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Local survival after fire in Mediterranean shrublands: combining capture-recapture data over several bird species

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Abstract Post-disturbance survival is a key factor in the onset of secondary successions. Here we analyse capture-recapture data from two before/after disturbance studies to estimate the effect of fire on local bird survival. Analyses of six bird species at two Mediterranean shrubland sites were combined using a meta-analysis approach. Two warblers, *Sylvia undata* and *S. melanocephala*, were studied at one site altered by prescribed burning, and five passerines (*Luscinia megarhynchos*, *Turdus merula*, *Parus major*, *P. caeruleus* and *S. melanocephala*) at one site disturbed by wildfire. Based on the combined analysis, annual survival probability significantly decreased from 0.49 to 0.18 (i.e. a 64% decline) after the fire. Our results further suggest a trend for a higher decrease in annual survival associated with wildfire (−72%, from 0.51 to 0.14) than with prescribed burning (−35%, from 0.41 to 0.27), although this should be properly tested with a specific experimental design. In *S. undata*, a decline in survival in the 'long-term' cannot account for the drop in density observed the first spring after fire. We suggest that a decrease in recruitment rate and an increase in the proportion of non-breeders immediately after the fire may contribute more strongly to the decline in the breeding population. Our results tend to support the idea that bird populations may respond to moderate disturbances with noticeable time lags, because of individual site tenacity.

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Introduction

Natural communities show various forms of resistance to disturbances, even to 'catastrophic' events such as fire, hurricanes, floods or avalanches (e.g. Kozlowski and Ahlgren 1974; Bazzaz 1983; Newsome and Catling 1983). Because of their ability to disperse, birds surviving a disturbance can either emigrate from the modified habitat or remain in it (the second is referred to as 'site tenacity' or 'local survival'). Each of these alternatives has an associated mortality risk—the failure to become established in a suitable habitat (Bélichon et al. 1996) on the one hand, or the impossibility of coping with the sudden decrease in shelter and resources on the other (Bendell 1974; Newsome and Catling 1983; Prodon and Pons 1993). Post-fire site tenacity has been suspected from observations of birds shortly after fire (Emlen 1970) or from evidence of limited changes in bird communities of burned forests (Prodon and Lebreton 1981, 1983). Indeed, the post-fire recapture of previously marked individuals demonstrated such tenacity in different biomes. The obtained return rates range from 9% to 22% in studies at the community level (Wooller and Brooker 1980; Loiselle and Blake 1984; Wooller and Calver 1988) and from 44% to 80% in single-species studies (Cowley 1974; Ellison 1975; Best 1979; Petersen and Best 1987; Rowley and Brooker 1987; Smith 1989). Few estimates are available for the Mediterranean Basin [Pons (1998) found a 15% return rate in a shrubland bird community], where fire is an important ecological force, driving vegetation dynamics (Trabaud 1981). All the above-mentioned studies rely, with two exceptions, on prescribed burning. This management-oriented fire is generally of uneven progression, besides being milder and smaller than wildfire.

Although post-fire site tenacity has been empirically demonstrated, quantification is difficult and estimates suffer from several weaknesses. Firstly, return rates, i.e. the product of capture and survival probabilities, cannot provide local survival measures when the capture rate varies with time, e.g. when fire drastically reduces vegetation cover. Secondly, most of the studies mentioned above did not include a comparison with return rates under undisturbed conditions, and did not take into account the variability of this parameter in the absence of fire. Thirdly, the small size of many data sets and inappropriate statistical procedures make the significance of many survival estimations questionable.

In this study, we took advantage of a prescribed burning in Mediterranean lowland vegetation, starting the study 2 years before the fire. Secondly, we took advantage of a wildfire in the same region. This second fire burned an area where a capture-recapture monitoring of passerine populations had already been operating for 4 years. The first aim of this paper is to investigate whether or not the local survival of the most common bird of the prescribed burning plot, the Dartford warbler *Sylvia undata*, differs before and after the alteration of its habitat by fire. The second aim is to perform a multi-species analysis of survival in order to test for a general effect of fire on Mediterranean passerine species. To this end, we combined data on six species in a meta-analysis approach (Hedges and Olkin 1985; Arnqvist and Wooster 1995), although the data were based on two fires with a single site each, and were not independent replicates within sites.

Materials and methods

Sites and study species

The prescribed burning plot of Torderes (42° 34′ N, 2° 45′ E) is 290 m a.s.l. in the Aspres massif, in the foothills of the Eastern Pyrenees, France. The relief is gentle, substrate siliceous, and the climate Mediterranean sub-humid (with a mean annual rainfall of 847 mm in 1991–1996). The 8.25 ha plot was included within an area of 12.5 ha which was to be experimentally burned. At the start of the study, in April 1991, the vegetation consisted of 15-year-old shrubland, developed after an intense wildfire in July 1976. This maquis had an average height of 1.5 m, and was dominated by *Erica arborea*, with scattered cork oaks *Quercus suber*. In January–March 1993, the site was altered by four successive fires, in the frame of a broader study on the impact of fire on shrubland communities. As a result, 76% of the plot area was burned unevenly (Fig. 1) and the foliage volume was reduced by 65% in the burned patches (Pons 1998). 133 Dartford and 79 Sardinian warblers *Sylvia melanocephala* were captured and marked in this plot.

The Dartford warbler is characteristic of fire-prone Mediterranean shrublands and shows a high breeding philopatry (Bibby 1979a). Warblers are dependent on shrubs for nesting and foraging (Bibby 1979b, 1979c; Martin and Thibault 1996) and cannot breed in recently and completely burned areas (Prodon and Lebreton 1983; Prodon et al. 1987; López and Guitian 1988; Llimona et al. 1993). Marking proved their site tenacity after a patchy fire (Pons 1998), but no estimation of local survival existed at that point. The Dartford warbler remained the dominant bird species at Torderes during the 6 years of study, despite a 44% reduction in its density after the fire (from 10.0 and 9.7 breeding pairs/10 ha before the fire, in 1991 and 1992 respectively, to 5.4, 7.6, 8.8 and 11.5 b.p./10 ha after the fire, in 1993–1996; Pons 1998). This drop in density was not due to a lack of potential immigrants as the Aspres massif included thousands of hectares of suitable habitat, with the species well distributed throughout.

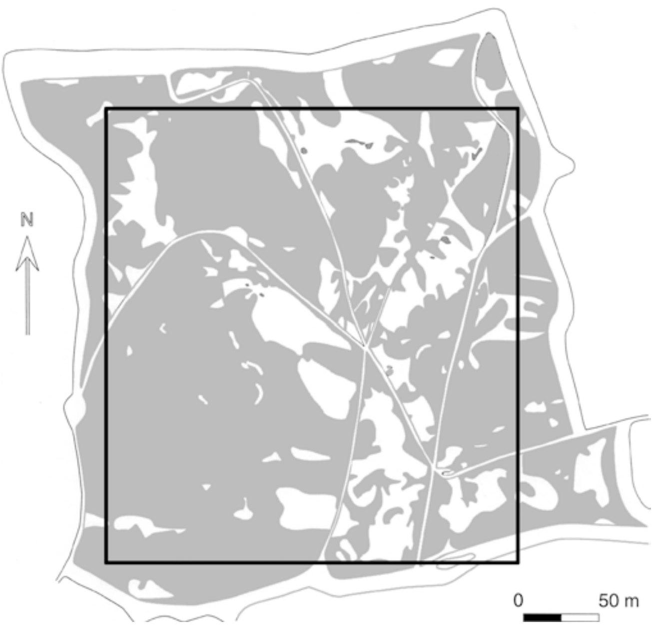

Fig. 1 Habitat heterogeneity following prescribed burning of the study plot at Torderes (8.25 ha, the whole altered area is 12.5 ha). The *thick solid line* represents the limits of the plot, burnt patches (76% of the plot area) are in *grey*

The wildfire study site is located at the Tiana bird ringing station (41° 30′ N, 2° 16′ E) in the Serralada Litoral at 200 m a.s.l., near Barcelona, Catalonia, Spain. The climate is Mediterranean sub-humid, with an average annual rainfall of 600 mm. Before the fire, the study area consisted of a mosaic of shrubland (58%), woodland (28%), and dry grassland (14%) (Vilalta 1983). The shrubland had an average height of 1–1.5 m, and was dominated by *Cistus* species, while the woodland was dominated by pines *Pinus pinea* and oaks *Quercus ilex* and *Q. pubescens*. Cultivated fields, mainly vineyards, surrounded the southern and western parts of this study site. In early August 1994, a wildfire of 914 ha completely burned the site. Birds were captured and marked from 1991 to 1998 following a standardised protocol. Mist-nets were used to trap birds from April to August at 10-day intervals, totalling ten trapping days per year. The nets were placed at fixed points on an area of 4 ha, and at a minimum distance of 10 m from the unburned fields. An ‘edge effect’ in the results is nevertheless unlikely, since the surrounding vineyards are unfavourable for the five bird species studied. These were the nightingale *Luscinia megarhynchos*, the blackbird *Turdus merula*, the great tit *Parus major*, the blue tit *P. caeruleus* and the Sardinian warbler, providing a total of 292 marked individuals.

Survival analysis of the Dartford warbler

In the prescribed burning plot, birds were captured using mist nets and marked with an individual combination of colour rings from spring 1991 to winter 1996–1997, on 24 consecutive ‘occasions’. One occasion consisted of a 3-month period (approximately a season of the year), and grouped together a 3-day mist net session (to mark new individuals and recapture already marked ones) and an average of four visits designed for visual controls. These controls were carried out in the morning, following all the paths of the plot and its periphery and mapping those colour-marked birds which could be identified. This activity was difficult before the fire when birds were concealed by vegetation, and much more effective afterwards. The trapping effort between consecutive mist net sessions was placed alternately on each of two overlapping halves of the plot. Total net length after the 1993 fires was increased (from 114 m to 174 m) in an attempt to minimise the adverse effect of reduced cover on warbler capturability. Temporal differences in capture probability, including both mist-net captures as well as visual controls, are however accounted for in the models (see below) so that they do not influence the estimation of survival. The 133 marked Dartford warblers were sexed according to plumage coloration (after their post-juvenile moult) and aged according to the colour pattern of primary covert feathers (Gargallo 1992). Three age classes were recognised: young (before or during their post-juvenile moult), first-year birds (up to the end of their first breeding season) and genuine adults (afterwards). Individuals' capture histories used as raw data for analysis included both physical recaptures as well as visual controls (hereafter both referred to as 'recaptures'). We only kept for analysis the birds captured during or after their first winter (44 males and 35 females).

Since it was impossible to recapture all marked individuals alive each season, the estimation of local survival probabilities (ϕ) had to rely on capture-recapture models accounting for recapture probabilities (p) (Lebreton et al. 1992). Survival probabilities correspond to 'local' survival because, as usual, it was impossible to distinguish between permanent emigration out of the study area and death. If S is the probability of survival and F the probability of remaining in the study area between two capture occasions, the local survival estimator is $\phi = S \times F$. A decrease in local survival ϕafter the fire can thus arise either from a decrease in S, i.e. mortality, in F, i.e. emigration out of the study area, or both processes.

The method used to estimate survival and recapture probabilities is fully detailed in Lebreton et al. (1992). Only necessary methodological principals are reported here. Multinomial likelihood functions describing capture-mark-recapture data, i.e. accounting simultaneously for the probabilistic processes of survival and recapture, are available (Lebreton et al. 1992) and implemented in specialized statistical software (e.g. Reboulet et al. 1999; White and Burnham 1999). These functions include one different parameter for each source of variation of the recapture and the survival process (e.g. one parameter for each sex). Maximum Likelihood estimation procedure is then used to obtain a descriptor of how the model fits to the data (i.e. $-2[\log(\text{likelihood of current model}) - \log(\text{likelihood of saturated model})]$, named deviance) and parameter values. This relies on a numerical determination of the set of parameter values that maximises the log(likelihood). Capture-mark-recapture models rely on the assumptions that:

1. All individuals of a given group (e.g. sex groups) have the same survival and recapture probabilities
2. Fates of individuals are independent.

Prior to identifying the best model according to data description (lowest deviance) and parsimony (lowest number of parameters), the verification of these assumptions has to be checked by goodness-of-fit tests. We followed this standard procedure, as recommended in Lebreton et al. (1992):

1. The starting point for model selection was the Cormack-Jolly-Seber model (CJS) generalized for several groups of individuals (i.e. different sexes). In this model, denoted $\phi(\text{sex*t})$ $p(\text{sex*t})$, both survival ϕ and recapture p probabilities vary between sexes (sex effect, male versus female) and between 3-month periods (time effect, noted t), temporal variations being independent among sexes (interaction between effects sex and t, noted by *).
2. The goodness-of-fit of this model was checked by contingency table tests (software RELEASE; Burnham et al. 1987). For each capture occasion, a χ^2 statistic is computed to test whether the distribution of recaptures is independent of past capture history and is homogenous across time and individuals. The χ^2 statistics are summed over all occasions to provide components (Test3.Sr, Test3.Sm, Test2.C) that reveal specific causes of departure from the CJS assumptions. The sum of χ^2 statistics over all components provides the overal χ^2 statistics of goodness-of-fit test for the CJS model. Test3.Sr checks that whether individuals are recaptured (occasion $i + 1$ or later) or not in the future is dependent on their past capture history (first capture at versus before i). This reveals the occurrence of transience, i.e. an excess of individuals captured only once (Pradel et al. 1997a). Test3.Sm checks, among those individuals recaptured later than i, whether their next recapture occasion (occasion $i + 1$ versus later) is dependent on their past capture history (first capture at or before i). This may reveal heterogeneity among individuals, for instance, because of age-dependence. Test2.C checks, among individuals recaptured later than i, whether their next recapture occasion (occasion $i + 1$ versus later) is independent of whether they have been captured at i. This reveals trap-dependence effects, i.e. the possibility that the probability of being recaptured is a function of the time elapsed since the last capture (Pradel 1993). For instance, this occurs when recently captured individuals avoid traps for some time, resulting in an excess of individuals which are not recaptured at occasion $i + 1$, but are recaptured later.
3. We then built contrasted biological meaningful models, i.e. with different parameterisations for recapture and survival probabilities, and selected the preferred one on the basis of minimum Akaike Information Criterion (AIC; Lebreton et al. 1992; Burnham and Anderson 1998). All models within two points of AIC from the preferred model are not statistically different. To make results presentation short, only these models are reported here. Power calculations were made according to Lebreton et al. (1992). The Logit-link function was used to constrain probability estimators to remain within the 0–1 interval. Models were fitted with software MARK (White and Burnham 1999).

Models were fitted for all combinations of the effects of sex and time (and the interactions potentially supported by the data) on survival and recapture probability. For local survival, temporal variability was parameterised as a season effect $\phi(s)$ (four categories), and the categorical covariates short-term $\phi(F_S)$ and long-term $\phi(F_L)$ for fire effect. 'Short-term' included the two 3-month periods following the prescribed burning, which may refer to an immediate fire effect, as the four fires were set during the first of these intervals. 'Long-term' effect included the seventeen 3-month periods from the fire (1993) to the end of the study (1997). For recapture probability, the two sexes were analysed separately, as territory defence and display behaviour was expected to induce a higher recapture probability for males. Temporal variability was described by the number of visits per occasion $p(v)$ as a measure of sampling effort, and short $p(F_S)$ and long-term fire effect $p(F_L)$ in the same way as for survival probabilities, because the probabilities of capture may be strongly affected by the changes in vegetation structure after fire (visual controls may become more effective; capture by mist nets less effective).

Meta-analysis

We then tested the prediction of a negative effect of fire on local survival of passerines in a meta-analysis of fire effect sizes over seven capture-recapture datasets (see Appendix). The mean standardised fire effect (i.e. mean of effect sizes) was expected to be significantly lower than zero. For this purpose, in addition to the Dartford warbler data set, we analysed:

1. Capture-recaptures and visual controls of 35 adult males of Sardinian warbler at Torderes (the 44 females and young provided too few recaptures for analysis), and
2. Capture-recaptures of adult nightingales ($n = 52$), blackbirds ($n = 104$), great tits ($n = 60$), blue tits ($n = 33$) and Sardinian warblers ($n = 43$) over eight consecutive occasions at Tiana.

Because of the small size of these six additional data sets, standard species-specific analyses of survival, i.e. goodness-of-fit tests and model selection, would not have been reasonable. We therefore built only biologically meaningful models, where temporal variations in survival or recapture rates were considered as due to the effect of the fire, but otherwise as non-significant. Model structures considered (with a logit-link function) for survival and recapture probabilities were short-term (F_S) and long-term fire effect (F_L), and constancy over time. The nine possible models resulting from the combinations of effects on survival and recapture rates were fitted. For the wildfire, 'F_S' included the first year after the fire (i.e. the smallest time interval possible) and 'F_L' the four subsequent years (i.e. from the fire to the end of the study). For the prescribed burning, 'F_S' and 'F_L' were defined as before (see 'Survival analysis of the Dartford warbler').

We then combined the results of the seven independent analyses. The procedure consisted of estimating a fire effect f and its standard error σ for each data set, and deriving a standardised effect, $z=f/\sigma$ (i.e. effect size). In the absence of fire effect, the combined test statistic z has a standard normal distribution $N(0,1)$. When there is a fire effect, the expectation will depart from 0. Whatever the magnitude of the true effect in each species, the expectation of the test statistic will be negative if there is a general decrease in survival. The power of the resulting meta-analysis will obviously depend on the magnitude of the effects in the various species. An advantage of this procedure is that the power will be non-negligible in the case of small to moderate effects in all species, i.e. the test has a good probability of detecting the fire effect, which is not the case for separate tests on each species. The procedure used implicitly amounts to using a confidence interval on the effect size, and checking whether 0 is within this interval. The data are too sparse to test for homogeneity of the effect and, at any rate, the null hypothesis according to which the effect sizes are equal across species has no special reason to hold on biological grounds.

The standardised fire effect was estimated for each species using four different models:

1. With or without fire effect on recapture probabilities (according to AIC values the preferred fire effect, either short- or long-term, was considered for each data set, therefore it was allowed to differ between species); and
2. With a long or a short fire effect on survival.

The mean standardised fire effect (the sum of all seven standardised slopes divided by the square-root of the degrees of freedom; df = 6) was then computed: (1) for each one of these four models, and (2) using only z-statistics from the preferred models selected for each species on the basis of AIC. We finally tested these statistics against no fire effect (null slope) with one-sided z-tests.

Table 1 Results of the goodness-of-fit tests of the CJS survival model for the prescribed burning data set on *Sylvia undata* (Torderes). Test notation according to RELEASE software (Burnham et al. 1987); see text for details. *NA* Not applicable due to insufficient data

Sex	Test component	χ^2	df	P
Male	Test3.Sr	4.893	13	0.977
Male	Test3.Sm	1.323	3	0.724
Male	Test2.C	4.303	12	0.977
Female	Test3.Sr	1.644	5	0.896
Female	Test3.Sm	NA		
Female	Test2.C	1.872	13	1.000

Table 2 Best supported models for the analysis of the effect of prescribed burning on survival for *S. undata* and males of *S. melanocephala* (Torderes). Recapture probability was constant over time for females *S. undata*, but was dependent on the number of visits and changed after the fire for males: $p(v+F_L)$. Only models within a two-unit AIC difference from the preferred model are given. Symbols for explanatory variables are: F_L long-term fire effect (from fire to the end of the survey, i.e. 17 3-month periods after fire); F_S short-term fire effect (two 3-month periods after fire); *sex* sex effect; *no symbol* constant

Species	Model	No. parameters	ΔAIC with preferred model
S. undata	ϕ	5	0
	$\phi(F_L)$	6	0.510
	$\phi(\text{sex})$	6	1.431
	$\phi(F_S)$	6	1.844
S. melanocephala	$\phi(F_L)$	3	0

Results

Survival of the Dartford warbler

We searched the surroundings of the Torderes plot shortly after the fire and we did not find any sign of short-distance dispersal or an increased use of margins by the plot inhabitants. Post-fire disappearance of warblers could be therefore due either to mortality or to long-distance dispersal. The term 'survival' in the following results must therefore be understood as an equivalent of 'local survival' (a survivor is thus a bird that both survives and remains in the study plot). The CJS survival model (Table 1) satisfactorily fitted to the capture-recapture data of males, as well as of females, despite the sparseness of the data and the resulting weak tests. There was no indication of transients or trap-dependence (Table 1). Model selection indicated that the data did not support:

1. The effects of sex, season, fire or time-dependency on survival probability, which could be considered as constant over time (Table 2) and was estimated at 0.437 per year, and
2. Time-dependency in recapture probability for females (annual $p=0.408$) but, for males, there was dependency on the sampling effort (overall number of visits per 3-month period, including trapping and visual controls; p ranges from 0.219 for 3 visits to 1 for 13 visits) and a positive effect of fire (for 7 visits, p rose from 0.170 before fire to 0.396 after fire; Table 3).

However, given the data available, there would be an approximate power of 0.53 to detect a 30% decrease in survival [quantified with the model $\phi(F_L)$ $p_{\text{males}}(v+F_L)$ $p_{\text{females}}(\text{constant})$] as significant. For a supposed 10% decrease in survival, the power would be 0.15. We cannot conclude, therefore, that fire had no effect on local survival. It is worth noting that the closest model to the preferred one includes a 'long-term' fire effect (model 'F_L'), hence this model tends to describe the data better than a 'short-term' effect (model 'F_S').

Meta-analysis

As stated above, it was impossible to run goodness-of-fit tests separately for each data set. However, after pooling over species, the data fitted the CJS model correctly,

Table 3 Estimates (±SE) of survival and recapture probabilities before and after fire (up to 4 years after fire). Estimates for each available dataset are retrieved from the closest model in AIC from the preferred model that includes a fire effect, either short- or long-term, on recapture and survival probabilities (Tables 2, 5). *NE* Not possible to estimate due to insufficient data

Fire/species	Probability	Survival		Recapture	
	Model	Before	After	Before	After
Prescribed burning					
Site: Torderes; 3-month time intervals					
S. undata[a]	$\phi(F_L)\ p(\text{sex}+v+F_L)$	0.871 ± 0.014	0.785 ± 0.039	0.170 ± 0.073 (males) 0.057 ± 0.019 (females)	0.396 ± 0.148 (males) 0.162 ± 0.067 (females)
S. melanocephala[a]	$\phi(F_S)\ p(v+F_L)$	0.736 ± 0.106	0.674 ± 0.313	NA	0.132 ± 0.073 (males)
Wildfire					
Site: Tiana; 1-year time intervals					
Luscinia megarhynchos	$\phi(F_S)\ p(F_L)$	0.464 ± 0.121	0.074 ± 0.073	0.238 ± 0.145	NE
Turdus merula	$\phi(F_S)\ p(F_L)$	0.345 ± 0.060	0.254 ± 0.132	0.724 ± 0.146	0.533 ± 0.355
S. melanocephala	$\phi(F_L)\ p(F_L)$	0.697 ± 0.098	0.094 ± 0.087	0.349 ± 0.219	NE
Parus caeruleus	$\phi(F_L)\ p(F_S)$	0.521 ± 0.099	0.191 ± 0.161	0.388 ± 0.185	NE
P. major	$\phi(F_L)\ p(F_L)$	0.369 ± 0.068	0.546 ± 0.123	0.703 ± 0.144	0.242 ± 0.196

[a] Recapture probabilities are given for a recapture effort of seven visits per 3-month period

Table 4 Results of the goodness-of-fit tests of the CJS model for the wildfire data sets (pooled data for five passerine species; Tiana). Test notation according to RELEASE software (Burnham et al. 1987); see text for details. *NA* not applicable due to insufficient data

Test component	χ^2	df	P
Test3.Sr	11.575	6	0.072
Test3.Sm	NA		
Test2.C	2.147	3	0.542

Table 5 Best supported models for the analysis of the effect of wildfire on survival at Tiana. All combinations of fire effects, both on survival and recapture probabilities, were considered. Only models within two units' difference in AIC from the preferred model are given. Symbols for effects are: F_L long-term fire effect (from fire to the end of the survey, i.e. 4 years);F_S short-term fire effect (1 year); *no symbol* constant

Species	Model	No. parameters	ΔAIC with preferred model
L. megarhynchos	$\phi(F_S)p(F_L)$	3	0
T. merula	$\phi\ p$	2	0
	$\phi(F_S)p$	3	1.10
S. melanocephala	$\phi(F_L)p(F_L)$	3	0
	$\phi(F_L)p$	3	0.65
P. caeruleus	$\phi(F_L)p(F_S)$	3	0
	$\phi\ p$	2	0.40
	$\phi(F_L)p$	3	1.70
P. major	$\phi\ p$	2	0
	$\phi(F_S)p$	3	0.25
	$\phi\ p(F_L)$	3	0.30
	$\phi(F_L)p(F_L)$	4	1.93
	$\phi(F_S)p(F_L)$	4	1.95

apart from a slight transient effect (Pradel et al. 1997b; i.e. Test 3.Sr; Table 4). The best supported models for Sardinian warbler males surveyed at Torderes, and for the five species surveyed at Tiana, are shown in Tables 2 and 5. Only the nightingale was significantly affected by fire ($\chi^2 = 5.070$, $P = 0.024$, df = 1). For the other species, the effect of fire was not significant but, for most, it was probably not detectable because of the limited sizes of the data sets.

For each different parameterisation of fire effect on local survival (short- vs long-term) and recapture probabilities (with vs without effect), no mean standardised fire effect was significant (Table 6). However, if we consider only the preferred models on the basis of AIC for each species (bold in Table 6):

1. The mean standardised fire effect was significantly negative. Considering, among the seven datasets, mean annual survival prior to fire and mean of the slopes for the fire effect in the preferred models (bold in Table 6), the mean decrease in survival was 63.6% (from 0.49 to 0.18).
2. A long-term fire effect was best supported after prescribed burning but a short-term fire effect was selected for three of the five species affected by the wildfire.
3. The fire effect represented a 10.2% decrease (from 0.80 to 0.72) in 3-month survival for the prescribed burning (i.e. 34.9% decline in the annual rate, from 0.41 to 0.27), and a 71.9% decrease (from 0.51 to 0.14) in annual survival for the wildfire. For the Dartford warbler in particular, the annual local survival rates can be tentatively estimated at 0.58 before the fire and 0.39 afterwards. This allows us to conclude that fire had a negative impact on survival, even if the data were not sufficient for estimating species-specific susceptibility to fire disturbance.

Discussion

The main goal of our study was to estimate the effect of fire on local survival in bird populations, with estimators unaffected by changes in recapture success before and after disturbance. Such changes in recapture success can be especially evident when fire leads to drastic modifi-

Table 6 Interspecific meta-analysis of fire effect on survival. Standardised slopes quantifying the strength of the fire effect on survival (i.e. effect sizes, on a logit scale) are given for four different models for fire effect on survival and recapture probabilities (standard errors were computed with second part procedure). Estimated effects in *bold* are from models with the lowest AIC (among those including a fire effect on survival). Two types of fire effect were considered: short-term (in the two 3-month periods after the prescribed burning and in the year following the wildfire) and long-term (in the 17 3-month periods after the prescribed burning and in the 4 years after the wildfire). One-sided *t*-tests were used to test for a negative fire effect on survival probability. *NS* Not significant ($P > 0.05$); *NE* not possible to estimate due to insufficient data

Recapture	Standardised fire effect on survival			
	Without fire effect		With fire effect (either long- or short-term)	
Fire effect on survival	Short-term	Long-term	Short-term	Long-term
Prescribed burning				
Site: Torderes; 3-month time intervals				
S. undata	0.744	−0.623	0.537[a]	**−1.195**[a]
S. melanocephala (males)	−0.148	−0.584	−0.192[b]	**NE**
Wildfire				
Site: Tiana; 1-year time intervals				
L. megarhynchos	−1.176	1.322	−1.927	0.243
T. merula	−0.978	−0.215	−0.472	0.712
S. melanocephala	−1.254	−1.908	−0.833	−2.094
P. caeruleus	0.227	−1.014	−0.632	−1.328
P. major	−1.367	−0.330	−0.855	0.776
Mean standardised fire effect	−1.494 NS	−1.267 NS	−1.653 NS	−1.178 NS
Mean standardised fire effect for preferred models	−3.432 $P < 0.01$			

[a] Fire effect on recapture probability only in males

[b] Next preferred model

cation of the habitat structure. As we found at the prescribed burning plot, fire decreased mist net capture rate but increased the number of visual controls, at least initially, due to reduced cover. The practical impossibility, however, of making true replicates both of prescribed (i.e. patchy) burning and wildfire plots, together with the lack of parallel controls, may limit the generalisation of our results. Nevertheless, to our knowledge, this kind of data and analysis is unique. Due to the heterogeneity of the Mediterranean landscape, a before/after disturbance design seemed to be the best way to control spatial variability, providing that the temporal variability in the absence of disturbance could be estimated (2 and 4 years were sampled in Torderes and Tiana, respectively, before the fire).

Initially, we showed that the survival probability of Dartford warbler adults, including first-year birds and adults, could be considered as constant over time despite the disturbance. However, the sampled population was modest, given the size of the prescribed burning plot, limited by management constraints. Power tests thus indicated that even a strong effect of fire on survival could not be excluded. Despite the difference in burned areas (12.5 ha vs 914 ha), the data from a second plot was combined to obtain an overall fire effect on local survival because the methods and the study areas (8.25 ha vs 4 ha) were comparable. The subsequent meta-analysis, allowing a test of fire effect over six species, and seven data sets, showed a significant decrease of 64%, from 0.49 to 0.18, of adult survival after fire. This result is comparable to the effect of a severe cold episode in the Mediterranean coast, after which the survival of the house sparrow also declined by 64% (from 0.47 to 0.17; Senar and Copete 1995). As is usual with capture-recapture studies, however, it was impossible to estimate the relative contribution of permanent emigration and genuine survival on the observed patterns of local survival.

The wildfire tended to affect local survival more intensely than the prescribed burning. Nevertheless, this should be properly tested with a specific and appropriate experimental design. The reduction in the annual survival was estimated at 35% after the prescribed burning and at 72% after the wildfire. The best supported ‘long-term’ effect (i.e. 4 years) of the prescribed burning on survival suggests a time lag in the response of the population (Wiens and Rotenberry 1985). The best supported ‘short-term’ effect of the wildfire on three of the five species concerned suggests a more rapid response through dispersal or local mortality. On the other side, the prefire annual adult survival rate of the Dartford warbler at Torderes (estimated at 0.58) is within the range of mean values for other non-migratory small Mediterranean passerines under undisturbed environmental conditions, e.g. 0.47 (females) and 0.68 (males) for the blue tit (Blondel et al. 1992), and 0.6 in the serin *Serinus serinus* (Senar and Copete 1990).

A moderate disturbance, such as a low intensity fire, allows birds and, in particular the Dartford warbler, not only to survive but also to remain on their home ranges provided unburned patches persist (see also

Martin 1983; Pons and Prodon 1996; Herrando et al. 2001). Such site tenacity implies that there must be some phenotypic plasticity for adaptation to the new environmental conditions (Winter and Best 1985; Brooker and Rowley 1991). At Torderes, fire decreased the carrying capacity of the warblers' nesting habitat in the burned patches, but not in the unburned ones. Foliage insects, the main food source for the species (Bibby 1979c), were more abundant on unburned patches inside the burned area than on nearby unburned shrubland (Pons 1998). This may explain why we did not find any increased use of the unburned external areas by the remaining adults. The majority of the site-tenacious Dartford warblers managed to maintain their territories, enlarging them to include enough unburned patches (unpublished data)—the species being reluctant to abandon a territory once it has been established (Bibby 1979a). In contrast, site tenacity is almost impossible for foliage-dwelling birds (Prodon and Lebreton 1983; Prodon et al. 1987; López and Guitian 1988; Llimona et al. 1993) after a severe disturbance like a Mediterranean summer wildfire that can completely destroy shrub and tree cover over large areas. This would be consistent with the trend for a higher decrease in local survival associated with wildfire than with prescribed burning.

The immediate drop in Dartford warbler breeding density (−44%) during the first year after the fire at the prescribed burning plot (Pons 1998) showed that the habitat alteration was sufficient to gauge a population response, not easily obtained in field experiments (cf. Wiens et al. 1986; Johannesen et al. 2003). However, the decrease in survival was, in the longer term, a result of the disappearance of most old breeders that composed the majority of the population in the first spring after fire. The observed population decrease did not result, therefore, from a sudden fire-induced mortality, or from an increased mortality during the first months after fire. It is more likely that it resulted either:

1. From an increase in the number of non-territorial, i.e. non-breeder, individuals. We did not include these birds in density measurements obtained by standard mapping method. However, non-territorial birds could be recaptured and, in survival analysis, were considered as alive. Visual controls showed that two adult males, which held territories before the fire, did not show territorial behaviour afterwards, although they remained on the site (a similar example of territory loss has been described in the red grouse *Lagopus l. scoticus*; Watson 1985), or
2. From a decrease in recruitment rates in the spring following the fire (only 25% of the 12 controlled birds were recruits, both sexes combined). In three other unburned Catalan sites pooled, 36% of breeders were new recruits ($n = 58$, personal observation, and J.M. Bas, personal communication). The frequency of recruits seemed lower, although not significantly so, at Torderes after the fire (one-tailed Fisher exact test, $P = 0.349$). The recruitment rate before the fire at Torderes unfortunately could not be assessed because, at that time, we were unable to separate first-year from older birds.

A variation in recruitment rates has been found after other types of disturbances, for example in the Pyrenean capercaillie *Tetrao urogallus*, following human disturbance (Brenot et al. 1996). However, a higher proportion of experienced breeders could, to some extent, compensate for the expected fall in reproductive success under disrupted environmental conditions. This fact may help to explain why the few existing demographic studies on passerines (Best 1979; Petersen and Best 1987; Robel et al. 1998) have failed to show any significant effect of fire on breeding success. In a Mediterranean heath in Australia studied for 20 years, fire extent (after eight different fires) affected the breeding densities of the splendid fairy-wren *Malurus splendens* with a time lag of 4 years. However, the variation in adult survival of the species was not related to the extent of the fire, but to environmental fluctuations (Brooker and Rowley 1995). The fire-induced change in the population in the Dartford warbler and the splendid fairy-wren are examples, at the plot scale, of population growth rates inconsistent with variation in survival rates (Siriwardena et al. 1998; Saether and Bakke 2000).

On a larger scale, extensive wildfires are not uncommon in the Mediterranean Basin and are expected to increase as a result of climatic warming (Piñol et al. 1998) and rural depopulation. Furthermore, prescribed burning is increasingly being used for wildfire prevention in this region. Therefore, the need for further long-term studies to assess the consequences of both types of fires on animal populations is worth stressing. The results should be carefully considered in future landscape management.

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Appendix

Table 7 shows capture-recapture data for *S. undata* and *S. melanocephala* at the prescribed burning plot. Table 8 shows capture-recapture data for the five bird species at the wildfire site.

Table 7 Capture-recapture data for *S. undata* and *S. melanocephala* at the Torderes site. Capture occasions are given per 3-month period (parenthesis) per year. R_i number of individuals captured at occasion i; m (i, j) number of individuals captured at occasion i and recaptured at occasion j

Occasion i	R_i	$j=$																						
		1991 (3)	1991 (4)	1992 (1)	1992 (2)	1992 (3)	1992 (4)	1993 (1)	1993 (2)	1993 (3)	1993 (4)	1994 (1)	1994 (2)	1994 (3)	1994 (4)	1995 (1)	1995 (2)	1995 (3)	1995 (4)	1996 (1)	1996 (2)	1996 (3)	1996 (4)	1997 (1)
S. undata (both sexes)																								
1991 (2)	13	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991 (3)	6		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991 (4)	1			0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (1)	3				1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (2)	8					0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (3)	0						0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (4)	7							3	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
1993 (1)	9								5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993 (2)	11									1	1	2	2	0	0	0	0	0	0	0	0	0	0	0
1993 (3)	4										0	1	0	0	0	0	0	0	0	0	0	1	0	0
1993 (4)	4											1	0	0	0	0	0	0	0	0	0	0	0	0
1994 (1)	11												2	0	0	0	0	0	0	0	0	0	0	0
1994 (2)	10													1	1	1	2	0	1	0	0	0	0	0
1994 (3)	2														0	0	0	0	0	0	0	0	0	0
1994 (4)	5															2	0	0	1	0	0	0	0	0
1995 (1)	12																7	0	0	0	0	0	0	0
1995 (2)	13																	4	2	1	0	0	0	0
1995 (3)	4																		0	0	0	0	0	0
1995 (4)	5																			1	1	0	1	0
1996 (1)	5																				1	0	0	0
1996 (2)	7																					0	0	2
1996 (3)	1																						0	1
1996 (4)	2																							0
S. melanocephala (males)																								
1991 (2)	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991 (3)	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991 (4)	2			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (1)	1				0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (2)	0					0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (3)	0						0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992 (4)	3							0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993 (1)	1								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993 (2)	3									0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1993 (3)	1										0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993 (4)	7											1	0	0	0	0	0	0	0	0	0	0	0	0
1994 (1)	1												0	0	0	0	0	0	0	0	0	0	0	0
1994 (2)	3													0	0	0	0	0	0	0	0	0	0	0
1994 (3)	0														0	0	0	0	0	0	0	0	0	0
1994 (4)	3															0	0	0	0	0	0	0	0	0
1995 (1)	2																1	0	0	0	0	0	0	0
1995 (2)	2																	0	0	0	1	0	0	0
1995 (3)	0																		0	0	0	0	0	0
1995 (4)	1																			0	0	0	0	0
1996 (1)	1																				0	0	0	1
1996 (2)	3																					0	0	0
1996 (3)	0																						0	0
1996 (4)	3																							1

Table 8 Capture-recapture data per species at the Tiana site. Capture occasions are year. R_i number of individuals captured at occasion i; $m(i, j)$ number of individuals captured at occasion i and recaptured at occasion j

Occasion i	R_i	$j=$						
		1992	1993	1994	1995	1996	1997	1998
L. megarhynchos								
1991	12	1	0	0	0	0	0	0
1992	10		2	0	0	0	0	0
1993	7			1	1	0	0	0
1994	9				0	0	0	0
1995	2					1	0	0
1996	2						2	0
1997	10							4
T. merula								
1991	13	5	0	0	0	0	0	0
1992	27		6	0	0	0	0	0
1993	29			6	1	0	0	0
1994	15				2	0	0	0
1995	10					2	0	1
1996	5						1	0
1997	5							1
S. melanocephala								
1991	3	1	0	0	0	0	0	0
1992	6		0	2	0	0	0	0
1993	6			2	0	0	0	0
1994	11				1	0	0	0
1995	6					1	0	0
1996	4						1	0
1997	7							0
P. caeruleus								
1991	11	2	1	0	0	0	0	0
1992	4		0	1	0	0	0	0
1993	7			2	0	0	0	0
1994	6				2	0	0	0
1995	3					0	0	0
1996	1						0	0
1997	1							0
P. major								
1991	14	2	0	0	0	0	0	0
1992	7		4	1	0	0	0	0
1993	11			2	0	0	0	0
1994	13				2	0	0	0
1995	10					1	1	1
1996	2						0	0
1997	3							1

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