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ORIGINAL ARTICLE

Do migratory pathways affect the regional abundance of wintering birds? A test in northern Spain

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ABSTRACT

Aim The abundance distribution of organisms at regional scales is commonly interpreted as the result of spatial variation in habitat suitability. However, the possibility that geography itself may affect patterns of distribution has received less attention. For example, the abundance of wintering bird populations might be influenced by the cost of reaching areas located far away from the main migratory pathways. We studied the abundance distribution of three common migratory passerines (meadow pipits, *Anthus pratensis*; common chaffinches, *Fringilla coelebs*; and European robins, *Erithacus rubecula*) wintering in farmlands located in the 600-km long Cantabrian coastal sector of northern Spain, roughly perpendicular to the west Pyrenean migratory pathway that drives European migrant birds into the Iberian Peninsula.

Location The study area occupies a belt located between the Atlantic coast and the Cantabrian Mountains in northern Spain.

Methods We counted wintering and breeding birds and measured the structure of vegetation and environmental variables (altitude, rainfall, temperature) in 68 farmlands distributed at different distances from the west Pyrenean migratory flyway. We also studied the distribution of birds ringed in central and northern Europe and recovered in the study area between October and February. Analyses were based on single univariate statistics (chi-square tests), ordination by principal components analysis and multiple regression.

Results Controlling for the effects of climate, vegetation structure and local abundance of breeding conspecifics, the winter abundance of all three species decreased with the distance from their main migratory route in the western Pyrenees. Such patterns fitted well to the observed distribution of ringing recoveries.

Main conclusions Our results support a link between the movements of birds along the Pyrenean migratory pathway and their winter abundance in northern Spain. According to this view, the sectors located near the migratory pathway seem to be more easily occupied by migrants, supporting the idea that proximity to passage areas may explain the fine-grain regional patterning of species abundance in wintering grounds.

Keywords

***Anthus pratensis*, bird migration, conservation biogeography, *Erithacus rubecula*, *Fringilla coelebs*, migratory pathway, Pyrenees, Spain, winter distribution, winter ecology.**

INTRODUCTION

The functional relationship between habitat and populations provides the conceptual background for current methodological approaches to bird conservation (Ausden, 2004; Morrison *et al.*, 2006). In fact, habitat quality, as determined by food availability or predation risk, is a major determinant of bird abundance, and it is commonly accepted that population levels

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are primarily determined by changes in the availability and suitability of breeding and wintering habitats (Goss-Custard *et al.*, 2002; Rappole *et al.*, 2003). However, there is increasing evidence that the abundance and distribution of birds are also affected by scale-dependent hierarchical processes that disturb the links between habitat suitability and bird numbers (Wiens, 1989; Kotliar & Wiens, 1990; Brown *et al.*, 1996). These processes are related to various factors affecting migratory bird populations, such as the temporal decoupling between food resources and bird numbers, variable climate harshness in different regions or the inability of individuals to reach isolated areas (Herrera, 1998; Henningsson & Alerstam, 2005; Carrascal & Díaz, 2006). Hence, a full understanding of the factors that affect the numerical evolution of migratory bird populations requires the study of such populations at different spatial and temporal scales (Baillie & Peach, 1992; Sherry & Holmes, 1996; Esler, 2000).

Migratory movements of birds may produce an uneven distribution of individuals in non-breeding grounds. The cost of migrating further away from the major route has been advocated to explain various patterns in the distribution of migratory birds, such as the existence of migratory divides (Chamberlain *et al.*, 2000; Henningsson & Alerstam, 2005) or the variation in the time of arrival at breeding grounds (Gordo *et al.*, 2007). However, the possibility that difficulties related to distance travelled may affect the large-scale patterns of bird abundance in wintering grounds has received little attention.

Each autumn, millions of birds migrate from their breeding areas in western Europe towards their wintering grounds in the Iberian Peninsula and North Africa. Such a massive flow of migrant birds becomes especially concentrated at geographical bottlenecks, such as coastlines and mountain passes (Alerstam, 1990). The Atlantic coast of France collects birds that reach Spain throughout the western Pyrenees (Fig. 1), forming the most important gateway for migrants to enter the Iberian Peninsula before they reach their Mediterranean wintering grounds. These grounds are mostly located in the warmest sectors of the south-western corner of the Iberian Peninsula and North Africa (Moreau, 1956; Bernis, 1966–71; Tellería *et al.*, 1999; Galarza & Tellería, 2003).

West of this important area of concentration of migrant birds, and roughly perpendicular to the main flow of migrants, the coastal lowlands located between the Atlantic coast and the Cantabrian Mountains form a 600-km long corridor in northern Spain (Fig. 1). This area is known as an important wintering ground for many European pipits, finches, thrushes, etc. (Tellería *et al.*, 1999; Wernham *et al.*, 2002; Milwright, 2006), which has been explained as being a function of suitable winter conditions resulting from the combination of the benign oceanic influence and a landscape in which farmlands

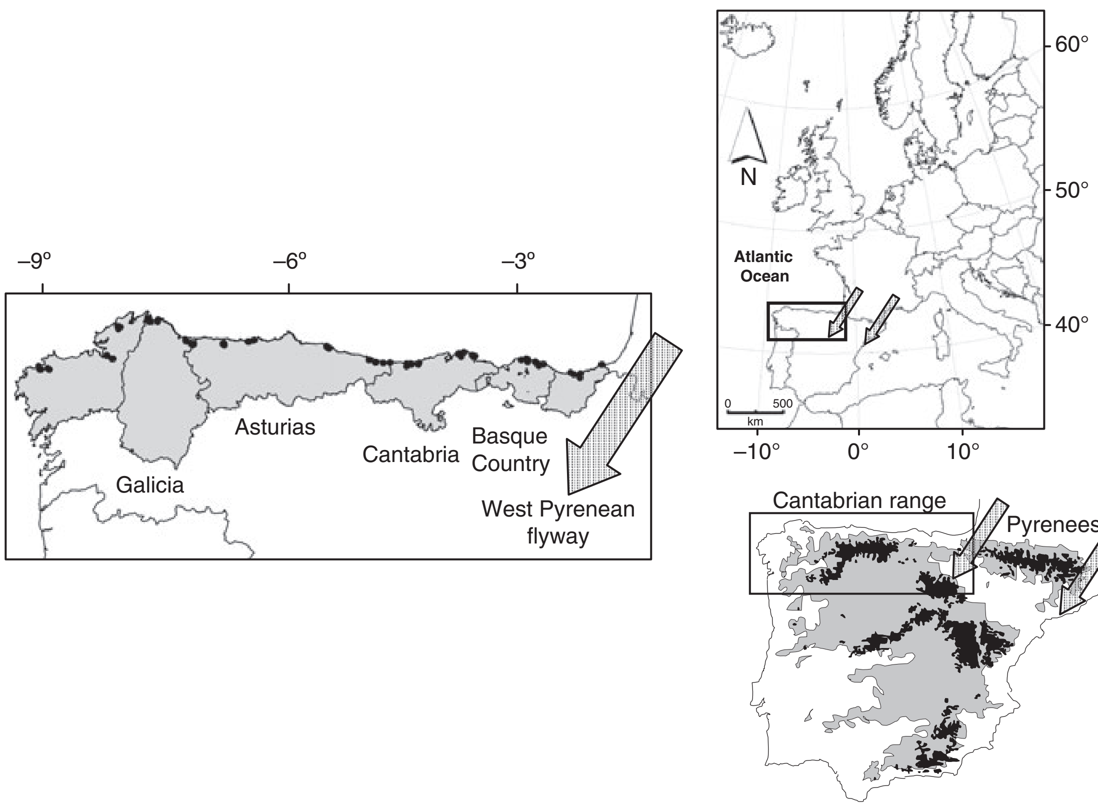

Figure 1 (Right) A view of the study area in Europe (above) and a detailed map (below) of the main topographic features of this area (areas shaded in grey and black represent areas above 500 and 1000 m, respectively). (Left) Distribution of the study sites in the four administrative sectors considered in this study. Arrows represent the main gateways for migrants to access the Iberian Peninsula.

are interspersed with tree plantations (Tellería & Galarza, 1990). Previous studies have reported a westward decrease in the numbers of wintering birds on these farmlands (Galarza & Tellería, 2003). Such patterns suggest that farmlands in north-western Spain may be less abundantly occupied by wintering birds because they are marginally located on the longitudinal span of migratory fronts in western Europe (Busse, 2001). Alternatively, the occupation of westernmost wintering areas may involve higher costs of migration from the west Pyrenean migratory gateway into the Iberian Peninsula.

Based on recoveries of ringed birds, we first determined whether European migratory individuals actually concentrate at the western Pyrenean point of access to the Iberian Peninsula. Proving this is critical if we are to interpret the area as the source of birds wintering along the northern Spanish coastline. Alternatively, the distribution of ringing recoveries may reveal a gradual decrease in abundance of migratory birds in the western sectors of the Iberian Peninsula simply because the area is at the edge of the continent; in which case we expect a positive relationship between the longitude of ringing and recovery localities of birds, rather than a concentration of migrants in the western Pyrenees.

Secondly, we explored the effect of distance from the Pyrenean migratory route on the abundance of birds wintering in northern Spanish farmlands, controlling for both environmental and demographic effects that may affect bird numbers. For instance, the concentration of migratory birds near the Pyrenees might be due to a mild climate or higher habitat suitability in these areas, rather than to their proximity to migratory pathways. In addition, a variable distribution of breeding conspecifics might affect the patterns of distribution of wintering robins and chaffinches in northern Spanish farmlands, either because resident populations contribute to total wintering numbers or because local migratory movements back and forth from nearby woodlands increase the wintering populations in open habitats.

METHODS

Study area

The study area occupies a 600-km long belt (10–30 km wide) located between the Atlantic coast and the Cantabrian Mountains in northern Spain (Fig. 1). Lowlands are covered by farmlands devoted to hay production, pine and eucalypt plantations and small villages, while areas over 400 m a.s.l. are covered by pasturelands and deciduous forests. The whole region is affected by prevailing moist Atlantic winds, and consequently receives abundant precipitation (over 1000 mm annually; Ninyerola *et al.*, 2005). Climatic conditions are deeply affected by the influence of the mountains, which create altitudinal and longitudinal variation in temperature. Thus, the mountain tops are generally covered with snow during the winter while lowlands have mild winters, particularly near the coast. Administratively, the study area is divided into four regions, which we used as study sectors for convenience (Fig. 1): Galicia (the area formed by the Galician provinces of Lugo and La Coruña, 17,800 km^2 and 1.49 million people), Asturias (10,604 km^2, 1.08 million people), Cantabria (5253 km^2, 0.57 million people) and the Basque Country (the coastal provinces of Vizcaya and Guipúzcoa, 4126 km^2, 1.83 million people).

The species

We studied the factors affecting winter distribution of three common passerines with different habitat preferences and migratory strategies: the meadow pipit (*Anthus pratensis* Linnaeus, 1758), the common chaffinch (*Fringilla coelebs* Linnaeus, 1758) and the European robin (*Erithacus rubecula* Linnaeus, 1758). The meadow pipit is a species associated with moist grasslands that does not breed in the Iberian Peninsula, meaning that all individuals wintering in Spain arrive there from central and northern Europe. Both the meadow pipit and the chaffinch (a species with preference for tree-covered farmlands) are diurnal migrants that follow coastlines and mountain passes, while the robin (which is usually associated with hedgerows) is a nocturnal migrant that moves in wider fronts (Alerstam, 1990). Relevant to our study, robins and chaffinches are abundant in northern Spain (Martí & Del Moral, 2003), both in farmlands and in nearby woodlands, which might blur their abundance patterns as shaped by the arrival of migratory birds. Our study excluded thrushes (including *Turdus philomelos* Brehm, 1834, which is common in the area) because they are locally popular game species whose abundance patterns may be distorted by hunting.

Ringing recoveries

We studied the distribution of birds ringed in European countries to the north of the Iberian Peninsula and recovered in the study area between October and February, a period that covers both the autumn migration and the wintering season. We used all ringing recoveries obtained in the study area until March 2007, which were deposited at the Spanish Ringing Scheme (meadow pipit, 204 recoveries; chaffinch, 67 recoveries; European robin, 76 recoveries). They were represented and analysed using the software ArcView® 3.2 (Redlands, CA, USA).

Bird counts, vegetation structure, altitude and climate

We counted wintering and breeding birds in 68 farmlands regularly distributed across northern Spain, 57 of which had woodlands located nearby, which were also sampled. We selected farmlands by using satellite images provided by SIGPAC (http://sigpac.mapa.es/fega/visor/). We measured the distance from each farmland to the western Pyrenees (more precisely to the French–Spanish border on the Atlantic coast). In the field, farmlands were located by means of GPS devices and maps.

We sampled one to four 500-m line-transects within each study site, depending on the size of each habitat patch; each was georeferenced using GPS devices and maps. Different teams of observers (two or three teams at a time, with two people in each team) sampled birds simultaneously early in the morning during the first half of June 2005, measuring the abundance of each species. Each observer recorded all birds seen or heard in farmlands at either side of the progression line irrespective of the distance at which each individual was detected. In this way we obtained for each species the number of individuals recorded per transect, a common index of bird abundance in extensive bird counts (Bibby *et al.*, 1992). We repeated the sampling in the same transects during mid January 2006, thus measuring the abundance of wintering birds in the same transects.

The structure of vegetation was measured in farmlands by means of two 25-m radius circles separated by 200-m intervals along each transect (Larsen & Bock, 1986). In each circle, we visually estimated shrub cover (the percentage of vegetation below 2 m in height) and tree cover (the percentage of vegetation above 2 m in height), counted the number of shrub and tree species and estimated the average height of the tree canopy. We averaged the scores of the two sampling circles to characterize each line transect. For each locality, we obtained mean monthly rainfall and temperature values by averaging long-term climatic data for December, January and February (Ninyerola *et al.*, 2005). We also measured elevation at each study locality as an additional surrogate of climate harshness (e.g. snow persistence). We did not measure vegetation cover in one of our sampling sites (located in Asturias), which rendered slightly different sample sizes among analyses.

Statistical analyses

To visualize the main pattern of distribution of ringing recoveries, we used concentric lines including 35, 50, 75 and 95% of recoveries as determined by kernel polygons (Hooge & Eichenlaub, 1997). We made sure that the density of recoveries per region was not affected by its surface area or human population (large or overpopulated areas may produce more data than small or less populated areas; Bairlein, 2001). We used chi-square tests (with Yates's correction for continuity when necessary) to compare the number of recoveries observed with those expected according to the surface area and human population of each region, under the null hypothesis that the number of ringing recoveries obtained in one region would be directly proportional to its surface area (should sampling effort depend on surface area) or to the size of its human population (should sampling effort depend on human population size; see Bairlein, 2001, for further details).

We conducted a principal components analysis (PCA) to reduce the number of variables used to describe vegetation structure. The PCA retained a single principal component with eigenvalue > 1 (PC1), which explained 68.01% of variance and was interpreted as a gradient of increasing vegetation cover (factor loadings for number of shrub species 0.71; shrub cover 0.71; tree cover 0.88; mean tree height 0.87; number of tree species 0.92).

To study how local and regional features affect bird abundance, we used a model selection approach based on the Akaike selection criterion, with bias correction term for small sample sizes (AIC_c; Burnham & Anderson, 2002). We searched for best models among possible parameter combinations in multiple regression models with normal structure of the error and identity as the link function, using maximum likelihood to assess the fit to the data. The original set of independent variables included the distance to the western Pyrenees, vegetation cover (PC1), rainfall, temperature, altitude and conspecific abundance in farmlands during spring. Because environmental variables (altitude, climate and habitat structure) might have nonlinear effects on bird abundance (for example if birds reach their highest or lowest abundance at intermediate values of these variables), we estimated both linear and quadratic effects of these variables when building our models. Because we predicted that bird abundance should decrease with increasing distance from the western Pyrenees, we compared models that included distance with the best model without distance. Finally, we used multiple regression models to compute the variance explained by each of the parameters included in the best model selected according to the AIC_c.

In a second step, we used a reduced sample of farmlands with nearby woodlands ($n = 57$) to test for the effect of seasonal changes in abundance of chaffinches and robins in woodlands on the abundance of the populations of these species wintering in farmlands. In this analysis, we controlled for the variables that best explained variation in abundance of birds wintering in farmlands, according to the models obtained using all farmlands. We measured the seasonal decrease in abundance in woodlands as the difference from spring to winter in the number of birds detected per transect.

RESULTS

Distribution of ringing recoveries

Recoveries of ringed birds were aggregated at the west Pyrenean entry route (Fig. 2). Such a concentration, which involved birds ringed in a wide longitudinal range outside Spain (from −10° W to 30° E north to the Spanish borders), blurred any significant correlation between the longitudes of ringing and recovery localities. This pattern strongly differed from the patterns predicted by the surface area (pipit, $\chi^2_{(3)} = 950.2$, $P < 0.001$; robin, $\chi^2_{(3)} = 201.6$, $P < 0.001$; chaffinch $\chi^2_{(3)} = 296.7$, $P < 0.001$) and human population (pipit, $\chi^2_{(3)} = 164.9$, $P < 0.001$; robin, $\chi^2_{(3)} = 29.74$, $P < 0.001$; chaffinch $\chi^2_{(3)} = 47.5$, $P < 0.001$) of the four study regions. Such a result suggests that the observed abrupt westwards decrease in the frequency of ringing recoveries does not result from a biased sampling of ringed birds, but is reliable evidence of the concentration of migratory birds at the western edge of the Pyrenees.

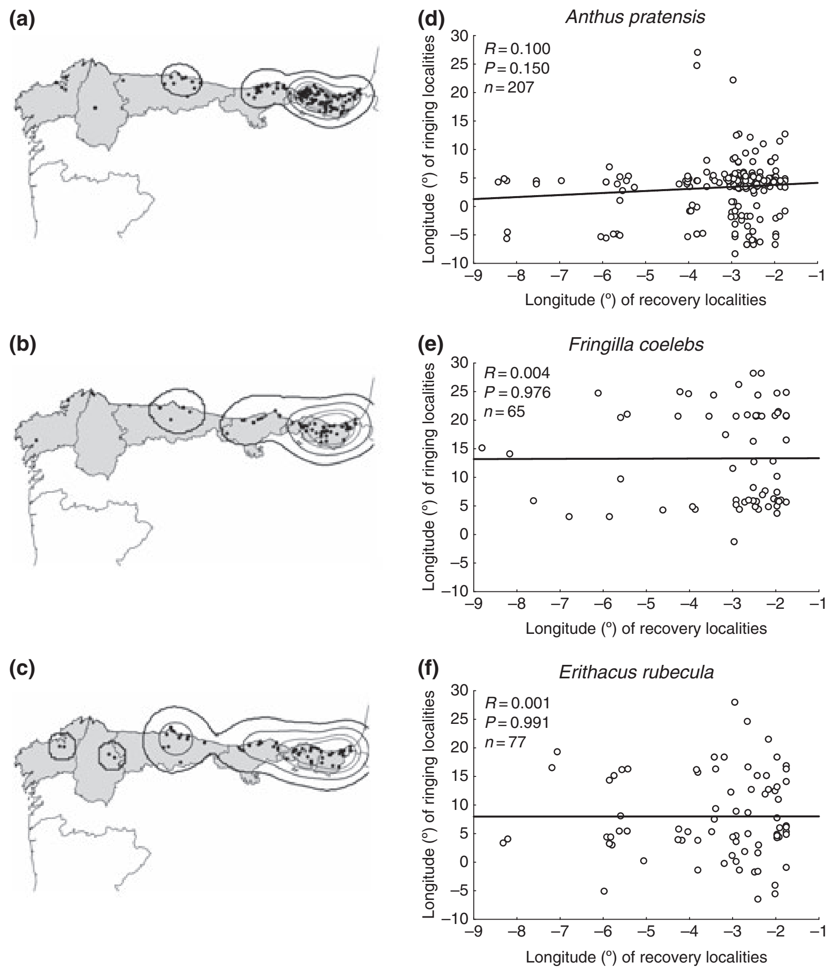

Figure 2 (Left) Distribution of ringing recoveries along the study area for (a) meadow pipits (*Anthus pratensis*), (b) chaffinches (*Fringilla coelebs*) and (c) robins (*Erithacus rubecula*). Concentric lines include 35%, 50%, 75% and 95% of recoveries, respectively, as determined by kernel polygons in ArcView 3.1. (Right) Relationships between the longitude of ringing and recovery localities of birds arriving at the study area from northern and central Europe for (d) meadow pipits (*Anthus pratensis*), (e) chaffinches (*Fringilla coelebs*) and (f) robins (*Erithacus rubecula*).

Factors affecting bird abundance

Average bird numbers differed among sectors (meadow pipit, $F_{3,64} = 5.30$, $P = 0.003$; chaffinch, $F_{3,64} = 3.84$, $P = 0.011$; robin, $F_{3,64} = 3.07$, $P = 0.07$), always reaching the highest abundance in the easternmost sector (Fig. 3). Both chaffinches and robins experienced a strong increase in abundance from spring to winter in the farmlands (Fig. 3; repeated measures ANOVA: chaffinch, $F_{1,67} = 92.65$, $P < 0.0001$; robin, $F_{1,67} = 38.73$, $P < 0.0001$). In addition, they showed a steep decrease in abundance from spring to winter in the woodlands neighbouring farmlands (mean ± SE birds per transect: chaffinch, 3.97 ± 0.65 in spring and 1.40 ± 0.43 in winter, $t = 3.32$, $P = 0.001$; robin, 11.82 ± 1.02 in spring and 2.84 ± 0.43 in winter, $t = 8.36$, $P < 0.001$).

Our model search based on AIC_c revealed that the distance from the western Pyrenees was a good predictor of the winter abundance of all three species. Thus, north Iberian farmlands located farther away from the Pyrenees had less abundant wintering populations of meadow pipits, chaffinches and robins. The best models to explain variation in abundance of these species included such an effect (Table 1), although it was absent from one plausible model (with $\Delta AIC_c < 2$) in chaffinches, in which abundance was more difficult to model than in the other species (Table 1: in chaffinches, $\Delta AIC_c > 2$ was not reached until the 23rd model sorted by increasing AIC_c). In view of this result, we looked at the second best model to explain winter abundance of chaffinches without considering distance, which ranked 38th and had $\Delta AIC_c = 2.58$. Therefore, we concluded that models excluding distance were unlikely in all three species, and used the parameters of the first models according to the procedure described above to compute multiple regressions to model variation in the winter abundance of each species. In these analyses, the effect of distance explained between 9% and 14% of the variance in winter abundance depending on the species (Table 2), and remained unchanged when we considered the possible influence of local movements of birds back and forth from nearby woodlands, measured as the decrease in bird abundance from spring to winter in such habitats (Table 2).

DISCUSSION

The west Pyrenean migratory pathway

It is commonly considered that birds face little limitation to dispersal unless they encounter large barriers such as oceans or

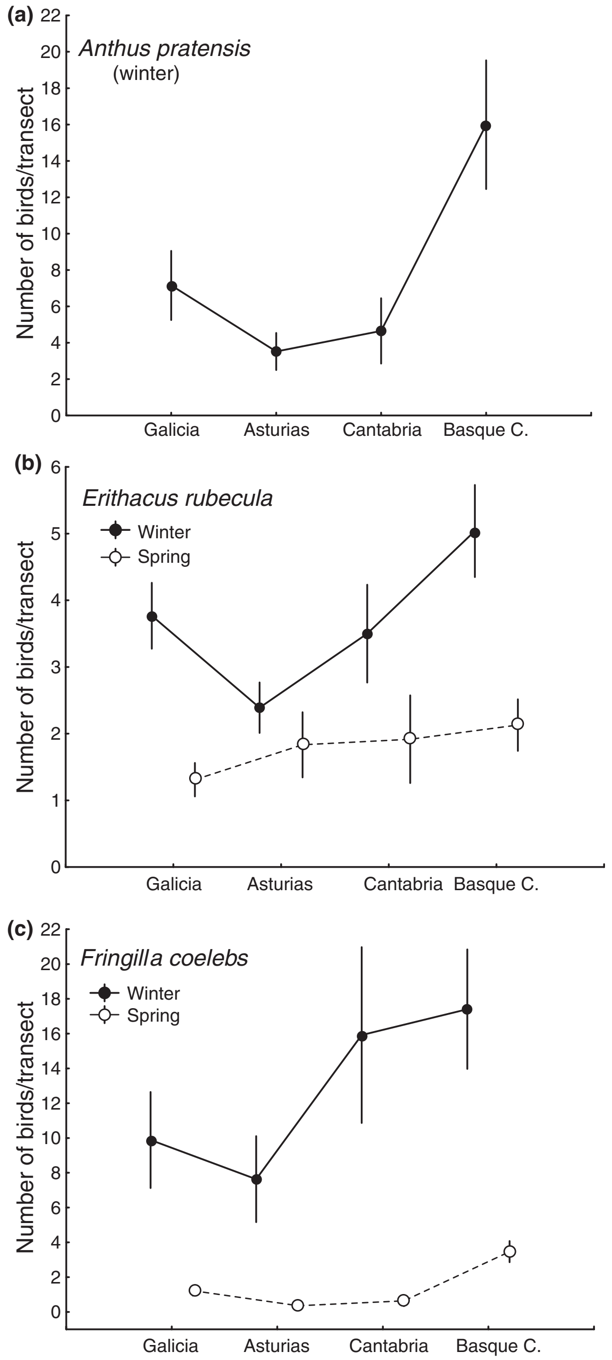

Figure 3 Abundance distribution (mean ± SE) of (a) meadow pipits (*Anthus pratensis*), (b) robins (*Erithacus rubecula*) and (c) chaffinches (*Fringilla coelebs*) among the four study sectors (Galicia, n = 26; Asturias, n = 16; Cantabria, n = 10; Basque Country, n = 16). Black dots refer to winter (January) and white dots to spring (June).

huge mountain ranges (Cox & Moore, 2000). However, less important geographical features can produce a spatial concentration of bird migratory flows (Alerstam, 1990) that, according to our results, may contribute to shaping the fine-grain regional patterning of bird abundance in wintering grounds.

Mountain ridges, valleys, rivers or coastlines are often used by migrants as leading lines, which are particularly important for diurnal migrants but are also used by nocturnal migrants (Åkesson, 1993; Bruderer & Liechti, 1998). As a consequence, the concentration of migratory birds is a common occurrence, which on the Atlantic French coast leads to the formation of a major gateway for migrants into the Iberian Peninsula located at the western edge of the Pyrenees. The distribution of ringing recoveries observed in this study reveals bottlenecked migration of pipits and finches (Fig. 2), two species that usually follow geographical features during migration (Zink & Bairlein, 1995; Wernham *et al.*, 2002). Interestingly, our results also support the idea that geography influences the migratory routes of the European robin, a nocturnal migrant which usually moves in wider fronts but seems to be influenced by coastal lines in western Europe (Remisiewicz, 2002). In all these cases, the origin of ringed birds recovered in northern Spain spans a broad range of longitudinal origins, with individuals arriving from regions located between 10° W and 30° E (Fig. 2). Uncorrelated longitudes of ringing and recovery localities further support the idea that the western edge of the Pyrenees is a major migratory pathway, at which western European populations of the three species converge to access the Iberian Peninsula.

Abundance patterns of wintering birds in northern Spain

Controlling for potential confounding factors (size of the regions and human population; Bairlein, 2001; Busse, 2001), our results revealed a sharp decrease westwards of the number of ringed migratory birds recovered in northern Spain (Fig. 2). Such a pattern agrees with the decrease in abundance of wintering birds with increasing distance from the Pyrenees detected by our censuses, and emerges in our analysis after controlling for the effects of the most important environmental determinants of the geographical distribution of wintering birds (Tables 1 & 2). Interestingly, we failed to observe any effect of local conspecifics (either breeding in farmlands or moving from nearby forests) on the abundance patterns of wintering robins and chaffinches. This further supports the idea that the bulk of the populations of these species, perhaps including local north Iberian populations, migrate to the main wintering grounds of the species (located in southern Spain; Tellería *et al.*, 1999). In turn, although the three species show great differences in habitat selection and migratory behaviour, their winter abundance in northern Spain decreased with increasing distance from the Pyrenean migratory pathway.

Migratory pathways and winter distribution

Our results support the view that the layout of the Pyrenean migratory pathway affects the regional patterns of bird abundance in winter, independently of the local environmental

Table 1 Selection of models to explain variation in abundance of meadow pipits (*Anthus pratensis*), chaffinches (*Fringilla coelebs*) and robins (*Erithacus rubecula*) wintering in northern Spanish farmlands. The table shows parameters (with signs indicating the direction of the effects) in the five best models for each species, ranked by decreasing likelihood according to the corrected Akaike information criterion (AIC_c). The increase in AIC_c of each model compared with the best model (ΔAIC_c) was used to calculate model weights (W), which represent relative likelihoods of each model. The table also shows the best of all parameter combinations that excluded the distance to the Pyrenees, and its rank (*) among all models arranged by AIC_c.

Rank	Variables in the model	AIC_c	ΔAIC_c	*W*
Meadow pipit				
1	+RAIN − DIST	82.43	0	0.153
2	+RAIN + ELEV − DIST	82.68	0.25	0.135
3	+RAIN + ELEV − $ELEV^2$ − DIST	82.72	0.29	0.132
4	+RAIN − VCOV − DIST	82.78	0.35	0.129
5	+RAIN + ELEV − VCOV − DIST	83.35	0.92	0.097
53*	+RAIN + ELEV	86.80	4.37	–
Chaffinch				
1	+ELEV − $TEMP^2$ − DIST	81.22	0.00	0.147
2	–DIST	81.39	0.16	0.136
3	+ELEV − $VCOV^2$ − $TEMP^2$ − DIST	81.98	0.76	0.101
4	–$TEMP^2$ − DIST	82.08	0.85	0.096
5	–TEMP − $TEMP^2$ − DIST	82.08	0.86	0.096
12*	–TEMP − $TEMP^2$	82.67	1.44	–
Robin				
1	+$RAIN^2$ + VCOV − DIST	−18.37	0.00	0.253
2	+RAIN + $RAIN^2$ + VCOV − DIST	−16.77	1.60	0.114
3	+$RAIN^2$ − ELEV + VCOV − DIST	−16.58	1.79	0.103
4	+$RAIN^2$ + VCOV + $VCOV^2$ − DIST	−16.52	1.86	0.100
5	+$RAIN^2$ − $TEMP^2$ + VCOV − DIST	−16.21	2.16	0.086
122*	+$RAIN^2$ + VCOV + $VCOV^2$	−9.23	9.14	–

RAIN, precipitation; ELEV, elevation; TEMP, temperature; VCOV, vegetation cover measured by PCA scores; BRAB, breeding abundance of each species (not estimated for pipits because they do not breed in the Iberian Peninsula); DIST, distance to the western edge of the Pyrenees.

Table 2 Results of multiple regression models of variation in abundance of meadow pipits (*Anthus pratensis*), chaffinches (*Fringilla coelebs*) and robins (*Erithacus rubecula*) wintering in northern Spanish farmlands. The models represent the best combination of parameters selected according to the corrected Akaike information criterion (AIC_c) (Table 1), in analyses conducted using all farmlands and a reduced sample of farmlands that had woodlands located nearby (in the latter case, the effect of spring-to-winter change in abundance of conspecifics in such woodlands is also estimated).

	All farmlands (n = 67)						Farmlands with nearby woodlands (n = 57)					
	Estimate	Beta	d.f.	*F*	*P*	Var (%)	Estimate	Beta	d.f.	*F*	*P*	Var (%)
Meadow pipit												
Intercept	0.716											
RAIN	0.175	0.371	1,64	9.61	0.003	12.51						
DIST	−0.149	−0.316	1,64	6.99	0.010	9.09						
Model			2,64	6.43	0.003	16.72						
Chaffinch												
Intercept	0.997						1.040					
ELEV	0.101	0.222	1,63	3.00	0.088	4.05	0.162	0.371	1,51	5.95	0.0182	9.49
$TEMP^2$	−0.096	−0.250	1,63	3.39	0.070	4.57	−0.133	−0.361	1,51	4.70	0.0348	7.50
DIST	−0.170	−0.373	1,63	9.06	0.004	12.22	−0.180	−0.393	1,51	7.74	0.0076	12.35
S–W							0.016	0.036	1,51	0.08	0.7828	0.12
Model			3,63	3.71	0.016	15.03			4,51	2.92	0.0299	18.64
Robin												
Intercept	0.547						0.543					
$RAIN^2$	0.075	0.435	1,63	11.65	0.001	13.56	0.073	0.430	1,51	10.08	0.0025	14.02
VCOV	0.080	0.343	1,63	9.95	0.002	11.58	0.090	0.379	1,51	10.04	0.0026	13.96
DIST	−0.103	−0.445	1,63	12.12	0.001	14.11	−0.099	−0.400	1,51	8.17	0.0061	11.36
S–W							0.002	0.009	1,51	0.01	0.9399	0.01
Model			3,63	7.63	< 0.0001	26.65			4,51	5.23	0.0013	29.08

RAIN, precipitation; ELEV, elevation; TEMP, temperature; VCOV, vegetation cover measured by PCA scores; DIST, distance to the western edge of the Pyrenees; S–W, spring-to-winter decrease in abundance of conspecifics in nearby woodlands (not estimated for meadow pipits).

conditions realized by birds in different parts of the northern Spanish coastal farmlands. According to this view, the seasonal occupation of this wintering habitat takes place in a spatially explicit context: most birds access northern Spain from the Pyrenean migratory pathway (Fig. 1), so that the areas located close to this pathway retain a surplus of individuals compared with sectors located further to the west. A nearly constant passage of birds through the migratory pathway, which reaches greatest importance during migration periods but may also canalize weather-dependent winter bird flows (Newton, 2008), may result in a higher abundance of birds close to the Pyrenees.

The concentration of birds on the move may facilitate the settlement of a surplus of birds in suitable habitats near the migratory flyway. However, this would be less likely further away, due to a diffusion of the supply of settlers with increasing distance from the source of colonizers. In winter, bird distribution seems to be regulated through the sequential settlement of individuals in habitat patches of differing quality (Brown, 1969; Fretwell & Lucas, 1970), with the first migrants to arrive in the area forcing surplus individuals to occupy less suitable sites (Greenberg, 1986; Sherry & Holmes, 1996). Thus, the seasonal occupation of wintering grounds located near migratory flyways will depend on the realized availability of suitable habitat patches, the landscape structure, the size of the populations involved, the costs of movements or the mortality rates associated with the distance travelled (e.g. Hanski & Ovaskainen, 2003).

Conservation implications

Migratory flyways are priority areas for the conservation of migratory bird populations (Hutto, 2000; van Eerden *et al.*, 2005). In fact, there is an increasing interest in understanding migratory connectivity of bird populations, a term coined to describe the latitudinal links between different breeding and non-breeding areas in species ranges, including the migratory stopover sites distributed along migratory pathways (Webster *et al.*, 2002). Our results support and extend this view, suggesting a relevant additional role of migratory pathways as seasonal sources of individuals wintering in nearby areas, which may end up producing a sequential colonization of habitat patches from their close proximity towards more distant areas.

The existence of purely geographical effects on habitat occupation by wintering birds has important conservation implications. Other things being equal (e.g. habitat suitability), farmlands located inside or near migratory pathways should be treated as cornerstone sites for the conservation of migratory birds, because they are used during both migration and wintering periods. In addition, there is a possibility that the location of major migratory flyways may explain variation in winter abundance of migratory land birds at larger geographical scales, for example in areas affected by continental migratory bird flows. The geographical layout of available habitat is known to play an important role in determining local abundances of species that use habitat patches linked by migration routes (such as waterfowl or waders; Newton, 2008). However, such geographical effects have been largely overlooked in studies of small passerines, which usually spread across large areas and occupy extensive habitats.

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