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Disentangling the origin of crossbills using morphology and isotopic (δ^2 H) characters. Are southern European crossbills restricted to population-specific key resources?

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Abstract Specialist foragers depend on specific prev commonly associated with limited habitat, which is often patchily distributed. Understanding how specialists use habitat patches is important to their conservation. Crossbills (Loxia spp.) are one of the best examples of a foraging specialist, because they exploit population-specific conifer species. In this work, we used morphology and stable isotopic analyses (δ^2 H) to test the use of two different key conifer species (Pinus spp.) by crossbills. This study was conducted in Spain to test whether a small patch of Aleppo pine (P. halepensis) from the Ebro Valley hosted native, resident common crossbill (L. curvirostra) populations or, by contrast, if it was used just as a "stopover" or a passage site between the two main mountain ranges situated to the north and south of this valley, which is mostly occupied by Scots pine (P. sylvestris). Crossbills caught at the Ebro Valley used this zone only temporarily, thus supporting the lack of a stable, strictly resident population. Morphological and isotopic analyses revealed that these birds were likely to belong to an Aleppo pine-associated population, and likely not to Scots pine crossbills moving between the Pyrenees and the Iberian System. Therefore, we observed evidence supporting high foraging specialization and population-specific use of key conifer resources in Spain. This work highlights the usefulness of combining morphological

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K. A. Hobson Environment Canada, 11 Innovation Blvd, Saskatoon SK S7N 3H5, Canada and stable isotopic analysis to infer the origin and possible movement patterns of crossbill populations.

Keywords Aleppo pine · Ebro valley · Iberian system · Pyrenees · Scots pine

Zusammenfassung

Mit Morphologie und Isotopenmerkmalen (δ 2H) der Herkunft von Kreuzschnäbeln auf der Spur: sind südeuropäische Kreuzschnäbel auf populationsspezifische Schlüsselressourcen beschränkt?

Nahrungsspezialisten hängen von spezifischen Beutetieren oder Futterquellen ab, deren Vorkommen normalerweise an einen begrenzten Habitattyp gebunden und daher oft lückenhaft verteilt ist. Zu verstehen, wie diese Spezialisten Habitaträume nutzen, ist wichtig für deren Schutz. Kreuzschnäbel (Loxia spp.) gehören zu den besten Beispielen für einen Nahrungsspezialisten, da sie sich von populationsspezifischen Koniferenarten ernähren. In dieser Studie kombinierten wir Morphologie und die Analyse Stabiler Isotope (δ 2H), um die Nutzung zweier verschiedener Hauptkoniferenarten (Pinus spp.) durch die Kreuzschnäbel zu erforschen. Die Untersuchung fand in Spanien statt und sollte klären, ob ein kleines Aleppokiefernwäldchen (P. halepensis) im Ebrotal ortsansässige Kreuzschnabelpopulationen (L. curvirostra) beherbergt oder ob dieses stattdessen nur als "Zwischenstopp"oder Durchzugsgebiet zwischen den beiden nördlich und südlich des Tales gelegenen, überwiegend mit Waldkiefern (P. sylvestris) bestandenen, Gebirgszügen dient. Im Ebrotal gefangene Kreuzschnäbel nutzten diese Region nur vorübergehend, was für das Fehlen einer stabilen, streng ortstreuen Population spricht. Morphologie und Isotopenanalysen zeigten, dass diese Vögel wahrscheinlich zu einer mit Aleppokiefern assoziierten Population gehörten und wohl eher nicht zu den Waldkiefern-Kreuzschnäbeln, die sich zwischen den Pyrenäen und dem Iberischen Gebirge bewegen. Unsere Beobachtungen liefern daher unterstützende Hinweise auf eine Nahrungsspezialisierung und eine populationsspezifische Nutzung wichtiger Koniferenressourcen in Spanien. Diese Arbeit unterstreicht außerdem die Nützlichkeit eines kombinierten Ansatzes aus Morphologie und der Analyse Stabiler Isotope bei der Erforschung der Ursprünge und möglicher Bewegungsmuster von Kreuzschnabelpopulationen.

Introduction

Among birds, foraging-specialists depend on specific prey commonly associated with a limited habitat (Newton 2003). Habitat loss is expected to differentially affect such specialist foragers, whose prey could be more likely to be patchily distributed (Summers et al. 2002). Understanding how foraging specialists use habitat patches is important to their conservation.

Crossbills (Loxia spp.) are an excellent example of a foraging specialist (Benkman 2003) because they feed almost exclusively on seeds of only a few species of conifer (Knox 1976; Groth 1993; Summers et al. 2002; Alonso et al. 2006). Such specialization evolves because conifers differ in the size and hardness of their cone scale, and no single type of bill of a given shape or size can feed equally well on all cones (Benkman 1987). Accordingly, a crossbill "type" exists (or is expected) for each conifer type, as it is well-reported for America (Groth 1993). In several regions of their range, however, crossbills are nomadic (Newton 2006; Marquiss et al. 2012), so "wrong" types could be observed at a given conifer patch (e.g., Edelaar and Terpstra 2004). Understanding to what extent crossbills specialized in foraging on a given conifer exist and are able to exploit alternative sources is important from evolutionary and conservation perspectives.

Situated in Southern Europe, the Iberian peninsula is inhabited by a number of presumably resident crossbill populations (Senar et al. 1993), considered to belong to the nominate subspecies that specializes in Norway spruce (*Picea abies*) (Cramp and Perrins 1993). However, recent studies suggest that populations specialized to feed on several pine species (*Pinus* spp.) have been uncovered (Alonso et al. 2006; Borrás et al. 2008; Edelaar et al. 2012). Thus, testing/confirming whether different patches of pines are monopolized by such specialists or, alternatively, whether other types might also use them is a question of key interest in understanding the population divergence and the identification of distinct evolutionary units of these Iberian populations.

Northeastern Iberia is occupied by several pine species, two among which are found to be distributed broadly. The Scots pine (P. sylvestris) is a typical mountain species, growing from 800 to 2,400 m a.s.l., thus being very abundant in the Pyrenees and the Iberian System including the two main mountain ranges from the area (Fig. 1). The Aleppo pine (P. halepensis), by contrast, is a thermophyle, Mediterranean pine growing between sea level and 200 m a.s.l. (exceptionally up to 1,000 m a.s.l.), so it is common in drier areas such as the Ebro Valley (Fig. 1). Whereas the Pyrenees and the Iberian System have large uninterrupted areas of Scots pine, Aleppo pine in the Ebro valley is patchily distributed. It is commonly argued that the Ebro Valley's Aleppo pine patches host viable, resident crossbill populations (Sampietro 1998; Borras and Senar 2003), which presumably would belong to an Aleppo pine crossbill type, well-differentiated from the Scots pine type (Alonso et al. 2006; Edelaar et al. 2012). However, ring-recovery data have provided evidence that Scots pine crossbills from the Pyrenees move to or pass over the Ebro Valley (D. Alonso, unpubl. data). Such findings pose the question of the origin of the crossbills observed in the Aleppo pine patches of the Ebro Valley, especially in small forest patches. Preliminary observations in the Pyrenees and the Ebro valley also show that crossbills tend to disappear at certain periods in a year (D. Alonso, per. obs.), thus suggesting that they could show some kind of dispersal or migration (i.e., they may be not strictly resident).

If the Aleppo pine forests from the Ebro Valley tend to be occupied by crossbills from nearby mountain ranges, we should expect the Ebro Valley crossbills to be detected only during some months per year, coinciding with displacements from such mountain ranges. Alternatively, (1) the Ebro Valley could host some Scots pine type resident crossbills, or (2) Aleppo pine crossbills could be local resident birds, or (3) belong to a nomadic, vagrant Aleppo pine-associated population.

Crossbills specializing on a certain conifer species are normally morphologically well-differentiated from crossbills using other feeding sources (Benkman 1993; Groth 1993; Summers 2002; Borrás et al. 2008). Crossbills that feed on Scots pine show narrower (depth/length ratio) bills than those that feed on Aleppo pine (Alonso et al. 2006; Edelaar et al. 2012). If crossbills from the Ebro Valley belong to an Aleppo pine-associated population, they should have a markedly different morphology than birds from the Pyrenees and the Iberian System, which are known to forage on Scots pine. By contrast, if crossbills from the Ebro Valley mainly belong to a transient population migrating or just moving between nearby mountain ranges, then we should expect to find a similar morphology between the Ebro Valley and the nearby mountain ranges.



Fig. 1 Sampling localities where the study was carried out: Bigüezal (Pyrenees); (2) Castejón de Valdejasa (Ebro Valley); (3) El Royo (Iberian System). Dominant pine species: *dark grey* Scots pine; *pale grey* Aleppo pine

Stable isotopic values in avian tissues are known to be associated with specific habitats and geographical location (Hobson and Wassenaar 2008). As such, we might expect stable isotope values to differ among crossbills raised in the Ebro Valley and the north and south mountain ranges. In particular, in any given region, stable-hydrogen isotope $(\delta^2 H)$ values in feathers are expected to show a lower value in more rainy areas than in drier areas or at higher altitudes vs. lower altitudes (Hobson and Wassenaar 1997; Hobson et al. 2004). So, all things being equal, we expect feathers grown in drier habitats, such as the Ebro Valley, should show a higher absolute $\delta^2 H$ value than tissues of birds from more rainy regions, such as the Pyrenees and the Iberia System. Alternatively, if crossbills from the Ebro Valley come from the nearby mountain ranges we should expect similar values among groups.

The aim of this work was to test whether a small patch of Aleppo pine from the Ebro Valley in Northern Iberia hosted native, Aleppo pine-associated crossbill populations or, by contrast, if it was used as just a "stopover" or a passage site between the two main mountain ranges situated to the north and south of the Ebro Valley. We used morphological- and isotope-based methods to test this hypothesis.

Materials and methods

Study area and data collection

The study was carried out in three sampling sites situated in pine (*Pinus* spp.) forests in the western Pyrenees (Bigüezal, $42^{\circ}40'N 01^{\circ}08'W$, 1,100 m a.s.l.), Ebro valley (Castejón de Valdejasa, $41^{\circ}59'N 00^{\circ}59'W$, 600 m a.s.l.), and the Iberian System (El Royo, $41^{\circ}54'N 02^{\circ}43'W$, 1,200 m a.s.l.; for details see Fig. 1). The dominant conifers in these sites are the Scots pine (*P. sylvestris*; Bigüezal, El Royo) and the Aleppo pine (*P. halepensis*; Castejón de Valdejasa). Scots pine forests from the sampling localities at Bigüezal and El Royo occupied broad areas while the Aleppo pine forest at Castejón de Valdejasa occupied a relatively small patch (Fig. 1).

Sampling was carried out during 2009. We used a sampling protocol consisting of checking the presence of crossbills throughout the year and catching them in order to obtain biometric measurements and feathers for stable isotopes analyses (SIA).

Crossbill presence at the sampling localities was tested twice a month (one survey per 15-day interval, one survey during the first and another one during the second half of each month), during a period of 15 min from dawn in the same sites where birds were regularly caught.

Crossbills were captured with mist nets at each site (16mm mesh, 2.5 m high). Nets were placed near sites used systematically by crossbills to consume salt and/or to drink. Once captured, crossbills were ringed, sexed, and aged either as first-year birds (with still some juvenile feathers in their wings or tail; EURING code 3 and 5) or adults (with no juvenile feathers; EURING code 4 and 6) (Svensson 1996). Moreover, we also measured wing length $(\pm 0.5 \text{ mm, method III by Svensson 1996})$ (WING), tail length (TAIL), tarsus length (TARS), head and bill length (HB), upper and lower mandible length (BUML and BLML, respectively), lower mandible width (BLMW; recorded at the mandibular symphysis), and bill width and depth (BWID and BDEP, respectively, recorded at the interlabial commissure) (for details see Alonso and Arizaga 2005). All measurements were recorded by DA. Moreover, we also checked whether females were breeding by examining their brood patch (0, no brood patch; (1) developing brood patch; (2) fully grown brood patch; (3) regressing brood patch). Females with either a developing or a fully grown patch were considered as breeders (Alonso and Arizaga 2011).

Finally, a primary feather (P1, the innermost one) was taken for stable isotope analysis. Feathers were taken only from the first-year birds in order to be sure that the P1 was grown where the birds were hatched (i.e., natal origin place), because the partial moult process undertaken by these birds in summer/autumn does not affect the P1 (Jenni and Winkler 1994). Sample sizes at each site were: Pyrenees, n = 20; Ebro Valley, n = 19; Iberian System, n = 16. Feathers were kept in individual paper envelopes prior to analysis.

Morphological analyses

We only consider here crossbills with known age and sex, and with all measurements recorded. Outliers (i.e., crossbills with abnormally high or low values for a particular variable) were removed. This was done with the aim of removing a few birds (<1 %) that had extreme values of (normally) a single variable, which hence could be due to observer-associated errors. Furthermore, due to the scarce number of adults caught within the Iberian System (Table 1), we only considered first-year birds for analyses. This gave us a sample size of 263 individuals (Pyrenees, n = 123; Ebro Valley, n = 27; Iberian System, n = 113).

All variables were standardized to make them nondimensional. A multivariate analysis of variance (MA-NOVA) was then performed with sex and site as factors. This MANOVA detected significant biometric differences both between sexes and among sites (Pillai's statistics: Sex,

 Table 1
 Number of crossbills caught at each site (three sampling sites from the North of Spain), with their age and sex known, and all the morphological measurements recorded

Site	First-yea	r	Adults	
	Male	Female	Male	Female
Pyrenees	74	48	99	38
Ebro valley	14	13	37	21
Iberian system	64	49	1	1

 $F_{10} = 13.562$, P < 0.001; Site, $F_{20} = 5.000$, P < 0.001; Site × Sex, $F_{20} = 0.950$, P = 0.523). Univariate ANO-VAs, however, revealed that only four variables differed between sexes: BDEP, HB, WING, and TAIL (statistics not provided). These four variables were corrected for the effect of sex. We then conducted a Principal Component Analysis (PCA) with the goal of reducing the measurements to only some variables that summarized bill morphology (Alonso and Arizaga 2005). Principle components with an eigenvalue >1 were used to test for the occurrence of significant morphological differences in relation to the site, once the sex effect was controlled for in the previous step. We used ANOVAs on PCs with site as a factor in order to test this.

Stable isotope analyses

We used P1 (1st primary feather) $\delta^2 H$ measurements because this isotope is well-associated with spatial and climatic variables (Hobson et al. 2004). While previous works have often used this isotope as an indicator of geographic origin at continental scales (Hobson and Wassenaar 2008), we considered $\delta^2 H$ measurements of bird feathers as a local proxy of habitat use and potentially larger-scale assignment to more distant regions. This approach is based on the fact that we could not absolutely assess the likelihood of local breeding at each of the three study sites and the fact that the three areas of interest were relatively close in terms of the resolution of the $\delta^2 H$ approach (Hobson 2008) although they differed dramatically in amount of rainfall and altitude. At more continental scales, crossbills dispersing from northern latitudes such as Scandinavia or northern Russia would have lower $\delta^2 H$ values compared to crossbills from Spain (Marquiss et al. 2012). Thus, we considered our data at two potential inference scales: local among our Spanish study sites, and continental.

All feathers were cleaned of surface oils using a triple 2:1 chloroform:methanol rinse and prepared for δ^2 H analysis at the stable isotope laboratory, Environment Canada, Saskatoon, Canada. The δ^2 H analyses were carried out following methods described in Wassenaar and Hobson

(2003), using calibrated keratin-isotope reference materials in order to avoid effects of H exchange with ambient water vapor. Measurements of δ^2 H were performed on H₂ derived from the high-temperature flash pyrolysis (1,350 °C) of the feathers with a HEKAtech HT-O AnalyzerTM linked to an Elementar IsoprimeTM continuousflow isotope-ratio mass spectrometer. All δ^2 H values were reported in δ -notation, in units per mil (‰), 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 a long-term (6-month running average) repeatability better than ±3.2 ‰.

We used an ANOVA on $\delta^2 H$ values with site as a factor in order to test for the occurrence of significant differences on this variable in relation to site.

Results

Crossbill presence

During 2009, crossbills were detected always at Bigüezal, during only four months at the Ebro Valley (from July to October) and during 10 months at the Iberian System (from March to December).

Morphological data

We found three principle components with an eigenvalue >1. PC1 was positively correlated with most skeletal-associated measurements, particularly with those

 Table 2
 Principal components (PCs) derived from a PCA on all the biometric variables

Variables	PC1	PC2	PC3
BLEN	+0.864	-0.038	+0.277
BUML	+0.890	-0.008	+0.250
BLML	+0.853	+0.002	+0.092
BLMW	+0.106	+0.012	+0.740
BWID	+0.155	+0.153	+0.678
BDEP	+0.307	+0.119	+0.767
НВ	+0.752	+0.172	+0.134
TARS	+0.165	+0.587	+0.216
WING	-0.063	+0.877	+0.030
TAIL	-0.002	+0.827	+0.032
Eigenvalue	3.72	1.87	1.08
Variance	37.16	18.73	10.80

See the text for abbreviations. Values in bold show a significant correlation of each variable with the corresponding PC. We only show those PCs which had an eigenvalue >1 in the PCA



Fig. 2 Mean ($\pm 95 \%$ CI) values of the PCs at each site (Pyrenees, Ebro Valley, Iberian System). A Tamhane's a posteriori test only revealed significant differences for the PC1 (*P < 0.05)

associated with bill length, so crossbills with high PC1 scores showed a longer, also more massive bill, as well as a longer tarsus (Table 2). PC2 showed higher correlation scores with WING and TAIL and, to a lesser extent, with some skeletal-associated measurements (Table 2), so crossbills with higher PC2 scores were birds with longer wings and tails, as well as a seemingly larger body structural size. The PC3 was mostly and positively correlated with bill width and depth and, to a lesser extent, with the rest of the skeletal-associated variables (Table 2). Thus crossbills with higher PC3 scores were birds with deeper and wider bills.

Only the PC1 and PC3 differed among sampling sites (ANOVA: PC1, $F_2 = 7.560$, P = 0.001; PC2, $F_2 = 1.932$, P = 0.147; PC3, $F_2 = 3.378$, P = 0.036). An a posteriori test, however, only revealed significant differences for the PC1 (Fig. 2). For this variable, crossbills caught at the Ebro Valley tended to have higher PC1 scores, i.e., a proportionally larger, more massive bill.



Fig. 3 Mean (±95 % CI) $\delta^2 H$ values (‰) of first-year crossbills caught at three different sites in Iberia

Stable isotopes analyses

Although crossbills from the Ebro Valley tended to have lower δ^2 H values (Fig. 3), the difference was non-significant (ANOVA: $F_2 = 2.027$, P = 0.142). The distribution of the values at the Ebro Valley was bimodal but unimodal at the other two sites (Fig. 4).

Discussion

Census data indicated that crossbills occurred for either the entire, or almost the entire year at the two localities in the Pyrenees and the Iberian System, both characterized by Scots pine. By contrast, crossbills from the Ebro Valley (Aleppo pine) seemed to be transients. Crossbills here were detected in summer, suggesting that they belonged to a non-resident population. This result demonstrates that crossbill populations in Iberia are not strictly resident (Senar et al. 1993; Clouet 2000; Edelaar et al. 2012), but they are likely to perform either nomadic displacements, as occurs in other areas of Europe (Newton 2006; Marquiss et al. 2012), or some kind of seasonal dispersal or migration-like movements. Such findings were compatible with the idea that crossbills in the Ebro Valley were either birds moving between forest patches of the Pyrenees and the Iberian System (Scots pine-associated crossbills) or, alternatively, that crossbills in the Ebro Valley were Aleppo pine-associated birds that would belong to highly mobile populations.

Morphological data revealed that crossbills from the Ebro Valley had a larger (relatively longer) bill than crossbills from the nearby mountain ranges, as also reported by Edelaar et al. (2012) for crossbills foraging on Aleppo pine. This suggests that the Ebro Valley crossbills belonged to a well-differentiated morpho-type, in this case



Fig. 4 Frequency distribution of $\delta^2 H$ values (‰) of first-year crossbills caught at three different sites in Iberia

v ariable	Male			remaie		
	PYRE	EBRO	IBER	PYRE	EBRO	IBER
BLEN	$18.8 \pm 0.1 \; (16.1 - 20.7)$	$19.6 \pm 0.2 \ (18.0-20.9)$	$19.2 \pm 0.1 \; (16.7 - 21.0)$	$18.6 \pm 0.2 \ (15.6 - 20.4)$	$19.7 \pm 0.1 \ (19.2 - 20.4)$	$18.7 \pm 0.1 \ (15.6-20.4)$
BUML	$17.8 \pm 0.1 \ (15.1 - 19.5)$	$18.4 \pm 0.2 \; (16.9 - 19.5)$	$17.9 \pm 0.1 \ (16.1 - 19.8)$	$17.5 \pm 0.1 \ (15.1 - 18.9)$	$18.4 \pm 0.1 \ (17.4 - 19.0)$	$17.5 \pm 0.1 \ (14.8 - 19.3)$
BLML	$16.6 \pm 0.1 \; (14.5 - 18.6)$	$17.1 \pm 0.2 \ (16.0 - 18.6)$	$16.8 \pm 0.1 \; (14.2 - 18.8)$	$16.4 \pm 0.1 \; (14.3 - 18.5)$	$17.0 \pm 0.2 \ (15.2 - 17.9)$	$16.5 \pm 0.1 \ (14.6 - 18.3)$
BLMW	$4.8 \pm 0.0 \ (3.7 - 5.4)$	$4.8 \pm 0.1 \ (4.1 - 5.2)$	$4.7 \pm 0.0 \ (4.0-5.4)$	$4.7 \pm 0.1 \ (3.4-5.4)$	$4.7 \pm 0.1 \ (4.3-5.2)$	$4.6 \pm 0.1 \ (3.7 - 5.4)$
BWID	$10.9 \pm 0.1 \ (10.1 - 11.9)$	$10.9 \pm 0.1 \ (10.2 - 11.4)$	$10.9 \pm 0.1 \ (10.0 - 11.7)$	$10.8 \pm 0.1 \ (9.8 - 11.8)$	$10.7 \pm 0.1 \ (10.2 - 11.3)$	$10.9 \pm 0.1 \ (9.9 - 17.1)$
BDEP	$10.7 \pm 0.0 \ (9.5 - 11.5)$	$10.6 \pm 0.1 \ (10.1 - 11.0)$	$10.7 \pm 0.1 \ (9.6 - 11.8)$	$10.7 \pm 0.1 \ (9.7 - 11.4)$	$10.5 \pm 0.1 \ (10.0 - 10.8)$	$10.5 \pm 0.1 \ (9.8 - 11.3)$
HB	$39.6 \pm 0.1 \; (36.4 - 41.8)$	$39.8 \pm 0.2 \ (38.5 - 41.6)$	$40.0 \pm 0.1 \; (37.3 - 42.2)$	$38.9 \pm 0.2 \; (36.5 - 40.9)$	38.8 ± 0.2 (38.0–9.7)	$39.3 \pm 0.2 \ (36.3 - 40.9)$
We show me	an 土 SE, ranges (in brackets)), Sample sizes as shown in T	able 1			

Table 3 Bill-associated biometric variables (in mm) of first-year birds at the three sampling sites in Iberia (Pyrenees, Ebro Valley, Iberian System)

selected to forage on Aleppo pine (Alonso et al. 2006), or that some larger-billed crossbills from the nearby mountain ranges (Table 3) may benefit from landing at the Ebro Valley, where they could forage successfully on the Aleppo pine. Stable isotope analyses support more strongly that crossbills from the Ebro Valley were local, since most of them showed $\delta^2 H$ values associated with drier environments. The hypothesis that crossbills seen during the summer in the Ebro may be Scots pine-associated crossbills moving between forest patches in the Pyrenees and the Iberian System cannot be fully rejected since we caught some birds that showed isotopic values associated to wetter origin localities. Although ring-recovery data demonstrated that some birds moved between both mountain ranges (D. Alonso, unpubl. data), meaning that they should pass or stop over in the Ebro Valley, it is possible that most of these birds would do this type of displacement quickly, would perform short stopovers in the Aleppo pine forests from the Ebro Valley, or would be scarce compared to the bulk of Aleppo pine-associated crossbills.

Crossbills from the Pyrenees and the Iberian System did not differ morphologically. This supports the idea that they all feed on a same key pine for which they are expected to be adapted (Alonso et al. 2006). The lack of significant morphological differences of these crossbill populations would also favor the hypothesis that they could belong to a single population (or meta-population), which would be able to move over broad areas throughout Iberia in order to search for suitable Scots pine forests with an abundant cone production, supporting the conclusions of Edelaar et al (2012).

The predicted long-term amount-weighted growingseason average δ^2 H value of precipitation at the three study sites based on Bowen et al. (2005) were -51 % for the Pyrenees and Iberian System and -43 ‰ for the Ebro. Applying a feather-precipitation relationship established for European passerines by Prochazka et al. (2013), namely $\delta^2 H_f = -10.29 + 1.28 \ \delta^2 H_p$, the expected feather isotope values of crossbills at the two mountain sites were -75.4 ‰, and -65.3 ‰ for the Ebro site. If we also consider an appropriate SD of ± 12 % (Hobson et al. 2012) to be reasonable for a single population, then the range in values we would expect at our sites (i.e., $\pm 2SD$) would range from -99.4 to -51.4 % for the Pyrenees and the Iberian System, and -89.3 to -41.3 ‰ for the Ebro site. These assessments fit for the Ebro site but were too positive for most of the samples we measured for the mountain sites. One possibility is that the mountain places were comprised of crossbills dispersing from further northern molting sites such as Scandinavia (see Fig. 1 in Marquiss et al. 2012) or that the years of study departed significantly from the long-term weighted-average annual precipitation δ^2 H values used in Bowen et al. (2005). That could occur if those sampling years were wetter than the mean in the mountains. However, mountainous areas are particularly challenging to model well using the isoscape approach for water isotopes. Thus, our data are compatible with a possible northern dispersal, but may have been also explained by particular local conditions in the Pyrenees and the Iberian System. As expected, crossbills from the Ebro site included a cohort enriched in δ^2 H compared to the other two sites, and this was consistent with their breeding at that site. However, in the Ebro the δ^2 H distribution was bimodal and some birds had lower δ^2 H values (i.e., <100 ‰). This suggests that perhaps some birds from the Ebro Valley could come from cooler and/or wetter regions, such as the nearby mountain ranges or from more northern latitudes (Marquiss et al. 2012).

Based on census data, crossbills at a small patch of Aleppo pine in the Ebro Valley appeared to use this zone only temporarily, thus supporting the lack of a stable, strictly resident population. However, morphological analyses revealed that these birds were likely to (mostly) belong to an Aleppo pine-associated population, and likely not to Scots pine crossbills moving between the Pyrenees and the Iberian System. The stable isotope results support the presence of one group of local breeding birds in the Ebro Valley associated with the Aleppo pine but also showed the presence of crossbills dispersing from other wetter areas elsewhere in Europe. Our evidence supports the presence of high foraging specialization and population-specific use of key conifers in Spain with potentially little movement of local breeders among these habitat types. Moreover, it could be mentioned that small patches of certain pines could serve to host the specialized types moving around as well as non-specialist types on dispersal, hence being of conservation value for both kinds of crossbills.

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