Factors influencing post-fire dynamics of Sardinian and Dartford Warblers in Mediterranean shrublands

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We studied the post-fire dynamics of two Mediterranean warblers (the Sardinian (*Sylvia melanocephala*) and the Dartford Warbler (*Sylvia undata*)) to determine whether these were influenced by local habitat recovery or by external population trends unrelated to the occurrence of fire. We used the point-count method to survey warblers from the first to the sixth breeding seasons after fire in burnt and unburnt control zones of the Iberian Peninsula. Both species increased similarly in the burnt zone until the fourth year after fire, but the Dartford Warbler increased faster than the Sardinian Warbler from then on. Six years after fire, the abundance of the Dartford Warbler was even higher in the burnt zone than in the control, where the population of this species remained constant during the study period. In contrast, a parallel increase in the populations of Sardinian Warbler in both zones was observed, thus suggesting that processes other than fire were profoundly involved in the dynamics of these two species greatly differ, the Dartford Warbler being highly influenced by local habitat changes in the burnt zone and the Sardinian Warbler being highly influenced by local habitat changes in the dynamics.

1. Introduction

Fires are a frequent disturbance in the Mediterranean area and are known to play a key role in the spatial and temporal dynamics of forest and shrubby systems (Blondel & Aronson 1999). The study of bird succession after fire in the Mediterranean Basin has focused on species turnover and its close association with vegetation recovery (e.g. Prodon *et al.* 1984, Prodon *et al.* 1987, Pons & Prodon 1996, Izhaki & Adar 1997). Prodon and Pons (1993) pointed out the importance of simultaneously monitoring burnt and unburnt control zones to eliminate the influence of temporal variations unrelated to the occurrence of fire. Therefore, as well as changes in the local habitat, factors with an effect on a larger scale, such as fluctuations in the nearby "source" population, mortality associated with migration, changes in predation or parasitism rates, climatic oscillations and so on, may influence local bird numbers (Wiens 1989). Several studies have reported how regional population trends greatly affect local bird abundance independently of habitat modifications (e.g. Hickey & Brittingham 1991, Böhning-Gaese & Bauer 1996, Bellamy *et al.* 2000). However, to our knowledge, to date no study has focused on the influences of regional population trends in the post-fire succession of burnt areas.

Two Mediterranean warblers, the Sardinian Warbler (Sylvia melanocephala) and the Dartford Warbler (Sylvia undata), often coexist in Western Mediterranean shrublands, although the former prefer low shrublands, whereas the latter seems to be favoured by medium and tall ones (Cody & Walter 1976, Martin & Thibault 1996). The post-fire abundance patterns of these shrubdwelling species is usually characterised by their absence during the first breeding season after fire and by a gradual increase in their numbers afterwards (Prodon & Lebreton 1983, Prodon et al. 1987, López & Guitian 1988, Llimona et al. 1993). Nevertheless, the temporal variations of these two warblers in burnt zones may be affected by temporal dynamics on a larger scale. Available data suggest that the population trends of these two warblers differ at a regional level. In contrast to the stability of the populations of Sardinian Warbler, the populations of Dartford Warbler have undergone a slow but progressive decrease since the 1970s in Spain (which has 75%-95% of the world population of this species) (Tucker & Heath 1994). Furthermore, the current tendencies of land abandonment and progressive afforestation in European countries in the Mediterranean have been reported to affect the Dartford Warbler negatively and the Sardinian Warbler positively (Preiss et al. 1997). Therefore, these two species of the genus Sylvia are an ideal set with which to study whether post-fire dynamics are influenced by factors other than local changes in habitat after fire.

Within this context, we propose two possible scenarios. First, if vegetation recovery determines the post-fire dynamics of the species, we hypothesise (1) a positive and strong effect of time since fire on the population trend in burnt areas, independently of that in unburnt areas. Furthermore, given the preference of the Dartford Warbler for low shrubby habitats, we also predict (2) a faster increase in the abundance of this species than in that of the Sardinian Warbler. Second, if regional population trends do affect the post-fire dynamics of the species, we hypothesise (3) that changes in bird abundance in burnt areas are associated with population trends in areas which have not been affected by fire. According to regional trends, we predict that in unburnt areas, the Dartford Warbler should show a decreasing abundance, whereas the Sardinian Warbler should show a stable or increasing population, which, if this second scenario is valid, should be related to their dynamics in burnt areas.

2. Material and methods

2.1. Study area

This study was carried out in the Garraf Natural Park (41°15'N, 1°55'E), situated 20 km to the south of the city of Barcelona, Spain (NE Iberian Peninsula). The vegetation in this park is dominated by shrubs such as Quercus coccifera, Pistacia lentiscus, Phillyrea latifolia, Olea europaea, Rosmarinus officinalis and Chamaerops humilis, and by pines (Pinus halepensis) in areas which have not been burnt recently. After a long period in which there were only some small fires, two large wildfires have profoundly marked the last two decades. The first burnt 10 000 ha in 1982 and the second, which burnt entirely within the zone previously burnt in 1982, affected 5000 ha in 1994. The 1994 fire was intensive and the total area covered by the remnant patches of unburnt vegetation accounted for less than 2% of the 5000 ha.

We did not find significant differences in relief and landscape structure between the zone burnt in 1994 and the zone not affected by this fire (Table 1). Moreover, the lithology (Mesozoic calcareous rocks) and phytosociologic composition (*Oleo-Ceratonion* with some plants of *Quercion ilicis* (Folch 1986)) was highly homogeneous. Therefore, we considered the zone that did not burn in 1994 as a suitable area for controlling the variations of Sardinian and Dartford Warbler populations unrelated to the occurrence of fire. To simplify the terminology of the study sites, hereafter the two zones are called burnt zone and control zone respectively.

2.2. Bird counting

The censuses were carried out in the burnt zone and the control zone during the breeding seasons of 1995, 1997, 1998 and 2000. We selected 35 stations (19 in the burnt zone and 16 in the control zone), which were located a minimum of 400 m apart to minimise pseudo-replication. Thus a total of 140 censuses was carried out during the study period. We also ensured that the area around each station was homogeneous and did not include farmland, urbanised areas or cliffs.

Point-counts were used to assess the abundance of the Sardinian Warbler and the Dartford Warbler (Bibby et al. 1992). We conducted censuses with several counting bands to analyse the differences in detectability between the two species (Bibby et al. 1992). Although detectability sharply decreased in the farthest bands (at more than 50 m from the observer) for both species, the detectability curve in relation to distance did not differ significantly between the two species $(\chi^2_3 = 1.036, P = 0.207$ for the control zone and $\chi^{2}_{3} = 2.731$, P = 0.565 for the burnt zone). Therefore, to maximise the number of contacts per census station, we decided to obtain abundance estimates by means of point-counts to infinity, that is, counting all birds seen or heard at any distance from the observer. Thus, from here onwards, abundance means the number of individuals detected per counting station.

Counting was conducted in the morning, during the hours of maximum bird activity, and started 1 h after dawn and 5 min after the arrival at the station. Point-counts taken by other authors have ranged from 5 to 20 min, but following the recommendations made by Fuller and Langslow (1984), 10 min was chosen as a compromise. Whenever we were sure that we had already observed the same individual it was not included as a new record. We carried out bird censuses exclusively under uniformly good weather, without rainfall or wind.

2.3. Data analysis

We used repeated measures ANOVA and the posthoc Tukey Honest Significant Difference (HSD) test to analyse temporal variations in the abundance of the two species throughout the study period in both the burnt and the control zones (Sokal & Rohlf 1995). All statistical analyses were run with Statistica Statsoft, Inc 1999.

3. Results

We found a continuous increase in overall abundance of the warblers in the burnt zone after the occurrence of fire ($F_{3,72}$ = 22.83, P < 0.001), but the speed of re-colonisation differed between the two species as the interaction between time since fire and the abundance of the two species was significant ($F_{3,72} = 4.00$, P < 0.05). The results of the Tukey HSD test showed that the abundance of both species did not differ until the forth year after fire; however, the Dartford Warbler became significantly more abundant than the Sardinian Warbler from then on (Fig. 1). Therefore, the two species colonised the burnt zone at a similar speed until the fourth year after fire, when the population of the Dartford Warbler began to increase faster.

Regarding the whole study period, the overall abundance of the Dartford Warbler did not differ between the burnt and the control zone ($F_{1,33}$ =0.179, P=0.674). Nevertheless, the abundance of this warbler increased significantly from 1995 to 2000 ($F_{3,99}$ = 5.570, P < 0.01). This trend was highly influenced by the zone ($F_{3,99}$ =7.488, P<0.001) since although the abundance of this species remained

Table 1. Similarities in relief (altitude, slope and orientation) and landscape structure (percentage of habitat burnt in 1994 within the zone affected by that fire, and percentage of habitat burnt in 1982 within the zone only affected by that fire) between study zones. Data comes from the comparison of 30 surveys (12.5 ha) randomly distributed in each zone. Mean (SD) and *t*-test for independent samples are shown for parametric variables, but for orientation, a circular variable, mean angle (angular deviation) and the Watson-Williams test are shown (Zar 1984).

	Burnt in 1982 and 1994	Burnt only in 1982	Test	Р
Altitude (m)	333 (101)	376 (104)	<i>t</i> = −1.62	0.111
Slope (degrees)	14.1° (8.8°)	17.0° (8.4°)	t = -1.28	0.207
Orientation (degrees)	–24° (63°)	-33° (72°)	F _{1.53} = 0.12	0.265
Habitat (%)	95.6 (8.28)	95.4 (7.03)	<i>t</i> = 1.26	0.900



Figure 1. Variation in the abundance (measured as number of individuals detected in a station during the 10-minute census) of the Dartford Warbler and Sardinian Warbler in the burnt zone. Bars indicate Standard Error. Significant differences between zones in a year, according to Tukey HSD test (P < 0.05) are marked *** at the top of the figure.

constant in the control zone, it steadily increased in the burnt zone (Fig. 2). The results of the Tukey HSD test showed that the abundance of the Dartford Warbler was significantly lower in the burnt zone than in the control zone in 1995 and 1997, did not differ in 1998 and was significantly higher in the burnt zone in 2000 (Fig 2). In summary, the temporal pattern shown by the Dartford Warbler in the burnt zone was characterised by a continuous increase in abundance, reaching even higher values than those measured in the control zone.

The populations of Sardinian Warblers differed between zones ($F_{1,33} = 17.347$, P < 0.001) and between years ($F_{3,99} = 12.120$, P < 0.001). These temporal variations were consistent between zones and the interaction between zones and years was not significant ($F_{3,99} = 0.580$, P = 0.981) (Fig. 3). Therefore, although the abundance of the Sardinian Warbler was always significantly lower in the burnt than in the control zone (*see* results of Tukey HSD test in Fig. 3), the pattern of variation was the same in both zones.

4. Discussion

Our results showed that Dartford and Sardinian Warblers occurred at low densities in the burnt



Figure 2. Variation in the abundance of the Dartford Warbler (measured as number of individuals detected in a station during the 10-minute census) after the 1994 fire in the two study areas. Bars indicate Standard Error. Significant differences between zones in a year, according to Tukey HSD test (P < 0.05) are marked *** at the top of the figure.



Figure 3. Variation in the abundance of the Sardinian Warbler (measured as number of individuals detected in a station during the 10-minute census) after the 1994 fire in the two study areas. Bars indicate Standard Error. Significant differences between zones in a year, according to Tukey HSD test (P < 0.05) are marked *** at the top of the figure.

zone from the first year after fire. These two warblers cannot usually breed the first year after a severe fire (Prodon & Lebreton 1983, Prodon *et al.* 1987, López & Guitian 1988, Llimona *et al.* 1993), but Martin (1983), Pons and Prodon (1996) and Pons (1998) reported their occurrence the first breeding season after fire. This was explained by the presence of remnant patches of unburnt vegetation within the burnt zone. In our burnt zone, as in the case of Pons and Prodon (1996), less than 2% of the surface covered by unburnt vegetation appears to be enough for the persistence of both species.

Our results allow the comparison between the abundance of the two species because we did not find differences in their detectability in any of the study zones (see methods). In the burnt zone, the abundance of the two species did not differ significantly until the fourth breeding season after fire, and hereafter the population of the Dartford Warbler increased faster than that of the other species. Therefore, we did not observe that the population of this species, which has a greater preference for low bushes (Cody & Walter 1976, Martin & Thibault 1996), increased faster than the other during the first years following fire, but it did increase from the fourth year onwards. We suggest that this pattern reflects that this species depends on remnants of unburnt shrubs at initial stages, but it rapidly colonises the burnt surroundings as soon as the sprouting shrubs have grown enough. However, the Sardinian Warbler seemed unable to colonise the sprouting shrubs and its population did not increase in a similar way to that of the Dartford Warbler.

Six years after fire, the Dartford Warbler reached higher densities in the burnt zone than in the control. Pons (1998) reported a similar pattern for this species in prescribed burnt shrublands of southern France. He found that the variations in Dartford Warbler abundance were closely related to the change in vegetation cover throughout succession, surpassing pre-fire densities in the fourth breeding season after fire, that is to say, two years sooner than in our drier study zone. The sharp increase of Dartford Warbler numbers in the burnt zone contrasted with their stability in the control zone, which does not confirm, at this geographical and temporal scale, the regional decline suggested by Tucker and Heath (1994). Our data suggest that Dartford Warbler population trends in the burnt zone are locally driven by habitat changes that are associated with post-fire dynamics. Rabenold et al. (1998) also reported that bird dynamics in disturbed habitats were inconsistent with regional population trends. However, when the same type of local habitat changes appear repeatedly here and there, the sum of local population trends can finally modify the temporal trends of birds on a larger scale (Holmes 1988, Virkkala 1991). In this respect, burnt areas (which are common in the Mediterranean, and have highly variable spatial and temporal occurrence patterns) can influence regional population trends. Because the abundance of the species varies rapidly with time since fire, modelling regional population trends in relation to fire distribution and frequency is difficult. It could, however, be relevant for the accurate monitoring of regional population trends of a species catalogued as vulnerable (Tucker & Heath 1994).

In accordance with its preference for medium and tall bushes (Cody & Walter 1976, Martin & Thibault 1996), the Sardinian Warbler showed a lower abundance in the burnt zone than in the control zone throughout the study. Herrando & Brotons (2001) actually showed that Sardinian Warbler juveniles from the burnt zone have a lower body condition (estimated by means of fluctuating asymmetry) than those living in the control zone, suggesting that burnt zones are of overall lower quality for this species. The progressive increase of Sardinian Warblers in both zones might be solely related to an enhancement of habitat quality resulting from post-fire dynamics, since the control zone was, in fact, also burnt in 1982. However, censuses conducted in 1997 and 1998 in a nearby area, which have not burnt for the last 50 years, showed no significant differences between the abundance of Sardinian Warblers in this area and that in the control zone (Herrando unpubl.), suggesting that the increase in the control zone is not associated with post-fire dynamics. Therefore, our results indicate that, independently of the occurrence of fire, this species increased its density throughout the study area, which suggests a regional increase for this species. Tucker & Heath (1994) considered that the population of Sardinian Warblers was stable in Europe, whereas Pérez de Ana (1993) found the species to be expanding its geographical distribution in the Iberian Peninsula. Similar trends have been suggested elsewhere (Andryushchenko et al. 1993, Hofmans 1998). This general pattern of increase is probably a result of more favourable climatic conditions during the last decade,

which was characterised by mild winters (Pérez de Ana 1993). But more interestingly, this increase in the abundance of Sardinian Warblers was parallel in the two study zones, suggesting that the temporal changes in the abundance of this species in the burnt zone are, to some extent, unrelated to the occurrence of fire and the consequent recovery of vegetation but rather related to population trends occurring at a larger scale.

In conclusion, our results fitted our first hypothesis for the Dartford Warbler, since habitat recovery had a strong effect on its post-fire dynamics. In contrast, the Sardinian Warbler fitted our second possible scenario, which suggested that population trend on a larger scale than the local disturbed habitat could be involved in the postfire dynamics of burnt areas. These results highlight that bird community succession is an assembly of responses of independent species to a variable number of environmental factors that reach further than simple changes in the local habitat.

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Selostus: Paikallisten ympäristönmuutosten ja laajemman mittakaavan tekijöiden vaikutus samettipääkertun ja ruoskokertun esiintymiseen Espanjan pensaikkoalueilla

Lintulajien runsauteen tietyllä alueella vaikuttavat sekä paikalliset tekijät (esim. metsäpalot) että laajemalla alueella vaikuttavat tekijät (esim. talvehtimisalueen sääolot). Kirjoittajat seurasivat samettipääkertun ja ruskokertun metsäpalon jälkeistä populaatiodynamiikkaa Iberian niemimaan pensaikkoalueella. Viimeaikaiset tutkimukset ovat osoittaneet, että ruskokerttujen määrä on vähentynyt jyrkästi Espanjassa. Samettipääkerttujen määrä on puolestaan pysynyt

vakaana. Ruskokerttu on oletettavasti kärsinyt Välimeren maiden maankäyttötavoissa tapahtuneista muutoksista, kun taas samettipääkertun on oletettu hyötyneen lisääntyneestä joutomaan määrästä sekä uusista metsitysprojekteista. Tutkijat halusivat selvittää, vaikuttiko tutkimuslajien runsauteen enemmän paikallisen tason elinympäristömuutokset vai tekijät, jotka operoivat paikallista tasoa laajemmalla alueella. Kerttujen runsaus arvioitiin sekä palaneelta alueelta (1-6 vuotta palon jälkeen) että palamattomalta kontrollialueelta pistelaskentamenetelmää käyttäen. Molemmat tutkimuslajit esiintyivät paloalueella verrattain vähälukuisina heti paloa seuranneena vuonna. Kummankin lintulajin runsaus kasvoi paloalueen iän myötä aina neljänteen palon jälkeiseen vuoteen saakka. Tämän jälkeen ruskokertun runsaus kasvoi nopeammin kuin samettipääkertun. Kuusi vuotta palon jälkeen ruskokertun runsaus oli suurempi paloalueilla kuin kontorollialueella. Kontrollialueella ruskokertun määrä oli pysynyt vakaana koko tutkimusjakson ajan. Samettipääkerttu sen sijaan runsastui tutkimusajanjaksona myös kontrollialueella. Samettipääkertun runsastumiseen paloalueella vaikuttivat siis muut tekijät kuin palodynamiikkaan liittyvät tekijät. Ruskokertun runsausmuutokset näyttivät sen sijaan liittyvän paikallisiin tekijöihin eli metsäpalon jälkeiseen sukkessioon tutkimusalueella. Tutkijat arvioivat, että palodynamiikkaan liittyvillä tekijöillä voi olla tärkeä merkitys ruskokertun runsausmuutoksiin. Kirjoittajien mukaan tutkittujen lintulajien vasteet ympäristönmuutoksiin olivat lajispesifisiä. Tämä olisi huomioitava arvioitaessa paikallisten ympäristönmuutosten linnustovaikutuksia.

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