Who are we sampling? Apparent survival differs between methods in a secretive species

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Survival is a fundamental parameter in population dynamics with increasing importance in the management and conservation strategies of wildlife populations. Survival probability in vertebrates is usually estimated by live-encounter data obtained by means of physical mark–capture–recapture protocols. Non-invasive acoustic marking relying on individual-specific features of signals has been alternatively applied as a marking technique, especially in secretive species. Nevertheless, to date no research has compared survival rate estimates obtained by acoustic and physical marking. We estimated half-yearly and annual survival and recapture rates of a secretive and threatened passerine, the Dupont's lark *Chersophilus duponti*, using two separate live-encounter data sets of males collected simultaneously by physical and acoustic marking in the same study area. The separate analysis of both methods led to different model structures, since transient individuals had to be accounted for in the acoustic marking but not in the physical marking data set. Furthermore, while reencounter probabilities did not differ between methods, survival estimates employing physical marking were lower than those obtained acoustically, especially between the postbreeding and the breeding period when the apparent survival of colour-banded birds was twice as low as for acoustic marking. The combination of marking methods suggested the existence of different subsets of individuals differentially sampled within the population: whereas colour-banded males seemed to represent the territorial fraction of the population, both resident and floater individuals were probably detected by acoustic marking. Using traditional mark–recapture methods exclusively could have misled our estimates of survival rates, potentially affecting prospective predictions of population dynamics. Acoustic marking has been poorly applied in mark–recapture studies, but might be a powerful complement to obtain accurate estimates of fundamental demographic parameters such as survival and dispersal.

Demographic models have an important role in the management of threatened species by predicting population size, population growth and extinction risk over a specified future time period (Sæther et al. 2005). Among the demographic parameters that noticeably affect population dynamics is survival, because of its great impact on population growth rate (Sæther and Bakke 2000).

Survival rates are usually calculated with live-encounter data obtained by physical recapture or resighting of marked animals, which are often the only practicable methods for estimating wild-living species' survival over several time intervals (Lebreton et al. 1992). Nevertheless, the use of physical recapture and resighting methods has been proved to be difficult when applied to secretive species of different animal groups, because of problems in detectability (Thompson 2004). Low reencounter rates can reduce the precision of estimates and condition our ability to detect survival differences among sampling periods, sex- and age-classes (Lebreton et al. 1992). In avian mark–recapture studies, physical marking and recapture by mist-netting is often characterized by low recapture rates and may impede

controlling for breeding status, movement rates, and other sources of heterogeneity (Faaborg and Arendt 1995). On the other hand, mark–resighting of colour-ringed birds tends to estimate higher reencounter probabilities than those typical of mist net studies (Sandercock et al. 2000).

As an alternative to physical marks for individual identification, several non-invasive methods have been applied to a wide array of taxa, such as DNA sampling recognizing genetic fingerprints (Lukacs and Burnham 2005), camera-trapping (Karanth et al. 2006) or visual recognition through individual morphological features (Meekan et al. 2006). Acoustic marking is another alternative technique to estimate survival; it is based on individual recognition through the specific spectrotemporal characteristics of vocalizations, whose repeated recordings over years can be considered as equivalent to recaptures. Acoustic marking has two main benefits compared to techniques relying on physical marks. First, it allows studying secretive species that do not allow mark detection or are difficult to catch (Galeotti and Pavan 1991). Second and maybe most important, it avoids the disturbance caused

by capture, handling and banding (Terry et al. 2005). In this sense, acoustic marking can be especially advantageous when studying sensitive or threatened species (Gilbert et al. 1994). Most individual recognition studies via acoustic signals have been carried out in territorial birds, but the technique has been used also in other taxa such as amphibians and numerous mammals (Ceugniet and Izumi 2004). In the latter group, however, the problematic identification of calling individuals due to variation associated to social factors has limited the applicability of the method (Mitani and Brandt 1994). Although vocal individuality has been extensively used as a census tool, and even to estimate annual survival in a few bird species (Gilbert et al. 1994, 2002), acoustic marking has never been used for estimating annual survival in passerines. Moreover, survival rates obtained with acoustic marking have never been compared to estimates derived from other traditional techniques, such as capture–mark–reencounter of ringed birds.

Although heterogeneity in catchability can be common (Crespin et al. 2008), a key assumption of most capture–mark–reencounter approaches is that individuals are equally probable to be caught (Bibby et al. 2000). Indeed, both acoustic marking and mark–resighting techniques are likely to suffer from biases that can mislead survival estimates (McGregor and Peake 1998, Sillett and Holmes 2002). For example, parameter estimates based on acoustic marking can be biased towards a subset of the sampled population when vocal activity varies with bird territorial or mating status (Amrhein et al. 2002). Mark–resighting studies on the other hand could fail to detect non-territorial individuals if territorial birds or breeders are more easily resighted (Sandercock et al. 2000). Since structured populations can be formed by various subsets of individuals, each characterized by different behavioural strategies and status (Smith and Arcese 1989), the simultaneous application of different marking methods could minimize possible sampling biases and permit a deeper insight into the ecology of the population under study (Crespin et al. 2008). Despite the low population size of our study model (below) we obtained extensive data for both marking methods, in contrast to previous monitoring studies on vocal individuality that were based on low sample sizes, sometimes less than 30 individuals (Terry et al. 2005).

Dupont's lark *Chersophilus duponti* is a rare species of conservation concern (B2000 territorial males were estimated for the whole Iberian Peninsula; Tella et al. 2005), and many aspects of the species' biology and ecology are poorly understood or totally unknown due to its secretive behaviour (Cramp 1988). In fact, its presence in Spain was largely unreported until the late 1970s (Aragüés 1992). In this study, we calculate and compare survival estimates of Dupont's lark using both acoustic marking and physical recapture combined with resighting of colour-banded individuals. Male territorial calls in the species are individually distinctive and constant over time and thus entirely satisfy the criteria for an individual-based monitoring of their populations (Laiolo et al. 2007). We discuss the results in terms of the potential differences in the status of target individuals and the consequences for the demographic monitoring of secretive species.

Material and methods

Study area and species

The study was carried out in Ebro Valley (north-eastern Spain), a dry plain covering approximately 10 500 km² characterised by widespread cereal cultivations and sparsely distributed patches of natural steppe vegetation of variable size. Despite hosting 450–500 male territories only, it is the second most important breeding population of Dupont's lark in Spain (Tella et al. 2005, Laiolo and Tella 2006).

The Dupont's lark is a small, sedentary and territorial passerine that exclusively inhabits flat shrub-steppe habitats of Spain and North Africa (Cramp 1988, Laiolo and Tella 2006, Seoane et al. 2006). The species is classified as endangered in the Spanish Red List (Garza et al. 2004) and near threatened in the IUCN Red List (BirdLife International 2005). Auditory contacts with this species are more frequent than visual ones, due to its cryptic colour, elusive behaviour and reluctance to fly at day even when encountered by humans. The song, the territorial call, the warning call, the distress call and the alarm whistles are the main vocalisations emitted by males (Laiolo et al. 2005, Laiolo and Tella 2005, 2006). Vocal activities are concentrated in two daily peaks: about one hour before dawn (the main peak) and shortly after sunset. The territorial call, the vocalization we used to identify individuals, is uttered both in the breeding (February to June) and postbreeding (September to November) periods. This species shows a strong territorial behaviour (Garza et al. 2005) but a large proportion of floater individuals might occur as adult sex ratio is heavily male-skewed, and males are overrepresented among captured birds even without using playback (Vögeli et al. 2007).

The study was carried out in sixteen habitat patches (hereafter 'subpopulations') of different size (from 5 to around 600 ha) and territory numbers (2–42 male territories, Tella et al. 2005), widely distributed across the study area. These patches constitute well-defined areas of natural steppe vegetation surrounded by a matrix of habitats that are unsuitable for the species. All these subpopulations were sampled in parallel by both physical and acoustic marking. Zimmerman et al. (2007) showed that survival estimates consistently increased when expanding the search area. Contrary to this approach we applied both physical and acoustic marking methods for sampling the identical subpopulations in our study area. Hence, a possible effect due to different sampling areas could be excluded.

Physical marking, recapture and resighting

Field work was performed in spring (March–June) and autumn (September–October), from autumn 2004 to spring 2007. We located singing birds during censuses carried out before dawn and then placed trap groups (3–4 spring loaded traps baited with yellow mealworms) near the detected singing points. A playback equipment (CD player and loudspeaker) forecasting the species calls and song was employed to attract the birds. After capture, they were banded with a metal ring and an individual combination of three colour rings for their identification at distance. We

applied a standardized protocol to measure the birds and extracted a drop of blood for molecular sexing (Vögeli et al. 2007). Finally, the birds were released at the capture sites. Playback was also used to attract birds and permit recaptures and resightings of colour banded individuals. However, resightings were much more frequent than recaptures (95% vs 5%, $n=183$ events). In a previous study, we detected no influence of forecasted sounds on either territory fidelity or dispersal movements (Laiolo et al. 2007). To facilitate reading, captures, recaptures and resightings were all considered as part of physical marking.

An exhaustive sampling of 11 entire subpopulations was possible due to their limited size (often below 100 ha), but not in five areas with more than 500 ha of available habitat, because of prohibitive workload. Inside these large patches we began to capture larks in spatially restricted areas that were successively enlarged during the study. If a marked bird was not detected in its territory in subsequent occasions, we performed intensive searches up to 250 m (mean nearest neighbour distance: 213.936 m, Laiolo et al. 2007) in the four cardinal directions from the capture point or until reaching the boundary of the territories of neighbouring birds. When the bird was not detected within this radius, we continued the search until arriving at the boundary of suitable habitat, which can be easily defined in this habitat-selective species (Garza et al. 2005, Laiolo and Tella 2006, Seoane et al. 2006). We determined the position of all birds captured, recaptured and resighted with GPS. For the purpose of this study, we only used male data ($n=183$ birds), which constitute 94% of the total number of captured birds from autumn 2004 to 2006 ($n=195$). Since adult survival rates were estimated, capturing events of juvenile individuals were suppressed. Both juvenile and adult birds undergo a complete moult in July–September and afterwards can not be differentiated anymore on morpho-anatomical basis (Svensson 1992). Therefore, all captured individuals in autumn were included in the physical marking data set.

Acoustic marking

In February–May and September–October 2004–2007, we recorded Dupont's lark territorial calls in individual territories by means of a microphone and recorder. Caller locations were established by means of a GPS. A typical Dupont's lark male utters from one to three types of territorial calls; only one male was found to give four call types. We measured from four (in the simplest call type) to 17 (in the longest one) spectrotemporal variables from 3756 territorial call types using Avisoft SASLab Pro 3.91 Software (Fast Fourier Transform: sampling frequency 22050 Hz, FFT length 512, time resolution 8.9 ms, frequency resolution 43 Hz, Window Function: Bartlett). A matrix was built in which caller identity was listed in rows and the acoustic variables of all call types arranged in columns, with 0-values entered for spectrotemporal variables of call types that were not uttered by an individual. We then performed a discriminant function analysis to calculate Euclidean distances (a measure of call dissimilarities) between calls of every pair of recorded males. Individuals recorded in different days were considered the same if their acoustic

distance was less than the maximum within-individual dissimilarity found in a sample of banded males (threshold value of 1.0, details in Laiolo et al. 2007). We also took into account Gilbert et al. (2002) criterion of incorporating knowledge on site fidelity to similarity measures, by removing matches within the same territory from subsequent matching in the same season. This is because the mechanisms promoting acoustic differentiation among neighbours do not operate when males are not close and interacting, and the same calls could appear in the repertoire of two or more distant individuals merely by chance. In our analysis, 263 males were classified as distinct individuals, and only 11 of these resulted to be misclassified when not applying Gilbert et al. (2002) criterion on site fidelity.

Survival analyses

Adult survival probabilities were estimated with MARK 4.3 (White and Burnham 1999) for both physical and acoustic marking data separately. We treated data separately because the same individuals could potentially be marked by the two methods and enter in both data sets, violating the assumption of independence. Moreover, time elapsed between occasions differed somewhat between both methods. Capture events were separated in breeding (February–June) and postbreeding (September–October) periods for each calendar year and marking method. For physical marking, the intervals between postbreeding and the next breeding period lasted 206–210 days (mean capture dates) and 143–153 days passed between breeding and the subsequent postbreeding period. For acoustic marking, the corresponding gaps ranged from 162 to 186 days and from 165 to 201 days respectively. Because of these differences, time intervals were independently set for each data set and accordingly adjusted in MARK.

For each method, we started with the fully time-dependent Cormack–Jolly–Seber model ($\phi_{(t)}$, $p_{(t)}$) where survival and recapture probabilities were denoted ϕ and p respectively (Lebreton et al. 1992). To test whether the general model fitted the data, we applied goodness of fit tests using the program U-CARE 2.2.5 (Choquet et al. 2005) to highlight possible violations of the assumptions underlying the CJS model (Pradel et al. 1997). Specifically, directional tests (Z-tests) were implemented in U-CARE to test for transience and trap-dependence (Pradel et al. 1997, Choquet et al. 2005). A further adjustment of the CJS model to the data was assessed with a parametric bootstrap approach in MARK. The parametric estimates from the model were employed to simulate data according to the assumptions contained in the CJS models (individuals were independent and no overdispersion of data occurred). This process was repeated 1000 times and the deviance of each model was calculated to control for possible exceeding deviance in the observed models comparing with the simulated data. The overdispersion parameter $\hat{c}$ was calculated as the ratio between the mean deviance of simulated models and the deviance of the observed model (Cooch and White 2004). No evidence of significant overdispersion ($\hat{c}=1.073$ for physical and 1.065 for acoustic marking respectively) was detected and the fates of individual birds could therefore be considered as

independent of each other (Anderson et al. 1994). We adjusted results obtained by both methods to their correspondent $\hat{c}$ (ideally $\hat{c}$ should be 1.000), although this adjustment had no qualitative effect on the results.

The CJS model ($8_{(t)}, p_{(t)}$) adequately fitted both the physical and acoustic marking data, but the presence of transients or emigrant individuals was detected in the latter (Results). Transients, opposite to residents, are individuals that disappear after marking and essentially have zero probability of recapture in subsequent occasions. When mixed in the data set with residents, these transients negatively bias survival estimates and lower the apparent survival of newly marked individuals (Pradel et al. 1997). To avoid this bias, for acoustic marking we used a 'transient' version of the CJS model that separated the first and subsequent encounters in the structure of the models (Pradel et al. 1997, Choquet et al. 2005). Following Perret et al. (2003), we additionally estimated the proportion of transient individuals (T_i) in each capture session.

Besides running constant and time dependent models, we additionally tested for overall differences between breeding and postbreeding seasons. For these models, capture events were merged into two annually independent episodes. The quasi Akaike information criterion corrected for sample size (QAIC_c, Burnham and Anderson 2002) was used to identify the model providing the most parsimonious fit to the data. Differences between the best-fitting and other models (DQAIC_c) and relative weights of evidence in favour of a particular model (QAIC_c weight) were employed to classify the obtained models. Model averaging procedures were applied in MARK to obtain model-weighted parameters and unconditional standard errors (Burnham and Anderson 2002). Annual survival probabilities were calculated by multiplying the two semestral survival rates (postbreeding-breeding and the subsequent breeding-postbreeding period). The program CONTRAST (Hines and Sauer 1989) was used to test for differences between the parameters estimated with both data sets.

Results

Physical marking

For the analyses of survival probabilities, 183 Dupont's larks were retained in the physical marking data set, which fitted the general CJS model adequately (global test: $\chi^2_{11} = 9.29$, $p = 0.60$). Neither transience (one sided directional test

$Z = 0.122$, $p = 0.452$) nor trap dependence ($Z = -0.653$, $p = 0.514$) were detected. Fully time-dependent reencounter probability was identified as the best estimator. Subsequently, we tried to constrain the general CJS model to obtain more parsimonious models, but the CJS model had overwhelming support (Table 1). Survival probabilities (95% CI) were low and very similar between postbreeding and subsequent breeding periods (0.3890.10, 0.3890.08) whereas they were more than twice as high (0.9390.32, 0.6390.13) between breeding and postbreeding periods (Fig. 1). The CJS model provided probabilities of reencounter ranging from 0.1390.05 (postbreeding period 2005) to 0.7790.19 (breeding period 2005) (Fig. 1). Annual apparent survival calculated as the product of the half-yearly survival rates were 0.2490.07 (autumn 2004–autumn 2005) and 0.3590.15 (autumn 2005–autumn 2006), respectively.

Acoustic marking

The CJS model ($8_{(t)}, p_{(t)}$) fitted well for the acoustic marking data (global test: $\chi^2_{12} = 248.42$, $p = 0.66$) and showed no evidence of trap dependence ($Z = 0.09$, $p = 0.93$). Nevertheless, we detected a significant presence of transient or emigrant individuals among all birds marked for the first time in the study area (one sided directional test for transience: $Z = 2.62$, $p < 0.01$). Indeed, 157 out of the 263 acoustically marked Dupont's larks were recorded only once. We recalculated the goodness of fit test for transience after suppressing the first encounter of each individual (Pradel et al. 1997), finding scarce evidence of remaining heterogeneity ($Z = 1.49$, $p = 0.07$). Following Pradel et al. (1997), we built therefore models accounting for the presence of transients in the marked sample ($8^*_{(t)}, 8_{(t)}, p_{(t)}$), estimating the initial apparent survival rate ($8^*_{(t)}$) separately from the survival rates of previously marked individuals in subsequent intervals ($8_{(t)}$). The limited evidence for lack of fit was corrected by the application of a variance inflation factor ($\hat{c}$). Hence, model selection for acoustic marking was preliminarily continued with the transient model. Due to the paucity of data and the resulting imprecise estimation of time-dependent survival rates in the first occasion ($8^*_{(t)}$), we built models with a constant initial apparent survival rate ($8^*_{(.)}$). The transient version of the CJS model was constrained after identifying the fully time-dependent reencounter probability model to fit best the data (Table 1). The best model ($8^*_{(.)}, 8_{(t)}, p_{(t)}$) had constant estimates for

Table 1. Models for survival (8), transient survival (8*) and reencounter (p) probabilities for Dupont's lark relying on physical marking and acoustic marking, respectively. The model subscripts refer to time dependence (t), seasonal time effect (t period) and constancy (.).

Model	QAIC _c	D QAIC _c	QAIC _c weight	No.	Q-deviance
Physical marking					
$8_{(t)}, p_{(t)}$	430.45	0.00	0.813	9	33.76
$8_{(.)}, p_{(t)}$	434.31	3.86	0.118	6	44.03
$8_{(t \text{ period})}, p_{(t)}$	435.40	4.95	0.069	7	43.00
Acoustic marking					
$8^*_{(.)}, 8_{(.)}, p_{(t)}$	552.13	0.00	0.595	7	35.06
$8^*_{(.)}, 8_{(t \text{ period})}, p_{(t)}$	553.89	1.76	0.247	8	34.73
$8^*_{(t)}, 8_{(t)}, p_{(t)}$	554.78	2.65	0.158	9	33.51

Figure 1. Survival (ϕ) and recapture (p) probabilities ($\pm$ SE) of Dupont's lark according to marking method. Note that the last parameter could not be estimated due to parameter redundancy with time dependent recapture probability. The first survival estimate in the first acoustic marking occasion (marked with an asterisk) includes a mixture of residents and transients because previous data was not available to estimate separately both parameters.

both the initial ($\phi_{(0)}^* = 0.52 \pm 0.06$) and the successive apparent survival rates ($\phi_{(1)} = 0.71 \pm 0.06$). Recapture probabilities ranged between 0.35 $\pm$ 0.07 (breeding period 2007) and 0.82 $\pm$ 0.11 (breeding period 2005) (Fig. 1). The mean transient rate was 19.9% (93.8%) in the sampled population, with a minimum of 16.7% in postbreeding period 2005 and maximum of 24.9% in post breeding period 2006. For both periods, annual apparent survival probability was 0.50 $\pm$ 0.06, corresponding to that of physical marking. Eventually, the three most parsimonious models (Table 1) were chosen for model averaging to facilitate the comparison between the models of acoustic and physical marking methods. The initial apparent survival estimate (for a mixture of resident and transient individuals) from model averaging was 0.52 $\pm$ 0.06, whereas in subsequent occasions the respective survival estimates ranged between 0.68 $\pm$ 0.10 (postbreeding period 2007) and 0.73 $\pm$ 0.10 (postbreeding period 2006). Recapture probabilities computed from model averaging varied between 0.34 $\pm$ 0.07 (postbreeding period 2007) and 0.82 $\pm$ 0.12 (breeding period 2005) (Fig. 1).

Comparing physical and acoustic marking

We used the most parsimonious model for physical marking and the model averaging outputs of the three best models for acoustic marking to compare the parameter estimates obtained by the respective methods. Both survival and recapture rates oscillated considerably using physical marking, whereas acoustic marking provided fairly stable estimates for both parameters (Fig. 1). However, there were no significant differences between recapture probabilities of physical and acoustic marking method (Sauer-Williams test, $\chi^2 = 1.56$, $DF = 1$, $p = 0.21$). Apparent survival probabilities, however, differed depending on the marking method (Sauer-Williams test, $\chi^2 = 9.31$, $DF = 1$, $p = 0.01$). The second survival estimate for physical marking was omitted while testing for differences between the two methods due to estimation problems (95% confidence interval: 0.001–0.999).

Given that estimates of apparent survival derived from CJS models strongly depend on the ability of each method to detect dispersed birds, we compared the dispersal distances inside the respective subpopulations obtained by each method between subsequent occasions in breeding and postbreeding periods, respectively (Fig. 2). In spite of sampling the same subpopulations and areas, acoustic marking detected significantly larger dispersal movements than physical marking in both intervals: Mann-Whitney $U_{7,26} = 37.0$, $p = 0.02$ (dispersal between breeding and postbreeding period); Mann-Whitney $U_{21,37} = 228.0$, $p = 0.009$ (dispersal between postbreeding and the next breeding period).

Figure 2. Comparison of dispersal movements detected by acoustic and physical marking. The boxes represent the interquartile range (IQR). The horizontal lines extend to, at most 1.5 times the IQR from either or both ends of the box, ending at an observed value. Mild and extreme outliers are differentiated by open dots and stars, respectively. Three times the box width marks the boundary between mild and extreme outliers. Differences between methods were significant in both periods (Mann-Whitney U-test, $p = 0.02$ and 0.009, respectively).

Discussion

To our knowledge this is the first study that compares survival estimates obtained through acoustic and physical marking using two large data sets from a secretive passerine species. Possible seasonal effects were also addressed by sampling in both breeding and postbreeding periods. In spite of focusing on the same population and years, physical and acoustic marking provided substantially different survival rates for Dupont's lark males, while reencounter probabilities did not differ significantly. The difference between methods was marked above all in the transition from postbreeding and breeding period, when the apparent survival of colour-banded birds was twice as low as for acoustic marking. Notably, survival estimates derived from the physical capture–recapture technique alone would have driven different conclusions, suggesting important seasonal differences in apparent mortality.

Previous studies with different marking methods highlighted differences between resighting studies that tend to have higher estimates of survival if compared with mist-netting (Salewski et al. 2007). Mist-net data may also include floaters or transients whereas mark–resighting studies usually examine only territorial birds or breeders, i.e. those segments that were easier to resight. This study shows that integrating the contrasting information obtained from physical and acoustic marking data seized an exceptional opportunity to achieve further knowledge of biological processes within the sampled population.

Transience and heterogeneity of capture

Whereas the physical mark–recapture data fitted the general CJS model, a transient model had to be used for the acoustic marking data set. The transience detected within the acoustic marking data set could be explained by the great variation in territorial and mating status among vocally active individuals (Amrhein et al. 2002, Laiolo and Tella 2005). Acoustically sampled territory owning Dupont's lark males and individuals that successfully established a territory (residents) remain within the subpopulation and show high apparent survival probabilities. In contrast, transient individuals uttering territorial calls, easily sampled by means of acoustic marking, might fail to establish a territory or to attract a female and consequently emigrate without being detected anymore by acoustic marking, or die whilst trying to move to another subpopulation. Part of these individuals could alternatively adapt a floating strategy, and stop advertising a territory. This would cause their disappearance from the acoustic sample although they can continue searching for mates through songs (Laiolo and Tella 2005). Transience was fairly constant across seasons and years, probably as a consequence of the species' pronounced territoriality during both breeding and postbreeding periods (Garza et al. 2005, Vögeli et al. unpubl). Additionally, high densities of Dupont's larks suggest that certain saturation at least in small and isolated subpopulations (Laiolo and Tella 2006) could lead to an increase in permanent emigration for newly seen individuals (Serrano and Tella 2007).

On the other hand, the use of playback for physical marking and reencountering could implicate a sampling bias towards established territory owners, with sufficient self-confidence to approach and challenge a hypothetical intruder (Nowicki et al. 2002). Under this logic, non-territorial or unmated males can remain undetected when playback is used (Legare et al. 1999). This could explain why the physical marking data set does not violate the CJS assumption of homogeneous survival, and specifically why the existence of transient individuals is not detected by this method.

Disentangling site fidelity and true survival

The constant and relatively high survival rates of acoustically marked Dupont's larks for all study periods outnumbered twice the apparent survival obtained by physical marking between postbreeding and breeding periods. As a consequence, apparent annual survival rates for banded Dupont's larks were extremely low compared with those sampled by acoustic marking. Since permanent emigration and mortality can not be distinguished by Cormack–Jolly–Seber approaches (Lebreton et al. 1992), asymmetries in the ability of both methods to detect local dispersers could explain this pattern. In this secretive species, physical marking relying on colour-banded individuals proved in fact to be weak in detecting local dispersal as compared to acoustic marking (Fig. 2). Dispersing individuals could have persisted alive within the subpopulation after leaving their territory. In this sense, the acoustic marking technique may be more efficient for sampling the local dispersers that are not detected by physical marking.

Local dispersal events in larks might be usual, given the high incidence of reproductive failure due to nest predation (Yanes and Suárez 1996), as frequently reported in birds (Serrano et al. 2001). Moreover, a high male-skewed adult sex ratio (Donald 2007) could increase intrasexual competition for establishing new or better territories. High competition levels are likely to persist after breeding, when juvenile males first attempt to recruit in the population, after moulting and learning their territorial calls. Furthermore, the low apparent survival rates of physical marked birds between postbreeding and breeding period coincides with the time dispersal is most probable.

Survival rates, behaviour and conservation

Individual-based monitoring techniques can highlight behavioural processes important in the dynamics of structured population, and the interpretation of the resulting demographic parameters can provide useful information for the conservation and management of animal populations (McGregor and Peake 1998). Acoustic and physical marking were found to draw on a slightly different sample of Dupont's lark males, probably because of differences in their territorial status, although the assignment to a corresponding population segment remains uncertain (Laiolo et al. 2007). However, our survival analysis combining simultaneously acoustic and physical marking suggested the existence of different subsets of individuals within Dupont's lark populations (see Fig. 3 for an

Figure 3. Hypothetical scheme of the segments of individuals within Dupont's lark populations detected by acoustic and physical marking. Both residents and transients are sampled acoustically, whereas transient individuals are not detected by colour-banding. Reencounter rates of acoustic marking are fairly constant for resident and null for transient individuals while they are biased towards residents with short dispersal movements for physical marking.

overview). Whereas colour-banded males seemed to represent the territorial fraction of the population, both resident and floater individuals were probably detected by acoustic marking, unlikely to we previously hypothesised (Laiolo et al. 2007). We suggest that this mismatch, together with the methodological bias in bird movement detection, is responsible for the observed diverging patterns of survival and dispersal. This finding is remarkable since physical mark-recapture methods alone, which in fact constitute the most used methods for monitoring individual birds, might have misled our understanding of Dupont's lark individual behaviour strategies, survival rates, and population dynamics. Acoustic marking as a non-invasive method has been scarcely applied to date for mark-recapture studies, but appears to be a powerful complement to traditional mark-recapture studies, not only for threatened or secretive species, but also for species difficult to capture or sensitive to handling. Identifying different segments within a species' population could shed light on their ecology and help us better calibrate conservation actions.

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