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Abundance variations, survival and site fidelity of Reed Buntings *Emberiza schoeniclus* wintering in central Spain

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Populations of the Reed Bunting (*Emberiza schoeniclus*) have suffered serious declines in western Europe during the last three decades. However, information on population parameters of migratory populations in their wintering quarters are scarce. Here, we examine variations in abundance, apparent survival and philopatry of Reed Buntings wintering in central Spain during five winters (spanning a period of seven years) using capture-recapture at a communal roost. Abundances were low during the first winters in the early 80s and increased steadily until the last winter in 1988–89. Model-averaged estimates, which account for model uncertainty, suggested that apparent survival fluctuations were small and did not follow any clear trend. There was some support for intersexual differences in apparent survival, although model-averaged estimates were similar for both sexes, and low support for an effect of winter weather conditions on survival rates. Return rate was 81% after correcting for mean apparent survival (62%) and low recapture probability (7%). However, this underestimates the return to the general area (feeding and roosting sites), because of high within- and between-roosts mobility of Reed Buntings during winter. Although population trends were not similar in different western European countries, our results are consistent with the overall recovery or stabilization of populations after the severe declines during the 1970s. Moreover, minor changes in survival rates and probable stability of winter food supply point to higher productivity on breeding grounds as the cause of the observed increase in abundance.

1. Introduction

Bird populations are regulated by processes that can act in different periods of the annual cycle (e.g, breeding, dispersal, wintering; Newton 1998). In migratory birds, breeding and wintering locations are widely separated, especially in long-distance migratory birds, and a number of stopover sites are used during migratory journeys. Therefore, factors underlying population dynamics of migratory birds include potential limiting factors at different locations and times during the year (Sillett & Holmes 2002, Newton 2004). However, population dynamics of migratory passerines have been studied more intensively during the breeding season (Böhning-Gaese & Hans-Günther 1996, Siriwardena *et al.* 1998, Murphy 2001), and only recently has detailed work been carried out in wintering quarters (Salewski *et al.* 2002, Sillett & Holmes 2002, Dugger *et al.* 2004). Moreover, evidence indicates that abundance of breeding passerines is sometimes more limited by factors operating on wintering grounds (Peach *et al.* 1991, Baillie & Peach 1992, Sherry & Holmes 1996, Marra *et al.* 1998).

Populations of farmland birds in western Europe have undergone serious declines in abundance during the last thirty years (Tucker & Heath 1994, Donald *et al.* 2001). Among this group, several species of small seed-eating birds have declined severely (Gregory *et al.* 2004). A long-term study in the UK on one such species, the Reed Bunting (*Emberiza schoeniclus*), identified reduced over-winter survival as the likely cause of population decline during the period of major reductions in abundance (Peach *et al.* 1999). Populations of Reed Buntings elsewhere in western Europe have also suffered declines in abundance during the last three decades, although trends were not parallel among countries (Donald & Gailly 1997, Fox 2004). Unlike the British population, Reed Bunting populations breeding in northern and central Europe are migratory or partially migratory, mainly overwintering in the Mediterranean area (Prys-Jones 1984, Villarán 1999). Therefore, factors that caused population declines in sedentary populations, namely winter food availability due to changes in agricultural practices (Peach *et al.* 1999), do not apply to migratory populations or would depend on agricultural practices on the wintering grounds (Fox 2004). However, information on demographic parameters of Reed Bunting populations wintering in the Mediterranean are scarce.

Here, we analyzed abundance, apparent survival and philopatry of a population of Reed Buntings wintering in central Spain. Specifically, we examined abundance variations during five winters (spanning a period of seven years), and discuss our results in the context of populations trends documented for breeding Reed Buntings in Western Europe. We also analyzed between-winter apparent survival, and specifically tested for differences between males and females, and among winters. Finally, we calculated the return or recurrence rate to the study area after correcting for apparent survival and recapture probabilities estimated for this population.

2. Material and methods

2.1. Study species

The Reed Bunting is a species with a wide Palearctic breeding distribution, although it is very scarce in the Mediterranean area. In Spain, breeding distribution is very scattered and the population has been recently estimated at 230–400 pairs. In northern Europe, populations are migratory, but increasingly sedentary towards the south. Migration is also differential in relation to sex, so males winter further north than females. During winter, Reed Bunting populations in Spain are locally abundant due to the important flux of migrants from northern latitudes. Analyses of ring-recovery data have shown that individuals wintering in Spain breed mainly in northern and central Europe and in some eastern European countries. In central Spain, almost all wintering individuals are migrants from northern latitudes, although some individuals from the small population breeding in Spain may mix with the migrants.

2.2. Study site and data collection

Fieldwork was conducted at the reed-bed of Villamejor (39º59’N, 3º47’W), in the Tajo basin, south of Madrid province, central Spain. The 25 ha reed-bed is dominated by *Phragmites australis* and surrounded by low shrubs, such as *Arthrocnemum macrostachyum* and *Atriplex halimus*. We selected a 4 ha plot, representative of the whole reed-bed, and erected ten mist-nets (12 m long). The number and position of nets were the same on each trapping occasion. We captured Reed Buntings during five winters, from 1982–83 to 1985–86 and in 1988–89. In 1986, there were some management changes in the property and banding activities were not allowed in the reed-bed. Therefore, we could not get data for two winters (1986–87 and 1987–88) until the reed-bed became public land in 1988.

Reed Buntings feed on seeds in the open countryside and cultivated fields surrounding the reed-bed of Villamejor, and use this and other reed-beds as communal roosts during winter (Villarán 2000). Thus, all birds were captured at dusk when they were entering the roost. Each captured bird was marked with a standard numbered aluminum ring (or the ring number was recorded if the bird had been previously ringed) and sexed according to plumage characters (Svensson 1992).

2.3. Data analysis

2.3.1. Abundance

The winter period was defined as the interval from 15 November to 15 February of the next year. This time period includes the overwintering period in Spain and excludes individuals in migration (Villarán 1999). Data analyzed include captures for a total of 40 trapping dates (1982–83, 4 trapping dates; 1983–84, 10; 1984–85, 10; 1985–86, 11; 1988–89, 5). As the mist-netting effort was constant on each trapping date, we used the number of individuals captured per trapping date as an estimation of abundance (Peach *et al.* 1996, Herrera 1998). To test whether bird abundance differed among winters, we used a one-way ANOVA (number of captures was square root-transformed). We first checked for linear or quadratic relationships between date of capture and the number of birds trapped, but no correlations were found (linear: $r^2_{38} = 0.0002$, $P = 0.92$; quadratic: $r^2_{37} = 0.033$, $P = 0.54$).

2.3.2. Apparent survival modeling

Apparent survival and recapture probabilities were estimated using the Cormack-Jolly-Seber (CJS) model in the program MARK (White & Burnham 1999). Because we missed two winters between 1985–86 and 1988–89, the length of time intervals was standardized to one year. We first constructed a general model that included the effects of sex and year on apparent survival and recapture probabilities. The program RELEASE (available in MARK) was used to test for goodness of fit of our general model to the CJS model. RELEASE generates three standard tests, two of which (TEST 2 and TEST 3) together provide the goodness of fit statistics for the general model.

We developed several submodels constraining different parameters of our more general model to test for sex and year differences in apparent survival and recapture probabilities. Given that our trapping effort was constant on each trapping date but not seasonally (number of trapping dates), we expected recapture probability to vary between winters. Nevertheless, we constrained recapture probability to remain constant among years in our two best ranked models to investigate whether annual differences were small and models might be simplified (lower number of parameters). Finally, we examined the effect of harsh weather conditions during winter on apparent survival. Weather data were obtained from the meteorological station nearest to the study area (Toledo station, distance: 17 km). Average minimum temperature and number of days with temperatures below 0ºC were calculated for each winter. We used the standardized values of meteorological variables as covariates in our most plausible model, forming a new candidate model. We used Akaike's Information Criterion (AICc) to assess the plausibility of the models. Models in the candidate set were ranked according to AICc and differences in AICc between models were calculated (ΔAICc). The model with the lowest value of AICc was considered the most parsimonious explanation for the data. Relative likelihood of each model in the candidate set was estimated with AICc weights. These Akaike weights sum to one in a candidate set and are interpreted as probabilities (Burnham & Anderson 2002). Besides the 'best' model in our candidate set, other models were also reasonably well supported (ΔAICc < 2). Therefore, we used model averaging to calculate average estimates, variances and confidence intervals of apparent survival and recapture probabilities (weighted by AICc weights) incorporating model uncertainty (Burnham & Anderson 2002).

2.3.3. Site fidelity

Site fidelity (also called return or recurrence rate) is the probability of return to a previously occupied location. Return rate is sometimes calculated as the proportion of marked individuals released in one year that are recaptured in the next year. However, this simple index is an unrealistic estimator of return rate because it includes both the probability of survival and the probability of recapture (Martin *et al.* 1995). To calculate a more reliable estimator of return rate, we divided the between-year recapture rate (proportion of individuals that were recaptured in years subsequent to initial capture) by the mean apparent survival and recapture probability (probability of being recaptured, conditional on being alive and in the sample) (see also Catry *et al.* 2004).

3. Results

3.1. Abundance

We captured a total of 1662 individual Reed Buntings during the five winters of study. Females (74.2% of captures) were more abundant than males (25.8%). Abundance varied significantly among winters (ANOVA $F_{4,35} = 8.3$, $P < 0.001$), increasing from 25.5 ± 6.4 captures/day in 1982 to 72.6 ± 14.2 in 1988 (Fig. 1), almost a three-fold increase.

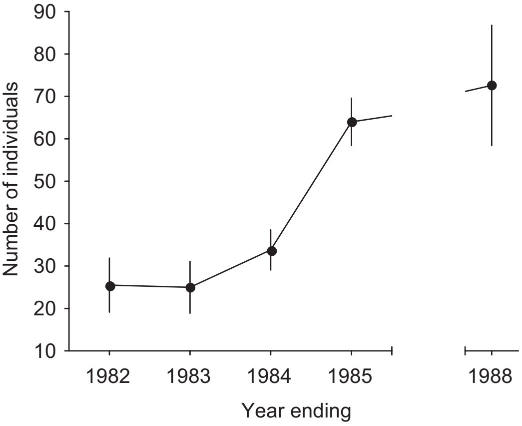

Fig. 1. Increasing abundance (mean ± SE captures/ trapping day) of Reed Buntings roosting in the reed-bed of Villamejor during winter from 1982–1989.

3.2. Apparent survival modeling

Results from the program RELEASE for TEST 2 and TEST 3 combined indicated that our general model [Φ(sex*t) p(sex*t)] fit the data (goodness of fit, $\chi^2_{10} = 11.3$, $P = 0.33$). There was low support for temporal sex-specific differences in apparent survival and recapture probability (Table 1). However, the model with constant apparent survival by sex and temporal variation in recapture probability [Φ(sex) p(t)] showed some support (ΔAICc = 2; Table 1). As expected, models that included year differences in recapture probability were better ranked than those with this parameter set constant (Table 1). The best model for our data included constant apparent survival and temporal variation in recapture probability (Table 1). However, the

Table 1. Model selection criteria for Reed Buntings captured during the winters 1982/83–1988/89 at the reed-bed of Villamejor, central Spain. Apparent survival (Φ) and recapture (p) probabilities were modeled as a function of sex, average minimum winter temperature (tmin), and number of days with temperatures below 0ºC during winter (db0). Parameters can be year-specific (t) or constant (.). Models were ranked according to AICc, and the model with the lowest AICc was considered best. * = interaction effect, np = number of estimable parameters.

Model	np	AICc	ΔAICc	Model weights
Φ(.) p(t)	5	491.10	0.00	0.41
Φ(t) p(t)	7	492.72	1.63	0.18
Φ(tmin, db0) p(t)	7	492.72	1.63	0.18
Φ(sex) p(t)	6	493.10	2.00	0.15
Φ(t) p(.)	5	494.89	3.79	0.06
Φ(.) p(.)	2	498.78	7.69	0.01
Φ(sex*t) p(sex*t)	14	499.79	8.70	0.01
Φ(sex*t) p(t)	11	500.32	9.22	0.00
Φ(.) p(sex)	3	500.44	9.34	0.00

Table 2. Averaged minimum temperatures (Tmin; ± 1 SE) and number of days with temperatures below 0ºC (Days Tb0ºC) for each winter (November through February). Standardized values were used as time-specific covariates in apparent survival modeling of Reed Buntings captured in the reed-bed of Villamejor, central Spain.

Winter	Tmin (ºC)	Days Tb0ºC
1982–83	1.4 ± 1.4	53
1983–84	3.6 ± 1.9	29
1984–85	3.5 ± 1.5	28
1985–86	2.4 ± 0.8	44
1988–89	1.9 ± 1.6	60

second best ranked model was reasonably well supported according to AICc criterion (ΔAICc < 2; Table 1), suggesting some inter-annual variation in apparent survival.

Average minimum temperatures and number of days with temperatures below 0ºC were similar among winters, except for the first and last winters when weather conditions tended to be colder on average (Table 2). Inclusion of meteorological covariates in our best candidate model (first model in Table 1) did not improve the plausibility of the model. AICc values were the same for this model and the model with temporal variations in apparent survival and recapture probability (Table 1). In our best model, apparent survival was 0.623 ± 0.139 (SE) and recapture probabilities were very low: 0.048, 0.135, 0.089, and 0.013, respectively (mean: 0.071 ± 0.030). Model-averaged estimates of apparent survival and recapture probabilities that include variance due to model selection uncertainty are shown in Table 3. Given the fully time dependent parameterization for apparent survival and recapture probability, and the very low recapture probability, parameters for the last year could not be properly estimated for our data (Table 3). Model-averaged estimates of apparent survival suggest some between-year fluctuations for both sexes, although no trend was apparent (Table 3).

3.3. Site fidelity

Overall 60 (3.6%) Reed Buntings were recaptured in a subsequent year after initial ringing from the 1662 individuals ringed. The percentage of recapture was similar for males (13 of 449; 3.0%) and females (47 of 1233; 3.8%). The estimated return rate was 81.2% after correcting for apparent survival and mean recapture probability.

4. Discussion

Our results showed that the abundance of Reed Buntings roosting at the reed-bed of Villamejor increased considerably throughout the years of study. Estimates of apparent annual survival were similar for both sexes, experienced minor between-winter fluctuations and were not influenced by weather conditions. Finally, we derived a more reliable percentage of return rate to the wintering area after accounting for apparent survival and the low recapture probability of this population.

Table 3. Model-averaged estimates of apparent survival for male and female Reed Buntings, and of recapture probability for both sexes. For each year, apparent survival or recapture probability estimates ± unconditional SE with 95% confidence intervals in brackets are shown. Parameters for the last interval are not reliably estimable under full-time parameterization given our data.

Year	Male	Female	Recapture probability
1982–83 to 1983–84	0.704 ± 0.239 (0.200–0.958)	0.703 ± 0.235 (0.207–0.955)	0.050 ± 0.033 (0.013–0.170)
1983–84 to 1984–85	0.581 ± 0.179 (0.247–0.854)	0.573 ± 0.173 (0.251–0.843)	0.145 ± 0.055 (0.066–0.287)
1984–85 to 1985–86	0.645 ± 0.323 (0.103–0.966)	0.648 ± 0.317 (0.107–0.966)	0.092 ± 0.050 (0.031–0.245)
1987–88 to 1988–89	0.593 (0.000–1.000)	0.589 (0.000–1.000)	0.023 (0.000–1.000)

Reed Buntings, as well as other farmland bird species, have suffered severe declines during the last quarter of the 20th century in western Europe (Tucker & Heath 1994). Long-term information on the Reed Bunting breeding population in the UK indicated a severe decline from the mid 1970s to the early 1980s and some increase or stable abundances since 1983 (Peach *et al.* 1999). Abundances of Reed Buntings wintering in our site in central Spain from the early to late 1980s showed certain similarities with that pattern. Abundances were low during the first winters and increased steadily until the last winter of study (Fig. 1). However, Reed Buntings wintering in Spain breed mainly in northern and central Europe and also in some eastern European countries (Villarán 1999). Detailed information on Reed Bunting population trends for western European countries other than the UK are not available, although European populations as a whole declined severely during the 1970s mainly because of habitat loss and agricultural intensification (Donald & Gailly 1997). Despite the general trend, severity of decline and trends afterwards were not similar in different countries for different reasons, particularly differences in agricultural intensification (Donald *et al.* 2001, Fox 2004). For example, by the late 1980s and early 1990s populations in many European countries were relatively stable (e.g., Norway, Poland, Sweden), others were declining (e.g., Germany, Belgium), and some increasing (e.g., Denmark, Ukraine; Donald & Gailly 1997). Overall, the increase in abundance of Reed Buntings wintering in central Spain broadly matched the general decline and subsequent recovery of breeding populations in western Europe.

Other regional or local factors could explain abundance variations at the reed-bed of Villamejor. Reed Buntings are known to move in response to harsh weather or persistent snow during winter (Prys-Jones 1984). Therefore, it is possible that more individuals could reach our site during severe winters. This is unlikely to be a primary explanation for variation in abundance because the two coldest winters (1982–83 and 1988–89) showed contrasting abundances, and the other three with similar weather conditions varied markedly in abundance (Fig. 1). At the local scale, the increase in abundance could also have been the result of changes or destruction of feeding or roosting sites nearby. However, cultivated fields and the general landscape surrounding the reed-bed of Villamejor did not seem to change appreciably (pers. obs.), and the area of farmland and meadow fields in Madrid province underwent little changes between 1985 and 1989 (AECM 1985–2004). Some reed-beds in the Tajo basin were burned during winter and thus more Reed Buntings could have used the reed-bed of Villamejor in response to those impacts. However, we did not detect a consistent increase in burning or destruction of roosting sites during the course of the study.

Our mean apparent survival of 62% for this wintering population is higher than the 54% adult survival estimated for British breeding populations (Siriwardena *et al.* 1998), although the accuracy of our point estimate is low and overlaps with the value reported for the British population. Nevertheless, we were more interested in analysing potential fluctuations or trends in survival rates than in the values of our point estimates. The model of constant survival was the best supported by our data, although the model of year-specific survival was also supported. Model-averaged estimates of apparent survival exhibited some interannual variation, but precision was low and last-year parameters could not be reliably estimated. This was due to the low recapture probabilities of Reed Buntings at the roosting site. Low recapture probabilities reduce the precision of estimates and could thus reduce power to detect survival differences among groups (e.g., sex-classes) or among sampling periods (Lebreton *et al.* 1992). Therefore, some interannual variation in apparent survival probably occurred, as is common in passerines. However, no trend was observed indicating that survival was not lower at the beginning of the study when abundances were lowest, and no relationship between survival and abundance was apparent, contrary to what was found for the British population (Peach *et al.* 1999).

Sex-specific differences in survival are common in birds because males and females usually differ in ecology (Siriwardena *et al.* 1998). We found some support for sex-dependent variation in apparent survival, although this difference is not appreciable in our model-averaged estimates. Again, the low recapture probability likely reduced the power to detect survival differences between sexes. Furthermore, sample size for males was low compared to females because central European populations are partially migratory and males winter further north than females, so Reed Bunting populations wintering in Spain consist mainly of females (Villarán 1999).

Winter weather did not seem to influence apparent survival in this population. Reed Buntings can suffer high mortality during severe cold weather in northern populations (Prys-Jones 1984, Peach *et al.* 1999), although those conditions are less frequent in Mediterranean latitudes (e.g., Senar & Copete 1995). In our analysis, the model including weather covariates was ranked similarly as the model with temporal variation in survival, so weather covariates did not improve the plausibility of the model given our data. In any case, the influence of winter weather conditions on Reed Buntings survival in Mediterranean climates remains to be better established.

Reed Buntings showed high site fidelity to the roosting site after correcting for apparent survival and the low recapture probability. The estimated 81% return rate is within the range of corrected estimations for other wintering passerines (usually between 40–100%; see examples in Catry *et al.* 2004). Roosting behavior and within-winter movements of Reed Buntings appear to be the cause of the low recapture probability at the roosting site and thus the low apparent return rate. First, Reed Buntings seem to move a lot within the roosting area, decreasing the probability of recapture of marked individuals (Schaub *et al.* 2001). Second, individuals are known to use different nearby roosts within the same winter (Fennell & Stone 1976, Villarán & Pascual-Parra 2003). In this sense, we recorded low within-winter recapture rates (proportion of individuals that were recaptured on subsequent trapping dates within a season), which on average (3.5%) were similar to the between-year recapture rate (3.6%) indicating that individuals regularly moved out the sampling area within a season. Moreover, several individuals marked at the study site have been trapped in other neighboring reed-beds (12–37 km apart) during the same or subsequent winters (Villarán & Pascual-Parra 2003). Studies using radiotelemetry in other passerine species found that individuals were highly faithful to feeding areas but used different roosts within the season (Morrison & Caccamise 1985, 1990). Whether wintering Reed Buntings show similar behavior is unknown, although it is likely that fidelity to the general area used by individuals (i.e., feeding and roosting sites) will be analogous or higher than our corrected estimate.

Although we cannot completely rule out regional or local factors, the increase in abundance of wintering Reed Buntings we recorded may reflect the recovery of breeding populations in at least some western European countries. Lower intensity in agricultural practices in Spain compared to other European countries (see Donald *et al.* 2001) and information on farmland area and yield in the Madrid province (AECM 1985–2004) suggest stable winter food availability for seed-eating passerines during the 1980s. This together with minor between-year fluctuations in apparent survival, which did not follow an apparent trend nor was related to winter abundances, suggest that the increase may have been due to higher productivity on breeding grounds.

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Espanjassa talvehtivan pajusirkun (*Emberiza schoeniclus*) kannanvaihtelut, selviytyvyys ja paikkauskollisuus

Pajusirkkupopulaatiot ovat pienentyneet huomattavasti Länsi-Euroopassa viimeisinä kolmena vuosikymmenenä. Tästä huolimatta populaatiosta niiden talvehtimisalueilla ei ole juurikaan tietoa. Tutkimme Espanjassa talvehtivien pajusirkkujen kannavaihteluja, selviytyvyyttä ja paikkauskollisuutta viiden talven ajan pyydystämällä ja rengastamalla lintuja niiden yhteisellä lepopaikalla. Lintuja oli 80-luvun alussa vähän, mutta lukumäärä kasvoi kohti tutkimuksen viimeistä talvea 88–89.

Arvioimme, että selviytyvyys ei heilahdellut vuodesta toiseen. Myöskään minkäänlaisia suuntauksia selviytyvyydessä ei havaittu. Sukupuolten välillä näytti olevan eroja selviytyvyydessä.

Myöskin talven säällä saattoi olla vaikutusta siihen. Palautuvuudeksi arvioitiin 81 % sen jälkeen, kun keskimääräinen selviytyvyys (62 %) ja alhainen todennäköisyys saada lintu uudelleen kiinni (7 %) oli otettu huomioon. Tämä saattaa kuitenkin olla alueellisen paikkauskollisuuden aliarviointia, jos ottaa huomioon, että pajusirkut liikkuvat talvisin paljon ruokailu- ja lepopaikkojen välillä. Vaikka populaatioiden muutokset eivät ole kaikkialla Länsi-Euroopassa samanlaisia, tuloksemme ovat yhdenmukaisia pajusirkkukantojen toipumisen ja vakiintumisen kanssa. Lisäksi pienet muutokset selviytyvyydessä ja talviruoan saatavuuden ilmeinen vakaus johtavat parempaan tuottavuuteen lisääntymisalueilla, joka taas näkyy yksilömäärien kasvuna talvehtimisalueilla.

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