Stable isotopes in a southern European crossbill population indicate restricted movement between regions with different pine species

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Abstract

The adaptation of irruptive birds to breed where they find abundant food allows them to be highly mobile and ubiquitous and opens a debate on the ecological and evolutionary impact of this behavior. Using δ^2H analyses, our aim here was to test whether the density fluctuation in a southern European crossbill population is caused by movements of irruptive northern European crossbills or of crossbills from nearby. Sampling was carried out in the western Pyrenees during four consecutive breeding seasons (2009–2012). During these four years, 2009 was a year with a much higher number of captures per day and this coincided with an invasion of crossbills in northern Europe. Only two out of 160 crossbills showed clear isotopic signatures of a northern European origin (and both were caught in 2009). Moreover, in 2009, we recaptured a bird ringed in The Netherlands. Otherwise, we found no differences among years in δ^2H and no significant effect of wing length (indicative of a northern origin) or residency status (long-term recaptures vs. non-recaptures) on δ^2H. Wing length also did not vary among these four years. Therefore, our results suggest that annual variation in local crossbill abundances is not only due to the movements of northern irruptive birds, but also to a large part due to the influx and local reproduction of individuals of Iberian origin. The lack of annual variation in isotopic signatures and similarity with values from a nearby mountain area with the same food resource (the pine *Pinus sylvestris*) suggests that movements are primarily between areas with the same type of resource. Thus, our results support recent morphological and genetic studies that indicate that crossbill populations within Iberia are not structured geographically but by resource use.

Introduction

Irruptive animals have the capacity to occupy very large geographic areas in short time periods. Their adaptation to breed where they find abundant food allows them to be highly mobile and ubiquitous and opens a debate on the ecological and evolutionary impact of this behavior (Summers, 1999; Benkman, 2003; Edelaar, Summers & Iovchenko, 2003; Edelaar *et al.*, 2012). Thus, their high natal and breeding dispersal would typically be expected to result in a genetically and ecologically homogeneous population (Lenormand, 2002; Coyne & Orr, 2004). However, recent studies suggest that this may not always be the case (Edelaar *et al.*, 2012).

A good example of this modern insight is the case of the common crossbill *Loxia curvirostra*. This species is a paradigmatic example among irruptive birds (Newton, 1972, 2006). In Europe, it breeds in association with several coniferous species, from a number of pines (*Pinus* spp.) in regions from

southern Europe fringing the Mediterranean Sea to mostly Norway spruce *Picea abies* within the boreal region in northern Europe (Cramp & Perrins, 1994). It has been reported that southern European crossbills (from now on: southern crossbills) are highly residential (e.g. Génard & Lescourret, 1987; Massa, 1987; Senar *et al.*, 1993; Edelaar *et al.*, 2012). In contrast, northern European crossbills (from now on: northern crossbills), in particular when associated with Norway spruce, make periodic irruptions that can reach south-western Europe (Newton, 2006). Thus, the presence of northern crossbills in Iberia is well documented (Cramp & Perrins, 1994; Borras & Senar, 2003; Newton, 2006). A recent analysis of apparent survival in crossbills in the Pyrenees has shown that many birds are resident (Alonso & Arizaga, 2013), indicating that a resident population occurs, presumably adapted to utilize Scots pine *Pinus sylvestris* (Alonso *et al.*, 2006; Edelaar *et al.*, 2012). Nevertheless, the population in this area fluctuates a great deal, suggesting that birds from elsewhere

also enter the local population every now and then. Given the presumed overall residency of southern crossbills, it was hypothesized that these more temporary members of the population are northern crossbills. Indeed, for our population, we documented evidence of long-term (>1 year) presence of presumably northern crossbills (Alonso & Arizaga, 2013), although genetic studies revealed that these northern birds differ genetically from those found in Spain, suggesting that most of them must stay for shorter periods and do not reproduce (Björklund, Alonso & Edelaar, 2013). However, because morphology alone is insufficient to identify birds as being northern or southern crossbills, it remains unclear whether these local population fluctuations are entirely because of the irruptions of northern crossbills or whether southern birds from elsewhere could also enter and leave the population.

This is important, as Edelaar *et al.* (2012) suggested that in Iberia several differentiated crossbill populations coexist, each specialized in exploiting a certain conifer species. They reported morphological, vocal and genetic differences (Summers & Jardine, 2005; Alonso *et al.*, 2006; Edelaar *et al.*, 2012). Moreover, they established that differentiation did not show the classical pattern of isolation-by-distance, but a pattern of isolation-by-ecology. This then implies that Iberian crossbills should move sufficiently such that dispersal among local populations specialized to the same pine species caused genetic cohesion, but without dispersal causing too much gene flow among populations using different pines as this would erase divergence. These results then predict that the fluctuations in our population may in fact be caused not only by immigration of northern crossbills, but also by immigration of southern crossbills from elsewhere in Spain. In this last case, the results predict that immigrants into our population should come from other populations using the same pine and not from populations using different pines. Given the relatively low and patchy ringing effort for crossbills in Iberia and elsewhere, the question of whether local density fluctuations are due to irruptions from northern Europe to Spain or due to movements within Spain cannot be settled by the ringing data.

The use of δ^2H can help to assess the origin of crossbills during irruptions (Marquiss, Hobson & Newton, 2008; Marquiss *et al.*, 2012). Given the existing isotopic gradient for δ^2H across Europe (Hobson *et al.*, 2004) and based on previous studies (Marquiss *et al.*, 2008, 2012), it can be stated that northern crossbills should have more negative (lower) values (characteristic range: −110 to −160‰) than southern ones (with expected values >−100‰). In Spain, crossbills using Scots pine or Mountain pine *Pinus uncinata* in the Pyrenees have lower values than crossbills using Aleppo pine *Pinus halepensis* in the more southern valleys and coastal areas of Spain (Arizaga, Alonso & Hobson, 2014). Accordingly, if immigrant crossbills in the Pyrenees are mostly northern birds, a clearly bimodal pattern for the δ^2H distribution is expected: the more negative peak should correspond to the fraction of northern crossbills, while the more positive peak should correspond to the fraction of local birds. By contrast, if these immigrant birds come from other Pyrenean areas, no
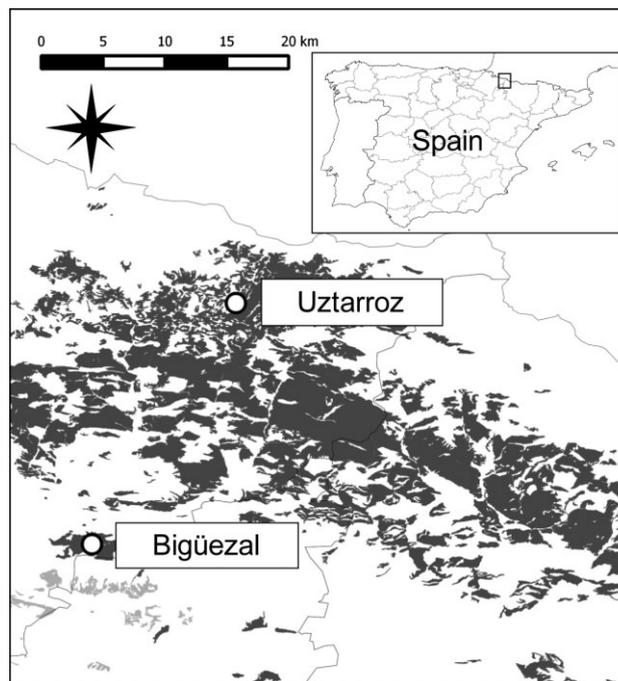
Figure 1 Geographic location of the two sampling localities in the western Pyrenees (North of Spain). Dark grey shadow area: Scots pine distribution. Pale grey shadow area: Aleppo pine (*Pinus halepensis*) distribution.

bimodal isotopic pattern is expected because of the relatively similar expected δ^2H values across this region (Hobson *et al.*, 2004). If these immigrant birds come from other Iberian areas with lower altitude and latitude, a bimodal pattern is also expected, but in this case the more negative peak should correspond to the fraction of local Pyrenean birds, while the more positive peak should correspond to the fraction of more Mediterranean crossbills.

Using δ^2H analyses, our aim here was to check where the apparently immigrant crossbills at our southern European locality come from, in order to understand better how crossbills manage to undergo adaptive divergence because of differential resource use despite being a potentially very mobile bird.

Material and methods

Study area and data collection

This study was carried out in the western Pyrenees (Navarra, North of Spain). Crossbills were sampled at two nearby sampling points (Fig. 1): Uztarroz (42°53' N 01°00' W, 1340 m a.s.l.), Bigüezal (42°40'N 01°08'W, 1100 m a.s.l.; Fig. 1). Data from these two sites were lumped for the analyses and considered as a single sampling unit as the possible isotopic variations between the two relatively nearby sites should be negligible (Marquiss *et al.*, 2012). Sampling sites were found in

mature forests of Scots pine, the dominant conifer species within the region (Loidi & Báscones, 2006).

Crossbills within our area have a main breeding season that starts in November–December and lasts until June (Alonso & Arizaga, 2011; D. Alonso, pers. obs.). This timing is tied to seed crop production by Scots pine, with the new, first seeds becoming available in late summer and the last ones dropping in late spring. Therefore, during summer, crossbills often disperse to other sites in search of food and new cone crops. Accordingly, as conducted in other studies (Newton, 2006; Edelaar *et al.*, 2012), we divided the study period not into calendar years but into 'crossbill' years, here defined as the period starting in November up to June of the next year, such that the samples of the same crossbill year belong to the same breeding population. Thus, for example year 2009 corresponds to the first six months of 2009 plus November and December of 2008.

Sampling was carried out during four consecutive 'crossbill' years (2009–2012), with a constant catching effort in each year (see succeeding text for details). Therefore, year-associated variations in the number of captures would show that local crossbill densities differ among years. A 6.6% of all captured crossbills are recaptured in subsequent crossbill years, suggesting that a substantial part of the population is resident (Alonso & Arizaga, 2013). Therefore, we infer that years with a higher number of captures per day represent years in which influxes of crossbills from elsewhere have occurred. For 2009, this is supported by a recapture (in January) of an individual ringed in The Netherlands.

The sampling protocol consisted of visiting each sampling site once every 2 weeks. Crossbills were captured with mist nets (16 mm mesh, 2.5 m high). At each site, we always used the same number of mist nets (linear meters: Uztarroz, 12 m; Bigüezal, 24 m), placed always at the same locations. Mist nets were open for a period of 4 h starting at dawn. Mist nets were placed around sites where birds gathered to ingest minerals (salt deposits at Bigüezal, a cattle-rail composed of stones at Uztarroz). Once captured, the sex of each bird was identified following Svensson (1996). According to feather color, form and wear, crossbills were aged as juveniles, second-year or older birds. Juveniles were crossbills in full or partial juvenile plumage; second-year crossbills were birds which have finished a nearly complete post-juvenile moult which affects all body feathers, but retaining juvenile flight feathers and normally a few inner greater wing coverts; older birds are crossbills which have performed a complete post-breeding moult; hence, they have no juvenile feathers left (Jenni & Winkler, 1994).

Because we were interested in assessing the origin of crossbills breeding within our area, only mature, potentially breeding crossbills (i.e. second-year and older birds) were considered for the analyses here. In these adult birds, we measured wing length (method III by Svensson, 1996) with 0.5 mm accuracy. In addition, we took from each bird the innermost primary feather (P1), which in second-year birds was a juvenile feather (i.e. grown when the bird was still a nestling), while in older birds, this was a feather moulted after breeding. This P1 was used for the δ^2H analyses. P1 within our region is replaced mostly before June (Alonso & Arizaga, 2011), so

northern crossbills reaching the Pyrenees during the second half of the year (Newton, 2006) should have replaced P1 in areas further north. However, if some of these irruptive birds stay >1 year in the area (Alonso & Arizaga, 2013), these will moult the P1 in the Pyrenees and, therefore, show local isotopic signatures. However, these long stays seem to be rare within the region, as shown by genetic studies (Edelaar *et al.*, 2012; Björklund *et al.*, 2013), and hence the effect of this bias should be minimal.

Stable isotope analyses

We used P1 (first primary feather) measurements of δ^2H because this isotope is well associated with spatial and climatic variables (Hobson *et al.*, 2004). For crossbills in particular, δ^2H has been successfully used to disentangle the geographic origin at continental scales (Marquiss *et al.*, 2008, 2012). P1 grows in (second-year/older birds) or presumably close (some older birds) to breeding sites; hence it is associated with a crossbill's origin.

Isotopic analyses were performed at the Stable Isotope Laboratory of the Biological Station of Doñana (LIE-EBD, Spain; www.ebd.csic.es/lie/Home.html). All feathers were cleaned of surface oils using a 2:1 chloroform:methanol rinse and dried (in an oven) overnight at 40°C. Samples were milled and homogenized in a Mixer Mill MM 400 (Retsch, Haan, Germany) and *c.* 300 μg of powdered material was placed into silver capsules for δ^2H determinations. Isotope measurements were performed on H_2 derived from high temperature conversion by means of a Flash HT Plus Elemental Analyzer coupled to a Delta-V Advantage isotope ratio mass spectrometer via a Conflo IV interface (Thermo Fisher Scientific, Bremen, Germany). The reactor temperature controller was set at 1450°C and the gas chromatography temperature was maintained at 85°C. The δ^2H analyses were carried out following methods described in Wassenaar & Hobson (2003), using calibrated keratin-isotope reference materials in order to avoid effects of H exchange with ambient water vapor. The typical sequence of samples and reference for δ^2H calibration in keratins was three reference materials followed by nine feathers samples. The reference materials used are CBS (Caribou Hoof Standard), KHS (Kudu Horn Standard), supplied by Environment Canada (Saskatoon, SK, Canada), and PA (Razorbill feathers), a working standard prepared in the laboratory. All δ^2H values are reported in δ-notation, in units per mil (‰), and normalized on the Vienna Standard Mean Ocean Water scale. Analytical reproducibility of references and samples was ±2‰.

Data analyses

Except for two outliers with very low δ^2H values, the δ^2H distribution showed a unimodal pattern (mean: −110.0‰, SD = 9.6‰; Fig. 3). Excluding these two outliers for now, we ran a general linear model (GLM) on δ^2H values with age, sex and year as factors, and sample weight and wing length as covariates. We included wing length as a covariate as long-winged crossbills in the Pyrenees are more likely to come from

Table 1 Number of crossbills sampled from 2009 to 2012 at two nearby sampling places in Navarra (west Pyrenees)

Year	2Y-Male	2Y-Female	>2Y-Male	>2Y-Female	Total
2009 (November 2008–June 2009)	8	8	0	1	17
2010 (November 2009–June 2010)	10	10	21	20	61
2011(November 2010–June 2011)	4	4	2	0	10
2012(November 2011–June 2012)	10	10	28	26	74

Abbreviations: 2Y, second-year crossbills; > 2Y, older birds. Year refers here to a 'crossbill' year, starting in November of one year up to June of the next one. Thus, year 2009 refers to the period from November of 2008 up to June of 2009. The number of samples does not reflect the number of crossbills caught (see Fig. 2).
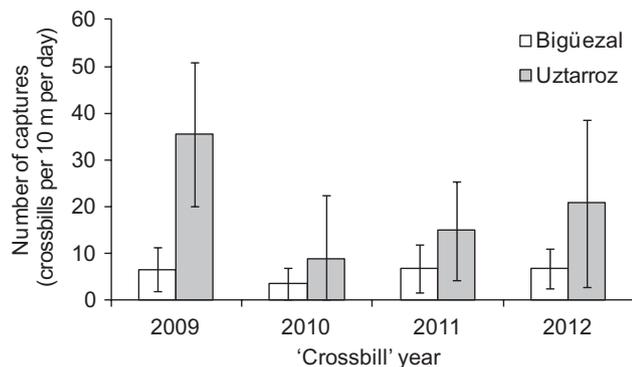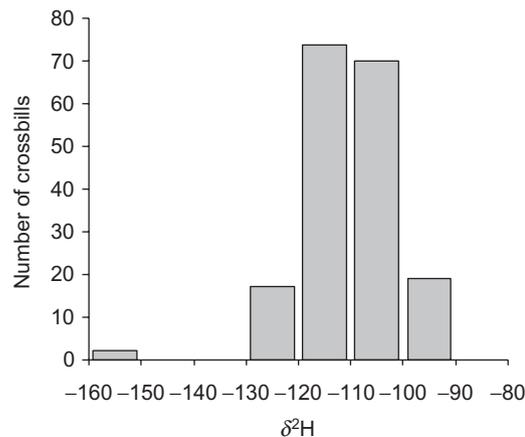

Figure 2 Crossbill densities varied considerably among years. We show here the number of captures per sampling day and 10 linear meters of mist nets (mean ± SD). Juvenile crossbills (EURING code = 3) are not included here. Year refers here to a 'crossbill' year, starting in November of one year up to June of the next one. Thus, year 2009 refers to the period from November of 2008 up to June of 2009.

Figure 3 Frequency distribution of the δ^2H values of the sampled crossbills (mean ± SD: −110.0 ± 9.6‰). Note the occurrence of two outliers with very low isotopic signatures. Sample size: n = 160.

northern Europe (Alonso & Arizaga, 2013). Our sample size was not sufficient to test for the effect of three-way interactions (Table 1), so we tested for the effect of each variable and all two-way interactions between age classes, sex and year. Moreover, we also included the year × wing length interaction.

A number of crossbills (n = 25) were long-term recaptures (mean: 814 days; range: 232–2136 days) caught in two different crossbill years. Hence, we assigned these birds to be local residents (Senar *et al.*, 1993; Alonso & Arizaga, 2013). We compared the δ^2H and wing length values of such birds with crossbills captured only once (i.e. more likely to be immigrants). All such recaptures were older birds, so we only controlled for the effect of sex. Therefore, we ran a GLM on δ^2H with wing length, sex and recapture status (resident vs. putative immigrants) as factors.

Results

During the four years in which the study was carried out, we found important local fluctuations in bird numbers (Fig. 2). Thus, 2009 was the year with a higher number of captures per day and, by contrast, few crossbills were captured in 2010 given this same catch/unit effort.

Only two crossbills had very low δ^2H signatures (Fig. 3), caught in March and April of 2009. These birds were first-year females and they had a relatively long wing compared with other birds of this age and sex (98.0 and 99.0 mm; first-year female population without these two outliers: mean ± SD, 95.6 ± 2.9 mm, n = 30).

Except for age, no variable was observed to have a significant effect on δ^2H (Table 2; Fig. 4). Older crossbills showed higher δ^2H signatures (−105.3 ± 6.4‰, n = 98) than second-year crossbills (−115.9 ± 6.0‰, n = 62).

Long-term recaptures (i.e. resident crossbills) showed similar isotopic values as crossbills captured only once (Table 3). Wing length was longer in males (Table 3; male: 99.4 ± 2.6 mm, n = 51; female: 96.0 ± 2.6 mm, n = 47), but did not differ between resident and putative immigrants.

Discussion

Based on isotopic (δ^2H) signatures of crossbills caught in the Pyrenees (northern Spain) during a period of 4 consecutive years, we found little evidence supporting the presence of northern European crossbills in this area. Two first-year birds were found to have very negative (low) δ^2H values (<−150‰) and a relatively long wing, implying a northern origin.

Table 2 General linear model conducted to test whether the isotope (δ^2H) signature of crossbills caught in the Pyrenees was influenced by sex, age, wing length, year ('crossbill' year) and the weight of the feather samples

Variable	SS	d.f.	F	P
Sex	6.617	1	0.172	0.679
Age	686.645	1	17.818	<0.001
Year	80.227	3	0.694	0.557
Wing	1.175	1	0.030	0.862
Sample weight	18.133	1	0.471	0.494
Year × Age	160.966	3	1.392	0.248
Year × Sex	168.918	3	1.461	0.228
Age × Sex	88.224	1	2.289	0.132
Year × Wing	81.068	3	0.701	0.553
Error	5472.185	142		

SS, sum of squares.

Table 3 General linear models conducted to test whether the isotope (δ^2H) signature and the wing length of crossbills caught in the Pyrenees was influenced by sex and recapture status (resident/immigrant)

Variable	SS	d.f.	F	P
δ^2H				
Sex	107.199	1	2.641	0.107
Recaptured	15.639	1	0.385	0.536
Recaptured × Sex	0.344	1	0.008	0.927
Error	3815.308	94		
Wing length				
Sex	275.138	1	39.329	<0.001
Recaptured	4.978	1	0.712	0.401
Recaptured × Sex	2.670	1	0.382	0.538
Error	657.603	94		

SS, sum of squares.
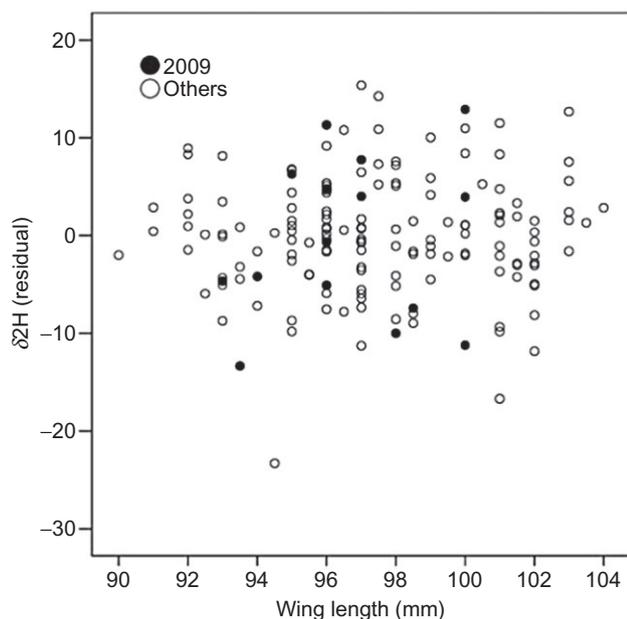
Figure 4 Residual (age, sex and sample weight effects removed) δ^2H values in relation to wing length of crossbills caught in 2009 and in the other study years (2010–2012).

Interestingly, these two birds were captured in the year with the highest local density of crossbills (2009), when also a ringed bird from northern Europe was caught (but not sampled for isotopes). Also in Scotland, 2009 was an invasion year (Marquiss *et al.*, 2012). These all suggest that immigrants from northern Europe were relatively more common in 2009.

However, this does not seem to be the only explanation for the two to three times higher number of crossbills in 2009, as only two out of 15 birds (13%) are clear northern immigrants. Instead, the higher number of crossbills in 2009 is most likely associated with a good local Scots pine seed production (D. Alonso, pers. obs.) attracting crossbills from other nearby areas and generating a high reproductive success, while at the same time allowing any northern crossbills morphologically adapted to Norway spruce to maintain themselves (Benkman, 1993, 2003; Smith & Benkman, 2007).

Excluding the two outlying crossbills, we observed a unimodal distribution of isotopic values from −130‰ to −90‰, suggesting a relatively homogeneous origin of crossbills caught within our area. The observed values indicate that these crossbills would not have come from the southern/eastern coastal forests of Aleppo pine, as based on latitude and altitude these birds should have more positive (up to −50‰) values (see map in Marquiss *et al.*, 2012; Arizaga *et al.* 2014). Instead, our values are very similar to values observed earlier for another nearby mountain area with Scots pine in the Iberian system (Arizaga *et al.*, 2014). Therefore, it can be inferred that most immigrants to our population seem to come from nearby areas likely having the same pine species and/or the same isotopic signatures. Hence, our results imply that movements of crossbills within Iberia between forest patches of Scots and Aleppo pine are limited. Instead, the data fit well with movements between patches of Scots pine. Overall, these interpretations based on our isotopic results confirm those based on genetic patterns (Edelaar *et al.*, 2012). They are also in line with the results of Arizaga *et al.* (2014), who found that birds from a forest of Aleppo pine did not seem to come from nearby areas with Scots pine.

Long-winged crossbills did not show more negative isotopic values suggesting a northern origin. This result is intriguing because we found earlier for the same sampling area and a longer study period that long-winged crossbills appeared more likely to be northern crossbills, as they tended to have lower apparent local survival rates and a color pattern more typical for northern European crossbills (Alonso & Arizaga, 2013). Perhaps, the numbers of these northern birds within our population are higher during other irruption years not included in this study. Alternatively, it is possible that we really had a non-marginal fraction of transients (potentially non-breeding) in our population, but that they may come from other nearby types of pine, for example Mountain pine in the high Pyrenees (Clouet, 2000; Borras & Senar, 2003), which are known to visit forests of other types of conifer species (Clouet, 2000). Based

on isotopic data, we cannot exclude the possibility of movements between forest patches with Scots and Mountain pine within the Pyrenees, as we have no isotopic data on crossbills from these latter areas. However, based on their higher altitude, we would expect lower values while our sample from the Pyrenees was very similar to that from a nearby mountain range further south with only Scots pine, where birds from Mountain pine are less likely to be found. Hence, such movements are probably rather limited.

Second-year birds had lower isotopic values than older birds. This result has been also reported in other studies (Marquiss *et al.*, 2012), as well as in other passerine birds (Langin *et al.*, 2006). In crossbills, nestlings and adults have the same diet (Cramp & Perrins, 1994), so a dietary difference between the two age classes is an unlikely reason to explain our results. Rather, these differences might be due to age-associated variations of the metabolism and physiology (Marquiss *et al.*, 2012).

In conclusion, except for two females with very negative δ^2H values, the δ^2H distribution within a crossbill population in the Pyrenees (northern Spain) was unimodal and δ^2H values were unrelated to year, wing length or residence status, despite great fluctuations in local crossbill densities among years. Hence, our results confirm the occurrence of northern crossbills in southern European localities but suggest that it might be more marginal than previously stated. In addition, they suggest that annual variation in local crossbill abundances is also partly because of the immigration/emigration of individuals of Iberian origin. Based on the absence of variation in isotope values between high density (many immigrants) and low density (only or mostly resident crossbills) years, and the high similarity to values observed for crossbills from a nearby mountain range with Scots pine, it appears that these movements would be mostly between areas sharing the same pine species and isotopic signatures. This then supports recent morphological and genetic studies that indicate that crossbill populations within Iberia are structured by resource use (isolation-by-ecology), but not by geography (isolation-by-distance). More generally, our results support the notion that the evolution of resource specialization is not necessarily prevented by a high dispersal rate, for example because settlement is selective in relation to environmental characteristics and hence gene flow is non-random (Edelaar, Siepielski & Clobert, 2008; Edelaar & Bolnick, 2012) or because natural and sexual selection act against immigrant locally non-adapted phenotypes (Van Doorn, Edelaar & Weissing, 2009).

Acknowledgements

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