The role of mountain ranges in shaping population-associated routes of migration: a case study of European Goldfinches in the Pyrenees

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We aimed to describe the morphologic and isotopic differences of European Goldfinches *Carduelis carduelis* according to their migratory behaviour or geographic origin. We compared morphologic and isotopic variables between birds caught in two different obligatory migratory pathways (eastern and western border of the Pyrenees) and throughout the post-breeding period (from late summer to winter). The isotopic and morphological traits varied across seasons (from autumn to winter), indicating that birds captured later in the season had traits typical of longer-distance migrants that come from regions situated further north. Moreover, our results suggest that Goldfinches caught in the eastern and western borders of the Pyrenees slightly differ in body size and in one of the two colour patch-associated traits, but not in their flight apparatus or isotopic values, these last being more strongly related to their areas of origin. Such observed regional differences, therefore, may be more strongly related to other selection pressures.

Key words: bird migration, *Carduelis*, flyways, Iberian Peninsula, morphology, stable isotopes

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Understanding spatio-temporal distribution patterns of populations during the non-breeding season is crucial to disentangle the biogeography and evolution of migration patterns and dynamics of bird populations (Newton 2004). Conditions at the non-breeding quarters can affect not only current survival, but also future survival or have individual fitness consequences through carryover effects (Roberge *et al.* 2008, Crossin *et al.* 2010). These can be studied only if birds or populations from given breeding areas can be linked to specific migration and wintering areas (Webster *et al.* 2002, Procházka *et al.* 2008, Finch *et al.* 2015).

For several passerine species with a broad distribution range across Europe, it is common to find a variety of migratory behaviours, from obligate migration to sedentary (Berthold 1996, Newton 2008). As a general pattern in Europe, it can be stated that populations of the same species breeding further to the north and east are more often migratory than those breeding further to the south and west (Fiedler 2005, Newton 2008, Förschler & Bairlein 2010, Andueza *et al.* 2013). Every year, the Mediterranean countries receive huge numbers of migrants coming from Northern Europe, which either cross the continent *en route* to their wintering sites in Africa or overwinter in Southern Europe. Iberia acts as either one of the main winter destinations or as a region of passage to West African winter quarters for several passerine species breeding in areas located further north and east (Tellería *et al.* 1996, 1999). The Pyrenees acts as a migration barrier for birds, so that main migratory flows entering Iberia in autumn pass through obligatory migratory pathways, either the western or eastern border of the Pyrenees (Galarza & Tellería 2003, Arizaga *et al.* 2015). It has been shown in several species, that migrants entering through the western edge of the Pyrenees come from more western origin regions, whereas those passing through the eastern edge have more eastern origins (Arizaga *et al.* 2012, Andueza *et al.* 2013), indicating parallel migration patterns.

During the non-breeding period, local Iberian birds are often sympatric with northern visitors (Tellería et al. 1999). The degree of sympatry among all these populations is still poorly known. Attempts to disentangle to what extent local breeders share the space with migrants coming from abroad during the nonbreeding period are scarce. In passerines, the majority of studies have focused on European Robins Erithacus rubecula or Eurasian Blackcaps Sylvia atricapilla in southern Iberia (Telleria et al. 2001, Perez-Tris & Telleria 2002, Domínguez et al. 2007, De la Hera et al. 2012, 2018); another study focused on whether local breeding Common Reed Warblers Acrocephalus scirpaceus shared their breeding sites with migrants from abroad during the autumn migration period in northern Iberia (Pagaldai & Arizaga 2015). The observed patterns vary substantially among species and regions: while in some cases resident birds tend to occupy the best habitats at a micro-scale level and, hence, the winter visitors occupy suboptimal habitats (e.g. Tellería et al. 2001), in other species those birds breeding in a given zone could disappear and be replaced by individuals coming from abroad (Domínguez et al. 2007). A third option would be that local breeding and migrant populations coexist without an obvious spatial segregation even at a micro-scale level (Pagaldai & Arizaga 2015).

A number of methods have been suggested to identify, or at least to differentiate, the relative origin and migratory behaviour of bird populations, including biometric and chemical approaches. For example, wing length and wing pointedness tend to increase with migration distance, while the tail/wing length ratio tends to be smaller (Mönkkönen 1995, Fiedler 2005, Arizaga *et al.* 2006, Delingat *et al.* 2010). As a consequence, and for Iberia in particular, local birds (defined as those that breed in Iberia) should be expected to have a shorter and less pointed wing and larger tail/wing length ratio as compared to those coming from abroad (i.e. having longer migration distances) during the non-breeding period. In parallel, stable isotopes also have been successfully used to describe the origin of given birds or populations (Hobson & Wassenaar 1997, Hobson et al. 2004). Across Europe, feathers grown in areas located further to the north and east show decreasing (more negative) signatures of deuterium (δ^2 H), which hence could be used as a proxy of birds' region of origin (Yohannes et al. 2005, Procházka et al. 2008, Gil et al. 2014). Finally, feather quality may be also used as a proxy of a birds' origin. In particular, more migratory bird populations have been reported to have relatively lower-mass feathers (i.e. a smaller mass/length ratio) when compared with sedentary populations of the same species (de la Hera et al. 2009). Feather colour patches might also be used as a proxy of feather quality, which might have a relationship with origin.

The European Goldfinch Carduelis carduelis is a widely distributed Western Palearctic species (Cramp & Perrins 1994). Northern populations are migratory and southern populations are sedentary, while those breeding at middle latitudes behave as true partial migrants with some individuals being resident and others migratory (Cramp & Perrins 1994). Iberia hosts from fully resident to partial migrant Goldfinch breeding populations, together with the bulk of migrants from abroad present from autumn to spring (Asensio 1986). According to previous phenological and morphological analyses, in September in northern Iberia most Goldfinches are local and from October to December, migrants from abroad are present and possibly mixing with local birds that may stay at their breeding sites for the whole annual cycle (Tellería et al. 1999, Arizaga et al. 2009). Moreover, using ring-recovery data, Asensio (1986) detected evidence supporting parallel migration in Goldfinches, with birds entering through the western part of the Pyrenees coming from more western regions than those passing through the eastern Pyrenees.

In this paper we aim to test whether birds coming from potentially different origins occur differentially in the eastern and western border of the Pyrenees (i.e. two different obligatory migratory pathways), throughout the post-breeding period (from late summer to winter). With that goal, we used the morphological and isotopic traits to infer these different areas of origin. We did not aim to identify the individual origin of each bird, but characterize the mean values obtained at different times, assuming that those values would belong to a representative sample of those populations which would be present at each site in each moment. We hypothesized that (1) Goldfinches caught late in summer (local breeders) differ from those caught during autumn migration or winter (migrant and winter visitors), the latter being expected to have longer and more pointed wings and a larger tail/wing length ratio as a consequence of the arrival or passage of birds more adapted to longer-distance movements (Tellería et al. 1999). (2) Since wintering birds hypothetically would come from areas located further north and east, they should be expected to have more negative δ^2 H values than those captured in late summer. Moreover, latesummer birds would be expected to have feathers of a relatively higher quality than those from birds captured in autumn or winter. (3) Goldfinches passing through the eastern part of the Pyrenees come from regions situated far to the east as compared to birds passing through the western part of the Pyrenees (Asensio 1986); a phenomenon also found in other passerines (Andueza et al. 2013). In this context, 'eastern' Goldfinches should exhibit traits more typical of longdistance migrants as compared to 'western' Goldfinches.

METHODS

Sampling area and data collection

Data were obtained in northern Iberia, both at the western and eastern edge of the Pyrenees. Goldfinches were caught in two localities from the Basque Country (W Pyrenees) and 15 localities in Catalonia (E Pyrenees), with mist and pull nets (Bub 1995), from September to December 2015. The localities in the W Pyrenees were situated in an Atlantic mosaic of meadows and forests and those from the E Pyrenees in a Mediterranean agroforestry mosaic of herbaceous and perennial crops combined with small forests and shrublands.

Once captured, each bird was ringed and its age and sex determined (Svensson 1996). The age was determined by looking for moult limits among the wing feathers (mostly within the greater coverts and tertials, since first-year birds undergo a partial moult and adult birds a complete moult (Svensson 1996). The sex was determined using a combination of characteristics, including amount of red on the head, presence of small black feathers in the nostrils and amount of black and brown in minor coverts (Svensson 1996). In addition, the following variables were measured: wing length (method III by Svensson 1996; accuracy ± 0.5 mm), tail length (±0.5 mm), primary feathers lengths (P1 to P9, number from innermost to outermost; ±0.5 mm), tarsus length (± 0.1 mm) and head-and-bill length $(\pm 0.1 \text{ mm})$. Also, the left and right P1's were collected in order to (1) measure additional feather-associated characteristics (length, mass, full feather area and yellow and white patch areas; Figure 1; these were taken from right P1), and (2) perform stable isotope analyses (left P1). As in most passerines, adult Goldfinches complete post-breeding moult close to their breeding quarters (July-August) with the replacement of the inner most primary feather (P1; Underhill & Zucchini 1988, Jenni & Winkler 1994). On the other hand, first-year birds undergo a partial post-breeding moult without affecting P1 (Jenni & Winkler 1994). Therefore, the isotopic values of P1 can be used to infer the breeding zones of a bird given that both age classes have replaced it in or near these zones.

Only those birds with their age and sex known were considered, and given the low sample size of adult birds, we only considered the analyses of first-year birds, i.e. 49 and 186 birds for W and E Pyrenees, respectively (for further details see Table 1). Birds in active moult were not used for the analyses, since they might show biased values of their wing or tail lengths. Feather and color patch areas (Figure 1) were measured using imageJ software (Schneider *et al.* 2012). The mass of P1 feathers were measured with a microscale (\pm 0.01 g accuracy).

Table 1. (Goldfinches cap	tured in the eastern a	and western Pyrenee	s, with at least one	e of the variable	s from Table 3 measured.
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		Western				Eastearn			
	Firs	t-year	Adults		First-year		Adults		
	Male	Female	Male	Female	Male	Female	Male	Female	
September	7	8	0	0	9	10	3	3	
October	5	3	1	2	23	23	0	6	
November	9	13	3	3	13	17	3	3	
December	1	3	0	0	31	60	2	9	
Totals	22	27	4	5	76	110	8	21	



Figure 1. Scheme of the P1 primary feather, with the white patch (WP) and yellow patch (YP) indicated.

Biometric and feather quality analysis

We analysed the biometric and feather quality variation from September (when we only capture local breeding birds) to December (when migrant wintering birds have already arrived). Ten variables were used in the analyses and these were lumped into three categories: (1) body size-associated: wing length, tail length, tarsus length, head-bill length, (2) wing morphologyassociated: (longest primary–P1)/wing length, tail length/wing length, (3) feather quality-associated: P1 length/P1 mass, P1 area/mass; yellow colour-patch area/P1 area, white colour-patch area/P1 area (P1Y, P1W, respectively).

Stable isotopes analyses

All feathers were cleaned of surface oils using a triple 2:1 chloroform:methanol rinse and prepared for stablehydrogen isotope analysis. The $\delta^2 H$ analyses were carried out following Wassenaar & Hobson (2003), with calibrated keratin-isotope reference materials to account for the H-exchange. Measurements of $\delta^2 H$ were performed on H² from the high-temperature flash pyrolysis (1350°C) of the feathers with a HEKAtech HT-O AnalyzerTM linked to a Elementar IsoprimeTM continuous-flow isotope-ratio mass spectrometer. All δ^2 H values were given in delta notation, in units per mille (%) and normalized on the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) scale. Repeated analyses of δ^2 H inter-comparison material IAEA-CH-7 (-100‰) and laboratory keratin references yielded within-run repeatability (n = 5) of < 2% and a long-term (6month running average) repeatability approximately ±3.2‰.

Statistical analysis

All variables were filtered in order to remove extreme outliers. This filter was carried using a box-plot for each variable and then removing those values identified as extreme outliers. Preliminary analyses were run using univariate linear models (ANOVA) on each variable with zone (Eastern, Western) and sex (male, female) as factors and date as a covariate, with interactions. However, due to the high number of tests we had a high risk of type 1 errors (significant results by chance). Therefore, we conducted a Principal Component Analysis (PCA) with all the variables, except δ^2 H (for

Table 2. Factor loadings from a Principal Component Analyses (PCA) on ten morphological and feather quality related traits of firstyear Goldfinches caught from September to December in the eastern and western Pyrenees. Abbreviations given in Methods.

Factor	PC1	PC2	PC3	PC4	PC5
Wing length	+0.478	-0.149	-0.202	+0.346	-0.242
Tail length	+0.429	-0.448	+0.288	-0.055	+0.011
Tarsus length	+0.248	-0.224	-0.267	-0.259	-0.055
Head-bill length	+0.322	-0.222	-0.457	+0.056	-0.144
(LP–P1)/Wing length	+0.071	+0.028	-0.248	+0.234	+0.801
Wing/Tail length	-0.091	+0.406	-0.521	+0.365	-0.223
P1 length/P1 mass	-0.449	-0.494	-0.169	+0.110	-0.050
P1 area/P1 mass	-0.442	-0.497	-0.173	+0.137	-0.053
P1W/P1 area	-0.089	+0.124	-0.304	-0.653	-0.229
P1Y/P1 area	+0.067	-0.074	-0.335	-0.402	+0.410
Eigenvalue	2.35	1.87	1.63	1.12	1.01
Explained variance (%)	23.5	18.7	16.3	11.1	10.1

which the sample size was much smaller; for details see Table S1). All Principal Components (PC) with an eigenvalue > 1 were then introduced as an object variable in univariate linear models with zone and sex as factors and date as covariate, with interactions. Statistics were done using R software (R Core Team 2014). In addition, we also conducted a Discriminant Function Analysis (DFA) in order to determine whether Goldfinch populations captured in the eastern or western Pyrenees can be separated according to the traits we measured. We used for this goal the 'lda' function of the package MASS in R (Venables & Ripley 2002). The DFA was run using the scaled raw variables and not the components from the PCA.

RESULTS

Five variables varied in relation to zone, date and sex, and only variables connected to feather quality did not (Table S1). Furthermore, we obtained few significant interactions, so the variation due to zone, date and sex was mostly additive.

The PCA with biometric measurements and feather quality related traits resulted in five PC's with an eigenvalue > 1. However, we considered only the first two, because they summarized sufficiently well both the size and the morphological relationships between variables. Overall, PC1 had positive, high factor loadings for the four main biometric traits (wing, tail, tarsus and headbill length), hence being associated with body size. PC1 also showed high, though negative, factor loadings with P1-length/P1-mass and P1-area/mass, indicating a positive association with birds with feathers of relatively lower quality. PC2 showed negative factor loadings for the P1-length/P1-mass and P1-area/mass, and was also positively associated with higher wing/tail ratios and shorter tails. PC2, therefore, may be positively associated with migratory behaviour, since migrant bird populations typically have proportionally



Figure 2. Marginal-effect plot representing the effect of date and sex on (A) PC1 and (B) PC2 scores, as obtained from models shown in Table 3. Both graphs show values for each sex separately.

longer wings and flight feathers of lower quality. PC3 showed high, negative factor loadings with the wing/tail ratio. PC3 associated negatively with colour patch size, head size and, to a lesser extent, wing and tarsus size, potentially being negatively correlated with migratory behaviour (and positively with sedentary behaviour). PC4 showed very high, negative factor loadings for the relative size of the yellow and white

Table 3. Results from ANOVAs used to test for the effect of zone (Z), date (D) and sex (S) on PC1 and PC2 (Table 2) on the morphological and feather quality related variables measured in Goldfinches caught from September to December in the eastern and western Pyrenees. Within each cell, we show the *F*- and *P*-values (*P*-values in parenthesis).

Factor:	Z	D	S	Z×D	Z×S	D×S	Z×D×S
df residual: 174	1	1	1	1	1	1	1
PC1	1.72 (0.192)	26.92 (<0.001)	51.41 (<0.001)	0.00 (0.996)	0.00 (0.999)	1.57 (0.212)	0.026 (0.872)
PC2	0.47	11.09	5.73	0.01	0.12	4.03	0.01
	(0.496)	(0.001)	(0.018)	(0.936)	(0.731)	(0.046)	(0.907)

patch in P1; to a lesser extent PC4 also had positive factor loadings with wing and wing/tail ratio, indicating relative length of wings. Finally, PC5 had very high, positive factor loadings for the wing-morphology associated variable, indicating relative length and pointiness of the wings. Overall, it seems that, apart from PC1 (associated with body size), PC2 to PC5 were correlated with migratory phenotype. Thus, in order to simplify the interpretation of our results, all analyses were limited to the first two PC's.

Univariate analyses revealed different patterns, depending on which PC was analysed (Table 3). We mostly detected single factor (i.e. additive) effects, with a few interactions. Date showed an effect on PC1 and PC2 (Figure 2). In particular, those birds captured later in the season had a larger body size but shorter bills, smaller colour patches and lower quality flight feathers. Sex also had a significant effect on PC1 and PC2, interacting with date in PC2 (Table 3, Figure 2). Overall, males were found to have larger body size and larger colour patches than females, and later in the season lower quality flight feathers.

The δ^2 H did not vary between regions and sex classes, but was observed to covary with date (Table S1), with birds captured later in the season having a lower isotopic value (Figure 3).



Figure 3. Marginal-effect plot (mean \pm 95% CI) representing the effect of date on deuterium signature (δ^2 H). Model shown in Table S1.

The DFA classified 74.2% of the birds correctly. By region, the percentage of correct classifications was higher in the East Pyrenees (83.0%) than in the West Pyrenees (52.6%). Selecting only those birds captured in November and December did not improve the DFA (percentage of correct classifications: 61.0%, East Pyrenees: 65.2%, West Pyrenees: 55.6%).

DISCUSSION

This study helps to disentangle the biogeographic patterns of migratory Goldfinch populations in western Europe. As we hypothesized, Goldfinches did not have the same biometric and feather quality characteristics across the sampling period. Those captured in September were smaller, with shorter wings and tails and a broader white wing patch. In a previous study, carried out at the western Pyrenean border, Arizaga et al. (2009) found that birds in winter had longer wings and tails and more pointed wings than those caught in autumn, supporting the influx of northern visitors in winter. Our results also support this pattern; therefore, Goldfinches in September should be mostly (if not entirely) local, which is also supported by ring-recovery analyses (Asensio 1986). In addition, Goldfinches caught late in the season had lower isotopic values suggesting a more northern/north-eastern origin (Hobson et al. 2004), in line with the morphological analyses. White wing areas are known to wear more rapidly than feather parts with melanin, becoming disadvantageous for flight (Bonser 1996). Our results are compatible with the idea that northern visitors migrate a longer distance and thus need stronger flight feathers with proportionally smaller white patches as an evolutionary adaptation to migration (Berthold 2001).

According to our hypothesis, wing length, the two skeletal measurements associated to body size (tarsus, head-bill length) and one of the two variables associated with feather quality (relative yellow patch area of the innermost primary feather) varied between the western and eastern Pyrenees. Goldfinches caught in the eastern Pyrenees showed on average longer wings, larger body size and had a proportionally broader vellow patch, independently of the period and sex. The on average longer wing found in the east was compatible with the idea that these Goldfinches would come from areas situated further to the north-east (Förschler & Bairlein 2010). Discriminant analyses were able to correctly classify just 75% of all samples. Contrary to other passerine birds (Andueza et al. 2013), biometrics and isotopes (deuterium) alone did not seem to be enough to distinguish between populations of Goldfinches occurring in the two studied regions. Probably, a larger data set and extending sampling over more years may improve this analysis.

In conclusion, the morphological feather quality and isotopic traits varied across the season (from autumn to winter), and this was likely to be associated with the origin of populations. Birds captured later in the season had morphological and isotopic traits typical of longer-distance migrants that would come from regions situated further north. This phenomenon has also been observed in other passerine birds, both in autumn (Arizaga & Barba 2011) and spring (Maggini et al. 2013). hence, the biometrics and deuterium levels can be used to detect the appearance of Goldfinches of northern European origin in Iberia, although we have not been able to correctly distinguish all birds from eastern and western populations. To conclude, our results suggest that Goldfinches caught at the eastern and western border of the Pyrenees slightly differ in body size and in traits associated with one of the two colour patches, but do not differ in wing size and shape and the deuterium signature, which would be more strongly related to their areas of origin. Such observed regional differences, therefore, might be more strongly linked to other selection pressures, such as local adaptations to particular main food supplies or climatic conditions at each region (Carbonell et al. 2003).

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SAMENVATTING

Wij onderzochten de variatie in morfologie en isotopenwaarden van Europese Putters *Carduelis carduelis* die in de herfstperiode aan de oost- en westkant van de Pyreneeën waren gevangen. De onderzochte kenmerken varieerden in de loop van het seizoen. De gegevens wijzen erop dat vogels die later in het seizoen werden gevangen, uit hoognoordelijke broedgebieden afkomstig waren. De Putters aan weerszijden van de Pyreneeën, verschilden enigszins in lichaamsgrootte en in een van de twee kenmerken van de kleurvlakken op de vleugels. Daarentegen werden geen verschillen gevonden in vleugellengte en vleugelvorm en in de isotopenwaarden (van de laatste wordt aangenomen dat die zijn gerelateerd aan de herkomstgebieden van de vogels). De waargenomen regionale verschillen hangen daarom mogelijk samen met andere selectiefactoren dan de geografische herkomst.

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SUPPLEMENTARY MATERIAL

Table S1. Results from ANOVAs used to test for the effect of zone (Z), date (D) and sex (S) on each variable. Within each cell, we show the *F*- and *P*-values in parenthesis, ns = non-significant: P > 0.05). Other abbreviations: LP: longest primary feather, P1: innermost primary feather length, P1W: P1's white colour patch area, P1Y: P1's yellow colour patch area.

	Factor	Z	D	S	Z×D	Z×S	D×S	Z×D×S
	df	1	1	1	1	1	1	1
Body size-associated	1:							
Wing length		6.59	12.62	118.56	0.45	3.11	0.05	1.30
df residual: 225		(0.011)	(0.001)	(<0.001)	(ns)	(ns)	(ns)	(ns)
Tail length		0.14	28.90	25.57	3.53	0.85	0.44	0.24
df residual: 216		(ns)	(<0.001)	(<0.001)	(ns)	(ns)	(ns)	(ns)
Tarsus length		22.17	1.25	7.43	1.10	0.22	0.14	0.07
df residual: 203		(<0.001)	(ns)	(ns)	(ns)	(ns)	(ns)	(ns)
Head-bill length		7.96	2.97	48.72	0.00	0.27	1.28	0.36
df residual: 197		(0.005)	(0.086	(<0.001)	(ns)	(ns)	(ns)	(ns)
Wing morphology-a	ssociated	l:						
(LP-P1)/Wing length		0.09	0.75	1.30	4.30	0.45	3.53	9.74
df residual: 225		(ns)	(ns)	(ns)	(0.039)	(ns)	(ns)	(0.002)
Wing/Tail length		3.93	15.06	5.62	10.26	3.58	0.86	0.83
df residual: 214		(0.049)	(ns)	(0.019)	(0.002)	(ns)	(ns)	(ns)
Feather quality-asso	ciated:							
P1 length/P1 mass		0.05	1.94	2.61	0.27	0.22	2.68	0.24
df residual: 205		(ns)	(ns)	(ns)	(ns)	(ns)	(ns)	(ns)
P1 area/P1 mass		0.14	2.07	2.11	0.49	0.41	2.88	0.47
df residual: 205		(ns)	(ns)	(ns)	(ns)	(ns)	(ns)	(ns)
Color patch-associat	ted:							
P1W/P1 area		2.73	14.17	0.56	0.10	4.84	0.23	0.11
df residual: 204		(ns)	(<0.001)	(ns)	(ns)	(0.029)	(ns)	(ns)
P1Y/P1 area		9.98	1.67	8.32	1.54	0.70	0.03	2.45
df residual: 205		(0.002)	(ns)	(0.004)	(ns)	(ns)	(ns)	(ns)
Stable isotopes:								
$\delta^2 H$		0.46	4.82	0.04	0.26	1.01	0.12	0.00
df residual: 73		(ns)	(0.031)	(ns)	(ns)	(ns)	(ns)	(ns)