

Short communication

Rediscovery of a second kind of crossbill for the Himalayan region, and the hypothesis that ecological opportunity drives crossbill diversification

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Crossbills *Loxia* spp. are unusual among birds, not only because of their remarkable crossed mandible tips, but also because of their high degree of ecological specialization. Different species and populations of crossbills have specialized to only a single conifer species, or even a single conifer variety, as a key food resource (Lack 1944, Benkman 1993, Cramp & Perrins 1994). According to Benkman (1993), key conifers need to fulfil the following criteria if they are to support an evolutionarily specializing population: (1) they produce sufficient cones each year somewhere in their geographical range, (2) they hold seeds during that time of the year when intake rates are lowest, and (3) their seeds are protected from depletion by potential non-crossbill competitors.

The evolution of extreme dietary specialization on a single key resource is understandable for geographically isolated crossbill populations to whom only a single conifer is available, e.g. for endemic crossbills of the Balearic Islands, Corsica, Cyprus, North Africa, Vietnam, Philippines and Hispaniola. However, even in regions with several conifers available, specialization by crossbills on a single conifer is found (Benkman 1993). As a result, a higher diversity of crossbills in regions with a higher diversity of suitable conifers is found. In northern Europe, three kinds of crossbills may co-occur (Two-barred Crossbill *Loxia leucoptera bifasciata*, Common Crossbill *L. curvirostra*, and Parrot Crossbill *L. pytyopsittacus*) in line with the diversity of resources (Siberian Larch *Larix russica*, Norway Spruce *Picea abies* and Scots Pine *Pinus sylvestris*; Lack 1944, Cramp & Perrins 1994). The highest diversity of crossbills is found on the Pacific coast of North America, with locally up to seven

different crossbills (White-winged Crossbill *L. leucoptera leucoptera* plus six *L. curvirostra* 'vocal types'; Groth 1993). This region has a high diversity of suitable conifers (Farjon 1990, 2005). Hence, the overall picture is that conifer diversity and crossbill diversity are fairly well correlated.

One conspicuous outlier concerns the Himalayan Crossbill *L. c. himalayensis*. This subspecies occurs from northeastern India (Punjab) east along the Himalayan range through Nepal, Bhutan and southern Tibet, to southwestern China (from southern Gansu south through western Sichuan to northwestern Yunnan provinces). This region supports a large diversity of conifers (Farjon 1990, 2005). I found no less than 11 conifer species that at this time cannot be excluded as suitable key conifers for crossbills, based on their relatively large geographical range, relative abundance where they occur, and dimensions of cones (length up to 13.5 cm) and seeds (length up to 6 mm, mass up to 12.9 mg) that fall within the range used by crossbills elsewhere (Benkman 1993, Cramp & Perrins 1994). These are *Tsuga chinensis*, *T. dumosa* and *T. forrestii*; *Larix griffithiana* and *L. otaninii*; *Picea asperata*, *P. brachytyla*, *P. likiangensis*, *P. smithiana* and *P. spinulosa*; and *Pinus yunnanensis*. Cone and seed traits differ considerably between these genera and species of conifers (Farjon 1990, 2005) creating selection for divergence of crossbills, as it is likely that no single crossbill population could optimally use them all (Benkman 1993). Although this list of conifers is most probably an overestimate of the number of true potential and distinct key resources that could support a specialized crossbill population, it does seem unlikely that only one crossbill population could be supported by all of these conifers. If indeed several morphologically varied key conifers are available but only one kind of crossbill is known, then either the hypothesis that diversity of key conifers dictates crossbill diversity is incomplete or wrong, or we have not fully uncovered crossbill diversity in the Himalayan region. With this in mind, I investigated the existence of any cryptic diversity in Himalayan crossbills.

METHODS

Specimens collected within the published range of the Himalayan Crossbill ($n = 39$) were borrowed from various bird collections (see Acknowledgments). Several measures were taken: wing length (maximum stretched), tarsus length (from the notch at the proximal caudal tarsometatarsus to last undivided scute), tail length (from implant of central remiges to longest outer remige), bill depth (at distal end of nostril, perpendicular to cutting edge), bill width at base (where rami enter the skin), bill width at joining of the rami, upper mandible length (from distal end of nostril to tip, opposite to the side of the tip of the lower mandible) and lower mandible length (from joining of rami to tip). Not all measures could be taken from each specimen due to damaged bills or missing tail feathers. Birds in wing moult always still had the old (full-grown) outer primaries.

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Table 1. Overview of differences between small and large crossbills from the Himalayan region in eight biometric traits.

Trait	Both groups (males only) CV	Small		Large		Percentage difference	df	F	P
		Mean	Range	Mean	Range				
Wing length	4.20	81.1	(78.5–84.5)	87.3	(83.0–92.5)	7.7	1,37	95.3	< 0.0001
Tail length	6.18	49.3	(47.3–51.5)	54.1	(51.0–56.9)	9.7	1,36	89.4	< 0.0001
Tarsus length	4.80	14.0	(13.3–14.8)	15.3	(14.5–16.3)	8.9	1,36	68.3	< 0.0001
Bill depth	6.96	7.50	(7.18–8.07)	8.57	(7.88–9.44)	14.2	1,35	92.1	< 0.0001
Bill width at base	6.79	7.66	(7.30–8.11)	8.74	(7.94–9.32)	14.1	1,33	84.7	< 0.0001
Bill width at rami	8.23	5.91	(5.44–6.36)	6.70	(5.92–7.25)	13.4	1,34	40.3	< 0.0001
Upper mandible length	7.08	11.6	(10.2–12.6)	13.6	(11.7–14.7)	17.0	1,36	88.3	< 0.0001
Lower mandible length	6.53	9.03	(7.49–9.72)	10.5	(9.59–11.3)	16.5	1,37	89.6	< 0.0001

Presented are coefficient of variation (males only, the two groups combined), the mean and range for each group, the difference between the groups (as % of the smaller), and the degrees of freedom, value for the *F*-statistic and *P*-value for one-way ANOVA. All means and ranges are in millimetres.

For bill depth I included all birds with complete bills. Some birds had slightly open bills, which means that some measurement error is included (some bill depths may have been over-estimated), but this is unbiased with respect to their other measurements.

Measurements were first ln-transformed, and then standardized (to a mean of 0 and a standard deviation of 1). I did not correct for sexual dimorphism (statistically significant for wing length and upper and lower mandible length), because this would exclude nine birds in full juvenile plumage with unreliable sex (more than one-quarter of all birds; conclusions were unaltered when juveniles were excluded).

I first calculated the coefficient of variation for each trait, to look for indications of unusually large variability, suggesting that more than one population was measured. As measurements on the same individual are normally correlated and thus not independent, I constructed new independent composite variables by performing a principal components analysis (PCA) on the correlation matrix, to see if plots of principal component (PC) scores showed bimodality. Finally, I performed univariate ANOVA and multivariate discriminant function analysis (DFA) on each group as indicated by PCA to determine how any groups differed.

RESULTS

All measured traits proved to be unusually variable, with large coefficients of variation (Table 1). All traits except tarsus length showed visual indications of bimodality. The first PC accounted for 77.9% of the total variation. All loadings on this PC were positive, and ranged from 0.32 (bill width at rami) to 0.37 (wing length). The remaining PCs accounted for only 6.4% or less, and are not treated further here. PC1 is clearly bimodal without any overlap between the two distributions (Fig. 1). Birds in the two

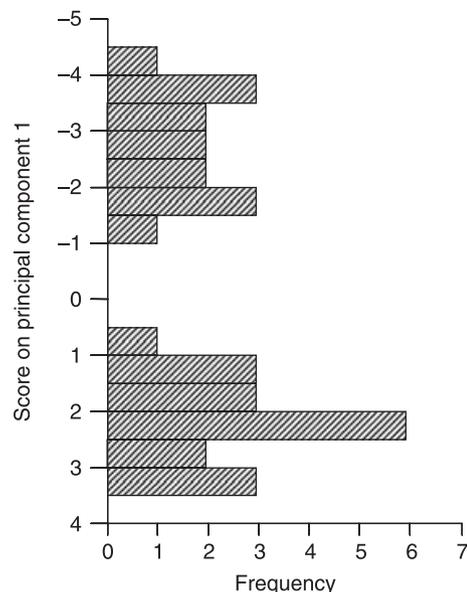


Figure 1. Frequency histogram of scores on the first principal component of 32 crossbills from the Himalayan region, showing two clearly separated groups.

distributions were then compared to test for statistical differences. One-way ANOVAs showed that these two groups differed significantly in PC1 scores ($F_{1,30} = 268.6$, $P < 0.0001$) and in all univariate measures (Table 1). DFA showed that small and large crossbills differed significantly in multivariate space ($F_{8,23} = 33.7$, $P < 0.0001$). Birds with larger discriminant function (DF) scores (larger birds) were mostly distinguished by a longer tail (loading 0.26), a longer upper mandible (loading 0.20) and a deeper bill (0.11), but by a relatively short lower mandible (-0.04).

DISCUSSION

The coefficient of variation (CV) for wing length of the Himalayan Crossbill is about one-third higher than for any other of 37 songbird populations, and the CV for upper mandible length is exceeded only by the highly polymorphic Black-bellied Seedcracker *Pyrenestes ostrinus* (Groth 1988). Compared with crossbills only, the CVs for the Himalayan sample were about twice as large as the average CV for the same traits across seven North American vocal types, and always exceeded their range (Groth 1993). Such large CVs indicate that more than one population is involved. Indeed, even without *a priori* designation to a particular group, PCA uncovered two groups that mainly differed in overall size, without any overlap in PC1 scores. These groups are not confused with sexual or age dimorphism, as both groups consisted of both sexes and age classes (small birds: six males, seven females, two juveniles; large birds: four males, thirteen females, seven juveniles). If anything, females and juveniles on average are smaller than adult males and so increase the variance of measures within each group, suggesting that differences between adults of the same sex are even more pronounced than presented here.

Based on previous descriptions of named taxa from the region, it seems that the group of small birds belong to *L. c. himalayensis* (Blyth 1845) and the group of large birds to *L. c. bangsi* (Griscom 1937). *L. c. bangsi* was synonymized with *L. c. himalayensis* soon after its description (Stanford & Mayr 1941, Vaurie 1956). It is not clear why this happened, but Stanford and Mayr (1941) write that Mayr's measurements – of what he believed to be the birds that Griscom measured – did not correspond to Griscom's published measures, and that not enough birds were included in the comparisons anyway. The results presented here vindicate Griscom's conclusion, and possibly Mayr's judgement was based on the wrong set of specimens.

How are these two groups related to conifer diversity? Judged by the *F*-values in Table 1, there are no indications that the groups have diverged more in bill traits than in body traits. On the other hand, the bill trait that seems to have the strongest impact on foraging efficiency, bill depth (Benkman 1993, 2003), differs in absolute terms by 1.07 mm. Bill depth of five distinct kinds of North American crossbills that are known to be specialized on different conifer species and varieties differ only by 0.10–0.61 mm (Groth 1993). Hence, the difference in bill depth between the two Himalayan groups seems more than enough for strong ecological differentiation. In addition, the difference in upper and lower mandible length, irrespective of whether this is innate or caused by wear, indicates use of a different resource. Both a deeper bill and a relatively shorter lower mandible are seen in crossbills specializing on conifers with cones whose scales take more force to separate (Lack 1944, Cramp & Perrins 1994).

The small birds were mainly collected in India and Nepal, with three out of 15 from the Chinese province of Yunnan. This distribution is in good agreement with specialization on Himalayan Hemlock *Tsuga dumosa* (Farjon 1990). Cones of hemlocks are the smallest from the list of potential key conifers listed earlier, and this agrees well with the fact that the smallest North American crossbill (vocal type 3, average bill depth 8.15 mm; Groth 1993) is specialized on similarly small-coned Western Hemlock *Tsuga heterophylla* (Benkman 1993). The large birds were collected from the Chinese provinces of Yunnan, Sichuan (Szechwan) and Gansu (Kansu). Based on published wing lengths, three large birds were collected in northern Myanmar (Stanford & Mayr 1941) and one in Sikkim (between Nepal and Bhutan; Stresemann *et al.* 1937). Taking its larger but still very small bill into account, and combined with the distribution of the conifers listed earlier (Farjon 1990, 2005), the larger crossbill might be specializing on Chinese Larch *Larix potaninii*. Studies on resource use in the field can help shed light on the particular key conifer on which each group might be specializing. Equally important would be to determine if and why the other listed potential resources do not support their own population of specialized crossbills, and how used and unused conifers fit the three criteria for key resources given by Benkman (1993).

The distributions of Himalayan Hemlock and Chinese Larch overlap from Nepal and southern Tibet eastwards to northern Yunnan and Sichuan. If indeed these conifers are the key resources, this suggests that geographical overlap of the two kinds of crossbills might be considerable. This is in agreement with the crossbill reports from Sikkim and Yunnan on apparent sympatry. Studies on differentiation in DNA and assortative mating in the region of geographical overlap are necessary to determine whether the two might be different biological species. If the two kinds indeed are found to remain distinct in sympatry, then somehow differentiation of crossbills specialized on different resources is maintained (or could even originate) in sympatry, in support of the hypothesis that ecological opportunity is driving global as well as local crossbill diversity.

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