J Ornithol (2015) 156:469–479
DOI 10.1007/s10336-014-1147-4

ORIGINAL ARTICLE

The roles of environmental and geographic variables in explaining the differential wintering distribution of a migratory passerine in southern Europe

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Received: 20 June 2014 / Revised: 17 November 2014 / Accepted: 28 November 2014 / Published online: 16 December 2014

Abstract In birds, spatial segregation between age or sex categories during the non-breeding period is a common phenomenon. The main single-factor hypotheses that have been stated to explain this are: (1) body-size variations (that result in more or less cold tolerance) interact with local climate, which promotes age- or sex-associated distributional optima; (2) the dominant age or sex monopolizes high-quality areas; and (3) the age or sex overwintering closer to breeding quarters does so due to the benefits of earlier arrival at the breeding quarters. Southern European countries host millions of birds from northern Europe during the winter period each year. In this work, we aimed to determine the ultimate causes (geographic location and distance to obligate migratory pathways, temperature and land use as a surrogate for food availability) explaining spatial segregation of Reed Buntings (*Emberiza schoeniclus*) by age and sex in winter. We used data from 38 sampling points across Iberia during the winter of 2011–2012. Reed Bunting abundance did not fit any of our possible models better than the null model, so we were unable to predict bird numbers across Iberia. Moreover, males were found to be predominant at sites close to presumably obligate migratory pathways (western/eastern Pyrenees). Body mass was higher in first-year birds and males, and tended to increase with distance to obligate migratory pathways, land use (in particular with a decreasing proportion of open habitats and urban areas), increasing minimum temperature, and decreasing mean temperature. Our data suggest that the increase in the proportion of males close to obligate migratory pathways is associated with the advantage to males in wintering as close as possible to breeding quarters.

Keywords Farmland · Migration pathway · Population structure · *Emberiza schoeniclus*

Zusammenfassung

Die Rolle von Umwelt- und geographischen Variablen bei der Erklärung unterschiedlicher Winterverbreitungen eines ziehenden Sperlingsvogels in Südeuropa

Bei Vögeln ist eine räumliche Trennung von Altersgruppen oder Geschlechtern außerhalb der Brutsaison ein weit verbreitetes Phänomen. Dies sind die einen einzelnen Faktor berücksichtigenden Haupthypothesen, die zur Erklärung herangezogen worden sind: (1) Unterschiede in der Körpergröße (die zu einer geringeren oder höheren Toleranz niedriger Temperaturen führen) interagieren mit dem lokalen Klima, was alters- oder geschlechtsspezifische Verbreitungsoptima begünstigt, (2) das dominante Alter oder Geschlecht monopolisiert hochwertige Gebiete und (3) das Alter oder Geschlecht, das näher am Brutgebiet überwintert, kann die Vorteile einer früheren Ankunft im

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Communicated by N. Chernetsov.

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Brutgebiet ausnutzen. Millionen nordeuropäischer Vögel überwintern jedes Jahr in südeuropäischen Ländern. In dieser Arbeit wollten wir die ultimaten Ursachen (geographische Lage und Entfernung zu obligaten Zugwegen, Temperatur und Landnutzung als Stellvertreter für Nahrungsverfügbarkeit), welche die räumliche Trennung von Rohrammern (*Emberiza schoeniclus*) im Winter nach Alter und Geschlecht erklären, ermitteln. Wir haben Daten von 38 Beobachtungspunkten in ganz Spanien aus dem Winter 2011–2012 herangezogen. Keines der möglichen Modelle erklärte die Abundanz der Rohrammern besser als das Nullmodell, wodurch wir nicht in der Lage waren, die Zahlen der Vögel in Spanien vorherzusagen. Darüber hinaus fanden wir, dass in der Nähe vermutlich obligater Zugwege (westliche/östliche Pyrenäen) überwiegend Männchen auftraten. Die Körpermasse war bei einjährigen Vögeln und Männchen höher und neigte dazu, mit der Entfernung zu obligaten Zugwegen, stärkerer Landnutzung (besonders mit einem abnehmenden Anteil offener Habitate und urbaner Flächen), steigenden Mindesttemperaturen und abnehmenden Durchschnittstemperaturen zuzunehmen. Unsere Daten deuten darauf hin, dass die Zunahme des Männchenanteils in der Nähe obligater Zugwege damit zusammenhängt, dass es für die Männchen vorteilhaft ist, so nah wie möglich am Brutgebiet zu überwintern.

Introduction

Each winter, southern European countries host millions of birds that breed in areas farther north (Senar and Borras 2004). The species involved range from waterbirds to passerines (Alerstam 1993; Newton 2008) and in many cases the mechanisms explaining their geographic distribution at their wintering areas by age and sex are still poorly understood (but see Cuadrado 1992, 1995; Catry et al. 2004; Tellería et al. 2008; Alves et al. 2013). Understanding such mechanisms is of key importance not only from an evolutionary and ecological standpoint (Cristol et al. 1999) but also from a conservation perspective (e.g., Tellería et al. 2005).

Spatial segregation of age and sex classes during the non-breeding season is a widespread phenomenon among birds (Cristol et al. 1999) on both large and small (microhabitat) geographic scales (Kettersson and Nolan 1983; Sherry and Holmes 1996; Catry et al. 2004, 2005a; Alves et al. 2013). Generally, adults and males spend the winter in areas farther north than first-year birds and females (Cristol et al. 1999). The main proximate single-factor hypotheses that have been stated to explain this pattern are as follows. (1) body-size variations between age or sex classes interact with local climate, which promotes age- or sex-associated distributional optima (Ketterson and Nolan 1976, 1979). This occurs when one sex and/or age is larger than the other sex or age(s), so that larger birds are able to live in colder environments as they have higher thermoregulation capacities. (2) The dominant age or sex class would monopolize, or preferably occupy, high-quality habitat (Pienkowski et al. 1985). (3) The age or sex overwintering closer to breeding quarters would do so due to the benefits of earlier arrival at breeding areas (Kokko 1999). From an evolutionary standpoint (sexual vs. viability selection), hypotheses 1 and 2 would be related to viability selection, whilst hypothesis 3 mostly supports sexual selection (Morbey et al. 2012) (although, theoretically, it is also hypothesized that males would reach the breeding quarters earlier than females in virtue of their higher capacity to survive under adverse weather early in spring; Møller 2004).

Depending on which of these causes promote spatial segregation by age or sex, the following predictions can be made. (1) If larger birds remain in colder areas, or the smallest birds are unable to survive below certain temperatures, we expect that the proportion of adults or males would be higher in areas with lower temperatures in those species where the males and adults are larger than the females and first-year birds, respectively. (2) If the dominant age or sex class occupies the best-quality areas then it could be expected to be linked to particular habitats and to avoid alternative habitats of lower quality, which would be occupied by subordinates. Furthermore, in this case, the dominant class would be expected to have a better body condition than the subordinate one, or at least the birds occupying preferred habitats should be in better condition (Catry et al. 2004). (3) If an age or sex class benefits from wintering closer to breeding quarters, then this age or sex would overwinter in areas located farther north, or closer to obligate migratory pathways (e.g., Galarza and Tellería 2003), regardless of temperature or habitat quality.

The Reed Bunting (*Emberiza schoeniclus*) is a widespread, seed-eating Palearctic songbird that breeds from Iberia to East Asia (Cramp and Perrins 1994) and spends the winter mainly within the circum-Mediterranean region, the Middle East, and southern Asia. Southern populations (*E. s. lusitanica* and *E. s. witherbyi*) are resident, while those farther north (*E. s. schoeniclus*) are partially migratory and mostly overwinter within the Mediterranean area (Prŷs-Jones 1984; Villarán 1999). During winter, Iberia is inhabited by the two resident subspecies, which differ markedly in size and bill characters from northern ones (Copete et al. 1999; Belda et al. 2009). From ring-recovery data, the species has been reported to segregate by sex in winter, with females overwintering farther south than males (Prŷs-Jones 1984; Villarán 1999). In some circumstances, however, the existence of great local variation in the population structure (i.e., in terms of sex or age ratios) has been reported to be of sufficiently high magnitude to invalidate conclusions about the segregation of Reed Buntings on larger geographic scales (Rubolini et al. 2000). In this case, data concerning age or sex ratios at a single locality cannot be considered representative of an entire region. Populations wintering in Iberia originate from several areas, from the European Atlantic region to central Europe (Villarán 1999). At their wintering areas, Reed Buntings roost in thick vegetation, mainly in reed beds, and normally in groups, which can vary from tens up to hundreds of individuals (Cramp and Perrins 1994).

Iberia is one of the main wintering areas in Europe for the Reed Bunting (Prŷs-Jones 1984; Villarán 1999). It is therefore a target area for the conservation of some European populations, and an excellent region for testing the ultimate causes of its sex- and age-associated differential geographic distribution during the non-breeding season. To achieve this goal, we used data obtained from Reed Buntings ringed at 38 sampling points, spread over much of Iberia.

Methods

Sampling area and data collection

Data were obtained from 38 sampling points (stations) from across Iberia (Fig. 1). Field work was done by volunteers, so the geographic distribution of the stations was conditioned by them. Accordingly, the sampling stations were situated, a priori, in sites known to be commonly used as roosts by Reed Buntings.

Reed Buntings were captured with mist nets, without using tape lures, during the winter of 2011–2012 (from December 2011 until January 2012) to ensure that no sampling occurred of migrating birds in autumn or spring. Sampling wetlands were mainly composed of reed beds (*Phragmites* spp.) (Table 4 in the Appendix), since this is the type of vegetation commonly used for roosting by the species, hence facilitating captures (Arizaga et al. 2011). Most stations (73.7 %) were situated in inland wetlands, with the remainder being found in or very near coastal marshes. The characteristics of the stations are shown in Table 4 in the Appendix: (1) except for two sites situated in coastal marshes and hence influenced by tide flow (GAUT-BI, HOND-GK), the ground was underwater, i.e., inundated, at 71.1 % of the stations; (2) at 79.0 % of the sta-

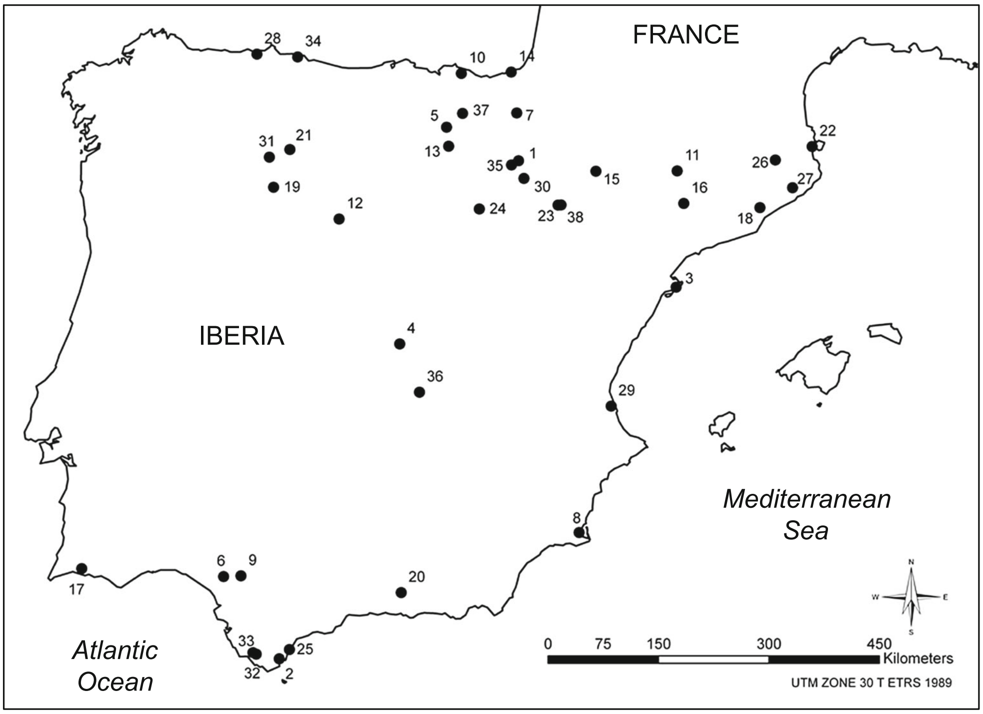

Fig. 1 Locations within Iberia of the 38 sampling points (stations) where the study was carried out during the winter of 2011. *Numbers* correspond to the codes shown in Table 4 in the Appendix

tions the reeds were more than 2 m high; (3) in the majority of the stations the reed bed covered more than 50 % of the area around the nets.

Wherever possible, the number of sampling days per site was at least 3, although it ranged from 2 to 11, with half of the stations (19) sampling on 3 days (Table 4 in the Appendix). The number and position of nets at each site was kept constant at most stations (Table 4 in Appendix). We used from 21 to 138 linear meters of mist nets (mean ± SD: 72 ± 31 m/site; Table 4 in the Appendix). Sampling lasted from 2 h before sunset to complete darkness and was carried out in good meteorological conditions (no rain or strong winds).

Once captured, Reed Buntings were ringed and their ages and sexes determined (Svensson 1996). Birds were aged as either first-year birds (with some juvenile feathers remaining in their wings) or adults (older birds, with no juvenile feathers in their wings) (for details see Jenni and Winkler 1994). We also measured P3 length (third primary feather, numbered from outermost to innermost; ±0.5 mm), and body mass (±0.1 g). Thick-billed and short-winged birds corresponding to local subspecies were excluded from analysis. We excluded these birds due to possible differences in habitat use and very small population sizes compared with the bulk of the *E. s. schoeniclus* winter visitors (Atienza and Copete 2003).

Data analyses

Overall, we considered four dependent variables, for which the effects of several environmental factors were tested separately: standardized number of captures, proportion of first-year birds, proportion of males, and body mass. The number of captures at each site and day was standardized to 100 linear meters of mist nets, and thereafter the mean number of captures for each site was calculated. Although we cannot fully reject some degree of nomadism in Reed Buntings during the winter, as found in other seed-eating passerines (Senar et al. 1992), it is well known that, for Reed Buntings in particular, a relevant fraction of the birds can be considered resident (Arizaga et al. 2011). This seasonal stability allows us to consider mean values (mean number of captures, age and sex ratios) from each site to be representative of the entire winter period. Considering those sites where three sampling days were conducted, we observed that the intrasite variance was marginally non-significant ($F = 3.237$; $P = 0.051$). The mean number of captures obtained at each site was therefore considered to be a good estimate of bird abundance. However, this variable did not fit the normal distribution (Kolmogorov–Smirnov test: $Z = 1.891$; $P = 0.002$), so it was log-transformed for the analyses (K–S test: $Z = 0.621$; $P > 0.05$). The proportion of first-year birds, males, and body mass fitted the normal distribution (K–S test: all $P > 0.05$). The proportion of first-year birds and males was calculated over the total number of first captures obtained at each site. Concerning body mass, we only considered each individual once, i.e., we only used data from the first capture event, in order to avoid pseudo-replications. This variable also fitted well to the normal distribution (K–S test: $P > 0.05$).

Thermoregulatory costs, mediated by food availability and temperature, are at the core of many trends in bird distribution during winter (Fretwell 1972; Newton 1980). Accordingly, eight potential explanatory variables linked to each station were considered: longitude (Long), latitude (Lati), distance to obligate migratory pathways (Dist), mean winter temperatures (of the daily means and minima; Tmea and Tmin, respectively), and land use (principal components 1–3; see below for further details), as a surrogate for habitat quality.

When dealing with wintering birds it is often difficult to determine which birds originate from which areas. Thus, monitoring the positions of these birds in winter is not always the best way to assess distance to breeding quarters. Alternatively, when birds must return to their breeding sites passing through obligate migratory pathways (e.g., if they must avoid oceanic areas or mountain ranges), distances to these pathways could be used as an indirect measure of distance to breeding quarters. In Iberia, it is well known that many birds enter the Peninsula through the eastern and western edges of the Pyrenees, and that the winter distribution is in part conditioned by the distances to these edges (Galarza and Tellería 2003; Tellería et al. 2009). Accordingly, apart from their geographic position in winter, we also included as an additional independent variable the distance of each location to the closest edge (western or eastern) of the Pyrenees (more precisely to the French–Spanish border on the Atlantic or Mediterranean coast).

Mean winter temperatures were obtained from the Iberian Climatic Digital Atlas (Ninyerola et al. 2005). We took historical mean values for the daily mean and minimum temperatures in the months of December and January from the Atlas. These two means were then averaged to obtain the mean winter temperature at each site. The data from the Atlas were used because, for some sampling points, the nearest meteorological station with complete climatic data was far away—in some cases more than 100 km. This could have led to significant biases if temperatures from these stations had been considered to be representative of the sampling sites where the Reed Buntings were captured. We observed that the mean temperatures for the sampling winter (December 2011–January 2012), for those meteorological stations with complete data that were close to sampling sites, were highly correlated (Pearson correlation: December: $r = +0.94$, $P < 0.001$; January: $r = +0.94$, $P < 0.001$) to the historical mean temperatures obtained from the Atlas. Therefore, we assumed that the data from the Atlas were a good representation of the mean temperature experienced by Reed Buntings during the winter of 2011–2012. Although temperatures were moderately correlated with latitude (mean: $r = -0.74$, $P < 0.001$; minimum: $r = -0.68$, $P < 0.001$), we included the two variables in our models in order to assess their effects separately. If only one variable appeared to be significant, we could not totally reject confounding effects between temperature and latitude.

In winter, Reed Buntings depend on farmland habitats such as stubble, fallows, etc. (Surmacki 2004), where they find seeds of weeds (Orlowski and Czarnecka 2007). Food resources, through habitat availability, seem to be a key factor influencing the winter distribution of Reed Buntings (Matessi et al. 2002). Land use around each sampling site was assessed using the Corine Land Cover 2006 map, which considers 44 different land uses. For the purposes of our study, the Corine land uses were re-codified into seven land uses: urban areas, arable land (cultivations), pastures, agricultural mosaic (both cultivated areas and noncultivated natural surfaces), woodland (forest, scrub), open areas with no or little vegetation, and wetlands. We calculated the percentage of each land use for a buffer of 5 km around each station. We assume that this buffer contains most/all of the Reed Buntings' winter foraging home range. Aiming to minimize autocorrelations, we conducted a principal component analysis (PCA) of the land use within each buffer.

When modeling body mass, we included four additional independent variables: P3 length [used as a body size surrogate (Gosler et al. 1998); we considered that birds with a larger body size relative to body mass had a better body condition], date [birds caught later in the season may be more fuel-loaded as they gain mass before the spring migration (Villarán and Pascual 2003)], sex, and age (Villarán and Pascual 2003). P3 length and date were included as covariates, and sex and age as factors. P3 length was included in all the models.

For each of the dependent variables (abundance, sex and age proportions, and body condition of wintering Reed Buntings in Iberia), generalized linear models (GLMs) with a Gaussian error distribution and identity link function were conducted with our potential explanatory variables. For models explaining the proportions of sex and age classes and body mass variations, we only considered stations with $\geq$10 captures.

Taking care not to overfit the GLMs, models were selected using an AIC approach (Burnham and Anderson 1998). An AICc difference >2 between two models was assumed to support differences in fit of the models to the data. All possible additive models were ranked in relation to their AICc value. Model averaging (Burnham and Anderson 1998) was used to obtain an averaged final model where the parameters for each variable were averaged across the models within the subset of models with AICc < 2 in relation to the top model. The AICc weight and the residual deviance for the subset of the best models were calculated. We also ran a null model in order to test whether it fitted better to the data than the alternative models.

Averaged final model β-parameter estimates, the standard errors in them, and the associated P values were obtained for the four dependent object variables. The effect of a variable was nonsignificant if P values associated with β parameters were >0.05. All analyses were run with R (R Development Core Team 2008), with the "MuMIn" (Barton 2014) package.

Results

The PCA provided three principal components (PC) with eigenvalues > 1 explaining, overall, 75.1 % of the variance (Table 1). When interpreting each PC, we looked for the highest absolute factor loadings. Arable land was the variable with the highest (absolute) coefficient of correlation with PC1, so PC1 was negatively correlated with cultivation (Table 1). PC2 was positively correlated with open habitat and negatively correlated with woodland (Table 1). High positive PC3 scores were correlated with zones with smaller urban areas.

Abundance

Overall, we caught 1,857 Reed Buntings (within-season recaptures excluded). We obtained a mean (±SE) standardized number of captures of 27.5 ± 8.8 Reed Buntings/day/100 m, although the actual range was from zero (at three stations: BIZA-NA, GUAR-LL, SOTO-AS) to 333.3

Table 1 Factor loadings of the PCs obtained from a PCA on seven land-use variables

Variable	PC1	PC2	PC3
URBA	+0.312	+0.229	−0.759
ARAB	−0.951	+0.247	+0.040
PAST	+0.671	−0.289	−0.020
MOSA	−0.260	−0.544	+0.451
WOOD	+0.655	−0.638	+0.051
OPEN	+0.429	+0.610	+0.506
WETL	+0.670	+0.556	+0.231
Variance (%)	36.87	22.59	15.62
Eigenvalue	2.58	1.58	1.09

URBA urban area, *ARAB* arable land, *PAST* pastures, *MOSA* agricultural mosaic, *WOOD* woodland, *OPEN* open surfaces with little or no vegetation, *WETL* wetlands

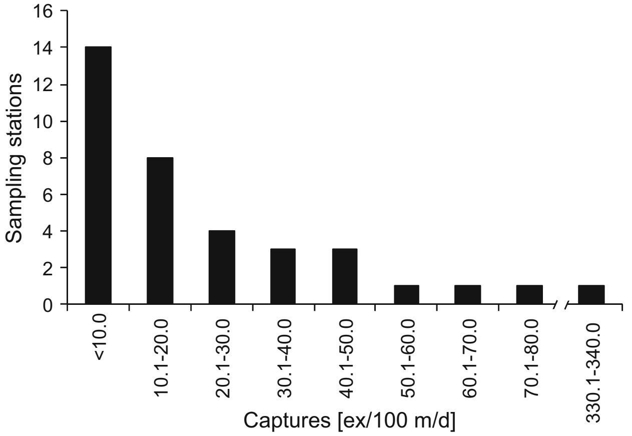

Fig. 2 Abundance distribution—Reed Buntings (*ex*) captured per day and 100 linear meters of mist nets—obtained during the winter for 38 sampling points in Iberia

Reed Buntings/day/100 m (AZNA-SE; for details see Table 5 in the Appendix; Fig. 2).

The standardized number of captures was observed to be best predicted by the null model and one model including the land use (PC1) (Table 2). However, the averaged β parameters were nonsignificant [Land (PC1): $\beta \pm SE = -0.11 \pm 0.08$, $P = 0.199$], so none of our potential explanatory variables predicted the geographic distribution of Reed Buntings across Iberia.

Sex and age percentages

Overall, 34.8 % of the captures were males, and this proportion differed from a 1:1 ratio ($\chi^2 = 174.203$, $P < 0.001$). We found three models that fitted to our data equally well (Table 2). According to the averaged β parameters, however, Dist was the only variable with a significant weight within the equation (Dist: $\beta \pm SE = -0.0003 \pm 0.0001$, $P = 0.013$; Lati: -0.05 ± 0.02, $P = 0.064$; Land (PC1): -0.03 ± 0.03; $P = 0.363$). Males were proportionally more abundant when they were closer to presumably obligate migratory pathways (Fig. 3).

We caught 63.9 % of first-year birds, a proportion that differed from a 1:1 ratio between the two age classes ($\chi^2 = 155.145$, $P < 0.001$). Although 16 models (including seven variables) were observed to have AICc < 2 in relation to the top model, there was a high degree of uncertainty (Table 2), and no explanatory variable predicted the proportion of first-year birds (averaged β parameters: $P > 0.05$).

Body condition

Two models (the global one and one including all but Land (PC1) variables; Table 2) were equally well supported by the data. Controlling for body size (here assessed using P3 length), body mass was observed to be higher in first-year birds and among males (Table 3). Moreover, body mass tended to increase with distance to obligate migratory pathway, latitude, longitude, land use (in particular a decreasing proportion of open habitats and urban areas), increasing minimum temperature and decreasing mean temperature (Table 3).

Discussion

Using ringing data from 38 stations across Iberia, we aimed—for the first time in this region—to assess the effects of geographic location, distance to the closest presumably obligate migratory pathway, climatic conditions, and land use on the distribution of Reed Buntings during the winter.

The geographic distribution of Reed Buntings in Iberia differed between sex classes, confirming a typical pattern of spatial segregation in winter (Cristol et al. 1999). Our results support the view that distance to the closest Pyrenean obligate migratory pathway affects winter male regional abundance, regardless of geographic position, climate, and land use. Interestingly, males were found to be proportionally more numerous at places located closer to such pathways. In part, this result is compatible with other studies where Reed Bunting males were found to winter in areas farther north than females (Prŷs-Jones 1984; Cramp and Perrins 1994; Villarán 1999; González et al. 2009). However, our results better support the idea that male Reed Buntings seem to prefer to winter in places closer to and with quicker and easier access to breeding grounds, and are consistent with the same distribution patterns observed in other farmland birds wintering in Iberia (Galarza and Tellería 2003; Tellería et al. 2009). This allows them to arrive in their breeding areas as soon as weather conditions improve in late winter and spring (Kokko 1999). Long-term phenological data on Reed Buntings in northern Europe show that this songbird is highly protandrous in spring (Coppack and Pulido 2009; Morbey et al. 2012). Our results hence support the hypothesis that the observed sex segregation during the winter is the result of a threshold between wintering in areas that could promote survival (viability selection) and those that guarantee a faster access to breeding grounds, which is often due to sexual selection (Morbey et al. 2012). Moreover, our data also give support to the idea that geographic segregation during the non-breeding period is one of the key determinants of protandrous arrival in spring in several bird species (Coppack and Pulido 2009). Alternative hypotheses associated with survival (viability selection) during the non-breeding period, such as the thermoregulatory hypothesis, or scenarios

Table 2 Small-sample-size-corrected Akaike information criterion values (AICc) of models that were considered when assessing the effects of several environmental factors on the standardized number of captures, proportions of males and first-year birds, and body condition of Reed Buntings spending the winter in Iberia

Models	AICc	ΔAICc	AICc weight	np	Deviance
Dep. variable: standardized number of captures					
Null	+32.42	0.00	0.58	0	4.445
Land (PC1)	+33.06	0.65	0.42	1	4.144
Global[a]	+54.75	22.33	–	8	3.441
Dep. variable: proportion of male Reed Huntings					
Dist + Land (PC1)	−32.01	0.00	0.52	2	0.3358
Dist	−30.84	1.16	0.29	1	0.3885
Dist + Lati + Land (PC1)	−30.03	1.98	0.19	3	0.3229
Null	−18.15	13.85	–	0	0.6831
Global[a]	−10.46	21.55	–	8	0.3074
Dep. variable: proportion of first-year Reed Buntings					
Land (PC1) + Tmea	−19.16	0.00	0.10	2	0.5407
Land (PC1) + Tmin	−19.08	0.07	0.10	2	0.5420
Long + Land (PC1) + Tmin	−18.67	0.48	0.08	3	0.4918
Tmin + Long	18.45	0.71	0.07	1	0.6150
Land (PC1) + Long	18.43	0.72	0.07	1	0.6153
Land (PC1) + Land (PC3) + Tmea	−18.38	0.78	0.07	3	0.4972
Long + Tmin	−18.29	0.87	0.06	2	0.5582
Dist + Long + Land (PC1)	−18.23	0.93	0.06	3	0.5000
Tmea + Long	18.11	1.04	0.06	1	0.6227
Long + Land (PC1) + Tmea	−18.01	1.15	0.06	3	0.5040
Lati + Land (PC1)	−17.92	1.24	0.05	2	0.5660
Land (PC1) + Land (PC3) + Tmin	−17.86	1.30	0.05	3	0.5068
Lati + Long + Land (PC1)	−17.68	1.48	0.05	3	0.5102
Dist + Tmin	−17.45	1.71	0.04	2	0.5758
Land (PC3) + Tmea	−17.40	1.75	0.04	2	0.5769
Land (PC3) + Tmin	−17.22	1.94	0.04	2	0.5807
Null	−13.12	6.00	–	0	0.8233
Global[a]	−1.32	17.84	–	8	0.4313
Dep. variable: body condition					
Global-Land (PC2)	+5350.76	0.00	0.72	11	2377.2
Global[a]	+5352.70	1.94	0.28	12	2377.0
Null	+6469.27	1118.51	–	0	4710.6

We show the best two models (with AICc < 2 in relation to the top model) and the global one

ΔAICc AICc difference in relation to the top model, *np* number of parameters

[a] Global model: Dist + Lati + Long + Tmea + Tmin + Land (PC1) + Land (PC2) + Land (PC3). The models for body mass also included Date, P3, Age, and Sex

where dominant males would occupy areas with better foraging conditions (Lundberg and Alerstam 1986), here assessed by proportion of arable land (PC1) and temperature, are not supported by our data.

Males were observed to be proportionally heavier than females (once body size was controlled for). This is compatible with the fact that (1) carrying higher fuel reserves would allow males to depart rapidly to their breeding areas as soon as weather conditions improve in late winter (Villarán and Pascual 2003) if a higher fuel load in winter correlates with a higher departure fuel load in late winter or spring, and (2) males may occupy a dominant social position that would allow them to have priority access to food (Moore et al. 2003).

We found no clear patterns supporting or explaining a possible segregation between age classes, suggesting that,

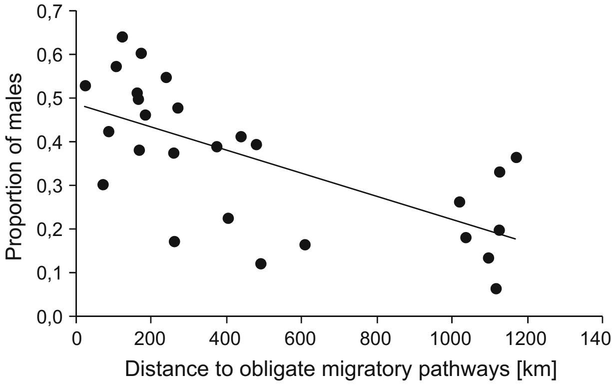

Fig. 3 The proportion of male Reed Buntings wintering in Iberia can be predicted from the distance to obligate migratory pathways (western/eastern Pyrenees)

Table 3 β Parameters obtained from the averaged model, which considered the effects of body size, age and sex, geographic position, distance to closest main migratory pathway (western/eastern Pyrenees), date, temperature, and land use (PC1–3) on Reed Bunting body mass in winter in Iberia

Variable	*B*	SE (*B*)	*P*
P3	+0.14	0.02	<0.001
Age	−0.14	0.06	0.026
Sex	−1.70	0.09	<0.001
Dist	+0.003	0.001	<0.001
Lati	+0.37	0.08	<0.001
Long	+0.13	0.04	0.001
Land (PC1)	+0.02	0.05	0.759
Land (PC2)	−0.14	0.04	0.002
Land (PC3)	+0.09	0.03	0.006
Tmea	−0.50	0.07	<0.001
Tmin	+0.44	0.07	<0.001
Date	+0.007	0.002	0.004

overall, both adults and first-year birds shared common wintering places, at least at their roosts. This result agrees with a study based on ring-recovery data in Spain (Villarán 1999). Our methodological approach, based on birds caught at roosts, is insufficient to determine whether there would be segregation between age classes on a microgeographic scale once the birds leave their roosting sites to forage. Contrary to what is normally found in birds, first-year birds were heavier than adults. Given that the former are normally subordinate to adults (Moore et al. 2003), their higher fuel loads do not seem to be caused by some kind of socially mediated mechanism of priority access to food. Rather, in the case of a food shortage, the dominant adult birds would be able to monopolize food access, so it would be advantageous for first-year birds to have extra fuel loads in order to overcome these possible starvation periods (Ekman and Lilliendahl 1993).

The abundance of Reed Buntings in Iberia during the winter was not explained by any of our candidate independent variables. Although Reed Buntings depend on farmland habitats in winter (Surmacki 2004; Orłowski 2005), so these areas play a key role in the conservation of the species during the non-breeding season (Peach et al. 1999), we were unable to find a direct link between bird numbers and land use around sampling points. Reed Buntings were caught at or near their roosts using mist nets, and this methodological approach is likely to be valid to study within-site seasonal fluctuations in abundance (Villarán and Pascual 2003; Arizaga et al. 2011), but may not be valid for comparing between-site abundances. This may be due to the fact that the number of captures at a site is influenced by several uncontrolled factors (positions of nets within the red bed, distances from mist nets to roosting places, etc.), and hence the number of captures may not reflect the real size of the Reed Bunting population. Alternatively (or as a complement) to this methodological bias, there might be other factors which also influence abundance. For instance, predation can influence spatial segregation (Nebel and Ydenberg 2005).

Finally, fuel load seemed to be influenced by several factors, giving rise to a rather complex scenario. It is not clear that males overwintered in regions which provided them with more food (indeed, body mass tended to increase with distance to obligate migratory pathways). The hypothesis predicting that the dominant sex would monopolize, or preferably occupy, high-quality habitat (e.g., with more food) is, accordingly, unlikely. The higher body condition of males might be due to the fact that they are dominant and have priority access to food (Moore et al. 2003; Villarán and Pascual 2003), although this is a question that should be investigated in detail.

In conclusion, our results suggest the existence of a link between the migration pathway used to reach Iberia and habitat quality at wintering sites as the explanation for segregation between sex classes of wintering Reed Buntings in Iberia. We found that males overwintered in regions located closer to presumably obligate migratory pathways than females, supporting the hypothesis that geographic segregation in winter may be due to the advantages of overwintering in places with better access to breeding quarters. Further research is needed to address the factors affecting spatial segregation between age classes or bird numbers.

Habitat quality in breeding and wintering areas is often considered to be one of the main determinants of bird abundance, and thus it is accepted that reductions in the availability and suitability of the selected habitats could strongly determine their population levels (Dolman and Sutherland 1995). Furthermore, when there is spatial segregation by sex, threats should be evaluated on a sex-specific basis (Catry et al. 2005b; Nebel and Ydenberg 2005), especially when the variables determining segregation are not manageable like large-scale geographical processes. Both aspects should be taken into account in the implementation of a conservation strategy, since the impact of habitat quality on the population will vary depending on its geographical location.

Acknowledgments We want to thank the many ringers who participated in the sampling of Reed Buntings: José L. Arroyo, Gorka Belamendia, Arnau Bonan, Alba Casals, Oriol Clarabuch, Ariñe Crespo, Emilio Escudero, Juan C. Fernández-Ordóñez, José L. Garzón, J. Gómez, J. Vicente González, Juan M. González, Rafael González, Óscar Gutiérrez, José L. Hernández, José I. Jauregi, Pere Josa, Iñigo López-Sarasa, Paco Martínez, David Miguélez, Alejandro Onrubia, Alfredo H. Ortega, Martín Pena, José M. Romero-Hiraldo, José M. Rivas, Lidia Roncero, Sergi Sales, Ángel Sallent, Víctor Salvador, Carlos A. Torralvo, Edorta Unamuno, Thijs Valkenburg. We also want to thank L. Cardador and M. de Cáceres for their advice about model averaging analysis. This research was partly funded by the Diputación de Gipuzkoa, Gobierno Vasco—Eusko Jaurlaritza, Grupo Ibérico de Anillamiento, Consorci de l'Estany d'Ivars-Vilasana, EGRELL, Fundación Migres, and Estació Biològica del Pallars Jussà. Two anonymous referees provided valuable comments that helped us to improve an earlier version of this work.

Appendix

See Tables 4 and 5.

Table 4 Station codes, sampling effort (sampling days, number of linear meters of mist nets used at each site), and habitat and vegetation structure around mist nets

No.	Code	Coor.	Days	Meters	W	H	S
1	ALFA-RI	42°13′N 01°50′W	3	72	<25	<2	75–99
2	ALGE-CA	36°10′N 05°26′W	4	54	100	<2	<25
3	AMPO-TA	40°40′N 00°47′E	7	132	<25	>2	25–50
4	ARAN-MA	40°02′N 03°39′W	3	90	0	>2	100
5	ARMI-AL	42°41′N 02°54′W	3	36	0	>2	50–75
6	AZNA-SE	37°09′N 06°19′W	3	21–33	<25	>2	75–99
7	BIZA-NA	42°51′N 01°44′W	3	24–138	<25	>2	75–99
8	CART-MU	37°43′N 00°52′W	3	30–48	<25	>2	50–75
9	CORI-SE	37°10′N 06°03′W	6	84	25–50	>2	25–50
10	GAUT-BI	43°21′N 02°40′W	4	144	Intertidal	<2	75–99
11	GUAR-LL	42°05′N 00°53′E	3	60	<25	>2	100
12	HERR-VA	41°33′N 04°39′W	3	60	0	>2	<25
13	HERV-RI	42°27′N 02°52′W	3	60	25–50	<2	50–75
14	HOND-GK	43°21′N 01°49′W	4	84	Intertidal	>2	100
15	HUES-HU	42°07′N 00°27′W	3	27	<25	>2	<25
16	IVAR-LL	41°41′N 00°58′E	3	96	0	>2	100
17	LAGO-FA	37°10′N 08°29′W	4	100	75–99	>2	75–99
18	LLIÇ-BA	41°35′N 02°12′E	3	48	25–50	>2	50–75
19	MILE-ZM	41°55′N 05°44′W	4	48	50–75	<2	75–99
20	PADU-GR	37°00′N 03°36′W	3	72	0	>2	100
21	PAJA-LE	42°23′N 05°29′W	3	96	<25	<2	50–75
22	PALA-GI	42°17′N 03°07′E	3	108	75–99	>2	75–99
23	PINS-ZA	41°43′N 01°05′W	4	54	0	>2	100
24	RABA-SO	41°41′N 02°22′W	2	54	25–50	>2	0
25	SANR-CA	36°17′N 05°17′W	5	84	0	>2	50–75
26	SANT-GI	42°09′N 02°30′E	3	48	100	<2	50–75
27	SILS-GI	41°48′N 02°45′E	3	96	25–50	>2	50–75
28	SOTO-AS	43°32′N 06°05′W	2	108	25–50	>2	100
29	SUEC-VA	39°15′N 00°19′W	4	90	<25	>2	75–99
30	TUDE-NA	42°03′N 01°38′W	2	24–60	<25	>2	100
31	VALD-LE	42°17′N 05°49′W	5	72	50–75	>2	75–99
32	VEJ1-CA	36°13′N 05°47′W	4	48–72	<25	<2	50–75
33	VEJ2-CA	36°14′N 05°50′W	7	72	0	>2	75–99
34	VILL-AS	43°31′N 05°24′W	4	108	50–75	>2	75–99
35	VILL-NA	42°16′N 01°43′W	2	96	50–75	>2	50–75
36	VILL-TO	39°27′N 03°20′W	3	120	<25	>2	75–99
37	VITO-AL	42°51′N 02°38′W	11	48	<25	>2	50–75
38	ZARA-ZA	41°43′N 01°02′W	4	54	0	>2	100

W area (in percentage) with water under the reed bed, *H* height of the reed bed in meters, *S* area (in percent) occupied by reed beds

Table 5 Number of captures of Reed Buntings in Iberia, during the winter of 2011

Code	Captures (Std.)	Captures (Abs.)	M-Ad	M-Fy	F-Ad	F-Fy
ALFA-RI	18.5	38	17	6	12	3
ALGE-CA	49.5	91	0	6	16	69
AMPO-TA	7.5	69	9	18	6	36
ARAN-MA	0.4	1	0	0	1	0
ARMI-AL	36.1	35	5	13	3	14
AZNA-SE	333.3	224	16	25	36	147
BIZA-NA	0.0	0	0	0	0	0
CART-MU	6.0	8	0	0	2	6
CORI-SE	7.7	35	1	8	6	19
GAUT-BI	4.3	23	2	5	1	15
GUAR-LL	0.0	0	0	0	0	0
HERR-VA	5.0	9	2	2	0	5
HERV-RI	57.8	97	23	22	23	29
HOND-GK	<0.1	1	0	1	0	0
HUES-HU	24.7	20	2	9	0	9
IVAR-LL	17.4	50	9	15	15	11
LAGO-FA	7.5	30	5	6	5	14
LLIÇ-BA	41.7	60	3	20	7	30
MILE-ZM	34.4	65	4	4	28	28
PADU-GR	4.6	10	0	1	1	8
PAJA-LE	25.3	71	13	14	24	16
PALA-GI	65.7	209	45	66	26	72
PINS-ZA	70.4	146	32	23	41	50
RABA-SO	1.9	2	0	2	0	0
SANR-CA	5.7	22	1	2	7	12
SANT-GI	38.2	54	10	13	12	19
SILS-GI	27.8	80	18	27	6	23
SOTO-AS	0.0	0	0	0	0	0
SUEC-VA	15.3	54	4	5	21	24
TUDE-NA	14.6	7	3	2	1	1
VALD-LE	15.6	54	17	4	20	11
VEJ1-CA	24.3	61	2	9	13	33
VEJ2-CA	10.1	49	5	11	7	25
VILL-AS	12.0	44	0	9	12	20
VILL-NA	15.6	30	9	6	11	4
VILL-TO	0.6	2	0	1	0	1
VITO-AL	2.8	14	3	4	3	2
ZARA-ZA	43.1	92	8	8	17	59

Std. standardized to 100 linear meters of mist nets, *Abs.* absolute.

We also show the number of captures of each age and sex class: *M* male, *F* female, *Ad* adults, *Fy* first-year. In some cases, not all of the birds could be aged or sexed, so the absolute number of captures is not always the same as the sum of the captures of birds of known age and sex

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