

- of Europe, the Middle East and North Africa. The birds of the western Palearctic. Vol. IV, Terns to woodpeckers. Oxford Univ. Press, Oxford.
- DANIN, A., G. ORSHAN, AND M. ZOHARY. 1975. The vegetation of the northern Negev and the Judean Desert of Israel. *Israel J. Bot.* 24:118-172.
- PAZ, U. 1986. Encyclopedia of the plants and animals of Israel, vol. 6. Ministry of Defense Publication, Tel-Aviv, Israel.
- PAZ, U. 1987. The birds of Israel. Ministry of Defense Publication, Tel-Aviv, Israel.
- YOSEF, R. 1989. The breeding biology of the Great-grey Shrike and the ecological implications of its impaling prey. M.Sc. thesis, Ben-Gurion Univ. of the Negev, Beer-Sheva, Israel.
- YOSEF, R., AND B. PINSHOW. 1988a. Polygyny in the Northern Shrike (*Lanius excubitor*) in Israel. *Auk* 105:581-582.
- YOSEF, R., AND B. PINSHOW. 1988b. Nestling transfer in the Northern Shrike (*Lanius excubitor*). *Auk* 105: 580-581.
- YOSEF, R., AND B. PINSHOW. 1989. Cache size influences female mate choice and reproductive success in the Northern Shrike. *Auk* 106:418-421.

Received 26 December 1991, accepted 20 November 1992.

The Auk 110(2):398-401, 1993

Call Matching and Positive Assortative Mating in Red Crossbills

JEFFREY G. GROTH¹

Department of Biology, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061, USA

Within some regions of North America, the morphological variability in Red Crossbills (*Loxia curvirostra*) is much greater than in most other songbird populations, leading some authors to consider the possibility that crossbill morphotypes are reproductively isolated from one another (Monson and Phillips 1981, Payne 1987, Groth 1988, 1993). I investigated this problem by measuring the morphology of mated crossbills in a single region, the southern Appalachian Mountains, in which individuals of divergent morphologies had opportunities to interbreed. I hypothesized earlier (Groth 1988) that crossbills in this region belonged to two distinctive groups, or species, based on vocalizations and morphology. Random mating in morphology would not support the hypothesis of reproductive barriers between the two groups. Instead, mixed matings between morphotypes might suggest alternative hypotheses, such as genetic polymorphism for bill and body size (e.g. Smith 1987), or that crossbills in the Appalachians were simply unusually variable for songbird populations, as in some Darwin's finches (Grant 1986).

Where their vocalizations have been studied, breeding pairs of other cardueline finches show precise flight-call matching between mates (Mundinger 1970, 1979, Marler and Mundinger 1975, Samson 1978), which may be a mechanism facilitating individual recognition in vocalizations. I used call matching as a means of deciding whether pairs I observed were

mated. Out of a larger sample of 157 adult and juvenile crossbills captured and recorded in Montgomery County, Virginia (Groth 1988), 48 individuals (all adults) were members of pairs showing the call-matching phenomenon (Fig. 1). Crossbill pairs were closely associated in the field, and once one member was in the mist net the other usually followed within a few minutes. Nests of most pairs were not found, but I did not make extensive efforts to search for them. Crossbills were uncommon in the Appalachian region during the study, and 14 call-matching pairs were captured on days for which no other crossbills were seen, reinforcing the idea that these birds were each other's mates. Seven pairs were associated with other adult crossbills in flocks of up to four individuals, but were considered "mated" because of the precise call matching they exhibited. Two pairs (G and U, Fig. 1) were each captured with begging juveniles, and another (pair V, Fig. 1) was found nesting. Also captured, but not used in the analysis, were three male-female pairs that were traveling alone but did not show call matching.

Six bill characters, wing length, and tarsus length (all to nearest 0.1 mm), as well as body mass (to nearest 0.1 gm), were measured for each individual. As a means of summarizing "size" (Rising and Somers 1989), principal components were calculated using SAS PROC PRINCOMP (SAS Institute 1985) from the correlation matrix of nine variables for the 48 birds in the analysis. This program equilibrated the variances of characters. All variables loaded approximately equally on the first component (PC1), which accounted for 73% of the total variance and can be interpreted as a function of overall bill and body size. Larger birds received higher scores along PC1. After

¹ Present address: Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, USA.

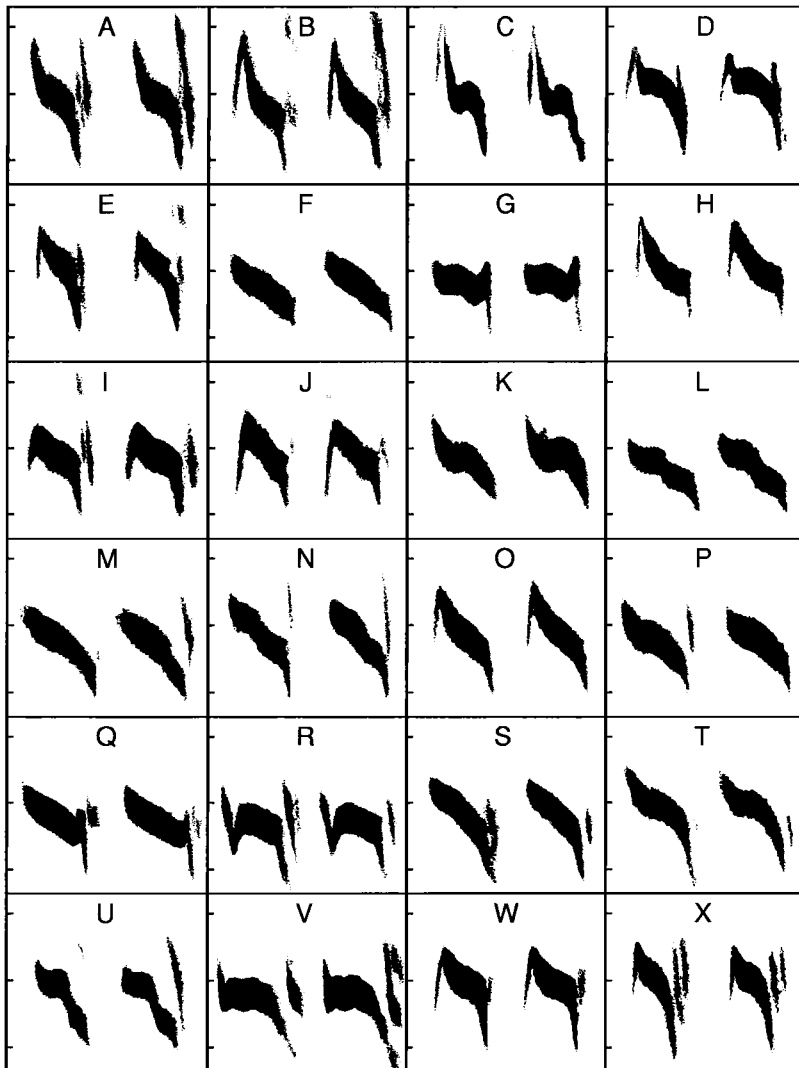


Fig. 1. Audiospectrograms of call notes for 24 pairs (labeled A-X) of crossbills in Virginia. For each pair, call note of male illustrated on left and female on right. Short horizontal marks along vertical axes are at 2, 4, and 6 kilohertz, and width of each box represents 140 msec. Note precise matching in call-note structure between members of each pair.

taking field measurements, crossbills were kept in captivity and their calls were recorded. Audiospectrograms were prepared from the recordings on a Kay Elemetrics model 7029A spectral analyzer at the 160-16,000 kHz setting using the wide-band filter. I observed that fine structure of calls was not influenced by presence or absence of mates during recording sessions.

Product-moment correlation coefficients (r) and their significances ($df = n - 2$) between male and female measurements were calculated for the nine univariate and one multivariate (PC1) morphological characters.

Because I hypothesized that crossbills in the sample fell into two distinctive groups based on calls (types 1 and 2), correlations within groups were computed to evaluate their contributions toward trends with all pairs pooled. Significances of correlation coefficients were evaluated *a posteriori* with sequential Bonferroni adjustments (Rice 1989).

In the sample with all pairs pooled, all bill and body-size characters were highly positively correlated between mates (Table 1; all $P < 0.05$). Considering the coefficient of determination (r^2), pairs shared more common variance in bill size characters than in body

TABLE 1. Product-moment correlation coefficients between measurements of males and females in mated pairs of Red Crossbills.

Character	Entire sample (<i>n</i> = 24)	Within	
		Type 1 (<i>n</i> = 11)	Type 2 (<i>n</i> = 13)
Body mass	0.59**	-0.37	0.65*
Tarsus length	0.43**	0.26	-0.42
Wing length	0.59**	0.54	-0.02
Upper mandible length	0.78***	0.24	0.45
Lower mandible length	0.72***	-0.18	0.73**
Upper mandible width	0.74***	-0.07	0.38
Lower mandible width	0.73***	0.72*	-0.37
Upper mandible depth	0.78***	0.09	0.43
Bill depth	0.64***	-0.08	0.04
PC1 score	0.84***	-0.21	0.44

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

size characters (mass, wing and tarsus). A scatter plot for PC1 scores (Fig. 2) shows that no pairs consisted of members widely different in overall size, and the distribution of data points indicates a gap between two morphologically distinctive clusters of pairs. Members of pairs with the largest bills and bodies gave flight calls without initial elements of rising frequency and with shorter elements of downward frequency modulation, which reflected the basis for earlier division of birds into two vocal groups.

The sample sizes for the two vocally defined groups were nearly equal and, within these samples, there was no trend for correlation coefficients to be positive between mates (sign tests). The few positive correlation coefficients were not consistent among characters between the two groups. Furthermore, the three within-group correlation coefficients (20 total) with P -values less than 0.05 could not be considered significant. Therefore, pairing trends within groups did not contribute in any substantial way to the positive correlations in total sample. The presence of two groups (based on vocalizations) that did not form mixed pairs was responsible for the highly significant positive assortative mating seen when birds of different vocalizations were pooled.

The Appalachian crossbills also showed a pattern of assortative pairing based on acoustic characters, but this observation is trivial because call matching was a prerequisite for identification of birds as mates. No information is available on the structure of the calls of these birds before they became associated with their mates. In two captive pairs with mates having initially different call structures that produced nests and successfully fledged young, the mates never matched each other's flight calls. Other captive pairs with different calls, monitored for months or years, never showed gradual changes in flight call structure (pers. observ.). However, the extent to which vocal learning in captive crossbills differs from those in wild populations is not known. A few captive adults

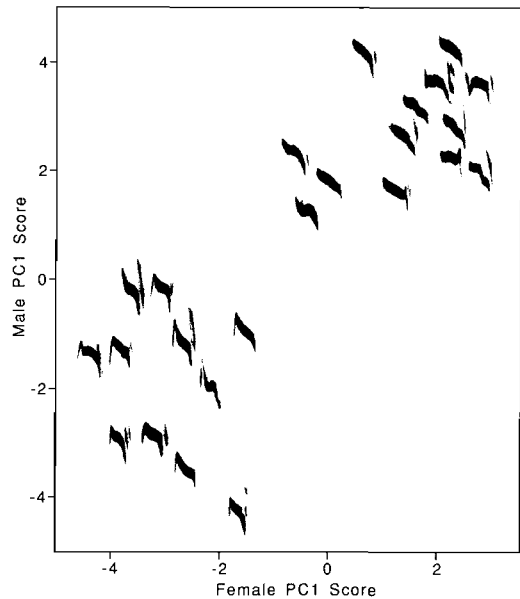


Fig. 2. Relationship between scores on principal component 1 ("size") of males and females in crossbill pairs. Pair-specific call notes illustrated at positions of data points for each pair (those of females used; absolute frequency of notes not accounted for). Note difference in call-note structure between small pairs (lower left) and large pairs (upper right).

and rare wild crossbills were recorded giving two distinctive call structures (Groth 1993), suggesting that call learning may involve additions and deletions of calls copied from other individuals. The three pairs captured that did not match in calls (see above) were vocally similar only insofar as belonging to the same vocal group, and they may have been prospective mates in early stages of courtship.

The first flight calls given by juvenile crossbills match the structures of the parents' or foster parents' calls (Groth 1993). Therefore, it is not possible, with the information available, to rule out the hypothesis that "mates" represent intrafamilial pairings (e.g. mother-son, father-daughter, brother-sister). However, these possibilities seem unlikely. All paired crossbills that I analyzed had lost all of the streaked juvenal plumage and had, therefore, left their nests months or years previously, providing ample time for association and intermingling with crossbills of other social groups. Additionally, if pair members were from the same families and the measured traits were highly heritable, as found in many birds (Boag and Van Noordwijk 1987), the correlation in morphology among mates should have been evident within vocal groups.

Intermingling among morphologically diverse and nomadic crossbills would be expected to reduce morphological variation among populations throughout

North America. This does not fit with the observation that the extent of bill and body-size differentiation in the complex (see Groth 1993) is among the highest in what is considered a single species of bird (AOU 1983). That pairings only occur within defined vocal and morphological groups suggests a mechanism by which the extensive morphological variation is maintained in this complex of presumably highly dispersive birds.

These observations do not support the hypothesis that vocal and morphological forms of crossbill are genetic morphs within single randomly breeding populations, nor are they best explained by the idea that crossbill populations are simply more variable than other songbirds. These findings are consistent with the hypothesis that distinctive forms of crossbill represent reproductively isolated groups (i.e. species). That the two forms were sympatric (both were producing young in the same region) does not agree with historically held concepts that crossbill forms represent geographic races. However, because crossbill "populations" appear to be ephemeral and the birds nomadic, it seems possible that members of one or both groups of birds originated outside of the southern Appalachians. Other regions of North America contain not only the two forms studied here, but also several additional forms with distinctive vocalizations and morphology (Groth 1993).

The process by which crossbills choose their mates is not known. Bill size correlates with conifer preference in crossbills (Kirikov 1940, Lack 1944, Groth 1988, 1993), and calls could function as signals giving information on morphology and, therefore, habitat preference, of individuals. A question that remains is whether vocalizations, visual assessment of morphology (e.g. some Darwin's finches; Ratcliffe and Grant 1985), habitat preferences, or combinations of these and/or other cues provide the bases for mate choice in crossbills.

I thank C. S. Adkisson for the use of his laboratory and for valuable advice in the early stages of this work. G. F. Barrowclough, C. C. Farquhar, and R. F. Rockwell critically reviewed the manuscript.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. American Ornithologists' Union, Washington, D.C.
- BOAG, P. T., AND A. J. VAN NOORDWIJK. 1987. Quantitative genetics. Pages 45-78 in *Avian genetics* (F. Cooke and P. A. Buckley, Eds.). Academic Press, London.
- GRANT, P. R. 1986. Ecology and evolution of Darwin's finches. Princeton Univ. Press, Princeton, New Jersey.
- GROTH, J. G. 1988. Resolution of cryptic species in Appalachian Red Crossbills. *Condor* 90:745-760.
- 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. Calif. Publ. Zool. In press.
- KIRIKOV, S. V. 1940. On the connection between the Red Crossbills and the coniferous trees. *Bull. Acad. Sci. USSR (Biol.)* 1940:359-376.
- LACK, D. 1944. Correlation between beak and food in the Crossbill *Loxia curvirostra* Linnaeus. *Ibis* 86: 552-553.
- MARLER, P., AND P. C. MUNDINGER. 1975. Vocalizations, social organization, and breeding biology of the Twite *Acanthus flavirostris*. *Ibis* 117:1-17.
- MONSON, G., AND A. R. PHILLIPS. 1981. The races of Red Crossbill, *Loxia curvirostra*, in Arizona. Pages 223-230 in *Annotated checklist of the birds of Arizona*, 2nd ed. Univ. Arizona Press, Tucson.
- MUNDINGER, P. C. 1970. Vocal imitation and individual recognition in finch calls. *Science* 168:480-482.
- MUNDINGER, P. C. 1979. Call learning in the Carduelinae: Ethological and systematic implications. *Syst. Zool.* 28:270-283.
- PAYNE, R. B. 1987. Populations and type specimens of a nomadic bird: Comments on the North American crossbills *Loxia pusilla* Gloger 1834 and *Crucirostra minor* Brehm 1845. *Occas. Pap. Mus. Zool. Univ. Mich.*, no. 714.
- RATCLIFFE, L. M., AND P. R. GRANT. 1985. Species recognition in Darwin's finches (*Geospiza*, Gould). I. Discrimination by morphological cues. *Anim. Behav.* 31:1139-1153.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.
- RISING, J. D., AND K. M. SOMERS. 1989. The measurement of overall body size in birds. *Auk* 106: 666-674.
- SAMSON, F. B. 1978. Vocalizations of Cassin's Finch in northern Utah. *Condor* 80:203-210.
- SAS INSTITUTE. 1985. SAS user's guide: Statistics, version 5 ed. SAS Institute, Inc., Cary, North Carolina.
- SMITH, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. *Nature* 329:717-719.

Received 5 March 1992, accepted 19 November 1992.