

## Is the nominate subspecies of the common crossbill *Loxia c. curvirostra* polytypic? II. Differentiation among vocal types in functional traits

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Vocally differentiated common crossbill *Loxia curvirostra* populations ('vocal types') in North America show a high degree of morphological and ecological specialization coupled with significant genetic differentiation and appreciable levels of assortative mating in sympatry. Similar vocally differentiated common crossbill vocal types have recently also been uncovered in Europe. These vocal types frequently overlap in space and time, and preliminary data indicate strong assortatively mating in sympatry. These observations suggest that the European nominate subspecies also consists of several independent evolutionary lineages, but so far morphological and ecological support for this view has been lacking. Bill morphology of crossbills is tightly linked to resource use, and we earlier showed that average morphology (of birds of unknown vocal type) indeed differed among years, consistent with the possibility that vocal types are morphologically differentiated if the proportion of each type caught varies among years. Here we test specifically for morphological differences between birds assigned to vocal type, at two sites and during two independent influxes. Differentiation between the two vocal types studied is highly significant, with the same pattern uncovered at each site and for each influx. Of eight traits investigated, in both univariate and multivariate analyses, the trait that differs most between the two types is the ecologically important bill depth. The difference in average bill depth between these two European vocal types (0.26 mm) is equivalent to the difference between some ecologically specialised North American vocal types. These results provide further evidence that the nominate subspecies of the common crossbill consists of several ecologically distinct populations, if not cryptic species.

Despite earlier expectations to the contrary the discovery of avian biodiversity has not slowed down (Peterson 1998), and does not even exclude (supposedly) well-known areas or genera. For example, recent studies on the North American red crossbill (=common crossbill *Loxia curvirostra*) have uncovered nine distinct kinds of crossbills, termed 'vocal types'. These populations are vocally, morphologically, and genetically differentiated and have partly overlapping distributions (Groth 1988, 1993a, b, Benkman 1999, Parchman et al. 2006). In line with this differentiation in regions of overlap, some of these types seem largely reproductively isolated in sympatry (Smith and Benkman 2007; see also Groth 1993a, b, and refs. in Knox 1990), supporting specific status. These nine vocal types only partially match up with earlier named subspecies, and the observed sympatric breeding without much hybridisation of some types suggests that a drastic departure from the old taxonomic system of allopatric subspecies (e.g. Newton 1972) may be needed to capture biological reality, even if other sympatric types are not fully reproductively isolated.

Discrete vocal types of common crossbills have recently also been identified in Europe (Clouet and Joachim 1996,

Robb 2000, Summers et al. 2002). High correspondence between these studies shows that these vocal types reflect true biological entities and are not products of arbitrary classification of continuous vocal variation (Edelaar et al. 2003). This discovery of vocal types in Europe begs the question whether cryptic biodiversity, as recently uncovered in North America, is also present in the European crossbills.

In contrast to the North American vocal types, rather little is known about the distribution, morphology, ecology, and evolutionary status of the European vocal types. Several vocal types are found to have largely overlapping distributions, from the British Isles and Central Europe to at least Scandinavia and the Baltic States (Robb 2000), and have regularly been found breeding within this area. Geographic overlap during the breeding season is by definition normally not observed in (allopatric) subspecies, but seems to be common for crossbill vocal types. While the amount of data are still limited to some 70 pairs, vocal types breeding in sympatry show almost complete assortative mating (Robb 2000, Edelaar et al. 2003, 2007), suggesting that vocal types are to some extent reproductively isolated, independent evolutionary lineages 'hidden' within the

nominate subspecies of the common crossbill *L. c. curvirostra* (see also Edelaar 2008 for more discussion).

Such independent lineages may arise due to ecological specialisation to different resources, as is true for the North American vocal types. Here significant morphological differences are most pronounced in the size and shape of the bill, which reflect adaptations to specialist feeding on different types of conifer cones (Benkman 1993, 2003). This is especially true for bill depth, since this trait is strongly linked to ecological performance in crossbills, determining feeding rate and efficiency (Benkman 1993). Out of five morphological traits including three bill traits, bill depth has been identified as the main target of selection in a natural crossbill population (Benkman 2003). Strong trade-offs in feeding efficiency result in low fitness for birds with maladaptive bill depths, and indeed each of the five vocal types investigated so far have a bill depth that is (near) optimal for utilizing a specific conifer as its key resource (Benkman 1993, 2003). Thus ecological specialisation and divergent selection on bill morphology seem to explain the origin and maintenance of distinct kinds of North American crossbills, even in sympatry (Smith and Benkman 2007).

It is logical to hypothesise that ecological specialisation and divergent selection on bill morphology may also have driven the origin of the European vocal types. If so, then morphological differentiation similar to North American vocal types is expected, especially in bill traits such as bill depth. Hence we compared morphological traits between European vocal types, in order to test for any population differentiation, which traits differed most, and by how much. By doing so this paper contributes to answering the question whether cryptic biodiversity exists in European common crossbills.

## Materials and methods

Individuals were attracted to caged common crossbills and small ponds for drinking and bathing, and were caught in mist nets upon approach. The surroundings of the first catching site (52°49'N–6°24'E) consisted of mixed conifer plantations of Scots pine *P. sylvestris*, larch species *Larix spp.* and Douglas-fir *Pseudotsuga menziesii*. We measured the following body and bill traits of a large sample of captured crossbills: mass, wing length (maximally flattened and stretched), tarsus length (from tarsometatarsal notch to front of bent foot), bill depth (from start of feathering to narrowest part of lower mandible), upper mandible length (from start of feathering to tip), lower mandible length (from most distal part at base to tip), lower mandible width (between left and right most distal part at base), length of head plus bill (largest distance between tip to back of head; see Svensson 1992 (pp. 304–308) and Edelaar and Terpstra 2004 for figures and details on catching, sexing, ageing, and measuring). Crossbill flight calls were recorded upon release (i.e. biometry was measured without prior knowledge of an individual's vocal type) and assigned to one of the six vocal types previously described in Robb (2000) by two different observers. A seventh call type ('X') discovered after the publication of Robb (2000) has here been conservatively included in call type A, which it resembles most in structure

of the calls, until its validity has been better established. For 14 ringed birds recaptured and remeasured several days to months later, repeatabilities of measurements (standardised and corrected, see below) were calculated following Lessells and Boag (1987) and found to be moderate to high: 0.71 (bill depth), 0.72 (mass), 0.72 (length head plus bill), 0.78 (lower mandible width), 0.83 (lower mandible length), 0.83 (wing length), 0.90 (upper mandible length), 0.94 (tarsus length). Assignment of these birds to call type was 100% identical.

We focus here only on the two most abundant crossbill vocal types A and C (from the scheme in Robb 2000; also termed vocal types 2B and 4E in Summers et al. 2002 or wandering crossbill and glip crossbill in Constantine and the sound approach 2006, respectively). All measures (cube root for mass) were ln-transformed and standardized to a mean of zero and a standard deviation of one. By doing this for each sex separately, we corrected for any (often statistically significant) sexual size-dimorphism (unsexed birds, including potentially still growing birds in full juvenile plumage, were excluded). First, stepwise-backward ANOVAs were performed on each morphological trait in order to test and correct for any confounding variables. The full model included the variables vocal type, age-class, and month number since the beginning of the study; non-significant variables were deleted one by one until all remaining variables were significant. After sequential Bonferroni-correction for multiple testing (alpha-level of 0.05 divided by the number of tests (traits) under evaluation), measurements did not differ between age-classes, but did differ between months for 5 out of 8 traits. Temporal variation in mass and upper and lower mandible lengths is well known for crossbills, and often related to food availability and intensity and substrate of feeding (affecting wear of the continuously growing horny covering of mandibles). Observed changes in bill depth and lower mandible width might be due to temporal observer variability in measuring, or perhaps even selection due to birds with particular characteristics dying or leaving the area. However, since here we are not interested in temporal changes yet these add variance to measurements, we corrected these five traits for month effects, where effect sizes were estimated in the presence of the factor vocal type only if this factor significantly contributed to the model. In the process six outliers (1.3% of all data) with highly significantly deviating residuals were encountered and removed (NB: including them did not alter any of the conclusions). Visual examination of the cumulative probability distributions of the remaining transformed and corrected data showed that the data conformed to normality.

Next, we tested for morphological differentiation of the two vocal types by univariate ANOVAs for each of the measured traits separately, and by multivariate Discriminant Function Analyses (DFA) on all traits simultaneously. DFA is used to test whether pre-defined groups differ significantly in multivariate trait-space, and we deleted traits stepwise from the full DFA model to identify those traits that contributed significantly to any detected population difference. Collinearity between variables was not too high for stepwise DFA (tolerance values varied from 0.45–0.86).

In order to gain confidence in any observed differentiation, we determined whether the obtained results were robust in the following ways. First, after performing a DFA on the whole dataset, we also analyzed males and females separately in order to see if each sex showed the same pattern. Second, during the study period two separate influxes of crossbills occurred in the Netherlands (summer 2002 to spring 2003, summer 2004 to spring 2005) with a virtual absence of birds in the intervening period of about a year, suggesting that these two influxes represent independent samples originating from outside the country. Hence we also analyzed birds from the first and second influx separately, to see if the results were temporally robust. Third, we performed ANOVAs and a DFA on measures of birds caught at a second site and measured by an independent observer (same measures except for tarsus length and lower bill length, which were not taken). Forest cover at this site (52°23'N–5°55'E) was predominantly dry Scots pine plantations with a one square kilometre plot of Douglas-fir nearby. Correction for month effects was not done because of unreliable estimates due to smaller sample sizes ( $n = 34$  type A and 22 type C at site 2 versus  $n = 284$  type A and 163 type C at site 1). This allowed us to test not only for spatial/observer robustness but also whether the results are similar when uncorrected data are used (only ln-transformed and standardized for each sex).

## Results

### Univariate differences

Except for upper and lower mandible length, the two vocal types differed significantly in all measured traits. The most notable difference was in bill depth (see Fig. 1, Table 1). This pattern of significance (and the direction of the difference) was the same for each sex when analyzed separately, except that wing length was marginally non-significant in males and tarsus length non-significant in females (Table 1). At site 2, types differed significantly in bill depth ( $F_{1,59} = 7.78$ ,  $P = 0.007$ ) and lower mandible width ( $F_{1,62} = 4.09$ ,  $P = 0.048$ ; other traits  $P > 0.05$ ): these traits also showed the most significant difference at site 1 (see Fig. 1).

### Multivariate differences

The two vocal types differed highly significantly in multivariate space (DFA, full model, Wilks' lambda = 0.82,  $P < 0.001$ ). In a stepwise-backward model, the final discriminant function (DF) was constructed of bill depth, upper mandible length, length of head + bill, and wing length (see Table 2). Jack-knifed classification correctly identified 68% of the individuals to vocal type (vs 50% expected by chance alone). When the sexes and influxes were analyzed separately, stepwise-backward models were very similar in that bill depth, upper mandible length, and length of head + bill or wing length were included and had similar loadings in both direction and magnitude (see Table 2). For site 2, the DF encountered by the stepwise-backward model was very similar to those of site 1 in that bill depth and

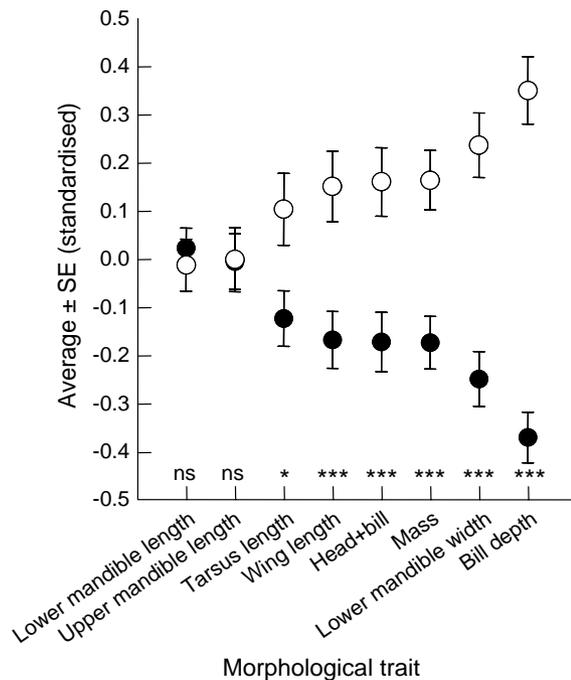


Fig. 1. Mean and standard error of eight standardized morphological traits, separately for type A (closed dots,  $n = 284$ ) and type C (open dots,  $n = 163$ ) crossbills caught at site 1 (sexes combined). Traits are ordered from left to right as having a larger average for type C. Stars give level of significance of univariate ANOVA ( $df_{1,445}$ ): \*  $P < 0.05$ , \*\*\*  $P < 0.001$ .

upper mandible length were included in all and had very similar loadings (see Table 2).

## Discussion

We detected highly significant univariate and multivariate morphological differences between the two most abundant, widespread and largely overlapping European crossbill vocal types (Robb 2000). We argue that these patterns are not statistical artefacts. First, all traits showing a significant month effect did not show a significant interaction between the factors month and vocal type ( $P$ -values were 0.27, 0.82, 0.82, 0.95 and 0.99), implying that even though some traits did fluctuate over time, the significant differences between vocal types fluctuated in parallel (i.e. were constant) during the whole study period. Second, multivariate differences were consistent across the sexes, across two different influxes of crossbills into the study area, and across two different observers measuring crossbills caught at different geographic locations, indicating that the observed differences are not a local or sampling artefact. For the second site we did not correct for a month effect, yet the observed pattern was similar. It is also worth noting that a third independent dataset from the UK also shows significant differentiation between types A and C (R. Summers unpubl. data).

Whilst the vocal types differed significantly in most traits (see Fig. 1), the univariate difference was by far the greatest for bill depth, which differed more than 0.7 standard deviations between the types. Bill depth was also most prominent in multivariate differentiation (see Table 2).

Table 1. Descriptive statistics for each of eight morphological traits for the two European common crossbill *Loxia curvirostra* vocal types A and C caught at site 1, and statistical significance of the difference between vocal types; males and females separately.

Trait	Males (n = 243)										
	Type A (n = 159)				Type C (n = 84)				Percent diff. (C-A)	F <sub>1,241</sub>	P
	Mean	SD	Min	Max	Mean	SD	Min	Max			
Mass (g)	39.29	2.42	33.7	46.5	40.26	2.35	34.8	45.6	2.45	11.0	0.001
Wing length (mm)	98.32	2.16	92.0	105.0	98.90	2.22	94.0	105.0	0.59	3.86	0.051
Tarsus length (mm)	17.70	0.47	16.7	18.8	17.86	0.46	16.2	19.0	0.90	6.56	0.011
Head+bill length (mm)	39.87	0.87	37.8	42.0	40.11	0.85	37.9	42.1	0.61	4.39	0.037
Bill depth (mm)	10.62	0.34	10.0	11.7	10.91	0.35	10.0	11.9	2.80	40.5	<.001
Upper mandible length (mm)	18.88	0.66	17.1	20.7	18.82	0.62	17.2	20.4	-0.33	1.05	0.31
Lower mandible length (mm)	16.15	0.93	13.8	18.9	15.66	0.80	13.9	17.6	-3.05	0.84	0.36
Lower mandible width (mm)	10.88	0.36	10.1	11.8	11.03	0.35	10.1	11.9	1.35	14.9	0.001

Trait	Females (n = 204)										
	Type A (n = 125)				Type C (n = 79)				Percent diff. (C-A)	F <sub>1,202</sub>	P
	Mean	SD	Min	Max	Mean	SD	Min	Max			
Mass (g)	37.83	2.66	31.2	46.4	38.44	2.06	33.8	43.6	1.60	4.89	0.028
Wing length (mm)	95.19	2.01	90.0	99.0	95.96	1.76	91.0	100.0	0.81	7.87	0.006
Tarsus length (mm)	17.69	0.48	16.1	18.8	17.75	0.46	16.5	18.7	0.32	0.69	0.41
Head+bill length (mm)	39.16	0.89	37.2	41.5	39.48	0.68	37.8	41.1	0.81	7.64	0.006
Bill depth (mm)	10.41	0.30	9.8	11.3	10.64	0.32	9.9	11.4	2.22	27.7	<.001
Upper mandible length (mm)	18.33	0.79	16.6	20.6	18.45	0.64	16.8	20.5	0.65	1.21	0.27
Lower mandible length (mm)	15.75	1.05	13.4	17.9	15.47	0.97	13.5	17.8	-1.79	0.03	0.86
Lower mandible width (mm)	10.66	0.42	9.6	11.7	10.84	0.36	9.8	11.5	1.62	13.8	0.001

Table 2. Results of stepwise-backward discriminant function analyses contrasting European crossbill vocal type A with vocal type C. Model 1 contrasts all birds of site 1 (sexes and inluxes pooled); models 2–5 describe the pattern for subsets of site 1 as indicated by their respective headers. Model 6 contrasts all birds of site 2. For each trait out of eight (six for site 2) that is significantly retained in the model we give its F-ratio and the magnitude and direction of its standardized loading on the final discriminant function. We also list for each model the value of Wilks' lambda ( $\lambda$ ) and its significance, and the proportion of birds that was correctly classified by Jack-knifed classification.

Trait	1: All individuals (n = 447)			2: Males (n = 243)			3: Females (n = 204)			4: First influx (n = 249)			5: Second influx (n = 198)			6: Second site (n = 56)			
	F	Loading		F	Loading		F	Loading		F	Loading		F	Loading		F	Loading		
Bill depth	61.9	0.91		47.4	0.96		22.1	0.90		30.5	0.85		31.3	0.97		7.21	0.94		0.94
Upper bill length	19.3	-0.68		20.8	-0.84		2.85	-0.45		11.8	-0.72		8.74	-0.56		2.43	-0.57		-0.57
Head+bill length	9.00	0.47		8.37	0.53		3.61	0.51		12.2	0.73		—	—		—	—		—
Wing length	2.10	0.18		—	—		—	—		—	—		4.25	0.37		—	—		—
Mass	—	—		—	—		—	—		—	—		—	—		—	—		—
Lower bill length	—	—		—	—		—	—		—	—		—	—		—	—		—
Lower bill width	—	—		—	—		—	—		—	—		—	—		—	—		—
Tarsus	—	—		—	—		—	—		—	—		—	—		—	—		—
	$\lambda = 0.83$			$\lambda = 0.79$			$\lambda = 0.86$			$\lambda = 0.83$			$\lambda = 0.83$			$\lambda = 0.86$			$\lambda = 0.86$
	$p < 0.001$			$p < 0.001$			$p < 0.001$			$p < 0.001$			$p < 0.001$			$p = 0.018$			$p = 0.018$
	correct: 68%			correct: 70%			correct: 61%			correct: 66%			correct: 67%			correct: 64%			correct: 64%

After manually forcing bill depth out of the statistical models, no other trait obtained a similarly high significance, and when allowed, bill depth would always and immediately re-enter the model. Our observation of population differentiation in such an important ecological trait suggests that divergent natural selection related to the use of different resources is acting on bill depth, because the functional importance of bill depth (Benkman 1993, 2003) would result in strongly stabilising selection against differentiation otherwise. In this context it is relevant that Groth (1988, table 8) also found larger differences in bill traits (especially bill depth) than in body traits in the ecologically differentiated North American vocal types 1 and 2.

Averaged over the sexes, bill depth differed by 0.26 mm between our type A and C. While this may not seem like a lot, this difference is similar to or even larger than the difference in average bill depth between some types known to be ecologically highly differentiated such as type 2 and type 5 (0.10 mm in Groth 1993, 0.30 mm in Benkman 1993) and type 2, and the highly localised South Hills crossbill (0.29 mm, Benkman 1999). From Fig. 1 in Benkman (2003), for the South Hills crossbill a positive or negative deviation of 0.26 mm from the optimal bill depth would result in a drop in survival probability from about 0.62 to about 0.39, a loss of 37%. The difference in bill depth between South Hills and type 2 crossbills, similar to the difference we found between type A and C, seems to causally explain the main part of the nearly complete reproductive isolation observed between these two crossbills (Smith and Benkman 2007). Hence, even a difference in average bill depth of only a few percent apparently has a large impact on the fitness and reproductive compatibility of populations feeding on the same food resource. This impact seems to be sufficient to explain why crossbills specialising on different conifer types have evolved different bill morphologies (Benkman 2003). Reversing this logic, the difference in average bill morphology of the magnitude we observed suggests specialisation on different resources.

Multivariate differentiation is such that the types differ not only in overall size but also in bill shape: type C has a more blunt bill and type A a more slender bill (see Fig. 2, Table 2). The evolution of deeper versus more slender bills is repeatedly observed in crossbill taxa (and other bird species) that feed on distinctly different resources (Benkman 1999, Schluter 2000, Benkman et al. 2001, 2003), further supporting the interpretation of some ecological differentiation between type A and C. Common crossbills invading to north-western France also had a significantly larger bill depth (difference 0.38 mm) but smaller upper mandible length (difference 1.23 mm) than crossbills from northern Europe (Massa 1987), even though they are thought to belong to the same population (the nominate subspecies).

We earlier (Edelaar and Terpstra 2004) suggested that annual variation in crossbill morphology (also reported by Davis 1964, Herremans 1988, Marquiss and Rae 2002) was in line with the presence of cryptic crossbill diversity within the nominate subspecies, potentially linked to the occurrence of several vocal types within its geographic distribution. Indeed the relative occurrence of type A and C during this study differed between years ( $\chi^2_1 = 49.1$ ,  $P < 0.001$ , Fig. 3). Annual variation in the proportion of different vocal types has also been reported by others (Robb 2000,

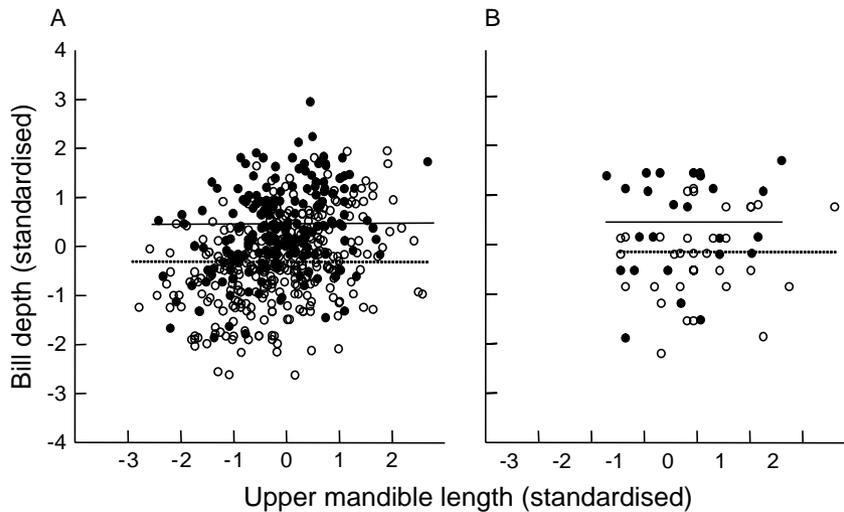


Fig. 2. Despite much overlap, type C crossbills (closed dots; continuous line indicating population average for bill depth) have a distinctly larger bill depth relative to their upper mandible length than type A crossbills (open dots; dotted line indicating population average for bill depth). This difference is independently observed both at catching site 1 (panel A) and site 2 (panel B). The difference in bill depth is significant in both panels (see text).

R. Summers pers. comm.). Moreover, the relative proportions of the vocal types caught also seemed to vary over time within invasions ( $\chi^2_5 = 8.34$ ,  $P = 0.14$  for 2002;  $\chi^2_3 = 5.88$ ,  $P = 0.12$  for 2003; Fig. 3), with type C apparently arriving later in both years. In addition to explaining temporal changes in average biometry (due to the unknowingly lumping of varying proportions of morphologically different populations), these changes in proportions over time also suggest that the vocal types originated from different areas and/or had differences in departure time or migration speed, further supporting some ecological differentiation between them.

Since crossbill vocal types differ more in vocalisations than in plumage and morphology, it has been suggested that perhaps sexual or social selection might explain their evolution, with no role for divergent natural selection

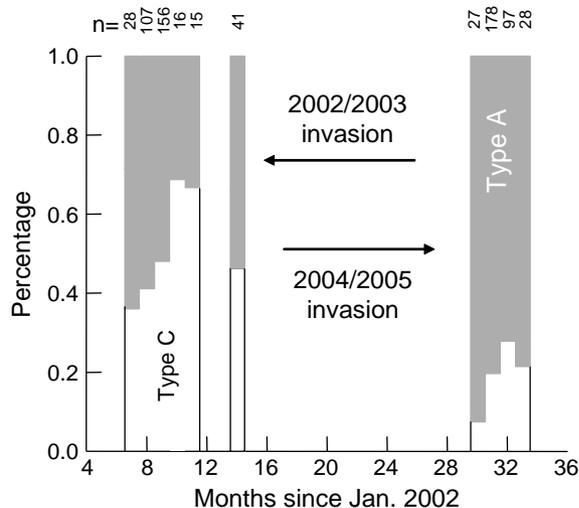


Fig. 3. The proportion of type A and type C common crossbills caught during two invasions, for each month when a minimum sample size of 15 vocally identified birds was caught.

(Galis and Van Alphen 2000). This hypothesis predicts that newly diverged populations or species are ecologically equivalent, and thus should not differ in functional traits due to stabilising selection. While it is presently unclear to what extent sexual and social selection are involved in the evolution of the European vocal types (and the North American ones for that matter), our results indicate that divergent natural selection is also involved since at least two vocal types were found to differ, and even mostly so, in functional traits.

In summary, we here show that two largely co-occurring vocal types differ significantly in morphology, and have diverged most in certain ecologically important bill traits. This leads us to draw two inferences: (i) vocal types are evolutionarily relevant lineages; and (ii) morphological differentiation is influenced by ecological differentiation and specialisation on different resources. Yet many questions remain. It is unclear whether the remaining vocal types also differ morphologically and ecologically. If so, it is not clear on which conifers each type might be specialising, given that the diversity of conifers in Europe seems much lower than in North America. In northern Europe only Norway spruce *Picea abies*, Scots pine *Pinus sylvestris* and Siberian larch *Larix sibirica* occur, but the latter two conifers are thought to be the key resource for parrot crossbill *L. pytyopsittacus* and two-barred crossbill *L. leucoptera bifasciata*, respectively, already (Lack 1944, Cramp and Perrins 1994). Additional conifer diversity is found in the Mediterranean countries and their islands, and indeed crossbills living in these regions differ morphologically (Cramp and Perrins 1994), and vocally (Summers and Jardine 2005). But these crossbills seem largely resident (Senar et al. 1993) and local birds give calls that are in fact more similar to those of parrot and Scottish crossbills *L. scotica* (Summers and Jardine 2005). Such calls do not correspond with any of the call types distinguished by Robb (2000), including type A or C treated here. The exception is type B (Robb 2000) which was recorded on Corsica, but

these may have been mainland birds (black pine *Pinus nigra* specialists?) temporarily staying at this island. Such immigrant/vagrant mainland birds have also been recorded within the range of the endemic *L. c. balearica* from the Balearic Islands (Summers and Jardine 2005) and *L. c. polioygna* from North Africa (Cramp and Perrins 1994).

In Central and southern Europe black pine might act as a key resource (for type B?), but the sparse data suggest that crossbills here are resident or leave the area only infrequently (Cramp and Perrins 1994). In the absence of parrot crossbill and two-barred crossbill in central Europe, there might be a role for European larch *Larix decidua*, Scots pine and/or mountain pine *Pinus uncinata* to support a distinct crossbill population in and around the Alps (see Glutz von Blotzheim and Bauer 1997), but again data linking vocal types with resource use and geographical distribution during periods of food scarcity (Benkman 1993) is mostly lacking. A wild hypothesis is that some vocal types have rapidly evolved in sympatry to utilise widely introduced and highly suitable North American conifers such as sitka spruce *Picea sitchensis*, Douglas-fir and lodgepole pine *Pinus contorta* which are known or suspected to support specialised crossbills in their native range (Benkman 1993), but data to test this hypothesis are still missing (smaller bills, as observed in their North American counterparts, would be expected). On the other hand, there might be ecologically significant regional variation in native conifers that we are insufficiently aware of. There is some geographical variation in Norway spruce cones that may be relevant for feeding crossbills (central European versus Scandinavian versus eastern European cones), but this remains to be tested experimentally. If geographical conifer variation indeed is relevant, this would suggest some kind of spatial structure or 'core areas' for the occurrence of the vocal types (Knox 1992). If such core areas are ultimately identified, it would mean that the nominate subspecies *L. c. curvirostra* consists of several regional populations that differ in vocalisations and biometry, probably deserving subspecific status (and specific status if reproductive isolation is confirmed in future studies). But the data and field impressions at hand, including evidence of average breeding dispersal of about 2000 km (Newton 2006), larger than for any other passerine species, so far do not support much scope for geographic population structure. Moreover, by definition subspecies interbreed when in sympatry, whereas the vocal types do not seem to do so (note that overlapping distributions, assortative mating, and morphological differentiation in ecologically important traits also do not support the interpretation that the vocal types are merely allopatric dialects). While an increasing dataset suggests complete reproductive isolation among the vocal types (Edelaar et al. 2003, Summers et al. 2007), data are few or absent for some types, and we need more experimental confirmation that complete assortative mating by calls as observed in the field is not due to the matching of calls between heterotypic individuals (as reported by Groth 1993b not to occur in two mixed pairs breeding in captivity).

Despite the lack of firm answers to some of these pressing questions, one thing is clear: the common crossbill provides for some uncommon empirical patterns.

*Acknowledgements* – Many thanks to M. Robb for co-identifying the crossbill calls and comments, to C. Benkman and D. Schluter for discussion and hosting during data collection, to A. Badyaev and M. Björklund for comments and hosting during analysis and writing, to C. Benkman, A. Badyaev, K. Oh and two anonymous reviewers for comments on a previous version. The study was financially supported by the Kluijver fund (Netherlands Ornithological Union) and a European Commission Marie-Curie OIF grant to PE. This paper reflects the author's opinion only, and the EU denies any responsibility for use of this information.

## References

- 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.
- Benkman, C. W., Holiman, W. C. and Smith, J. W. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. – *Evolution* 55: 282–294.
- Benkman, C. W., Parchman, T. L., Favis, A. and Siepielski, A. M. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. – *Am. Nat.* 162: 182–194.
- Clouet, M. and Joachim, J. 1996. Premiers éléments de comparaison de trois populations françaises de beccroisés *Loxia curvirostra*. – *Alauda* 64: 149–155.
- Constantine, M. and The Sound Approach 2006. The sound approach to birding—a guide to understanding bird sound. – Publ. by author.
- Cramp, S. and Perrins, S. C. 1994. The birds of the western Palearctic. – Oxford University Press, Oxford.
- Davis, P. 1964. Crossbills in Britain and Ireland in 1963. – *Brit. Birds* 57: 477–501.
- Edelaar, P. 2008. Assortative mating also indicates that common crossbill *Loxia curvirostra* vocal types are species. – *J. Avian Biol.* 39: 9–12.
- Edelaar, P. and 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.
- Edelaar, P., Robb, M., Van Eerde, K., Terpstra, K., Bijlsma, R. and Maassen, E. 2004. Zijn er meerdere soorten 'gewone' kruisbek in Nederland? – *Limosa* 77: 31–38.
- Edelaar, P., Summers, R. and 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.
- Galis, F. and Van Alphen, J. J. M. 2000. How fast do crossbills speciate? On assortative mating and vocalisations. – *Trends Ecol. Evol.* 15: 357.
- Glutz von Blotzheim, N. and Bauer, K. M. 1997. Handbuch der Vögel Mitteleuropas. Bd. 14. Passeriformes-part 5. – Aula-Verlag GmbH, Wiesbaden.
- Groth, J. G. 1988. Resolution of cryptic species in Appalachian red crossbills. – *Condor* 90: 745–760.
- Groth, J. G. 1993a. Call matching and positive assortative mating in red crossbills. – *Auk* 110: 398–401.
- Groth, J. G. 1993b. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the north american red crossbill (*Loxia curvirostra*) complex. – University of California, Berkeley and Los Angeles, California.

- Herremans, M. 1988. Measurements and moult of irruptive common crossbills (*Loxia curvirostra curvirostra*) in Central Belgium. – *Gerfaut* 78: 243–260.
- Knox, A. G. 1990. The sympatric breeding of common and Scottish crossbills *Loxia curvirostra* and *L. scotica* and the evolution of crossbills. – *Ibis* 132: 454–466.
- Knox, A. G. 1992. Species and pseudospecies: the structure of crossbill populations. – *Biol. J. Linn. Soc.* 47: 325–335.
- Lack, D. 1944. Correlation between beak and food in the crossbill, *Loxia curvirostra* Linnaeus. – *Ibis* 86: 552–553.
- Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities—a common mistake. – *Auk* 104: 116–121.
- Marquiss, M. and Rae, R. 2002. Ecological differentiation in relation to bill size amongst sympatric, genetically undifferentiated crossbills *Loxia* spp. – *Ibis* 144: 494–508.
- Massa 1987. Variations in Mediterranean crossbills *Loxia curvirostra*. – *Bull. B.O.C.* 107: 118–129.
- Newton, I. 2006. Movement patterns of common crossbills *Loxia curvirostra* in Europe. – *Ibis* 148: 782–788.
- Parchman, T. L., Benkman, C. W. and Britch, S. C. 2006. Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: *Loxia*). – *Mol. Ecol.* 15: 1873–1887.
- Peterson, A. T. 1998. New species and new species limits in birds. – *Auk* 115: 555–558.
- Robb, M. 2000. Introduction to vocalizations of crossbills in north-western Europe. – *Dutch Bird* 22: 61–107.
- Schluter, D. 2000. The ecology of adaptive radiation. – Oxford University Press, Oxford.
- Senar, J. C., Borrás, A., Cabrera, T. and Cabrera, J. 1993. Testing for the relationship between coniferous crop stability and common crossbill residence. – *J. Field Ornithol.* 64: 464–469.
- Smith, J. W. and Benkman, C. W. 2007. A coevolutionary arms race causes ecological speciation in crossbills. – *Am. Nat.* 169: 455–465.
- Summers, R. W. and Jardine, D. C. 2005. Vocal similarities between Mediterranean and north European pine crossbills *Loxia* spp. – *Ardeola* 52: 269–278.
- Summers, R. W., Dawson, R. J. and Phillips, R. E. 2007. Assortative mating and patterns of inheritance indicate that the three crossbill taxa in Scotland are species. – *J. Avian Biol.* 38: 153–162.
- Summers, R. W., Jardine, D. C., Marquiss, M. and Rae, R. 2002. The distribution and habitats of crossbills *Loxia* spp. in Britain, with special reference to the Scottish crossbill *Loxia scotica*. – *Ibis* 144: 393–410.
- Svensson, L. 1992. Identification guide to European passerines. – Svensson, Stockholm.