Articles

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Are European birds leaving traditional wintering grounds in the Mediterranean?

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Climate warming and other environmental changes seem to be causing a shift in the wintering grounds of European birds northwards. We tested this hypothesis by exploring whether the abundance of 14 common migratory passerines (Passeriformes) wintering in Spain has decreased during recent decades. We used data on ringed birds provided by the European Union for Bird Ringing (EURING) with a capture per unit of effort approach to detect whether the number of foreign ring recoveries controlled by the total number of ringed birds has decreased during the last 60 yr. We also explored if trends of breeding populations, diet and body mass explained the observed patterns. Results show that the arrival of extra Iberian wintering birds has decreased since the 1980s. This tendency was weakly associated with the trends of breeding populations reported by the European Bird Census Council (EBCC). However, diet produced some suggestive patterns since frugivorous birds, a group adapted to tracking spatiotemporal changes in food availability, depicted sharper reductions in the number of wintering individuals. In addition, larger birds, less affected by winter thermoregulatory requirements, lessened their migratory movements to the south more than small birds. The results suggest a long-term rearrangement of migratory movements of European birds in which the Mediterranean basin is losing its traditional role as primary wintering ground.

Many European populations of partial migratory birds move to winter in the Mediterranean Basin (Busse 2001). In recent years, environmental changes related to climate warming and habitat alterations seem to be affecting these movements with migratory populations moving further north of traditional wintering grounds (Siriwardena and Wernham 2002, Fiedler et al. 2004, Visser et al. 2009). However, empirical evidence on the extent of these changes in the Mediterranean region is as yet sparse (Onrubia and Tellería 2012) or concern to some isolated species (Tellería 2014a, b).

The lack of information on the ongoing changes in the Mediterranean Basin as a wintering ground for European partial migratory species could be explained by the difficulties of overcoming three methodological obstacles: a) the availability of long-term assessments of the number of birds moving to winter in Mediterranean countries; b) the complexity of assessing the true migratory status of partial migratory birds in wintering grounds where foreign individuals mix with local conspecifics (De la Hera et al. 2012); and c) the difficulties of controlling for some alternative processes affecting the number of overwintering individuals, such as the long-term trends in the size of their European breeding populations. These challenges can be overcome, however, with data provided by two cooperative monitoring programs supported by European amateur and professional ornithologists: ring recoveries gathered over the years by the European Union for Bird Ringing (Euring, <www.euring.org/>) and inter-annual counts of breeding bird populations carried out by the Pan-European Common Bird Monitoring Scheme launched by the European Bird Census Council (EBCC, <www.ebcc.info>). These programs provide a long-term perspective on the origin and numerical trends of ringed birds and the evolution of their breeding populations. This information can be used to explore whether the number of birds moving to winter in the Mediterranean Basin over the last decades has changed, and whether such changes can be explained by a simple effect of long-term variations in the size of the European breeding bird populations involved in these movements.

In this study, we use the above-mentioned datasets and some complementary information on bird biology to explore whether the role of Spain as a wintering ground of several partial migratory passerines (Passeriformes) has changed in recent decades. More specifically, we use data on ring recoveries of birds that breed in central or northern Europe and winter in Spain (hereafter foreign recoveries) to do the following.

1) We investigate whether the number of foreign recoveries has decreased in recent decades as a result of the decline in the number of wintering birds. If no change has occurred

in the migratory movements of birds, we would expect the number of foreign recaptures to follow the patterns of ringing activity, which has increased dramatically in Europe since the 1970s (Du Feu et al. 2009).

2) We explore whether such a potential reduction in the number of foreign recoveries is related to long-term changes in the size of the bird populations involved in these movements. Since the size of breeding populations of many birds has changed in Europe (Gregory et al. 2007, EBCC <www.ebcc.info>), we would expect concomitant trends in the number of birds involved in migratory movements to the Mediterranean. A lack of relationship between wintering and breeding trends would point to other effects related to changes in the migratory schedules of birds (e.g. a reduction in the migratory fraction of these partial migratory species as a response to global warming; Møller et al. 2010, Pautasso 2012).

3) Finally, we test the effect of two traits of species on the potential changes in bird movements. a) Food tracking. Diet may affect the migratory reaction of birds to environmental changes. For instance, frugivorous birds actively track fruit abundance, a resource that changes dramatically among sites and years (Levey and Stiles 1992, Boyle and Conway 2007). Since these birds are in fact omnivorous, they can translate fruit tracking ability to the exploitation of other emerging food resources in northern areas, such as invertebrates or food resources related to urban areas (Robinet and Roques 2010, Jokimäki and Kaisanlahti-Jokimäki 2012, Møller et al. 2014). This could lead to a reduction in migratory movements to South as winter conditions improve in northern areas of Europe. b) Body mass. Larger birds show less thermal conductance than small birds, a trait that improves their ability to cope with thermal restrictions in colder areas (Schleucher and Withers 2001, Meehan et al. 2004). Since wintering birds actively react to temperature changes (Carrascal et al. 2012), this difference suggests that, in a context of climate warming, larger species could be the first to reach thermal thresholds suitable for survival in colder regions of Europe and to reduce their movement to wintering grounds in the south.

Material and methods

Data on bird movements

Our study focused on 14 common passerine species (Passeriformes) that winter in mild areas of Spain and show differences in diet and body mass (Tellería et al. 1999; Table 1). We used data on ringed birds provided by the Office of Migratory Species of the Spanish Ministry of Agriculture, Food and Environment integrated within Euring. These data referred to ring recoveries provided by ringing activity gathered over six decades by mist-netting, the main method used by ringers to capture small passerines (recoveries included as code 20 of the EURING exchange code 2000; Speek et al. 2001; in the case of multiple recaptures of the same individual, we only considered the first one). Within this databank we selected two kinds of records: 1) birds ringed in Spain (peninsular Spain and the Balearic Islands) during winter (December, January and February) and then recovered more than 1000 km to the north outside of the wintering

Table 1. Main characteristics of the bird species included in this study. Species are classified according to body mass (g) and winter diet (G, granivorous, I, insectivorous, F, frugivorous). Breeding population trends in Europe since the 1980s are also reported (excluding *Saxicola torquatus* whose trends have been provided by the European Bird Census Council only since the 1990s). The countries from which most rings have been recovered in Spain are also reported.

Family	Species	Body mass (g)	Diet	Population trend (%)	Country (number of ring recoveries)
Alaudidae	Skylark *Alauda arvensis*	40.0	G	−51	Belgium (1)
Motacillidae	Meadow pipit *Anthus pratensis*	18.4	I	−68	Belgium (73), United kingdom (15), Netherlands (12), Germany (7), Russia (6)
	Wagtail *Motacilla alba*	21.0	I	−8	Belgium (28), Germany (12), United Kingdom (4), Netherlands (4), Czech R.–Slovakia (3)
Turdidae	Eurasian robin *Erithacus rubecula*	18.2	F	17	Sweden (72), Poland (36), Germany (32), Belgium (26), Finland (20)
	Black redstart *Phoenicurus ochruros*	16.5	I	62	Germany (11), France (3), Belgium (2), Denmark (1), United Kingdom (1)
	Stonechat *Saxicola torquatus*	15.3	I	34	France (3), Germany (2), Belgium (1), United Kingdom (1), Netherlands (1)
	Song thrush *Turdus philomelos*	67.8	F	5	Finland (33), Sweden (30), Germany (28), Belgium (18), Poland (15)
	Redwing *Turdus iliacus*	61.2	F	−22	United Kingdom (6), Belgium (5), Finland (5), Netherlands (4), Russia (2)
	Blackbird *Turdus merula*	113.0	F	20	Denmark (1), Germany (1)
Sylvidae	Blackcap *Sylvia atricapilla*	15.5	F	150	Belgium (154), Germany (31), France (29), United Kingdom (28), Netherlands (20)
	Chiffchaff *Phylloscopus collybita*	7.5	I	98	Belgium (44), Germany (35), United Kingdom (21), Netherlands (13), France (10)
Fringillidae	Chaffinch *Fringilla coelebs*	21.4	G	8	Russia (25), Switzerland (5), Germany (5), Finland (3), Poland (2)
	Common linnet *Carduelis cannabina*	15.3	G	−63	Belgium (71), United Kingdom (28), Germany (14), Netherlands (7), France (5)
	Goldfinch *Carduelis carduelis*	15.6	G	4	Germany (16), United Kingdom (12), Switzerland (8), Belgium (7), France (6)

season; and 2) birds recovered during winter in Spain that had been ringed outside of the wintering season more than 1000 km north. In this way, all records referred to long-distance migratory birds arriving at the Spanish wintering localities from central and northern Europe.

To assess the effort (E) applied to obtain foreign recoveries in Spain (C), we used the temporal distribution of birds ringed by the Spanish ringing scheme (Table 2). In this way, we designed a capture per unit of effort approach (CPUE; Seber 1982, Robinson et al. 2009) to have an index of the numerical evolution of wintering populations (expressed in number of foreign individuals recovered per 1000 ringed birds; CPUE: [C/E] $\times$1000). This index was applied to report the trends in the arrival of migratory birds to Spain. We also looked for the numbers of ringed birds in Europe to control for their effect on the number of ringed birds recovered in the wintering grounds of Spain. As this information is not available for all European countries, we used the number of ring recoveries of live birds available in EURING as a surrogate of ringing effort (Du Feu et al. 2009; <www.euring.org>). Previously, we tested that the number of ring recoveries per decade in Spain was significantly correlated to the total number of ringed birds.

Statistical analyses

We used chi-square tests to compare whether the evolution of foreign recoveries (C) per decade was predicted by changes in the number of ringed birds (E) or, alternatively, they depicted smaller numbers than expected in recent decades (Table 2). We used product-moment correlation analyses to test if changes in the numerical trends of breeding bird populations (%) offered by EBCC for the 1980–2010 period were related to changes in the number of foreign recoveries (% of change in the CPUE indexes) between the 1980s and the 2000s (only after the 1980s was the effort applied to ringing birds large enough for most species; see below). We also used correlation analysis to test whether changes in foreign recoveries were related to differences in the species' body mass (Dunning 1992). The effect of diet was tested by one-way ANOVA after sorting the species according to winter food preferences (insectivores, granivorous and frugivorous; Table 1), and GLM analyses were used for exploring potential interactions among diet, population trends and body mass on changes in CPUE indexes. All analyses were carried out using Statistica 7.0 (StatSoft, Tulsa, OK).

Results

General patterns

Our analyses on the temporal distribution of ring recoveries and ringing effort reflected four main issues (Table 2). First, the number of foreign recoveries of the skylark *Alauda arvensis*, the black redstart *Phoenicurus ochruros*, the stonechat *Saxicola torquatus* and the blackbird *Turdus merula* were too small. Thus, these birds were excluded from further analyses. Second, the number of birds ringed before the 1980s was too small to make a comprehensive assessment of the sampling effort in several species (Table 2). Third, a simple observation of rough data in Table 2 suggests that, in spite of a dramatic increase in the number of ringed birds in Spain over the years, the number of foreign recoveries decreased in most cases. In some species, this decrease was evident from the 1970s onwards (the Eurasian robin *Erithacus rubecula*, the chaffinch *Fringilla coelebs* and the wagtail *Motacilla alba*; Table 2). Finally, the total numbers of ringed birds in Spain per decade was strongly correlated to the number of ring recoveries ($r = 0.93$, $p = 0.002$, $n = 7$ decades; <www.euring.org>) supporting the use of ring recoveries as a surrogate of ringing effort in Europe.

Temporal trends in ring recoveries

Most European countries from which birds arrived to winter in Spain, particularly the ones located in northern and continental areas, reported a decrease in the number of ring recoveries of birds wintering in Spain despite a general increase in ringing activity (Fig. 1). This reduction was more evident when CPUE indexes were used to explore the trends in Spain (Fig. 2). Chi-square tests used

Table 2. Number of ring recoveries (C) of birds breeding in central and northern Europe and wintering in Spain per decade. The total number of birds ringed in Spain per decade is shown in brackets (E) as a measure of sampling effort. Records before the 1950s have been omitted.

	Decade C(E)					
	1951/1960	1961/1970	1971/1980	1981/1990	1991/2000	2001/2010
Alauda arvensis	0 (0)	0 (3)	0 (7)	1 (433)	0 (347)	0 (990)
Anthus pratensis	3 (0)	26 (4)	26 (222)	57 (6694)	10 (6709)	4 (6559)
Carduelis cannabina	10 (2)	42 (74)	16 (2297)	12 (24 831)	38 (43 647)	10 (38 212)
Carduelis carduelis	2 (30)	15 (214)	22 (3761)	9 (46 360)	3 (83 313)	1 (93 610)
Erithacus rubecula	30 (5)	76 (215)	51 (3202)	47 (54 348)	25 (82 998)	30 (166 558)
Fringilla coelebs	1(1)	21(65)	10 (2152)	9 (32 009)	6 (39 855)	2 (69 167)
Motacilla alba	3 (0)	18 (27)	8 (301)	8 (8627)	4 (9415)	11 (30 619)
Phoenicurus ochruros	3 (0)	8 (15)	3 (284)	3 (748)	1 (11 093)	1 (15 931)
Phylloscopus collybita	0 (1)	8 (194)	6 (2673)	19 (42 896)	42 (106 481)	63 (210 102)
Saxicola torquata	0 (3)	5 (7)	0 (386)	2 (5702)	0 (9333)	1 (13 523)
Sylvia atricapilla	0 (0)	8 (94)	27 (3569)	70 (83 388)	78 (167 735)	95 (302 595)
Turdus iliacus	0 (0)	2 (14)	9 (129)	13 (526)	2 (626)	2 (940)
Turdus merula	0 (1)	0 (133)	1 (1543)	1 (21 565)	0 (36 236)	0 (72 939)
Turdus philomelos	1 (1)	50 (41)	31 (423)	70 (926)	10 (12 791)	11 (30 874)
Total	53 (44)	279 (1100)	210 (20 949)	321 (329 053)	219 (610 579)	231 (1 052 619)

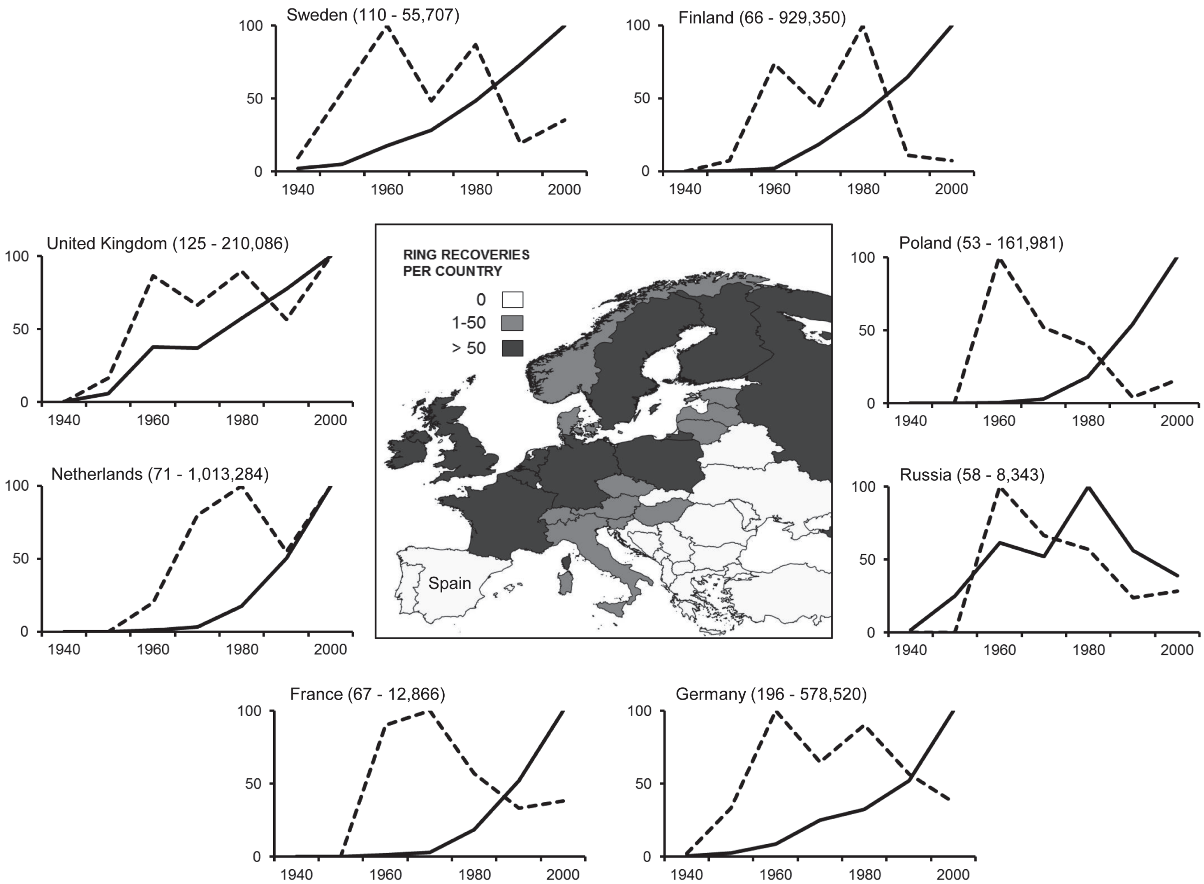

Figure 1. Temporal trends in the number of ring recoveries per decade of wintering birds in Spain (dotted lines) according to their country of origin and the total number of ring recoveries of live birds reported per country (continuous line). The number of ring recoveries in Spain and the number of ring recoveries of live birds per country are reported in parenthesis. All graphs have been re-scaled to show 100 in the largest scores. Graphs for countries with less than 50 recoveries in Spain have been omitted (Belgium has been not included due to incomplete information on ring recoveries in the EURING data bank; note that the trends in Russia can be affected by changes in the 1980s of former Soviet Union).

to analyse whether temporal changes in the number of ring recoveries were predicted by the temporal distribution of the ringing effort in Spain, showed that all but two species (the chiffchaff *Phylloscopus collybita*, $\chi^2 = 3.16$, DF = 2, p = 0.205, and the white wagtail *Motacilla alba,* $\chi^2 = 5.07$, DF = 2, p = 0.079) reported significant differences ($p < 0.001$) between observed and predicted patterns. Most species depicted a continuous loss of ring recoveries with the exception of the common linnet *Carduelis cannabina* that experienced an increase of ring recoveries during the 1990s and then decreased (Fig. 2).

Features affecting the patterns

Bird species showed a decreased rate of foreign recoveries in Spain despite the trends of European breeding populations (Fig. 3A). The relationship between the changes in CPUE indexes and the trends of breeding populations was weak (r = 0.38, p = 0.280, n = 10; Fig. 3A), particularly by the disrupting effect of the common linnet *Carduelis cannabina* (this relationship improved when this species was removed; r = 0.67, p = 0.048, n = 9). No significant effect was detected when the trends in foreign recoveries reported by CPUE indexes were arranged according to diet (ANOVA; $F_{2,7} = 0.67$, p = 0.543). However, a visual inspection of Fig. 3A suggests some emerging patterns: trends in the number of foreign recoveries of insectivorous and frugivorous birds were positively related to populations trends, with frugivorous birds showing stronger reductions in foreign recoveries than insectivorous birds. When these two groups of birds were considered together, a significant effect of population trends and diet was reported on the changes in the number of foreign recoveries gathered in Spain (GLM; population trends $F_{1,4} = 18.49$, p = 0.013; diet $F_{1,4} = 11.75$, p = 0.027; $R^2 = 0.86$, p = 0.019, n = 7).

Body mass was negatively correlated to the trends in foreign recoveries (r = −0.69, p = 0.027, n = 10) suggesting that large birds reduced their migratory movements to wintering grounds in Spain more than small birds (no effect of diet was detected on this pattern; Fig. 3B). Body mass predicted the changes in foreign recoveries better than changes in European breeding populations (GLM; body mass $F_{1,7} = 4.98$, p = 0.061; population trends $F_{1,7} = 0.29$, p = 0.604, $R^2 = 0.50$, p = 0.089, n = 10). This result did not change when only insectivorous

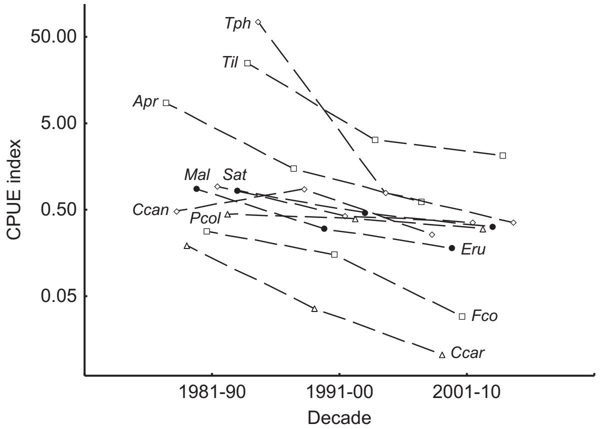

Figure 2. Trends in the number of ten species of foreign wintering birds recorded in Spain in recent decades based on an index of capture per unit of effort (CPUE; number of foreign ring recoveries in Spain/1000 birds ringed in this country). CPUE is plotted on a log10 scale. *Apr*: *Anthus pratensis*; *Ccan*: *Carduelis cannabina*; *Ccar*: *Carduelis carduelis*; *Eru*: *Erithacus rubecula*; *Fco*: *Fringilla coelebs*; *Mal*: *Motacilla alba*; *Pcol*: *Phylloscopus collybita*; *Sat*: *Sylvia atricapilla*; *Til*: *Turdus iliacus*; *Tph*: *Turdus philomelos.*

and frugivorous birds were considered in the analysis (body mass $F_{1,4} = 5.72$, $p = 0.075$; population trends $F_{1,4} = 1.69$, $p = 0.263$, $R^2 = 0.78$, $p = 0.049$, $n = 7$).

Discussion

Temporal trends in ring recoveries

The evolution of ring recoveries reported in this paper is congruent with a reduction in the number of European birds arriving to winter in Spain (Fig. 1). This statement is supported by two main features of our research. First, from a methodological perspective, it should be noted that these patterns were detected after controlling for the effects of some common biases in the use of ring recoveries, such as the uneven distribution of effort devoted over time to collecting or producing the data (Perdeck 1977, Fiedler et al. 2004). For instance, illegal bird-catching was a common activity in Spain until the 1980s, when the legal protection of small passerines was strictly applied (Santos et al. 1988). However, to control for the potential effect of this hunting pressure on ring recoveries, or on the willingness of catchers to communicate the recoveries of an illegal activity, we have only handled recoveries provided by ringing activity (Robinson et al. 2009). As in other countries, bird ringing is strongly regulated in Spain, where only trained people are authorized to handle wild birds. This guarantees high quality data with which we have applied a CPUE approach similar to that used in monitoring exploited animal populations (Maunder et al. 2006). In addition, if the decrease in the number of foreign recoveries cannot be explained by a reduction in ringing activity in Europe (Fig. 2), the most parsimonious explanation of patterns reported in this study is that the number of overwintering individuals in Spain of most species has declined.

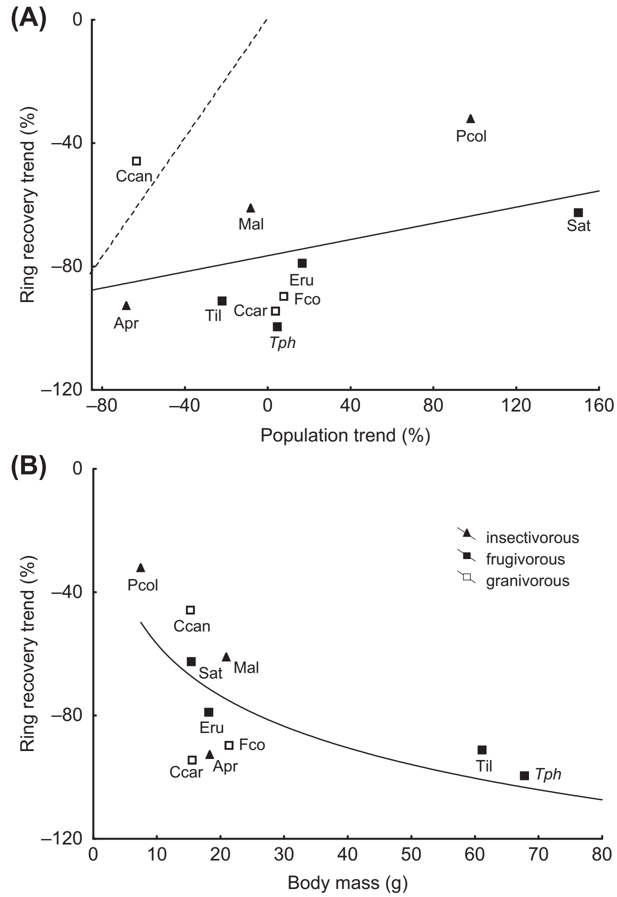

Figure 3. (A) Correlation between changes in breeding populations in Europe (horizontal axis) and the number of ring recoveries of long-distance migratory birds wintering in Spain (vertical axis) for ten passerine species since 1980. Breeding population data as % in population change between 1980 and 2010 (reported by the European Bird Census Council), and ring recovery trend expressed in number of foreign individuals recovered per 1000 ringed birds; CPUE indexes). Broken line shows the hypothetical distribution of a regression line produced by similar scores in ring recoveries and populations trends. (B) Relationships between the number of ring recoveries of long-distance migratory birds wintering in Spain and body mass (in grams) of the study species. Species are classified according to their diet: insectivorous (triangles), frugivorous (closed squares) and granivorous (open squares). Acronyms for species as in Fig. 2.

Second, the changes in the number of foreign birds arriving to winter in Spain were weakly related to the numerical trends of European breeding populations. Rather, the number of foreign recoveries of most species declined irrespective of numerical changes in their breeding grounds (Fig. 3A). It can thus be rejected that the reduction of overwintering individuals is a simple collateral effect of long-term changes in the size of the European bird populations and, alternatively, it can be interpreted as a result of the reported shift to the north of the wintering grounds of many land birds (La Sorte and Thompson 2007, Visser et al. 2009). This interpretation agrees with previous studies in which a decrease in the arrival of partial migratory species to wintering grounds in Iberia and Northern Africa has been reported (Onrubia and Tellería 2012, Tellería 2014a, b).

Effects of diet and body mass

Despite the reduced sample size (ten species), the results in this study suggest two mechanistic explanations of the reported decrease in the arrival of migratory birds to wintering grounds in Spain. First, we detected stronger losses in ring recoveries of those insectivorous and frugivorous species whose breeding populations depicted sharp reductions in Europe. In addition, after controlling for the effect of population changes, frugivorous birds experienced sharper reductions in wintering grounds. Numerical trends and diet explained a convincing 86% of variation in the number of foreign recoveries, then supporting the view that, at least for these two groups of birds, the numerical trends of European breeding populations affected the number of wintering individuals, and that this effect changed according to diet. Unfortunately, we have been unable to include granivorous finches in this explanation because of the atypical trends in the common linnet (Fig. 3A).

The increased reduction in wintering migratory frugivores in Spain supports the hypothesis of the enhanced aptitude of these fruit trackers to adjust movements to the extant availability of food if compared to other species adapted to more predictable food sources (e.g. insectivores; Levey and Stiles 1992). Great variation between years is a central characteristic of fruit–frugivore interactions, which makes the patterns observed in a year hardly generalisable to all years. This ability of wintering blackcaps, thrushes and, to a lesser extent, Eurasian robins to move according to fruit resources is usually observed in wintering grounds in Spain, where their abundances are regulated by the annual availability of fruits (Rey 1995, Tellería et al. 2008, 2014). The reported changes in the migratory behavior of the Blackcap, one frugivorous species for which foreign recoveries in Spain has declined despite the sharp increase in the European population (Fig. 3A), support this interpretation. This change of migratory schedules of this species has been related to its ability to adapt migratory journeys to increasing food availability offered by urban areas in central Europe (Berthold 2001, Bearhop et al. 2005; see also Møller et al. 2014).

Our results also suggest a comprehensive role of body mass as a predictor of the reported changes in the migratory behavior of species, with larger birds showing sharper reductions in the number of overwintering individuals (Fig. 3B). This result is congruent with the effect of climate warming on bird movements from colder areas. Wintering birds show strong preferences for warm sectors (Carrascal et al. 2012) given that low temperatures increase the risk of starvation if food is insufficient to cope with energetic demands for thermoregulation (Calder and King 1974). As a result, the northern range limits of bird species have been related to ambient winter temperatures through its effect on metabolic demands of birds that, because of the lower thermal conductance of larger species (Schleucher and Withers 2001), are negatively related to body mass (Root 1988, but see Repasky 1991). This pattern has been observed in winter bird assemblages of North America, which are composed of larger species in colder sectors (Meehan et al. 2004). Our results support the view that, in a context of climate warming, thermal constraints could play a key role in shaping the migratory behavior of birds, with larger species being the first to benefit from warming in colder regions of Europe.

Prospects

The numerical reduction in wintering migrant birds in Spain reported in this study appears to have been taking place since at least the 1970s (Fig. 2, Table 2). However, this reduction may have been in progress earlier, since several partially migratory passerines began to winter in Northern Europe in the mid-twentieth century and earlier (Møller et al. 2014). This trend is supported by the eloquent reduction in ring recoveries of Eurasian robins, chaffinches and wagtails in Spain since the 1960s reported in this study (Table 2). Since partial migratory birds maintain a high genetic variation related to migratory behavior and can change from partially migratory to resident in a few generations (Berthold 2001, Liedvogel et al. 2011, Pulido 2012), this trend seems to suggest an ongoing process. Then according to current predictions of global warming (IPCC 2013), such trends will continue to increase the number of sedentary populations in Europe and to reduce the number of overwintering birds in the Mediterranean.

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