure, post-fire succession, burned zones, Mediterranean shrublands.

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The study of avian post-fire dynamics in Mediterranean shrublands has traditionally focused on bird-community turnover and its clear association with changes in vegetation structure (*e.g.* Lawrence 1966, Prodon *et al.* 1984, Stanton 1986, Prodon *et al.* 1987, Vicente 1991, Pons & Prodon 1996, Izhaki & Adar 1997, Herrando *et al.* 2003). Most of these works showed that bird abundance usually increases progressively, matching vegetation recovery. However, an association between the vegetation and the avian community may be due to an indirect effect of the increase in food available to birds following vegetation recovery. An association between food availability and bird abundance is often detected during the breeding season (as a consequence of high food requirements for feeding nestlings) as well as during the winter (when there may be food scarcity). However, there is a wide disparity of results over all periods, from strong associations between bird abundance and food availability to no correlation at all (e.g. Newton 1980, Martin 1987, Wiens 1989, Diaz & Pulido 1993, Morris & Thompson 1998). The lack of a relationship may be found when these resources are so abundant that they do not impose any constraint on the exploiters. This is a common pattern when there is a second, more limiting resource for individuals, or when populations are in a growing stage (Begon *et al.* 1987).

In addition, in Mediterranean ecosystems, studies on the post-fire dynamics of invertebrates, the main food source for many breeding passerines, have usually focused on soil arthropods (Prodon *et al.* 1987, Athias-Binche *et al.* 1987, Sgardelis *et al.* 1995, Broza & Izhaki 1997), whose numerical responses to fire seem to be very variable depending on the soil layer in which they live, as well as on the severity of the fire in terms of temperature and duration. Only a few studies have dealt with the effects of fire on foliage invertebrates (e.g. Woinarski & Recher 1997, Pons 1998). As with birds, these authors reported a fast increase in foliage-arthropod abundance in the vegetation regenerating rapidly after fire. However, despite the trends described for both birds and arthropods after fire, our understanding of the associations between these two groups remains poor.

The main aim of our study was to test the hypothesis that bird communities are structured by arthropod availability. If this is true, there should be an association between arthropod availability and bird numbers. Since successional dynamics show a progressive increase in the number of interactions between elements of the ecosystem (Margalef 1968, Odum 1969), we hypothesized that the association between arthropod availability and bird requirements is greater in mature unburned areas than in recently burned ones. Most studies conducted on the relationship between arthropods as a food resource and birds have, in general, focused on one bird species. In contrast, our study attempts to consider the entire bird community feeding on shrub invertebrates.

Methods

Study area and design

This study was carried out during the breeding and wintering seasons of 1998 in the Garraf Natural Park, situated 20 km south of the city of Barcelona (NE Iberian Peninsula). The study area (41°15'N 1°55'E) consists of low hills and small valleys located at 100–500 m a.s.l. The average annual rainfall is about 500 mm, but the karstic lithology of these hills provides only skeletic soils, which offer extremely dry conditions for plant communities. The vegetation of the study area is dominated by shrubs such as *Arbutus unedo, Quercus coccifera, Pistacia lentiscus, Ulex parviflorus, Rosmarinus officinalis, Thymus vulgaris, Chamaerops humilis* and *Olea europaea*, and by *Pinus halepensis* trees. These plant species are widespread in the natural park, regardless of the frequency of fire, which has basically affected species abundance but not species composition, although grasses such as *Ampelodesmos mauritanica* and *Brachypodium retusum* were more abundant in recently burned zones than in others (Herrando *et al.* 2003); this is a common pattern in Mediterranean shrublands (Trabaud 1981).

The area that is the Garraf Natural Park does not now support any economic resources apart from those related to leisure activities. At the end of the nineteenth century, however, the area was extensively cultivated, and vineyards occupied the belts of terraces built into the stony slopes of the mountains. After the phylloxera crisis, most of the human population migrated to nearby urban areas, although livestock and timber exploitation continued until the middle of the twentieth century. From then on, human activity has sharply decreased, and fire has been the main form of disturbance affecting the landscape and habitats. A knowledge of this historical process is essential for understanding the current aspect of the Garraf massif.

The natural park has had two extensive fires in the last decades: the first burned 10,000 ha in 1982; and the second, which burned the area again in 1994, affected 5,000 ha. The periphery of the park, about 1,000 ha, has not been damaged by fire in recent years and consists mostly of pine woods grown since the end of the timber exploitation (40–50 years ago). Although we could not directly reconstruct a succession from the synchronic study of these three adjacent zones (Prodon & Pons 1993), the historical processes that occurred throughout the whole massif (see above) and the similarity of climate, relief and plant species composition led us to assume that fire was the main factor involved in the current physiognomy of each of these zones. Other authors have used the synchronic approach to study successional post-fire dynamics (e.g. Vicente 1991, Crête *et al.* 1995, Ding *et al.* 1997, Imbeau *et al.* 1999), and we think that our study area provided an appropriate framework within which to study the relationships between bird and arthropod abundance after fire. We established 18 randomly placed survey zones: 6 within the habitat burned in 1982 (referred to as "F82"), 6 within the habitat burned in both 1982 and 1994 ("F94"), and 6 in the fire-free zone ("Control").

Arthropod sampling

We used sweep-net sampling to collect arthropods from shrubs. This method is probably the most widely used for sampling arthropods from vegetation, and it is especially suitable in ecosystems where the plants of interest are small. Sweep-netting does not provide a measure of absolute density; however, this is not needed when examining the relationships between arthropods and bird abundance (Cooper & Whitmore 1990). Arthropods are not expected to be uniformly distributed in plants, but, rather, concentrated in the areas where leaves and branches are especially dense and with the highest physiological activity, that is, in the most external layers of the shrubs. Hence, although the sampling device only allows surveying these external layers, we think that the method could be appropriate for estimating overall arthropod abundance, independent of shrub size.

Arthropods were collected in each of the 18 survey zones in a transect that involved beating shrubs at intervals of 1 m during a route of 100 m. Each transect was repeated twice (at intervals of at least 3 weeks) in both the breeding and wintering seasons. We carried out a total of 72 transects and thus obtained 72 samples. Each sample was obtained in just 10–15 minutes to minimize the effects of temperature and weather changes within the sampling time. We assumed that each arthropod sample was a reliable indicator of the foliage arthropod community in the survey zone. This assumption was supported by the fact that the transect was relatively long and designed to maximize spatial heterogeneity in plant species composition and vegetation structure. Finally, we analysed differences in arthropod order abundance in each of the two samples in each season and habitat, and found them to be not significant in 42 out of the 48 tests carried out. Thus, we considered them as true replicates and used means between the two samples for a given taxon as the most reliable indicator of its abundance in the given period.

Samples were dried for 72 hours at 70°C, the numbers of individuals were counted, and each sample was weighed. Next, we classified arthropods to the taxonomic level of order. We then determined whether the different taxons encountered had been detected in previous studies on shrubland bird diets. According to the feeding data compiled in Cramp (1988, 1992), Cramp & Perrins (1993) and Hódar (1994), the bird species found in our study show a notable flexibility in diet depending on the frequency of the different potential prey types in the habitat. All the arthropod orders present on the studied shrubs occur in the diets of the breeding birds found in the area, except Phasmida, which was very rare and accounted for less than 0.01% of total arthropod biomass in all zones. Although Wolda (1990) indicated that some arthropod species included in abundance estimates may not be potential prey for birds because they are unpalatable or require excessive time or energy for capture, we assumed that the total arthropod biomass of each sample could be considered a measure of resource availability for the whole insectivorous bird community inhabiting this zone.

Bird sampling

The point-count method was used to assess the abundance of bird species (Bibby *et al.* 2000). In each of the 18 survey zones, five point-count stations were randomly selected. The sampling was carried out twice at each station during the breeding season (March to June) of 1998 and wintering season (November to January) of 1998/99. Thus a total of 360 point-counts were performed during the census period.

Birds heard or seen were recorded, and the distance between the observer and the bird was estimated. Following the recommendations of Fuller & Langslow (1984), sampling time was 10 minutes. Bird counts were carried out during the first three hours after sunrise, during maximum avian activity. Censuses were performed only in good weather conditions, without heavy rainfall or strong wind (Bibby *et al.*

2000). To calculate densities for each species, we considered the maximum number of individuals detected at either of the censuses conducted at each station as the most reliable indicator of abundance. We then used the method proposed by Reynolds *et al.* (1980) to estimate bird density.

We attempted to determine the kind of association between the availability of arthropods from shrubs and the bird species that gleaned these invertebrates. Therefore, from the total bird species recorded in the census, only those that, according to literature and personal observations, gleaned arthropods from shrub surfaces were considered. These were as follows: Wren *Troglodytes troglodytes*; Stonechat *Saxicola torquatus*; Dartford Warbler *Sylvia undata*; Sardinian Warbler *Sylvia melanocephala*; Blackcap *Sylvia atricapilla*; Bonelli's Warbler *Phylloscopus bonelli*; Chiffchaff *Phylloscopus collybita*; Goldcrest *Regulus regulus*; Firecrest *Regulus ignicapilla*; Long-tailed Tit *Aegithalos caudatus*; and Great Tit *Parus major*. We made notes of the feeding activities observed during the fieldwork, and took into account the foraging substrata reported by Cramp (1988, 1992) and Cramp & Perrins (1993) for these bird species in Western Mediterranean shrublands and pine woods. The percentage of food taken from shrubs by each species has been established as follows; 100% for the Wren; 6% for the Stonechat; 100% for the Dartford Warbler; 100% for the Sardinian Warbler; 100% for the Blackcap; 10% for Bonelli's Warbler; 50% for the Chiffchaff; 20% for the Goldcrest; 20% for the Firecrest; 40% for the Long-tailed Tit; and 60% for the Great Tit.

To obtain a reliable indicator of the food requirements of these birds, we calculated their field metabolic rate (FMR), a parameter that shows the amount of food required per day by birds in a given area. Given our specific interest in the relationships between arthropod abundance in shrubs and the birds that feed on them, we calculated the field metabolic rate derived from foraging on shrubs (FMRS). Thus, the FMRS quantified the weight of food required per day by all birds that glean from shrubs in our study plots, and was expressed as g/day/10 ha. The field metabolic rate (FMR) of each bird species was estimated using the allometric regression for passerine birds of appropriate size proposed by Nagy (1987); the FMRS for each species was calculated by multiplying its FMR by the proportion of food taken from shrubs. The FMRS of a population was calculated by multiplying the FMRS of each species by its abundance and, finally, the overall FMRS of the bird community was calculated by adding together the FMRS of each bird species population inhabiting the study zone.

Statistical Analysis

We compared arthropod density, arthropod biomass, bird density, bird biomass and FMRS of the three zones studied by means of an ANOVA. A Newman-Keuls test was used for post hoc comparison. When data transformation did not meet the ANOVA assumptions, we used the Kruskal-Wallis test (Sokal & Rohlf 1995). A multiple comparison rank extension of the Kruskal-Wallis for pairwise comparisons was performed (Siegel & Castellan 1988); since there were $k = 3$ groups, the level of significance was $\alpha' = \alpha/k(k-1) = 0.0083$ (one-sided Z distribution). For dependent samples, the t-test was used to analyse differences between the breeding and wintering season, but the non-parametric Wilcoxon matched pairs test was chosen when data transformations did not meet the parametric assumptions (Sokal & Rohlf 1995). Standard linear regression was used to test the relationship between arthropod biomass and bird requirements (Sokal & Rohlf 1995), and residual analysis was used to analyse differences in this relationship among the three zones. The residuals obtained from this regression were used as an index of predation pressure, being negative when there were lower FMRS than expected from the model and positive when they were greater. All statistical analyses were run with Statistica Statsoft, Inc 1999.

Results

Arthropod community

Altogether 3,827 individual arthropods were collected from the shrubs. The most abundant orders were Araneida, Homoptera, Heteroptera, Diptera, Coleoptera and Hymenoptera; these

Table 1. Shrubland arthropod community descriptors in the breeding and wintering seasons in the three zones. Values: Mean (standard error). We performed a multiple comparisons rank extension of the Kruskal-Wallis test for pairwise comparisons (Siegel & Castellan 1988). Significant differences are marked ***.
*Descriptors de la comunitat d'artròpodes dels arbustos en la estació reproductora i hivernant en les tres zones. Valors: Mitjana (error típic). Amb l'objectiu de comparar entre parelles es va dur a terme una extensió del test de rangs Kruskal-Wallis per a comparacions múltiples (Siegel & Castellan 1988). Les diferències significatives estan marcades amb el símbol ***.*

	F94	F 82	Control	Kruskal-Wallis	P	F94 vs Cont.	F94 vs F82	F82 vs Cont.
BREEDING SEASON								
Total individuals	43.50 (3.11)	83.33 (6.58)	128.41 (18.27)	12.78	<0.01	***	***	n.s.
Biomass (mg/ transect)	61 (16)	127 (21)	120 (13)	6.89	<0.05	***	***	n.s.
WINTERING SEASON								
Total individuals	35.00 (9.47)	38.33 (7.75)	54.00 (6.92)	3.80	0.146	n.s.	n.s.	n.s.
Biomasss (mg/ transect)	19 (8)	19 (6)	44 (19)	3.03	0.219	n.s.	n.s.	n.s.

had more similar relative frequencies in the breeding season than in winter (Fig. 1). The other orders found were Collembola, Orthoptera, Lepidoptera, Tysanoptera, Phasmida, Psocoptera, Neuroptera, Acari and Opilionida, which together accounted for less than 15% of the total number of individuals. The abundance of most of the orders did not show any significant difference among the three zones in either breeding or wintering seasons. In the former, only Homoptera, Araneida and Heteroptera showed significant differences between study zones: Homoptera numbers were lower in F94 than in the other habitats (Kruskal-Wallis test H' = 11.40, p<0.01, p<0.0083 for pairwise comparison with both, F82 and the Control); Araneida numbers were higher in the Control than in the burned zones (Kruskal-Wallis test H' = 10.43, p<0.01, p<0.0083 for these pairwise comparisons); and Heteroptera individuals were less abundant in F94 than in F82 (Kruskal-Wallis test H' = 8.74, p<0.05, p<0.0083 for pairwise comparison between F94 and F82). In the breeding season, the total number of individuals per transect and arthropod biomass per transect were significantly higher in the Control and F82 than in F94 (Table 1). In the wintering season there were even fewer significant differences: only Araneida showed the same pattern as in the breeding season (Kruskal-Wallis H' = 11.46, p<0.01, p<0.0083 for the two pairwise comparisons between the Control and the burned zones). It is worth noting that the total number of individu-

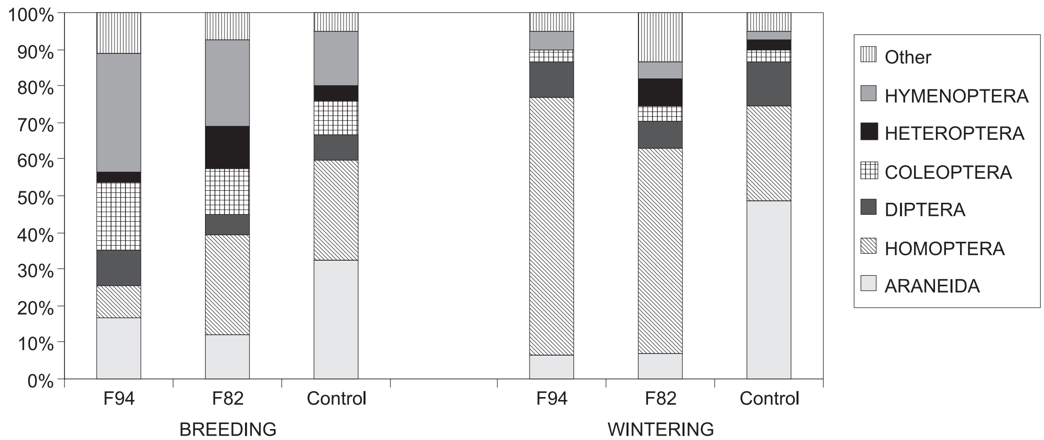

Fig. 1. Percentages of arthropod orders in each study zone in the breeding and wintering seasons.
Percentatge de cada ordre d'artròpodes en cada zona d'estudi durant l'estació reproductora i nidificant.

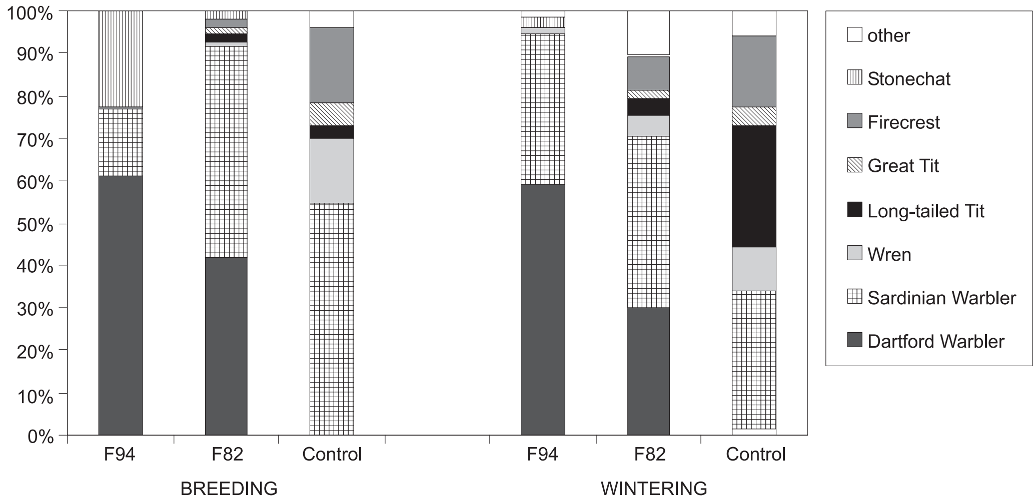

Fig. 2. Percentages of bird species in each study zone in the breeding and in wintering seasons. Numbers refer only to those species that feed on shrubs.
Percentatge de cada espècie d'ocell en cada zona d'estudi durant l'estació reproductora i nidificant. Les xifres fan referència exclusivament a aquelles espècies que s'alimenten als arbusts.

als per transect and arthropod biomass did not differ among zones during the winter (Table 1).

From the breeding to wintering seasons, F94 showed no significant differences in total individuals (Wilcoxon test Z = 0.94, p = 0.345) or in arthropod biomass (Wilcoxon test Z = 178, p = 0.074; Fig. 3); F82 showed a significant decrease in total individuals (Wilcoxon test Z = 2.20, p<0.05) and in arthropod biomass (Wilcoxon test Z = 2.20, p<0.05; Fig. 3). The Control also showed a significant decrease in the number of total individuals (Wilcoxon test Z = 2.20, p<0.05) and in arthropod biomass (Wilcoxon test Z = 1.99, p<0.05; Fig.3).

Bird community

We found that, in both the breeding and wintering seasons, the shrubland bird communities were always dominated by: Wren, Dartford Warbler, Sardinian Warbler, Great Tit, Long-tailed Tit, Stonechat and Firecrest. The two warblers accounted for more than 70% of the total individuals inhabiting the burned habitats,

Table 2. Shrubland bird community descriptors in the breeding and wintering seasons in the three zones. Values: Mean (standard error). We used the ANOVA and the Newman-Keuls test for pairwise comparisons. Variables were log-transformed in order to fit ANOVA assumptions. Significant differences are marked ***.
*Descriptors de la comunitat d'ocells dels arbustos en la estació reproductora i hivernant en les tres zones. Valors: Mitjana (error típic). Es va utilitzar l'ANOVA i el test de Newman-Keuls per fer comparacions entre parelles. Les variables es van transformar mitjançant logaritmes per acomplir les assumpcions de l'ANOVA. Les diferències significatives estan marcades amb el símbol ***.*

	F94	F82	Control	F	P	F94 vs Cont.	F94 vs F82	F82 vs Cont.
BREEDING SEASON								
Total density (ind/10ha)	8.83 (1.07)	24.69 (3.75)	28.42 (1.95)	17.32	<0.001	***	***	n.s.
Total biomass (g/10ha)	99.5 (13.5)	274.3 (41.3)	303.3 (27.9)	13.63	<0.001	***	***	n.s.
FMRS (g/day 10ha)	19.85 (2.36)	78.56 (10.78)	71.30 (7.52)	17.21	<0.001	***	***	n.s.
WINTERING SEASON								
Total density (ind/10ha)	39.54 (2.44)	47.00 (3.84)	55.87 (13.96)	0.95	0.408	n.s.	n.s.	n.s.
Total biomass (g/10ha)	448.8 (29.1)	478.2 (24.0)	515.2 (107.2)	0.25	0.777	n.s.	n.s.	n.s.
FMRS (g/day 10ha)	119.8 (7.9)	133.3 (7.0)	104.0 (14.7)	1.95	0.176	n.s.	n.s.	n.s.

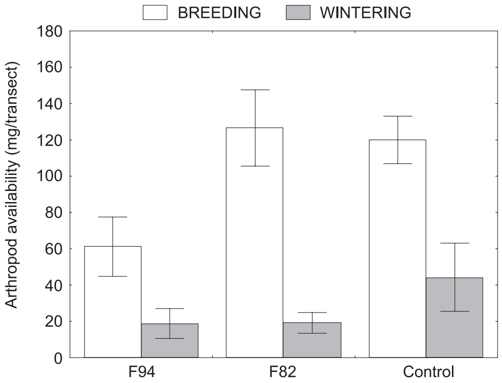

Fig. 3. Arthropod availability in the breeding and wintering seasons in the three zones (n=18). Bars indicate standard error.
Disponibilitat d'artròpodes en l'estació reproductora i hivernant en les tres zones (n=18). Les barres indiquen els errors típics.

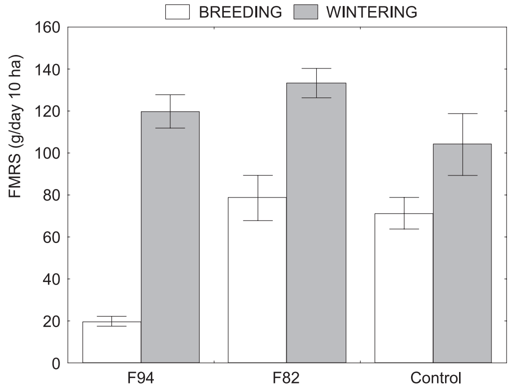

Fig. 4. Field metabolic rate deriving from foraging on shrubs (FMRS) in the breeding and wintering seasons in the three zones (n=18). Bars indicate standard error.
Taxa metabòlica derivada de l'alimentació en arbusts (FMRS) durant l'estació reproductora i hivernant en les tres zones (n=18). Les barres indiquen els errors típics.

whereas in the Control, the bird species were more equally distributed (Fig. 2). In our study area, Bonelli's Warbler was only present in the breeding season, whereas the Blackcap, Chiffchaff and Goldcrest were only present in the winter.

The comparison of shrubland-bird-community descriptors between zones differed depending on the season. During the breeding period, the F94 shrubland bird community had significantly fewer individuals and lower biomass and FMRS than the shrubland bird communities of the other two zones. In contrast, during the wintering season, no significant differences were found between zones (Table 2).

From the breeding season to the wintering season, F94 showed a significant increase in total shrubland bird density (t-test = -13.17, df = 5, $p<0.001$), total shrubland bird biomass (t-test = -12.62, df = 5, $p<0.001$) and in the FMRS (t-test = 12.53, df = 5, $p<0.001$; Fig 4). F82 presented significant differences in total bird density (t-test = -3.62, df = 5, $p<0.05$), total bird biomass (t-test = -3.45, df = 5, $p<0.05$) and in FMRS (t-test = -3.74, df = 5, $p<0.05$; Fig. 4). Finally, the Control did not show a significant increase in total shrubland bird density (t-test = -1.88, df = 5, p = 0.117), total shrubland bird biomass (t-test = -1.96, df = 5, p = 0.106) or in the FMRS (t-test = -2.39, df = 5, p = 0.062; Fig. 4). Thus, seasonal variation in the FMRS was greater in F94, where it was six-fold greater in winter than in the breeding period (Fig. 4).

Relationships between arthropod availability and birds

In the breeding season, arthropod availability was positively correlated with the FMRS (r = 0.548, $p<0.05$, n = 18; Fig. 5). In winter, arthropod availability was not correlated with the FMRS (r = 0.391, p = 0.109, n = 18). The residual analysis of the first of these regressions

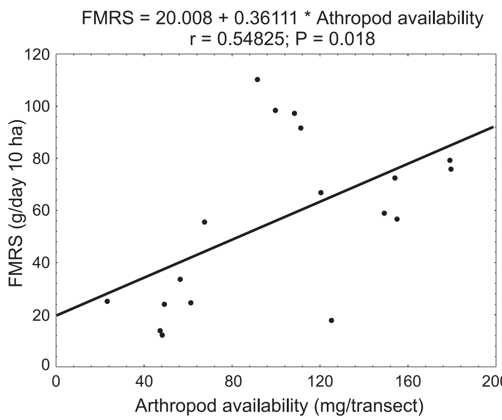

Fig. 5. Relationship between FMRS and arthropod availability during the breeding season.
Relació entre FMRS i disponibilitat d'artròpodes durant l'estació reproductora.

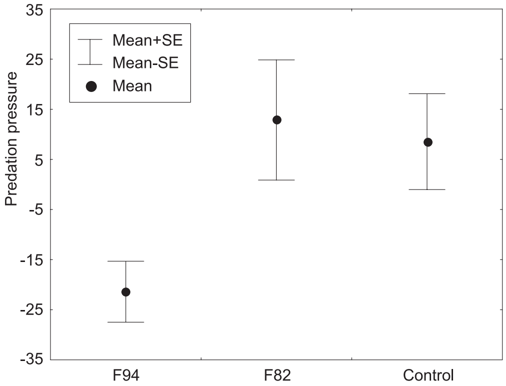

Fig. 6. Predation pressure (estimated as the residuals of the linear regression) in the breeding season in the three zones. Bars indicate standard error.
Pressió de depredació (estimada com el residual de la regressió lineal) en l'estació reproductora en les tres zones. Les barres indiquen els errors típics.

showed significant differences between habitats ($F = 3.84$, $df = 2,15$, $p<0.05$). The average residual score for F94, F82 and the Control was used as an index of the predation pressure in each zone. Thus, the Newman-Keuls post hoc multiple comparison showed that the index of predation pressure in the Control and in F82 (which were 8.53 and 12.86 respectively) did not significantly differ ($p = 0.753$), but the index of predation pressure in F94 (-21.4) differed from both the index of predation pressure in F82 ($p<0.05$) and in the Control ($p<0.05$) (Fig. 6).

Discussion

Seasonal changes in arthropod and bird numbers

In temperate areas, arthropod numbers usually have a marked peak in spring and summer and then decrease sharply in winter because the biological cycles of these invertebrates are strongly affected by low temperatures and adverse weather conditions (Berryman 1986). This may explain why we detected a significant decrease in arthropod biomass from breeding to wintering seasons in F82 and in the Control but, surprisingly, F94, the most recently burned zone, did not show significant differences between seasons. Brown (1986) pointed out that a high proportion of early-successional insect species overwinter as immature individuals, which is an advantageous strategy because in the initial stages of succession the time for development is often limited by the death of herbaceous species. Therefore, the pattern observed in F94 may be related to the higher quantities of grasses observed there compared with the other two zones.

In contrast to arthropods, birds were more abundant in winter than in the breeding season in all of the three zones. To explain the high abundance of wintering birds we should bear in mind that many European birds overwinter in coastal Mediterranean areas, such as the Garraf, where they feed basically on fleshy fruits (Blondel & Aronson 1999). Large quantities of fleshy fruits from shrubs such as *Pistacia lentiscus, Phillyrea latifolia* and *Olea europaea* are available during autumn and winter in the study area. In a study carried out in a similar Mediterranean plant community in southern Spain, Herrera (1984) calculated an annual fruit biomass production of 98 kg/ha, with a peak in December, when there were more than 100,000 fruits/ha. He also suggested that the presence of a large number of passerines in winter is only possible in mild climates with an abundant supply of energy-rich fruits.

Successional changes in arthropod and bird numbers

Our results showed that the relative abundance of arthropod orders varied among zones, although the most abundant groups were always Araneida, Homoptera, Diptera and Hymenoptera. These results are similar to those found by Pons (1998), who reported Homoptera, Diptera and Hymenoptera to be the most abundant orders in burned and unburned Mediterranean shrublands of southern France. In both Pons's study and ours, the abundance of foliage arthropods was lower in burned areas than in nearby unburned areas. This is a typical pattern in most ecosystems when they have recently been affected by fire, and it provides plants with a short-term release from insect herbivory (Swengel 2001).

Our results showed that shrubland bird densities were lower in the recently burned area than in the other two zones during the breeding season. In contrast with this, if we consider the whole bird community and not only that linked to shrubs, overall bird abundance did not differ between F94 and F82 (Herrando *et al.* 2002), thus indicating that the abundance of other species that do not feed on shrubs is particularly important in the recently burned area. Interestingly, after a controlled fire in a Mediterranean shrubland of southern France, Pons (1998) found that bird abundance did not follow a decrease in shrub arthropod abundance and suggested an increase in flying and terrestrial invertebrates which might enhance prey availability, thus contributing to maintaining bird densities.

Bird community and arthropod availability

During the breeding season, we found a significant positive association between the arthropod availability from shrubs and the food requirements of the bird community that gleans these invertebrates. In contrast, during the wintering season, the use of fruits as a food resource may explain the lack of correlation between bird requirements and arthropod availability. An association between bird requirements and arthropod availability is an expected prediction if a bird community is constrained by food availability (Martin 1987, Wiens 1989). Arthropod abundance is likely to limit bird density because during breeding individuals forage mostly on these invertebrates for both their own sustenance and that of their nestlings. Arthropod availability sets an upper limit on bird abundance at equilibrium stages and does not allow bird populations to grow beyond the carrying capacity of the system. In such conditions, other factors, such as competition between similar species for scarce resources, may contribute to shaping community structure (Wiens 1989).

However, after a disturbance event, such as a fire, both the bird and arthropod communities undergo a successional process that follows vegetation recovery. The residual analysis showed that in F94, the most recently burned zone, there were fewer birds than expected from the arthropod availability. In contrast, F82 (burned 16 years before the fieldwork) and the Control (not damaged by fire) showed the opposite relationship, suggesting a closer dependence of the bird community on arthropod availability. These results indicate that arthropod biomass is greater than bird requirements soon after fire, thus suggesting that birds are not limited by arthropod availability. In such case, birds could be limited by an alternative resource, such as breeding sites. Pulido & Díaz (1997) found that the abundance of Blue Tits *Parus caeruleus* was not constrained by food resources, but by the availability of tree holes for nesting. In our study, the presence of this type of structural constraint in F94 would be applicable for the scarce Great Tit, but even if this were the case (highly improbable in a area with an abundance of holes among the karstic rocks and walls of abandoned terraces), it is difficult to imagine this forest species reaching high densities in a burned area. Nesting sites for the commonest cup-nesting species are generally presumed to be readily available (Wiens 1989) and therefore are likely to be highly abundant in our study area, so would not limit bird numbers. Other types of potential resource, such as perches, roost locations or cover from predators were not quantified in this work, but these structural components of habitats have not been reported to date as constrictors of shrubland bird communities.

We suggest that the actual fire dynamics could be responsible for the disassociation between bird requirements and arthropod availability. Invertebrate life cycles are very short, and their community characteristics and abundance may recover sooner than for vertebrates such as birds, whose responses may take longer. Typically, bird predation on arthropods shows a sigmoid-shaped curve, that is to say, there is a slow initial response to increasing prey density, followed by increased predation until predation levels off (Kirk *et al.* 1996). In our study, during the first years after fire, the bird community does not seem to be related to arthropod availability (and predation pressure on the invertebrates is consequently lower), probably because of the distinct recovery speeds of these two groups. Pons & Prodon (1996) found that some bird species colonized a 140-ha burned area from similar open areas nearby, while others showed marked site tenacity and managed to persist in spite of the drastic modification of the vegetation. However, neither of these responses may be enough to recover five thousand hectares of burned vegetation rapidly, and successive colonization waves should be added to the juveniles produced in the burned area. The sigmoid-shaped theoretical curve is consistent with the increase in density, biomass and the FMRS after the first years of succession, and the stabilization of these numbers 16 years after fire (the Control and F82 did not differ in the values of these parameters). Therefore the hypothesis that bird communities are limited by arthropod availability seems to be only suitable for middle and later successional stages when the interactions between elements of the ecosystem are probably stronger than during initial stages after fire.

It is commonly assumed that early successional habitats are variable in quality and that resources are more patchily distributed than in later successional habitats (Helle & Mönkkönen 1990). Thus, at initial successional stages birds are often not yet fully adapted to the main features of the vegetation structure (Wiens 1989). However, in a concurrent study in the same area (Herrando *et al.* 2003), we found that three years after fire, vegetation structure was already a reliable predictor of bird community. This pattern has repeatedly been reported in several studies relating birds and vegetation structure after fire in the Mediterranean Basin (Prodon *et al.* 1987, Vicente 1991, García 1997). The high historical occurrence of perturbations in Mediterranean ecosystems may have led some species to include early successional stages as favourable habitats. The results of the present study may help to clarify the dynamics of Mediterranean bird communities after fire. Even when the bird community is highly predictable from vegetation structure soon after fire, it does not seem to be limited by food until later stages, when, in addition to habitat structure, food abundance may set an upper limit to bird numbers.

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Resum

Dinàmica post-incendi en ambients arbustius mediterranis: la disponibilitat d'artròpodes modela la comunitat d'ocells?

Es va estudiar la relació entre la disponibilitat d'artròpodes i els requeriments energètics dels ocells en una zona coberta de brolles, garrigues i màquies. Específicament es va testar la hipòtesi que la disponibilitat d'aliment constituïa un possible limitant en la recuperació de la comunitat d'ocells dins la dinàmica de recolonització post-incendi. Es va utilitzar un sistema de captura estandarditzat amb salabres per recol·lectar artròpodes i estacions puntuals per estimar l'abundància d'ocells. Els censos es van dur a terme durant la temporada de nidificació i d'hivernada dels ocells en una zona que no havia estat afectada pel foc i en dues zones cremades (la primera incendiada 4 anys abans del treball de camp i la segona 16 anys abans). Durant la temporada de nidificació vàrem trobar una associació positiva entre la disponibilitat d'artròpodes i els requeriments energètics dels ocells a les tres zones. No obstant això, comparada amb les altres dues, la zona afectada recentment pel foc contenia menys ocells que els esperables a partir de la seva abundància d'artròpodes. D'aquesta manera sembla que els ocells exercien una pressió de depredació menor sobre les poblacions d'artròpodes en aquesta zona que a les altres dues, les quals no diferien entre si respecte a aquest paràmetre. Aquests resultats suggereixen que la disponibilitat d'artròpodes no limita el nombre d'ocells reproductors pocs anys després del foc, però sí que ho pot fer en estadis posteriors. A l'hivern, quan la comunitat d'ocells estudiada també s'alimenta de fruits, no es va trobar cap associació entre ocells i artròpodes.

Resumen

Dinámica post-incendio en ambientes arbustivos mediterráneos: ¿la disponibilidad de artrópodos modela la comunidad de aves?

Se estudió la relación entre la disponibilidad de artrópodos y los requerimientos energéticos de las aves en una zona cubierta de matorral mediterráneo. Específicamente se testó la hipótesis de que la disponibilidad de alimento constituía un posible factor limitante en la recuperación de la comunidad de aves

dentro de la dinámica de recolonización post-incendio. Utilizamos un sistema de captura estandarizado con embudos entomológicos para recolectar artrópodos y estaciones puntuales para estimar la abundancia de las aves. Los censos se llevaron a cabo durante la temporada de nidificación y de invernada de las aves en una zona que no había sido afectada por el fuego y en dos zonas quemadas (la primera incendiada 4 años antes del trabajo de campo y la segunda 16 años antes). Durante la temporada de nidificación se encontró una asociación positiva entre la disponibilidad de artrópodos y los requerimientos energéticos de las aves en las tres zonas. No obstante, comparada con las otras dos, la zona afectada recientemente por el fuego contenía menos aves de las esperables a partir de su abundancia de artrópodos. De esta manera parece que las aves ejercían una presión de depredación menor sobre las poblaciones de artrópodos en esta zona que en las otras dos, las cuales no diferían entre sí respecto a este parámetro. Estos resultados sugieren que la disponibilidad de artrópodos no limita el número de aves reproductoras pocos años después del fuego, pero sí que lo puede hacer en estadios posteriores. En invierno, cuando la comunidad de aves estudiada también se alimenta de frutos, no se encontró ninguna asociación entre aves y artrópodos.

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