Morphological diversification of Common Crossbill *Loxia curvirostra* populations within Iberia and the Balearics

Daniel Alonso¹, Juan Arizaga^{1,2,*}, Rafael Miranda² & M. Ángeles Hernández²



Alonso D., Arizaga J., Miranda R. & Hernández M.A. 2006. Morphological diversification of Common Crossbill *Loxia curvirostra* populations within Iberia and the Balearics. Ardea 94(1): 99–107.

Two subspecies of Common Crossbill *Loxia curvirostra* are currently accepted to be present in Iberia and the Balearics: *L.c. curvirostra* and *L.c. balearica*. Nonetheless, some populations in S Iberia are yet to be known, especially regarding their taxonomy. Biometrics of Crossbills from Navarra in N Iberia, Alicante and Málaga in S Iberia, and Mallorca in the Balearics were analysed by means of Discriminant Function Analysis, to describe their morphological diversification, and to quantify their degree of differentiation. Crossbills from Navarra and Mallorca strikingly differed from each other, supporting their status of nominate and *balearica* subspecies, respectively. By contrast, individuals from S Iberia belong to an intermediate morphotype that differ significantly from Crossbills in N Iberia and the Balearics. Thus, data support that either adaptation to different resources or isolation, or both, cause morphological differentiation of populations of Crossbills.

Key words: Common Crossbill, *Loxia curvirostra*, biometrics, Iberia, Balearics, discriminant function analysis

¹Department of Vertebrates, Aranzadi Sciences Society, Zorroagagaina 11, E-20014 Donostia, Spain; ² Department of Zoology and Ecology, Faculty of Sciences, University of Navarra, Irunlarrea 1, E-31080 Pamplona, Spain; * corresponding author (jarizaga@alumni.unav.es)

INTRODUCTION

One of the main issues in the study of evolution of organisms is to determine how the environment promotes adaptation. Divergence of populations as a consequence of adaptation to resource diversity is of particular relevance to the process of speciation (Futuyma 1998, Schluter 2001). Speciation among Crossbills seems linked to morphological diversification promoted by adaptation to foraging on cones of a variety of conifers (Benkman 1987, 1993, 2003, Summers & Piertney 2003). Alternatively, processes of speciation in Crossbills have also been associated with either geographical or breeding isolation (Knox 1976, Groth 1993).

Due to the high heterogeneity of populations, the systematics of Common Crossbills *Loxia curvirostra* has been the aim of several studies within the Palearctic (Knox 1976, 1990, 1992, Eck 1981, Massa 1987, Clouet & Joachim 1996) and the Nearctic (Groth 1993). For the Common Crossbill in N America, Groth (1993) described seven different types proposedly belonging to distinct sibling species. Taxa of Common Crossbills, such as subspecies, have been classified by means of external features, such as biometrics and plumage colouring, as well as by feeding ecology, geographic distribution and breeding isolation (Cramp & Perrins 1994).

In Iberia and the Balearics, Common Crossbills are irregularly distributed in areas with coniferous forests (Borrás & Senar 2003), where currently two subspecies are accepted to be present: L.c. curvirostra, in N Iberia (up to S Pyrenees and the Cantabrian Mountains), and L.c. balearica, in the Balearics. Nonetheless, the status of Crossbills from S Iberia remains unsettled: some biometrics indicate that these Crossbills are intermediate of curvirostra and balearica (Cramp & Perrins 1994) or even constitute a separate subspecies, L.c. hispana (Hartert 1904 in Cramp & Perrins 1994). Alternatively, Crossbills from S Iberia have been considered as belonging to either the curvirostra subspecies (Newton 1972, Knox 1997, Tellería et al. 1999) or to balearica (Jutglar & Masó 1999). In a recent work on calls of Crossbills from S Iberia and the Balearics, Summers & Jardine (in press) observed that they were much more similar to larger-billed Crossbills, such as the Scottish one (L. scotica), than to curvirostra. Thus, a detailed analysis of the biometrics of Crossbills in Spain would help to better understand the status of Crossbills from this region, paying particular attention to the S Iberia population, as well as to complement data on calls, hence improving our understanding of the diversity of populations of Common Crossbills in Iberia and the Balearics.

We deal with three main hypotheses to explain the patterns of morphological diversification of Crossbills in Spain:

First, populations or species of Crossbills might be often recognised by key food sources, rather than by geographical location (Benkman 1993, Groth 1993, Edelaar *et al.* 2003, Edelaar & Terpstra 2004). Therefore, the presence of various conifer species in Iberia should predict the presence of distinct Crossbill species. Accordingly, it seems sensible to include populations from S Iberia with *balearica* rather than *curvirostra*, since birds in S Iberia and the Balearics feed on the same food source (Aleppo pine *Pinus halepensis*), whilst populations from N Iberia feed mainly on Scots pines *Pinus sylvestris* (see methods for further details). In addition, Mediterranean birds perfectly serve this ecological approach to investigate taxonomy, since these populations seem to be much more resident than those from N Europe (Senar *et al.* 1993), allowing us to assign a particular individual to a specific key resource.

Secondly, it is well documented that seed predation by Red Squirrels *Sciurus vulgaris* causes selection for larger cone scales (Mezquida & Benkman 2005). In those areas where Crossbills and squirrels live together, cone scale size and bill morphology of Crossbills may change accordingly. Particularly, Mezquida & Benkman (2005) showed that, due to the absence of squirrels in the Balearics, cone scales were smaller and bill morphology of Crossbills was different from the one observed in Crossbills from S Iberia. Consequently, two distinct morphological clusters are to be expected in S Iberia and the Balearics respectively, in addition to the one expected in N Iberia (see hypothesis 1).

Thirdly, a possible morphological diversification between Crossbills in S Iberia and the Balearics is expected if we consider that birds from the Balearics are to some extent isolated from those in S Iberia (assuming that Mediterranean Crossbills are largely sedentary, Senar *et al.* 1993), and hence may show separate life histories. This hypothesis, as the previous one, also supports the existence of two distinct morphological clusters in S Iberia and the Balearics, respectively, or even more clusters (in addition to the one from N Iberia), if we consider the existence of an isolated nucleus in S Iberia. Note that hypotheses 2 and 3 are not necessarily exclusive but complementary.

METHODS

Sampling localities and biometrics

We compiled data on four populations of Crossbills within the following localities: Navarra (Sierra de Leire, 42°40'N, 01°07'W, Sierra de Uztarroz,

42°52'N, 01°00'W), Alicante (Sierra de Maigmó, 38°30'N, 00°40'W), Málaga (Montes de Málaga, 36°50'N, 04°23'W) and Mallorca (Sierra de Tramontana, 39°33'N, 02°31'E and 39°56'N, 03°08'E) (Fig. 1). In Navarra, the predominant conifer is the Scots pine, whilst in Alicante, Málaga and Mallorca it is the Aleppo pine.

Crossbills were captured with mist nets that were placed near water. Individuals were released as soon as the biometric variables had been measured. We use data from nine years (1994-2002): Navarra (1994–1999), Alicante (1998–2001), Málaga (1996, 2001) and Mallorca (2001, 2002). Crossbills were ringed (or the ring was read) and age and sex determined (Svensson 1992). Two age categories were considered: adults (AD; EURING code 4/6) and juveniles (JV; EURING code 3/5). We recorded the following ten biometric variables (Fig. 2), according to Svensson (1992): wing length (flattened and straightened, WL, ± 0.5 mm), tail length (TL, ± 0.5 mm), tarsus length (TS, \pm 0.1 mm), upper and lower mandible length (UML, LML, respectively; from the tip of each mandible to the interlabial commisure, ± 0.1 mm), lower mandible width (LMW, recorded within mandibular symphysis, ± 0.1 mm), culmen



Figure 1. Distribution of the Common Crossbill (shaded areas) in Spain and the sampling localities: 1) Sierra de Leire and Sierra de Uztarroz (Navarra); 2) Sierra de Maigmó (Alicante); 3) Montes de Málaga (Málaga); 4) Sierra de Tramontana (Mallorca).



Figure 2. Some of the bill measures taken on Crossbills: LML = lower mandible length, UML = upper mandible length, BD = bill depth, CLL = culmen length. This specimen was caught in Navarra (photo J. Arizaga).

length (CLL, from the tip to the feathering, \pm 0.1 mm), skull plus bill length (SB, \pm 0.1 mm), bill width and depth, (BW and BD, respectively; the first one recorded within the base of the lower mandible, for the second one see also Edelaar & Terpstra (2004); \pm 0.1 mm). All measurements were made by the same observer (DA). Crossbills of unknown sex or age and individuals with worn or missing feathers (primaries or rectrices) were removed from posterior analyses.

In the present analysis, we used data on 607 Crossbills (Navarra: n = 256; Alicante: n = 230, Málaga: n = 88, Mallorca: n = 33). Descriptions of their biometrics are summarised in Table 1.

Statistics

We conducted a MANOVA on the ten biometric variables, with sex and age as control factors, for each of the sampling localities. In all but one (Málaga) significant differences were detected in relation to sex (P < 0.05; Málaga, P = 0.086), and in all cases but one (Mallorca) we observed age-associated variations (P < 0.05; Mallorca, P = 0.943). Accordingly, four age-sex categories should be considered: AM (adult males), AF (adult females), JM (juvenile males), JF (juvenile females). Nonetheless, it is here relevant to notice that sample size of some age-sex groups in some

		Adults (EU	JRING 4/6)			Young (EU	RING 3/5)	
MALES	Navarra $(n = 102)$	Alicante $(n = 79)$	Málaga (n = 33)	Mallorca $(n = 6)$	Navarra $(n = 51)$	Alicante $(n = 40)$	Málaga (n = 30)	Mallorca $(n = 12)$
Wing length	97.1 ± 2.0	94.9 ± 2.8	95.3 ± 2.0	93.7 ± 2.3	96.6 ± 2.3	95.0 ± 1.9	94.5 ± 1.8	93.2 ± 2.5
Tail length	58.7 ± 3.7	58.5 ± 2.0	57.8 ± 2.3	56.9 ± 1.0	59.6 ± 4.1	58.2 ± 2.0	58.5 ± 1.6	57.2 ± 1.9
Tarsus length	21.7 ± 0.7	21.8 ± 0.6	21.5 ± 0.5	21.5 ± 0.8	21.8 ± 0.7	21.5 ± 0.7	21.4 ± 0.5	21.2 ± 0.6
Upper mandible length	18.1 ± 0.6	18.8 ± 0.7	18.5 ± 0.9	18.8 ± 1.0	18.0 ± 0.7	18.6 ± 0.7	18.3 ± 0.4	18.3 ± 0.4
Lower mandible length	16.7 ± 0.8	17.1 ± 0.8	17.0 ± 1.0	16.8 ± 0.9	16.5 ± 0.8	16.9 ± 0.9	17.5 ± 0.7	16.7 ± 0.7
Lower mandible width	4.0 ± 0.6	4.7 ± 0.4	4.6 ± 0.7	4.7 ± 0.4	4.0 ± 0.5	4.8 ± 0.3	5.1 ± 0.1	4.8 ± 0.2
Culmen length	19.2 ± 0.7	20.0 ± 0.9	19.4 ± 0.8	19.3 ± 1.1	19.2 ± 0.7	19.7 ± 0.8	20.0 ± 0.6	19.3 ± 0.7
Skull + bill length	39.5 ± 1.2	40.8 ± 1.4	39.8 ± 1.4	40.2 ± 1.1	39.5 ± 1.4	40.8 ± 0.9	40.9 ± 0.6	39.7 ± 0.9
Bill width	10.6 ± 0.5	10.7 ± 0.4	10.9 ± 0.2	10.6 ± 0.4	10.5 ± 0.5	10.6 ± 0.4	10.9 ± 0.3	10.6 ± 0.3
Bill depth	10.5 ± 0.5	10.6 ± 0.4	10.6 ± 0.6	10.6 ± 0.3	10.3 ± 0.5	10.6 ± 0.3	11.0 ± 0.2	10.7 ± 0.3
FEMALES	Navarra $(n = 80)$	Alicante $(n = 61)$	Málaga (n = 23)	Mallorca $(n = 8)$	Navarra $(n = 23)$	Alicante $(n = 50)$	Málaga $(n=2)$	Mallorca $(n = 7)$
Wing length	94.5 ± 2.0	92.1 ± 2.7	93.4 ± 2.0	89.1 ± 4.2	93.7 ± 1.6	93.0 ± 2.4	93.0 ± 1.4	90.3 ± 1.8
Tail length	56.6 ± 3.5	56.5 ± 2.5	55.8 ± 3.2	57.0 ± 5.6	57.3 ± 3.0	57.0 ± 2.6	58.0 ± 1.4	55.9 ± 1.6
Tarsus length	21.6 ± 0.7	21.6 ± 0.6	21.5 ± 0.6	21.1 ± 0.3	21.6 ± 0.5	21.5 ± 0.7	21.1 ± 0.1	21.1 ± 0.6
Upper mandible length	17.8 ± 0.8	18.3 ± 0.6	18.0 ± 0.9	17.9 ± 0.8	17.7 ± 0.7	18.0 ± 0.8	18.8 ± 0.4	17.8 ± 0.3
Lower mandible length	16.4 ± 0.8	16.6 ± 0.8	16.6 ± 1.1	16.0 ± 0.9	16.1 ± 0.8	16.5 ± 0.7	16.8 ± 0.4	16.2 ± 0.9
Lower mandible width	3.9 ± 0.6	4.4 ± 0.4	4.3 ± 0.9	4.6 ± 0.3	4.1 ± 0.5	4.6 ± 0.4	5.0 ± 0.0	4.5 ± 0.3
Culmen length	18.7 ± 0.8	19.2 ± 0.7	18.6 ± 0.8	18.8 ± 0.9	18.9 ± 0.8	19.0 ± 0.8	19.9 ± 1.3	18.7 ± 0.7
Skull + bill length	38.9 ± 1.3	40.0 ± 0.9	39.0 ± 1.4	39.4 ± 0.9	39.2 ± 1.0	39.9 ± 1.1	39.9 ± 0.5	39.5 ± 0.5
Bill width	10.4 ± 0.4	10.4 ± 0.3	10.7 ± 0.4	10.6 ± 0.4	10.4 ± 0.4	10.4 ± 0.4	10.7 ± 0.2	10.6 ± 0.3
Bill depth	10.3 ± 0.4	10.3 ± 0.4	10.3 ± 0.7	10.7 ± 0.4	10.3 ± 0.4	10.3 ± 0.4	10.7 ± 0.2	10.6 ± 0.4

Table 1. Biometrics of Common Crossbills Loxia curvirostra within Iberia (Navarra, Alicante, Málaga) and the Balearics(Mallorca), captured from 1993 to 2002. Means are given \pm SD. All measures are in mm.

localities was low (n < 10 in Mallorca, except in JM) and very low (n = 2 in JF from Málaga), so analyses with these groups are statistically not very robust. Thus, to pool all data within each locality (i.e. to make the sample size larger, combining data on all the age-sex categories), we conducted an ANOVA on each of the variables, with sex and age as control factors, and used the residuals of each measurement within a Discriminant Function Analysis (DFA).

The DFA was used to quantify morphological diversification of populations of Common Crossbills in Iberia and the Balearics (Hair *et al.* 1999). We also used this analysis to determine which variables had the greatest discriminating capacity. With this purpose, standardized coefficients derived from the obtained discriminant functions (DF) were used (Dillon & Goldstein 1984).

As a complement, we also used univariate ANOVA's on each of the variables (corrected for age and sex effects), to know which variables showed significant univariate differences among sites. The software SPSS v.11.0 for Windows was used.

RESULTS

The Discriminant Function Analysis provided 3 significant DF (Function 1: $\lambda_{Wilk} = 0.426$, canonical correlation r = 0.688, P < 0.001; Function 2: $\lambda_{Wilk} = 0.808$, r = 0.375, P < 0.001; Function 3: $\lambda_{Wilk} = 0.940$, r = 0.244, P < 0.001). Standardised coefficients of the functions are described in Table 2. When focussing on DF 1 only, which explained 79.8% of the variance, the most contributing biometric variables (based on their absolute values) were LMW (0.892) followed by WL (-0.518; see Table 2 for further details).

Overall, 70.0% of individuals were correctly classified by the DFA (Table 3, Fig. 3), with a decreasing proportion from Navarra to S Iberia and the Balearics.

Table 2. Standardised coefficients of canonical discriminant functions, and the percentage of variance explained. Variables used in the DFA were corrected for the effect of age and sex.

Corrected variables	Function 1	Function 2	Function 3
Culmen length	-0.06	0.48	-0.05
Upper mandible length	0.25	-0.24	0.21
Lower mandible length	-0.01	-0.14	0.42
Lower mandible width	0.89	-0.01	0.49
Bill width	0.23	-0.55	0.30
Bill depth	-0.31	-0.57	-0.46
Skull + bill length	0.15	0.80	-0.30
Tarsus length	-0.12	0.15	0.22
Wing length	-0.52	0.17	0.66
Tail length	-0.30	-0.08	-0.13
Explained variance (%)	79.8	14.5	5.6

Birds from Navarra were never classified as belonging to Mallorca by the DFA, and the proportion of Crossbills from Navarra classified as belonging to other sites was smaller than 16.0% (Alicante 13.7%; Málaga 2.3). By contrast, many birds from Mallorca were classified as belonging to Alicante (45.5%, note that only 30.3% of individuals from Mallorca were correctly classified), some as belonging to Málaga (15.2%) and very few to Navarra (9.1%). Thus, Crossbills from Navarra and the Balearics were morphologically clearly differentiated, and Crossbills from Navarra seemed to be relatively well differentiated from those from S Iberia, while individuals from Mallorca, though



Figure 3. Scatter plot provided by the first and the second discriminant functions. Z values are plotted for each studied population: Navarra (1), Alicante (2), Málaga (3) and Mallorca (4). Centroids are represented by the marked dots.

Table 3. Table 3.	Classification matrix	provided by t	he DFA or	n four p	oopulations	of Common	Crossbills	from	Iberia a	and
the Balearics. Con	rrect classifications, ir	bold.								

	Navarra	Alicante	Málaga	Mallorca	Correct classifications (%)	
Navarra ($n = 256$)	215	35	6	0	84.0	
Alicante ($n = 230$)	39	170	13	8	73.9	
Málaga ($n = 88$)	18	39	30	1	34.1	
Mallorca ($n = 33$)	3	15	5	10	30.3	

relatively well differentiated from Crossbills from Navarra and Málaga, showed a large morphological overlap with those from Alicante.

In Alicante, 17.0% of specimens were classified as Crossbills from Navarra, whilst only 9.2% as individuals from the rest of Mediterranean sampling localities (Málaga 5.7%; Mallorca 3.5%). With regards to Málaga, 20.5% of Crossbills were classified as individuals from Navarra, while 45.4%, as specimens belonging to other Mediterranean sites (Alicante 44.3%; Mallorca 1.1%). Thus, concerning the two localities in S Iberia, an average of 17.9% of Crossbills were classified as belonging to Navarra. By contrast, less than 10.0% of the individuals from Alicante were classified as Crossbills from the other Mediterranean localities. while for Málaga many birds were considered by the DFA as Crossbills from other Mediterranean sites. The proportion of individuals from S Iberia classified as belonging to Mallorca was very low (mean 2.3%).

Univariate ANOVA's revealed that all the corrected variables showed significant differences among sampling zones (Table 4). Afterwards, a Tukey-B test showed that localities were included into distinct clusters according to different variables, which made the interpretation of data rather confusing and difficult (Table 4).

DISCUSSION

Discriminant Function Analysis showed that Crossbills from Iberia and the Balearics differ in biometry among locations. To find causes explaining this variation we must consider some biometric variables linked to bill morphology, since the lower mandible width contributed most to the canonical discriminating functions. This measure supports the idea that adaptation for foraging is one of the main causes of diversity among Crossbill populations (Massa 1987, Benkman 1993, 1999). Indeed, Crossbills from Navarra captured in forests of Scots pines showed a smaller bill than Crossbills from S Iberia and the Balearics, captured in forests of Aleppo pine. Scots pine shows smaller, less hard cone scales than Aleppo pine (Castroviejo et al. 1986), so optimal bill morphology of specimens foraging on Scots pine may be more delicate than of birds which forage on Aleppo pine (see Benkman 1993).

We also observed that individuals from Navarra had a longer wing than Mediterranean ones. Though this variable is used as an estimator of body size (Gosler *et al.* 1998), it is considered to work best to make comparisons within populations, rather than between them (P. Edelaar pers. comm.). By contrast, wing length well reflects

	F_3	P^1				
Culmen length	21.01	***	Alicante ^a	Málaga ^{ab}	Mallorca ^{bc}	Navarra ^c
Upper mandible length	26.26	***	Alicante ^a	Málaga ^a	Mallorca ^b	Navarra ^b
Lower mandible length	12.26	***	Málaga ^a	Alicante ^a	Navarra ^b	Mallorca ^b
Lower mandible width	81.65	***	Málaga ^a	Alicante ^a	Mallorca ^a	Navarra ^b
Bill width	16.25	***	Málaga ^a	Mallorca ^b	Alicante ^b	Navarra ^b
Bill depth	9.73	***	Mallorca ^a	Málaga ^a	Alicanteab	Navarra ^b
Skull + bill length	35.39	***	Alicante ^a	Málaga ^b	Mallorcabc	Navarra ^c
Tarsus length	5.99	**	Navarra ^a	Alicante ^a	Málagaa ^b	Mallorca ^b
Wing length	47.83	***	Navarra ^a	Málaga ^b	Alicante ^b	Mallorca ^c
Tail length	2.97	*	Navarra ^a	Alicantea ^b	Málaga ^{ab}	Mallorca ^b

Table 4. Univariate ANOVA's on biometrics of four populations of Crossbills from Iberia and the Balearics. Within each variable, populations were ordered from small to large. Locations across which no significant differences were observed according to a Tukey-B test, are indicated by similar superscripts.

 $^{1} * P < 0.05, ** P < 0.01, *** P < 0.001$

flight performance, with migrant species or populations having a longer wing than resident ones (Mönkkönen 1995, Calmaestra & Moreno 2001), which improves flight efficacy and promotes higher migratory speeds. If we consider that Aleppo pine is a more stable food source (Senar *et al.* 1993), Aleppo pine Crossbills might move less in their lives, hence showing shorter wings, as we observed in this work. Accordingly, also note that the island-dwelling Crossbills on Mallorca had the shortest wings.

The DFA showed that less than 10% of Crossbills from Mallorca were classified as belonging to Navarra, whilst no Crossbills from Navarro region were classified as belonging to Mallorca. This agrees with data on subspecies of Common Crossbill in N Iberia and the Balearics (Cramp & Perrins 1994, Knox 1997).

The DFA results also showed that Crossbills from S Iberia seemed to be intermediate between individuals from Navarra (curvirostra subspecies) and Mallorca (balearica), as suggested by Cramp & Perrins (1994). A more detailed analysis revealed that populations from S Iberia showed more similarities with those from Navarra than with those from Mallorca. Indeed, Crossbills from Málaga overlapped mainly with individuals from Alicante, and at the same time more with Crossbills from Navarra than from Mallorca, and a similar trend was shown by Crossbills from Alicante. Accordingly, we must reject that Crossbills from S Iberia and the Balearics belong to a single morphologically undifferentiated subspecies balearica. What phenomenon does explain then this divergence among Mediterranean sites? As pointed out in the introduction, a possible isolation of Crossbills from the Balearics may have caused this divergence (populations from S Iberia and the Balearics may have evolved independently). Nonetheless, due to the fact that Crossbills from these two areas feed on the same key pine (Aleppo pine), it is unlikely that geographic location by itself explains some of the biometric variation between these two sites, particularly if we regard bill-associated variables. By contrast, as argued before, shorter wing lengths in Crossbills from Mallorca than from S Iberia were well explained if we consider that birds from Mallorca move less as a consequence of living on a small island. Alternatively, as suggested by Mezquida & Benkman (2005), biometric variations of Aleppo pine Crossbills from S Iberia and the Balearics are consistently supported by variations of cone scale traits (such as scale length or thickness), as a result of co-evolutionary interactions of cone traits, squirrels and Crossbills.

In conclusion, both ANOVA's and DFA showed that Crossbills from S Iberia have an intermediate morphotype between the curvirostra and the balearica subspecies, occurring in N Iberia and the Balearics, respectively. Considering the assignments in the DFA, Crossbills from S Iberia were more similar to those from N Iberia than to those from the Balearics. Hence, morphological diversification among Crossbill populations was found to be mainly related to insularity. At present it is unclear whether this is due to isolation, or due to resource adaptation (the evolution of a phenotype that is best able to utilise the distinct food resource on the Balearics that has evolved in the absence of squirrels). Resource adaptation may well explain the difference in biometry between birds from N and S Iberia, since birds feeding on cones with weaker scales had a smaller bill width. Further studies on movements of Crossbills within Iberia and between the Balearics and Iberia could help to clarify how the flow and hence the hybridization among populations of Spanish Crossbills occurs. To improve our understanding of the factors driving population differentiation in Crossbills, it is necessary to next test how genetic diversification is related to morphological diversification, resource use, and isolation.

ACKNOWLEDGEMENTS

T. Santamaría collaborated during the field work. Governments from Navarra, Andalucía, Valencia and Baleares authorised us to ringing activities. We also extend our thanks to A. Zaragozí, C. Palanca, J. Castany, A. Lara, F. Fernández, and M. Suárez, for their hospitality. P. Edelaar provided us with very interesting ideas which aided to shape the paper. Useful comments from P. Edelaar and R. Summers on earlier drafts improved this work.

REFERENCES

- Benkman C.W. 1987. Food profitability and the foraging ecology of crossbills. Ecol. Monogr. 57: 251–267.
- Benkman C.W. 1993. Adaptation to single resources and the evolution of Crossbill (*Loxia*) diversity. Ecol. Monogr. 63: 305–325.
- Benkman C.W. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. Am. Nat. 153: S75–S91.
- Benkman C.W. 2003. Divergent selection drives the adaptive radiation of crossbills. Evolution 57: 1176–1181.
- Borrás A. & Senar J.C. 2003. Piquituerto Común. In: Martí R. & del Moral J.C. (eds). Atlas de las aves reproductoras de España.: 588–589. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid.
- Calmaestra R. & Moreno E. 2001. A phylogeneticallybased analysis on the relationship between wing morphology and migratory behaviour in passeriformes. Ardea 89: 407–416.
- Castroviejo S., Laínz M., López González G., Montserrat P., Muñoz Garmendia F., Pauci J. & Villar L. (eds). 1986. Flora Ibérica. Plantas vasculares de la Península Ibérica e Islas Baleares. Volume I. Real Jardín Botánico-C.S.I.C., Madrid.
- Clouet M. & Joachim J. 1996. Premiers élements de comparaison de trois populations françaises de Beccroisés *Loxia curvirostra*. Alauda 64: 149–155.
- Cramp S. & Perrins C.M. 1994. Handbook of the Birds of Europe, Middle East and North Africa. Volume VIII. Oxford University Press. Oxford.
- Dillon W.R. & Goldstein M. 1984. Multivariate analyses: methods and applications. Wiley & Sons, New York.
- Eck S. 1981. Reflexionen über die Taxonomie westpalaearktischer Loxia-Arten (Aves, Passeriformes, Fringillidae). Zool. Abh. 37: 183–207.
- Edelaar P., Summers R. & Iovchenko N. 2003. The ecology and evolution of crossbills *Loxia* spp.: the need for a fresh look and an international research program. Avian Sci. 3: 85–93.
- Edelaar P. & Terpstra K. 2004. Is the nominate subspecies of the Common Crossbill *Loxia c. curvirostra* polytypic? I. Morphological differences among years at a single site. Ardea 92: 93–102.
- Futuyma D.J. 1998. Evolutionary Biology. Sinauer Associates, Sunderland.

- Gosler A.G., Greenwood J.J.D., Baker J.K. & Davidson N.C. 1998. The field determination of body size and condition in passerines: a report to the British Ringing Committee. Bird Study 45: 92–103.
- Groth J.G. 1993. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American red crossbill (*Loxia curvirostra*) complex. Univ. California Publ. Zoology 127, Berkeley.
- Hair J.F., Anderson R.E., Tatham R.L. & Black W.C. 1999. Análisis multivariante. 5th Edition. Prentice Hall Iberia, Madrid.
- Jutglar F. & Masó A. 1999. Aves de la Península Ibérica. Editorial Planeta, Barcelona.
- Knox A.G. 1976. The taxonomic status of the Scottish Crossbill Loxia sp. Bull. Brit. Orn. Club 96: 15–19.
- Knox A.G. 1990. Probable long-term sympatry of Common and Scottish crossbills in northeast Scotland. Scot. Birds 16: 11–18.
- Knox A.G. 1997. Crossbill. In: Hagemeijer W.J.M. & Blair M.J. (eds). The EBBC Atlas of European Breeding Birds: 726–727. Poyser, London.
- Massa B. 1987. Variations in Mediterranean Crossbills Loxia curvirostra. Bull. Brit. Orn. Club 107: 118–129.
- Mezquida E.T. & Benkman C.W. 2005. The geographic selection mosaic for squirrels, crossbills and Aleppo pine. J. Evol. Biol. 18: 348–357.
- Mönkkönen M. 1995. Do migrant birds have more pointed wings?: a comparative study. Evol. Ecol. 9: 520–528.

Newton I. 1972. Finches. Collins, London.

- Schluter D. 2001. Ecology and the evolution of species. Trends Ecol. Evol. 16: 372–380.
- Senar J.C., Borrás A. Cabrera T. & Cabrera J. 1993. Testing for the relationship between coniferous crop stability and common crossbill residence. J. Field Ornithol. 64: 464–469.
- Summers R.W. & Jardine D.C. In press. Vocal similarities between Mediterranean and north European pine crossbills *Loxia* spp. Ardeola.
- Summers R.W. & Piertney S.B. 2003. The Scottish Crossbill – what we know and what we don't. Brit. Birds 96: 100–111.
- Svensson L. 1992. Identification guide to European passerines. Oxford University Press, Oxford.
- Tellería J.L., Asensio B. & Díaz M. 1999. Aves Ibéricas. II. Paseriformes. J.M. Reyero Editor, Madrid.

SAMENVATTING

Op het Iberisch Schiereiland worden momenteel twee ondersoorten van de Kruisbek onderscheiden, namelijk *L.c. curvirostra* (op het vasteland) en *L.c. balearica* (op de Balearen). Over de Kruisbekken van Zuid-Spanje heerst enige onzekerheid omtrent de status van de ondersoorten. Deze studie beoogt de morfologische variatie met behulp van biometrische gegevens in kaart te brengen. Daartoe werden deelpopulaties bemonsterd in Noord-Spanje (Navarra) en Zuid-Spanje (Alicante en Málaga), en op de de Balearen (Mallorca). De Kruisbekken van Noord-Spanje en Mallorca verschilden duidelijk van elkaar, wat een bevestiging opleverde van hun subspecifieke status. De Kruisbekken van Zuid-Spanje vormden een tussengroep, zij het met een duidelijker overlap met de Noord-Spaanse dan met de Balearische vogels. Het lijkt dus uitgesloten dat de Zuid-Spaanse en Balearische Kruisbekken een morfologisch ongedifferentieerde *balearica* ondersoort vormen, ondanks het feit dat beide groepen op de kegels van de Aleppo-den *Pinus halepensis* foerageren (in tegenstelling tot de Noord-Spaanse, die afhankelijk is van Grove den *Pinus sylvestris* met zijn minder stugge schubben) en dientengevolge aan dezelfde coevolutionaire interacties tussen kegels, Eekhoorns *Sciurus vulgaris* en Kruisbekken onderhevig zijn geweest. De Kruisbekken van de Balearen hadden wel de kortste vleugels van alle onderzochte deelpopulaties op het Iberisch Schiereiland, geheel in lijn met hun status van standvogel. Overigens moet worden benadrukt dat de steekproef van Mallorca erg klein was. (RGB)

Corresponding editor: Rob G. Bijlsma Received 26 July 2005; accepted 17 March 2006