RESOLUTION OF CRYPTIC SPECIES IN APPALACHIAN RED CROSSBILLS[1]

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Abstract. Two distinct and sympatric forms of Red Crossbill (*Loxia curvirostra*) from breeding populations in Virginia and North Carolina were resolved using multivariate analysis of vocalizations and morphology. Five characters were used to describe individually distinctive flight calls of 135 adults which were also measured for a set of nine bill and body size characters. Call notes were bimodal for two characters, and a principal components plot separated birds into two clusters based on call note shape. Univariate distributions of morphological data showed some weak bimodalities and higher coefficients of variation than other passerine bird populations. Distributions along multivariate first principal component axes from morphological data (sexes in separate analyses) were bimodal, dividing fully grown adults into two distinct bill and body size classes. The vocal and morphological multivariate clusterings of individuals were entirely congruent, but no univariate character in either data set could completely separate the two forms. The matrix correlations between vocal and morphological interindividual distances were 0.441 for males and 0.423 for females and were highly significant using Mantel tests. However, within each hypothetical cryptic species, vocal and morphological characteristics were uncorrelated, showing a lack of pattern in the sample beyond the division into two nonreducible clusters. Other vocal differences between the two forms are described, and observations of ecological differences are summarized. The type specimens representing the two names which have been applied to Appalachian crossbills, *L. c. pusilla* (Gloger 1834) and *L. c. minor* (Brehm 1845), were compared to birds of known vocalizations. The type of *pusilla* matched the larger Appalachian form, but the type of *minor* was smaller than all adult males in the sample. The taxonomic problem of *L. curvirostra* is discussed, and an argument is made in favor of the species level for the two Appalachian vocal and morphological forms.

Key words: Morphometrics; cryptic species; bioacoustics; vocalizations; Red Crossbill; Loxia curvirostra; Carduelinae; multivariate analysis; sexual dimorphism.

INTRODUCTION

The Red Crossbill (*Loxia curvirostra*) in North America is known for its extreme variability in coloration and bill and body size. Strong philopatry and low dispersal would allow local differentiation of subspecies or populations, but Red Crossbills are nomadic with year-round breeding (McCabe and McCabe 1933, Bailey et al. 1953, Bent 1968), suggesting the potential for high gene flow. The paradox of pronounced morphological variation with strong dispersal has not been ex-

plained. Collections of breeding Red Crossbills from some regions have included birds of divergent morphologies (Jollie 1953, Kemper 1959, Monson and Phillips 1981, Dickerman 1987, Payne 1987), questioning the division of the complex into geographic subspecies. The European sibling species of red crossbill, *L. scotica* and *L. curvirostra,* are extremely similar in morphology (Knox 1975, 1976) but differ in vocalizations (Nethersole-Thompson 1975).

This paper searches for cryptic species limits in a highly morphologically variable sample of crossbills from breeding populations in Virginia and North Carolina. Cryptic species of birds have been resolved in other instances in which morph-

specific vocalizations have been identified (see reviews by Selander [1971] and Payne [1986]). Morphologically similar species of birds, such as in *Myiarchus* (Lanyon 1978), *Vidua* (Payne 1973), and *Empidonax* (Stein 1958, 1963; Johnson 1963) have invariably been shown to have different vocalizations. The objectives of this study were to obtain individually distinctive flight call sonograms from a sample of Red Crossbills from breeding areas in Virginia and North Carolina, and also capture and measure bill and body size characters for the same set of individuals. Vocal and morphological data sets were then directly compared in a search for biological pattern.

METHODS

STUDY AREA AND FIELD METHODS

I observed, tape recorded, and captured crossbills in the southern Appalachian mountains from 7 January 1983 to 3 July 1984. Most of the fieldwork was done near Blacksburg, Virginia (Brush Mountain, 790 m elevation; Poverty Hollow, 600 m elevation; and Price Mountain, 750 m elevation). Additional fieldwork was done in Highlands, North Carolina (1,150 m elevation), 26–31 October and 19–21 November 1983, and on Roan Mountain, North Carolina (1,900 m elevation), 20–21 June 1984. Crossbills are highly specialized feeders on seeds within cones of many conifer species. The forests near Blacksburg were of mixed conifers and hardwoods, with Virginia pine (*Pinus virginiana*), pitch pine (*P. rigida*), table mountain pine (*P. pungens*), white pine (*P. strobus*), and hemlock (*Tsuga spp.*) predominating among the conifers. At Highlands, white pine had a locally heavy cone crop in the late summer of 1983 which supported the breeding of crossbills. The Roan Mountain site was in the red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) assemblage, but cone crops were poor during my fieldwork there.

Crossbills were captured in mist nets using live crossbills as decoys and branches with pine cones as attractants. I remained vigilant at net sites and recorded vocalizations in encounters between decoys and wild crossbills. Birds were sexed by plumage characters (according to Phillips 1977) and divided into two age classes: (1) juvenile (*n* = 80), possessing at least some streaked juvenal plumage, and (2) adult (*n* = 136), no streaked plumage. I assumed that all individuals classified as adults were fully grown. A total of 53 crossbills

(17 adults, 36 juveniles) was captured at Highlands and a total of seven (one adult, six juveniles) was captured on Roan Mountain. The remaining 156 (118 adults and 38 juveniles) were captured near Blacksburg. All were pooled into a single data set. Evidence for breeding by crossbills in this region included many observations of adults feeding newly fledged young, adults travelling as male-female pairs, females with incubation pitches, singing males, specimens with enlarged gonads, and the discovery of a nest (on Price Mountain) that fledged two young.

MORPHOLOGICAL ANALYSIS

The following morphological measurements were taken for each individual: body mass (MA, to the nearest 0.1 or 0.5 g); tarsus length (TR, posterior surface of bent tibiotarsal/tarsometatarsal joint to distal edge of lowest scute on right leg); wing length (WG, chord, with the wing held 3–4 cm from the body); upper mandible length (LU, anterior edge of nostril to tip); bill depth (BD, compressed at a line perpendicular to anterior edge of nostril); upper mandible depth (DU, with bill open, at anterior edge of nostril); upper mandible width (WU, between tomia, at anterior edge of nostril); lower mandible width (WL, at points where rami intersect the skin); and lower mandible length (LL, juncture of rami to tip). All lengths were taken with dial calipers to the nearest 0.1 mm.

VOCAL ANALYSIS

Like other members of the Carduelinae, Red Crossbills have species-specific flight calls (Mundinger 1970, Newton 1973), which are given both in flight and while perched. In several species of breeding carduelines, flight calls are individually distinctive and are used in individual and mate recognition (Mundinger 1970, 1979; Marler and Mundinger 1975; Samson 1978). Because of their importance within the pair bond, flight calls may provide useful information in studies of near-species systematics, where reproductive behavior defines the species level (Mayr 1970). In this paper, I treated sonagraphic representations of flight calls as two-dimensional objects that could be measured in the same way as any other phenotypic feature to provide quantitative data for use in numerical taxonomic analyses (Goldstein 1978, Sparling and Williams 1978, Payne and Budde 1979, Johnson 1980, Miller 1986).

I kept captured birds individually in small wire

cages and tape recorded them. Caged crossbills placed outdoors often gave bouts of flight calls at rates of up to five calls per second. Recordings were made on a Uher Report IC recorder at 9.5 cm using either a Dan Gibson parabola and microphone or a Uher cardioid microphone mounted in a Sony PBR-330 parabola. I usually stood about 5–15 m from calling birds while recording. Sonograms were prepared with a Kay Elemetrics Sona-Graph model 7029A at the 160–16,000 Hz analysis range with the wide band filter. Periodic checks were made of the rotor speed and frequency calibrations of the spectrograph, but variations were minute. One clearly recorded flight call was selected to characterize each individual. From three to over 100 additional flight call sonograms were available for each individual to evaluate within-individual variation, but most of the variation within individuals appeared to be the result of "ghosting" of fine structural features due to depression of recording signal. Sonograms of several individuals recorded both before and after capture showed that captivity did not influence the structure of flight calls. Some juveniles gave only begging calls and others were less consistent than adults in the structure of flight calls; therefore, I used only adults in analyses described below, based on a set of five continuous ratio-scale variables (defined in Fig. 1). Measurements were made by first drawing thin pencil lines on the sonograms to delimit each character and then measuring with a clear plastic ruler and protractor. Measurement error would account for additional within-individual variation, but this variation would be slight compared to the extensive variation among individuals.

A total of 127 crossbills were given U.S. Fish and Wildlife Service bands and released; the remainder were kept for further behavioral observations or prepared as specimens and deposited either in the Bailey-Law collection of Virginia Polytechnic Institute or the Museum of Vertebrate Zoology, University of California.

STATISTICAL METHODS

The search for cryptic species began with univariate histogram analysis and calculation of the coefficient of variation (CV) for each character. The CV is widely known as an indicator of homogeneity of population samples, especially in birds (Mayr et al. 1953).

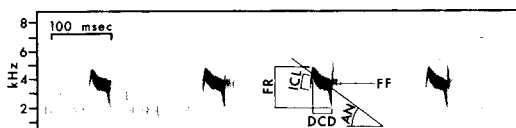The second approach consisted of numerical taxonomic methods (Sneath and Sokal 1973).

FIGURE 1. Series of flight calls and illustration of the five vocal characters as follows: frequency range (FR, to nearest 0.1 kHz); initial component length (ICL, to nearest 1 mm); downward component duration (DCD, to nearest 0.1 mm and converted to milliseconds by multiplying by 3.99); fundamental frequency (FF, at estimated strongest frequency, to nearest 0.1 kHz); and main angle (AN, line drawn through central axis of downward component, to nearest 1°).

Variables in each data set were first standardized to zero mean and unit variance to account for differences in magnitude and measurement units of characters. To search for possible clusters of individuals based on either call note structure or bill and body morphology, it was first essential to graphically portray the range of variation for each data set such that individuals would be separated by the measured distances among them. Two separate measures of distance (one vocal, one morphological) were then calculated as the multivariate Euclidean distance in standardized characters between each pair of individuals. Eighty adult males and 55 adult females with complete data sets were used, providing 3,160 pairwise comparisons for males and 1,485 for females. These distances were described graphically by two-dimensional principal components (PC) plots, and the qualities of the plots were assessed by the cophenetic correlation coefficient (r_{cc}) between the original Euclidean distances (measured) and the observed Euclidean distances in the two-dimensional plots. Since the variables were first standardized, PCs derived from correlation and covariance matrices were identical, and the results were also equivalent to PCs derived from correlation matrices of raw, unstandardized variables. PC analysis using the combined data set of 14 acoustic and morphological variables was also performed.

All PC plots were drawn so that the variances in scores in each dimension were proportional to the eigenvalues (and percentages of explained variance), making distances between points in the plots (i.e., the observed distances) equivalent to Euclidean distances using the PC1 and PC2 factor coordinates. This method avoids the distortion that is created when PC plots are drawn
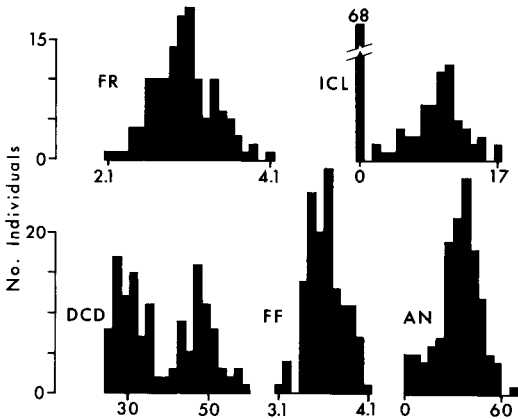
FIGURE 2. Frequency distributions for the five characters of flight call structural variation. FR, ICL, and FF are plotted in ranks as measured; DCD values were placed into categories of 2 msec, and AN values were placed into 5° categories.

"square," which often expands the observed distances between points along PC2 relative to PC1.

Congruence between vocal and morphological data was assessed in two ways. First, clusterings in the separate vocal and morphological PC plots were compared visually. Second, the matrix correlation (r_{cc}) between vocal and morphological distances was calculated because this descriptor estimates how well a distance value in one data set predicts the distance value in the other data set for any pair of individuals. Matrix correlations were tested for significance using Mantel's t statistic (Mantel 1967, Schnell et al. 1985).

Although the presence of cryptic species was not assumed initially, the hypothetical cryptic species resolved in the study were analyzed in a second phase using the methods described above to test for further reducibility. After reduction, the phenotypic differences between groups were evaluated by analysis of variance (ANOVA) between means and qualitative assessment of the range of overlap for each character. Discriminant function analysis (DFA) was performed to assess separability of the hypothetical cryptic species using morphological variables.

Calculations were performed using SAS (SAS Institute 1982), SPSS (Nie et al. 1975), NTSYS (Rohlf et al. 1980), and the GEOVAR computer program of D. M. Mallis and R. R. Sokal.

TAXONOMIC ANALYSIS

The names that have historically been applied to Appalachian crossbills are *L. c. minor* (Brehm

TABLE 1. Correlations among vocal characters in the entire sample of Appalachian adults ($n = 135$).

Variable	DCD	ICL	FF	FR
ICL	−0.77***	—		
FF	−0.38***	0.28**	—	
FR	−0.20*	0.31***	0.14	—
AN	−0.23**	0.04	0.60	0.05

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

1845) and *L. c. pusilla* (Gloger 1834). The type specimens representing these names were measured and compared directly to Appalachian specimens. To account for differences between dried study skins and measurements of live birds, correction factors were calculated by measuring a set of 47 crossbills first as live birds and then 1 year later as dried study skins. The differences between means for the characters were added to the measurements of the old types.

RESULTS

UNIVARIATE ANALYSIS OF
VOCAL CHARACTERS

Estimates of population variability in absolute frequency and temporal characters (comparable to FF and DCD in this study) have been made for vocalizations in other avian populations (summarized by Miller 1986). FF had a CV of 6.07 and DCD had a CV of 23.73, placing the sample of Appalachian crossbills near the middle of the range of these other species. ICL (CV = 111.56) and AN (CV = 38.93) were extremely variable, and FR (CV = 12.16) was moderately variable. Because FF had relatively less variation than the other four characters, it can be stated that most of the call note variability was in "shape" and not the positions of the calls in the vertical (frequency) dimension.

Histograms show that DCD and ICL were strongly bimodal (Fig. 2). ICL was also discontinuous, with 68 of the 135 adults having flight calls completely lacking initial components, and the remaining 67 individuals having at least small initial components. The characters ICL and DCD were highly negatively correlated (Table 1) and gave nearly identical placement of individuals into modes. All individuals with ICLs greater than zero had DCDs less than 39.8 msec, and the birds with longer DCDs typically had ICLs of zero. The exceptions to a perfect agreement between ICL and DCD were four individuals with short DCDs and ICLs of zero.

TABLE 2. Correlations (factor loadings) between acoustic variables and the first two principal components, with percentages of variance explained by each axis.

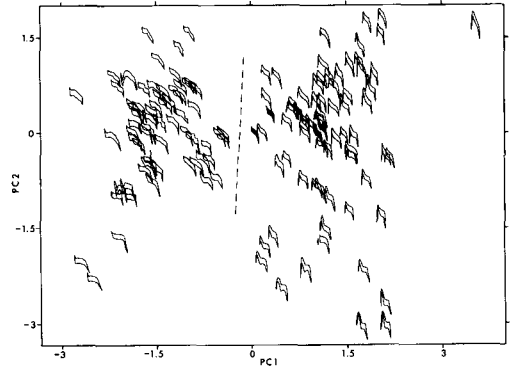| Variable	PC1	PC2
FR	0.464	−0.260
DCD	−0.893	−0.085
ICL	0.867	−0.178
FF	0.571	−0.063
AN	0.249	0.941
% variance	43.0	19.9

FIGURE 3. Principal components plot based on flight call data on all adults. Outlines of call notes were traced from sonograms at the positions for each individual. Dashed line shows division between Type 1 (right) and Type 2 (left) vocal groups. Blackened notes represent Type 1 individuals lacking initial components. The r_{cc} between plot distances and original standardized vocal Euclidean distances = 0.842.

PATTERN OF CALL NOTE SIMILARITY

A plot of the first two principal components was a good summary of the original Euclidean distances among individuals (Fig. 3). Two major clouds of points resulted from strong bimodality along PC1, and this division reflects the strong negative correlation between the characters DCD and ICL which provided the basis for the high loadings of these characters on PC1 (Table 2). The calls (and thus, birds) were divisible at the PC1 value of about −0.070 into a cloud of 71 birds on the right of the plot (Type 1) and 64 birds on the left (Type 2).

UNIVARIATE ANALYSIS OF MORPHOLOGICAL CHARACTERS

Table 3 indicates the pronounced morphological variation within each sex. Wing and bill lengths are among the most commonly published measurements in surveys of avian population variation, and the Appalachian sample was highly variable in comparison to other passerine bird populations (Fig. 4).

Histograms of the morphological data are presented in Figure 5. There were no outlying individuals consistently different from the remainder of the sample, and no discontinuities, revealing no obvious divisions between hypothetical cryptic species. Skewness was negative in six and positive in 12 of the 18 distributions, which is not significantly different from chance expectations if all had been drawn from normal populations (Sign Test [Snedecor and Cochran 1965], $\chi^2 = 2.0$, ns). For both males and females, each of the morphological variables except MA showed negative kurtosis (platykurtosis), which is greater than expected if all were drawn randomly from normal distributions ($\chi^2 = 10.89$, $P < 0.001$). Additionally, seven of the 18 intrasexual morphological distributions (DU, WU, WL,

and TR in males and BD, DU, and WU in females) were significantly different (at $P < 0.05$) from normally distributed as indicated by Kolmogorov-Smirnov tests using the t distribution as the null model, and this is greater than the number of nonnormal distributions expected by chance ($\chi^2 = 41.32$, $P < 0.001$) if all distributions were drawn from normal populations. A combination of high CV values and platykurtosis has been described by Grant et al. (1985) for some *Geospiza* populations, but these and the Appalachian crossbills were not typical of other songbird populations.

PATTERN OF MORPHOLOGICAL SIMILARITY

Of the 36 morphological character correlations within each sex, all were positive and highly sig-

TABLE 3. Coefficients of variation (CVs) for morphological measurements on adults in Appalachian crossbills.

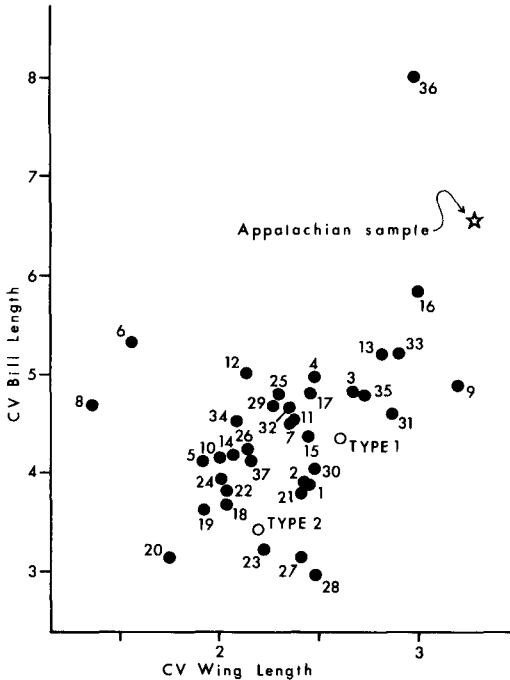| Variable	Males	Females
MA	7.06	9.11
TR	3.72	4.23
WG	3.28	3.02
LU	6.55	5.63
BD	5.10	4.56
DU	4.87	4.48
WU	6.25	6.14
WL	5.70	5.40
LL	6.62	5.70

FIGURE 4. Morphological variability within populations of passerine birds. Dots = estimates for within-population CVs (males only) in wing and bill length for different species using values from a representative single population or mean CV for more than one population; star = Appalachian sample (adult males). Species, numbers of populations (wing, bill length) and literature sources are as follows: 1) *Zonotrichia leucophrys* (20, 20) Banks 1964; 2) *Empidonax difficilis* (30, 30), 3) *E. flavescens* (7, 6), 4) *E. hammondi* (10, 11) Johnson 1980; 5) *E. oberholseri* (1, 1); 6) *E. wrightii* (1, 1) Johnson 1963; 7) *Carpodacus mexicanus* (9, 9) Power 1983; 8) *Carduelis spinus* (1, 1) Sellers 1986; 9) *Passerella iliaca* (31, 31) Zink 1986; 10) *Icterus galbula* (48, 48) Rising 1970; 11) *Campylorhynchus rufinucha* (9, 9), 12) *C. gularis* (3, 3), 13) *C. zonatus* (7, 7), 14) *C. megalopterus* (2, 2) Selander 1964; 15) *Geospiza magnirostris* (5, 5), 16) *G. fortis* (9, 9), 17) *G. fuliginosa* (11, 11), 18) *G. difficilis* (6, 6), 19) *Pinaroloxias inornata* (1, 1), 20) *Camarhynchus crassirostris* (6, 6), 21) *C. psittacula* (4, 4), 22) *C. parvulus* (6, 6), 23) *C. pallidus* (5, 5), 24) *Certhidea olivacea* (12, 12) Lack 1947; 25) *Pinicola enucleator* (6, 6) Adkisson 1977; 26) *Melospiza melodia* (1, 1) Smith and Zach 1979; 27) *Loxia scotica* (1, 1), 28) *L. pityopsittacus* (1, 1), 29) *L. curvirostra* (3, 3) Knox 1976; 30) *Junco hyemalis* (13, 13), 31) *J. phaeonotus* (4, 4), 32) *J. vulcani* (1, 1) Miller 1941; 33) *Parus gambeli* (7, 7) Behle 1956; 34) *Sitta pygmaea* (23, 23), 35) *S. pusilla* (8, 8) Norris 1958; 36) *Pyrenestes ostrinus* (1, 1) Smith 1987; 37) *Loxia leucoptera* (this study: sample of all adult males from Alaska and Yukon Territory [*n* = 30] in the Museum of Vertebrate Zoology). "Population" samples ranged from single localities (e.g., Rising 1970) to broad areas including entire species or subspecies (e.g., Johnson 1963, Adkisson 1977).
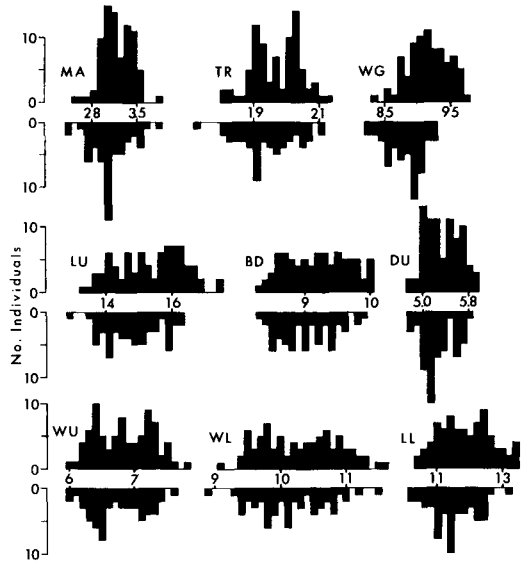

FIGURE 5. Frequency distributions for morphological characters. Males are stacked above scale and females below for each character. BD, DU, WU, and WL are plotted in ranks as measured; MA values were placed into 1-g categories, TR, LU, and LL values were placed in 0.2-mm categories, and WG values into 1-mm categories.

nificant (Table 4). These high correlations indicate that when considering the entire sample, individuals varied in a manner consistent with differentiation in overall size. Other populations of birds generally have lower character correlations (Selander and Johnston 1967, Adkisson 1977) but few works have published correlations among study skin measurements within songbird populations that could provide a more substantial basis for comparison.

With these strong positive correlations, the morphological PC1s for both sexes accounted for large fractions of the total measured variance. All nine characters loaded positively and nearly equally on the PC1s, indicating that the vectors summarized overall "size" or "bill and body size" (Table 5). Furthermore, the distributions (by sex) of PC1 scores were bimodal (Fig. 6), reflecting an unexpected deficiency of medium-sized birds. A division into "small" and "large" forms along the PC1 axes seemed appropriate, but the exact cut-off values would be arbitrary due to lack of large discontinuities. Two-dimensional PC plots not including PC1 (not shown) showed no obvious group structures and were poor reflections of original interindividual Euclidean distances.
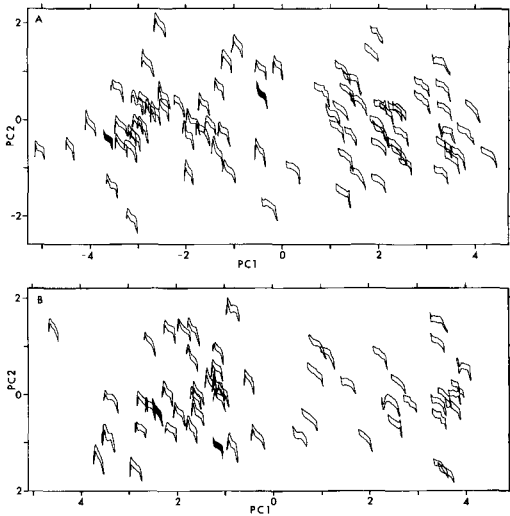
FIGURE 6. Principal components ordinations of the morphological data for (A) males, and (B) females. Factor loadings for the two plots were very similar (Table 5). Outlines of flight call sonograms were traced at the positions of individuals, and blackened individuals are Type 1 birds lacking initial components in their flight calls. The r_{cc}s between distances among points in the PC plots and original standardized morphological Euclidean distances = 0.972 for males and 0.961 for female, indicating that these plots are excellent representations of original Euclidean distances in morphology.

INTEGRATION OF VOCAL AND MORPHOLOGICAL DATA

Concordance of morphological and vocal characters is one way of identifying limits between closely related species (Löhrl 1963, Lanyon 1969). Both vocal and morphological PC1 scores were indicators of the placement of individuals into hypothetical cryptic species (see above), and Table 6 shows that for both sexes the correlation between vocal and morphological PC1 scores was

TABLE 5. Correlations (factor loadings) between morphological variables and the first two principal components with percentages of total variance explained by each axis.

Variable	Males		Females	
	PC1	PC2	PC1	PC2
MA	0.746	0.338	0.756	0.262
TR	0.794	0.224	0.763	0.211
WG	0.739	0.453	0.682	0.641
LU	0.878	−0.024	0.866	−0.031
BD	0.929	−0.245	0.905	−0.229
DU	0.916	−0.235	0.888	−0.287
WU	0.895	−0.130	0.884	−0.155
WL	0.849	−0.304	0.854	−0.228
LL	0.832	0.088	0.816	−0.030
% variance	71.3	6.7	68.4	8.2

highly significant, revealing congruence between the two data sets. Table 6 also shows that interindividual distances in flight call structure and morphology were positively correlated at a level which is highly significant using the test of Mantel. These comparisons show that vocalizations and morphology were congruent in the sample, but do not in themselves reveal any discontinuities betweeen taxa.

With call notes illustrated as data points in the morphological PC ordinations (Fig. 6), it is possible to use both sets of characters in forming hypotheses about taxonomic structure. The Type 1 and Type 2 vocal subgroups did not intersect in the morphological PC plots and were separated along the PC1 axes, showing that the morphological difference between the groups was mainly based on bill and body size. Discriminant function analyses (DFAs) using the multivariate Type 1/Type 2 division as the grouping variable (not shown) produced functions (sexes in separate analyses) separating the vocal groups with

TABLE 4. Product-moment correlations between morphological variables for the entire sample of Appalachian adult crossbills. Values for females above diagonal; males below. All values are significant at $P < 0.001$.

	MA	TR	WG	LU	BD	DU	WU	WL	LL
MA	—	0.63	0.54	0.56	0.63	0.59	0.62	0.61	0.49
TR	0.59	—	0.54	0.55	0.65	0.65	0.67	0.55	0.47
WG	0.55	0.57	—	0.60	0.49	0.46	0.48	0.47	0.61
LU	0.58	0.63	0.58	—	0.73	0.73	0.77	0.71	0.76
BD	0.66	0.67	0.66	0.76	—	0.92	0.78	0.76	0.68
DU	0.65	0.67	0.65	0.75	0.95	—	0.77	0.78	0.64
WU	0.63	0.64	0.63	0.78	0.85	0.82	—	0.74	0.69
WL	0.51	0.62	0.51	0.70	0.81	0.79	0.74	—	0.70
LL	0.56	0.66	0.56	0.81	0.70	0.67	0.65	0.67	—

TABLE 6.   Multivariate correlations between vocalizations and morphology.

Sample	PC1 scores[a]	Distance matrices[b]	
	r	(r_cc)	t-value[c]
All males	−0.811***	0.429	15.511***
All females	−0.881***	0.441	9.375***
Type 1 males	0.201	−0.123	−1.458
Type 1 females	−0.301	−0.019	−0.174
Type 2 males	0.091	0.015	0.194
Type 2 females	−0.398	0.156	1.282

[a] Product-moment correlation coefficients between morphological and vocal PC1 scores.
[b] Comparisons of original standardized Euclidean vocal and morphological distance matrices within the indicated samples.
[c] Student's t-distribution, values from Mantel tests.
*** $P < 0.001$.

100% correct classification using morphological variables. Additionally, PCA using the combined total of 14 morphological and vocal characters in a single data set clearly resolved two groups of males and two groups of females with substantial discontinuities between them in the PC1/PC2 plot (not shown; this clustering was concordant with the separate multivariate call note and size class groupings). These analyses showed a morphological, size-based division between two distinctive vocal types of crossbill.

COMPARISON OF TWO CRYPTIC SPECIES OF RED CROSSBILL

The two forms of crossbill resolved in the above analyses were delimited on the basis of flight call note structure. Table 7 shows the univariate comparisons for the five vocal characters used in this study. AN was not important in distinguishing the two forms. All but four of the Type 1 calls had at least a small initial component, and all Type 2 calls lacked an initial component. DCD also differed greatly between the two forms. The shorter duration of Type 1 calls gave them a harsher, more attenuate "chip" compared to the slightly tonal "choop" of Type 2. Type 1 calls averaged slightly higher in pitch (as measured by FF) and greater in FR than Type 2.

Type 2 birds averaged 4–12% larger than Type 1 birds of the same sex for the nine morphological characters, and the differences between means were highly significant (Table 8). With respect to bill length, the difference between the two forms was in the low range for other congeneric and sympatric avian species (Hutchinson 1959, Schoener 1965). Within each sex, Type 1 and Type 2 samples overlapped in each character, explaining the continuity and apparent near-normality in most morphological characters when birds were pooled.

PATTERNS WITHIN CROSSBILL FORMS

Males were slightly larger than females within each form (Table 9). WG showed the highest significance of difference between sexes in both forms as is typical for songbirds (Amadon 1959), but males also had significantly longer upper mandibles in both forms, which is in contrast to the findings of Grant et al. (1985) for Geospiza and Selander and Johnston (1967) for Passer domesticus, for which sexual dimorphism in bill length was less than other morphological characters. Otherwise, after division into flight call groups, each form had a typical level of sexual dimorphism.

TABLE 7.   Descriptive statistics and ANOVAs for differences in flight call characters between Type 1 and Type 2 crossbills. See Figure 1 for measurement units for each character.

Variable	Type 1 (n = 71)				Type 2 (n = 64)				F-ratio[a]
	x̄	CV	Min	Max	x̄	CV	Min	Max	
FR	3.15	11.33	2.1	4.1	2.90	11.72	2.2	3.7	16.40***
ICL	9.2	42.21	0	17	0	0	0	0	358.0***
DCD	32.12	10.64	26.3	39.9	49.56	8.96	39.9	60.2	661.7***
FF	3.76	5.91	3.2	4.2	3.58	5.07	3.1	4.1	27.01***
AN	34.5	43.87	3	69	31.5	30.69	0	47	1.810

[a] ANOVA, df = 1, 133.
*** $P < 0.001$.

TABLE 8. Descriptive statistics and ANOVA between means of the morphological characters for the two Appalachian crossbill forms.

	Males									
	Type 1 ($n = 39$)				Type 2 ($n = 41$)				% diff.[a]	F-ratio[b]
Variable	$\bar{x}$	CV	Min	Max	$\bar{x}$	CV	Min	Max		
MA	30.49	5.81	25.8	34.5	33.09	5.76	29.0	38.5	8.53	39.8***
TR	19.16	2.94	18.0	20.4	20.14	2.65	18.8	21.3	5.11	62.9***
WG	89.41	2.61	83.8	95.4	93.52	2.19	89.5	97.5	4.60	70.3***
LU	14.49	4.35	13.3	15.7	16.11	3.43	14.9	17.5	11.18	149.5***
BD	8.80	2.91	8.3	9.4	9.59	2.70	9.1	10.0	8.98	185.1***
DU	5.08	2.52	4.8	5.4	5.50	2.90	5.2	5.8	8.27	171.7***
WU	6.46	3.48	6.0	7.0	7.17	3.48	6.7	7.8	10.99	176.3***
WL	9.81	3.06	9.1	10.4	10.78	3.25	10.0	11.6	9.89	176.6***
LL	11.32	4.86	10.5	12.9	12.48	4.14	11.5	13.5	10.25	94.9***
	Females									
	Type 1 ($n = 32$)				Type 2 ($n = 23$)				% diff.[a]	F-ratio[c]
Variable	$\bar{x}$	CV	Min	Max	$\bar{x}$	CV	Min	Max		
MA	29.21	7.44	24.5	35.1	32.72	6.85	30.2	38.5	12.02	34.0***
TR	18.90	2.98	17.3	20.3	20.03	3.30	18.0	21.0	5.98	46.2***
WG	86.64	2.62	82.1	90.3	90.09	1.86	85.8	92.5	4.60	38.1***
LU	14.17	3.61	12.9	15.0	15.51	3.10	14.6	16.3	9.46	96.7***
BD	8.73	2.72	8.3	9.2	9.38	2.89	8.8	9.9	7.45	90.5***
DU	5.05	2.41	4.8	5.3	5.42	3.19	5.1	5.7	7.33	86.1***
WU	6.42	3.26	6.0	6.9	7.14	2.79	6.8	7.6	11.22	165.5***
WL	9.78	3.26	8.9	10.3	10.65	3.38	9.8	11.5	8.90	90.1***
LL	11.12	4.04	10.3	12.4	12.08	3.78	11.3	13.2	8.63	60.6***

[a] Expressed as a percentage of the smaller form (Type 1).
[b] ANOVA, df = 1, 78.
[c] ANOVA, df = 1, 53.
*** $P < 0.001$.

The question of residual pattern and substructure was assayed to assess the discreteness of the two hypothetical taxa. The set of 36 univariate morphological distributions *within* the four subgroups showed no significant tendencies for direction of skewness or kurtosis (Sign Tests). Deviations from normality (at $P < 0.05$) using the test of Shapiro and Wilks (1965) occurred in only four distributions, which is not different from the number expected by chance if all were drawn from normal populations. Within each taxon, the CVs for morphological characters (see Table 8) were like most passerine populations (Fig. 4), in contrast to the analysis of the entire sample of Appalachian males.

The correlations between vocal characters within the two call types (Table 10) did not resemble those when call types were pooled (Table 1). Type 1 calls with short ICLs were not necessarily long in DCD, so Type 1 birds could not be perfectly ordered as more or less Type 2-like in these two distinguishing characters. The strong positive correlation between FR and DCD in Type 2 calls suggests variation related to "size"

of call notes for this form, but the biological meaning of this is unclear. Because correlations in vocal characters within the two forms were generally low, no combination of any two PCs within each form explained more than 55% of the variation, all two-dimensional PC plots (none

TABLE 9. Sexual dimorphism in morphological characters within each of two forms of Appalachian crossbill.

	Type 1		Type 2	
	% diff.[a]	F-value[b]	% diff.[a]	F-value[c]
MA	4.38	7.45**	1.13	0.48
TR	1.38	3.78	0.55	0.53
WG	3.20	25.33***	3.31	46.77***
LU	2.26	5.40*	3.87	18.94***
BD	0.80	1.59	2.24	8.77**
DU	0.59	0.78	1.48	3.76
WU	0.62	0.66	0.42	0.20
WL	0.31	1.22	1.22	2.07
LL	1.80	2.94	3.31	9.92**

[a] Expressed as a percentage of the smaller (female) mean.
[b] ANOVA, df = 1, 69.
[c] ANOVA, df = 1, 62.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 10. Product-moment correlation coefficients between flight call characters within two forms of crossbill. Matrix for Type 1 birds ($n = 71$) above diagonal; matrix for Type 2 ($n = 64$) below.

	DCD	ICL	FF	FR	AN
DCD	—	0.07	0.07	0.04	-0.28*
ICL	0.00	—	-0.19	0.07	-0.15
FF	-0.08	0.00	—	-0.14	0.01
FR	0.49***	0.00	0.20	—	0.02
AN	-0.35**	0.00	0.02	0.00	—

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

shown) were poor reflections of measured vocal Euclidean distances, and none revealed obvious subgroup structure.

Compared to correlations among morphological characters in the entire Appalachian sample (Table 4), those within the separate forms were far reduced (Table 11). For example, within a call type, birds with long upper mandibles showed only weak and nonsignificant tendencies to have long wings. The few strong positive correlations, like between BD and DU in all four matrices, were usually explainable as measurement of the nearly the same feature. Like the within-group vocal PCAs (above), the within-group morphological PC plots (none shown) were poor reflections of measured interindividual Euclidean distances and showed no obvious clusterings.

Hybrid songbirds may be intermediate in both vocalizations and morphology (e.g., Robbins et al. 1986). If the two forms of crossbill found in this study were intergrading, it may be expected that some individuals would be intermediate in both data sets; inversely, those most unlike the opposing taxon in morphology (i.e., the smallest and largest) would also be farthest from vocal intermediacy. PC1 scores for both data sets in the analyses when all birds were pooled measured relative intermediacy in both data sets, but were uncorrelated within each of the four subgroups (Table 6), giving no support to the hypothesis of hybridization between these forms. Additionally, standardized Euclidean distances between individuals in vocalizations and morphology showed no significant matrix correlations within subgroups (Table 6). In other words, flight call structure predicted nothing about morphology beyond random placement within the morphotypic range of a vocal type.

TABLE 11. Product-moment correlation between morphological variables within two cryptic species of crossbill. For each matrix, females above diagonal; males below. See Table 8 for sample sizes.

	MA	TR	WG	LU	BD	DU	WU	WL	LL
				Type 1					
MA	—	0.35	0.13	0.16	0.33	0.16	0.25	0.23	-0.01
TR	0.22	—	0.20	-0.04	0.19	0.09	0.08	-0.01	-0.22
WG	0.31	0.25	—	0.15	-0.11	-0.16	-0.31	-0.10	0.41*
LU	0.17	0.32*	0.17	—	0.26	0.27	0.24	0.38*	0.49**
BD	0.36*	0.25	0.36*	0.30	—	0.72***	0.27	0.33	0.17
DU	0.15	0.22	0.15	0.26	0.82***	—	0.09	0.45**	0.01
WU	0.29	0.36*	0.29	0.27	0.61***	0.51***	—	0.23	0.17
WL	0.09	0.27	0.09	0.20	0.34*	0.29	0.28	—	0.22
LL	0.29	0.56***	0.29	0.58***	0.24	0.20	0.27	0.14	—
				Type 2					
MA	—	0.36	0.43*	0.02	0.24	0.24	0.13	0.23	0.17
TR	0.44**	—	0.16	0.05	0.32	0.37	0.37	0.03	0.16
WG	0.18	0.18	—	0.20	0.07	-0.04	-0.04	-0.11	0.01
LU	0.30	0.08	0.30	—	0.27	0.29	0.20	-0.07	0.33
BD	0.41**	0.29	0.41**	0.21	—	0.85***	0.37	0.36	0.34
DU	0.51***	0.32*	0.51***	0.25	0.87***	—	0.46*	0.37	0.28
WU	0.33*	0.05	0.33*	0.40*	0.42**	0.38*	—	0.06	0.18
WL	0.02	0.07	0.02	-0.03	0.42**	0.35*	0.08	—	0.35
LL	0.17	0.10	0.17	0.49**	0.21	0.12	-0.10	0.16	—

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

ADDITIONAL VOCAL EVIDENCE

Red Crossbills have a repertoire of distinctive, nongraded (Miller 1979, Morton 1982) calls like other cardueline finches (Mulligan and Olsen 1969, Coutlee 1971, Marler and Mundinger 1975, Adkisson 1981), and other species of *Loxia* (Nethersole-Thompson 1975, Mundinger 1979). The alarm call (Fig. 7) was given during handling, disturbance, or when hawks flew over. Of the captured adults recorded giving alarm calls, the Type 1 birds ($n = 5$) gave alarm calls consistently of longer duration, higher absolute frequency, and purer tone than the Type 2 birds ($n = 8$), which had alarm calls of lower absolute frequency and with greater frequency modulation. The excitement call (Fig. 7) was given as a component of nesting behavior, in greeting sessions, and in social aggression. Sixteen of the captured adults were recorded giving excitement calls, and the Type 1 birds ($n = 8$) all gave relatively higher pitched calls with simple upward and downward frequency modulation. Type 2 birds gave excitement calls of more complex structure, with lower elements first falling, then rising, and again falling in frequency, and with upper elements above initial portions of the lower elements. Nethersole-Thompson's (1975) "toop" of *L. scotica* and his "alarm call" of European *L. curvirostra* are both probably homologous to my excitement call since they were described as given in the same behavioral contexts. In all casual observations of birds in the field and captivity, crossbills of known flight call type did not give alarm or excitement calls typical of the other form.

ECOLOGICAL OBSERVATIONS

Sympatric congeners are probably each other's closest ecological competitors, and should display morphological and ecological differences to allow their sympatry (Hutchinson 1959, Schoener 1965), but the degree of morphological difference required has been questioned (Simberloff and Boecklen 1981, Wiens 1982). Bill size differentiation within *Loxia* and the associated differentiation in habitat and food selection has been used as a classic case of niche partitioning (Lack 1944, Newton 1973). Type 1 and Type 2 crossbills moved through the same habitat near Blacksburg during the same seasons (both with associated juveniles), showing that the two forms can occur syntopically. Both forms were seen on pitch pine, Virginia pine, and eastern white pine. Table mountain pine cones are large, spiked, and
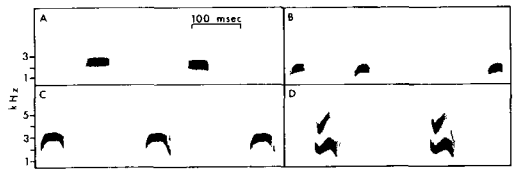

FIGURE 7.   Representative sonograms of (A) Type 1 alarm calls, (B) Type 2 alarm calls, (C) Type 1 excitement calls, and (D) Type 2 excitement calls.

thick-scaled, and in the 16 instances I recorded different individuals foraging on this species, all were of Type 2, the larger-billed form. While the habitat near Blacksburg had a diversity of conifer species and thus the potential to attract crossbills with different conifer preferences, the predominant conifer at Highlands, North Carolina, was eastern white pine, which has relatively thin cone scales. Of the 53 birds captured at Highlands and perhaps 100 more encountered, only one was a Type 2 bird. One juvenile Type 2 bird was captured on Roan Mountain on 21 June 1984, but the six other birds captured (one adult, five juveniles) and possibly 10 more heard, were all Type 1. These observations indicate both differences and overlap in the conifer utilization of two forms.

ANALYSIS OF TYPE SPECIMENS REPRESENTING APPALACHIAN CROSSBILLS

The name *pusilla* (Gloger 1834) is available under the the 1985 Code (International Trust for Zoological Nomenclature 1985) and is represented by a lectotype which originated in Georgia (Payne 1987). The AOU (1931) first used *pusilla* to replace *minor* for a northern and eastern North American subspecies. The type specimen of *pusilla* was in Berlin when van Rossem (1934) examined it, and he regarded *percna* (Bent 1912, from Newfoundland) as a synonym of *pusilla* although he did not compare the type directly to Newfoundland specimens. Griscom (1937) and the AOU (1957) agreed with this interpretation, and most museums today use *pusilla* to represent Newfoundland Red Crossbills or large-billed eastern birds. The assessment of Monson and Phillips (1981) was that *pusilla* was not representative of Newfoundland birds but rather crossbills from the southern Appalachians. Payne (1987) showed that the type of *pusilla* was outside the range of variation of Newfoundland birds but within the range of several populations from
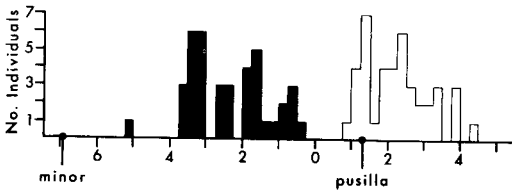
FIGURE 8. Ordering of males along the between-groups discriminant function axis for six skin characters. Black distribution = Type 1 males; hollow distribution = Type 2 males. The positions of the type specimens of *L. c. pusilla* and *L. c. minor* are indicated.

North America, including the southern Appalachians.

Other than *pusilla,* no names are available for an endemic southern Appalachian subspecies. Griscom (1937) suggested the existence of an unnamed one by describing color and size differences between the Appalachian specimens and his more northern *neogaea.* He did not name it as a new subspecies due to the small number of specimens. The AOU (1957) considered Appalachian crossbills to be part of the eastern subspecies *minor.*

Measurements of five bill dimensions and wing chord were lower for study skins than for the same measurements made on live birds (Table 12). The bill may get smaller as it dries, and wings were measured in a more folded position in preserved specimens. Discriminant function analysis using the six skin measurements separated 100% of the Appalachian males (grouped by calls into Type 1 and Type 2 populations, Fig. 8). The type of *minor* was far smaller than any of the birds I measured in the Appalachians in 1983 and 1984, obtaining a discriminant score of −6.953. The type of *pusilla* was near the middle of the range of Appalachian birds and obtained a discriminant score of 1.293, placing it within the distribution of Type 2 birds and outside that of Type 1. The type of *pusilla* was within the range of Type 1 birds for three of the six characters (WL, LL, and WG), and it was within the range of Type 2 birds for all six characters.

DISCUSSION

THE BIOSYSTEMATIC LEVEL OF THE TWO CROSSBILL FORMS

The crossbills from Appalachian breeding populations formed two distinctive, nonreducible units (taxa). This finding is in conflict with the traditional view that North American *L. curvi-*

TABLE 12.   Analysis of the type specimens of *Loxia curvirostra pusilla* and *L. c. minor.* The df coefficients were calculated as a separation of males of Type 1 and Type 2 for the set of six morphological characters. The resulting df scores for the type specimens (see text) were obtained by multiplying the corrected determinations of the characters by the raw df coefficients, summing the resulting values across all six characters, and adding the negative constant. The standardized df coefficients indicate relative weight of each character on the df axis.

Variable	Measurements		Corr. factor[a]	df coefficients	
	pusilla	minor		Raw	Standardized
WG	90.0	85.3	+1.78	0.149	0.326
LU	15.9	12.4	+0.09	0.491	0.290
BD	9.5	8.2	+0.10	0.838	0.215
WU	7.1	5.8	+0.25	1.228	0.292
WL	10.2	8.3	+0.13	1.488	0.487
LL	11.5	10.1	+0.03	0.224	0.119
Constant				−55.253	

[a] Correction factor, which is the average decrease (in mm) for each character in the set of 47 crossbills measured after preparation and drying.

rostra is divisible into geographic and morphologic subspecies.

According to Mayr (1970) both subspecies and semispecies (= allospecies) are defined on the basis of geography, with the difference between the two categories representing an assessment of the level of differentiation between the taxa. Without evidence, Griscom (1937) argued that morphotypes of Red Crossbill are subspecies, and not species, because they return to home breeding ranges after invasions into ranges of other forms. Smaller crossbills the size of Type 1 birds are most strongly represented as specimens from the Appalachians (Payne 1987), suggesting that larger Type 2 birds would have been the invading form under this scenario. However, large crossbills are frequent residents of the southern Appalachians. Adults exhibiting breeding behavior in Georgia (described by Sciple 1952) were the size of Type 2 birds (Payne 1987, p. 15). The nesting pair described by Goetz (1981) fed and nested on table mountain pine, indicating that these were probably large-billed birds. Some large crossbills associated with juveniles in North Carolina were described by Sykes (1974). The type specimen of *pusilla* was large (Payne 1987, this study).

Another scenario that would fit crossbill call types as subspecies is that both Type 1 and Type 2 were invaders of the southeastern region from elsewhere. However, despite the assumed volatility of crossbill populations, there is evidence

that crossbills are not merely irregular invaders of the southeastern mountains. Fair numbers have been seen by observers in Virginia since the early 1960s (cf. records of the Virginia Society of Ornithology). Few successful nests have been reported in the entire southeastern region (six total: Warren et al. 1977; Goetz 1981; Haggerty 1982; Simpson 1987; McNair, unpubl.; this study) but additional nest-building behavior has been observed (Jones 1932, Sciple 1952, Johnston 1963, Stupka 1963, Simpson 1974) and juveniles have been seen with some frequency (Scott 1964, 1981; Murray 1971; Swindell 1974; Sykes 1974; Carter 1976; C. S. Adkisson, pers. comm.). A low density of resident crossbills probably ranges through the pine forests of the southern Appalachians, and concentrations may occur at local seed abundances such as at Highlands, North Carolina, or when "true" invasions of nonbreeders occur (Brooks and Lund 1942). There is no evidence that the southeast region experienced an invasion of crossbills prior to this study (cf. reports in *American Birds*). Available evidence suggests that large- and small-billed crossbills have both resided in the southern Appalachians in historical times. The mixing of birds in 1983 and 1984 (and probably also in earlier years) shows that crossbills of the two call types occurred over the same general region and had opportunity for social mixing, qualifying the situation as a sympatric one, which is in opposition to the subspecies or semispecies definitions.

An unfavorable hypothesis to explain the results of this study is that the two forms represent morphs within a single population. Morphism in birds is generally restricted to plumage characters (Huxley 1955); however, polymorphism in bill and body size has been suggested by Smith and Temple (1982) for *Chondroheirax* kites and found by Smith (1987) for *Pyrenestes* seedcrackers. However, there are no examples of distinctive within-population morphs showing vocal differences. A single possible exception was a population of *Geospiza conirostris* in which two song types of males showed a significant 6.3% difference in bill length (Grant and Grant 1979). In this case other bill and body size characters did not differ between the song types, and the song type phenomenon in this population was not stable (Grant 1986). In contrast, the Appalachian forms had consistently large differences in nine morphological characters. As the fine structure of cardueline calls has a large learned component (Mundinger 1970, 1979), different

morphs should occasionally have the same vocalizations since they should occasionally occur in the same nests. In this study no instances were found in which birds classifiable as different size classes had the same vocal type, giving no evidence that these forms are within-population morphs.

That North American *L. curvirostra* is a single species which is divisible into subspecies should be questioned. With evidence that distinctive vocal and morphological forms coexist sympatrically disagrees with the subspecies argument, and lack of swamping of morphological types in North America suggests an absence of hybridization. A series of continental subspecies implies zones of contact in identifiable regions, but it is difficult to envision this for mobile birds such as crossbills. The evidence presented here suggests that crossbill call types can overlap in geographic ranges and maintain vocal and morphological distinctiveness, favoring the hypothesis that they are cryptic species. Mated pairs found by Groth (1984) were never of mixed size class, and further analysis of pairing behavior, song, and biochemical genetics will address reproductive biology in more detail (Groth, unpubl. data). Reproductive separation of the different species could be accomplished by an unknown combination of vocal (Becker 1982), morphological (Ratcliffe and Grant 1983), and ecological (Lack 1971) differences. Even though call types may be largely learned, young birds may imprint differentially on their parents' calls. Bill size differentiation and associated ecological differences may play additional roles in at least providing some spatiotemporal separation of crossbill forms. The situation for North America appears to be similar to that in northern Britain where the Scottish Crossbill (*L. scotica*) and the Common Crossbill (*L. curvirostra*) are considered species.

CALLS IN THE SYSTEMATICS OF CROSSBILLS

Mundinger (1979) has argued against the use of the vocalizations in the systematics of cardueline finches because species may share calls through vocal imitation. This restriction does not apply to this study because systematic relationship was not determined by sharing of calls, but rather by the pattern of fine structure of homologous calls. However, it is not certain whether the characters of the notes were truly homologous. It is con-

ceivable that the gross similarity in flight calls (downward frequency-modulated) of the two Appalachian forms may be the result of convergence, with the possibility that separate ancestors of Type 1 and Type 2 may have had cultural-evolutionary phases in which they were more different from one another in flight call structure. Other North American crossbill forms with different flight call structures may be more closely related on genetic or morphological grounds to either one of the Appalachian forms than the latter are with each other (Groth, unpubl. data). Although calls intergraded in the characters that I used, this continuity may be artificial and show nothing of true relationship. It is not known whether these two forms are sister taxa.

THE TAXONOMIC PROBLEM

Given that I found no distinctive crossbill forms other than Type 1 and Type 2 in the southern Appalachians, it seems reasonable to conclude that the type specimen of *pusilla* represents one of them. The taxonomic implications of this finding may bring yet another interpretation of the correct placement of the name *pusilla*. With the evidence that Type 2 birds also range widely throughout North America (Groth, unpubl. data), including areas traditionally the ranges of the large-billed western subspecies *benti, bendirei,* and *grinnelli,* these names may all be synonyms of *pusilla* because they may be referring to the same wide-ranging taxon. It is not known whether another distinctive vocal population with large bills could have resided in the Appalachians in the early 1800s from which the type of *pusilla* was collected. Because neither *minor* nor *pusilla* should represent Type 1 birds, this form may be an unnamed Appalachian endemic. Further work on the geography and morphology of crossbill vocal populations is necessary to solve this interesting taxonomic problem.

ACKNOWLEDGMENTS

LITERATURE CITED

ADKISSON, C. S. 1977. Morphological variation in North American Pine Grosbeaks. Wilson Bull. 89: 380–395.

ADKISSON, C. S. 1981. Geographic variation in vocalizations and evolution of North American Pine Grosbeaks. Condor 83:277–288.

AMADON, D. 1959. The significance of sexual differences in size among birds. Proc. Am. Phil. Soc. 103:531–536.

AMERICAN ORNITHOLOGISTS' UNION. 1931. Checklist of North American birds. 4th ed. American Ornithologists' Union, Lancaster, PA.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds. 5th ed. American Ornithologists' Union, Baltimore, MD.

BAILEY, A. M., R. J. NIEDRACH, AND A. L. BAILEY. 1953. The Red Crossbills of Colorado. Museum Pictorial No. 9, Denver Museum of Natural History.

BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow Zonotrichia leucophrys. Univ. Calif. Publ. Zool. 70:1–123.

BECKER, P. H. 1982. The coding of species-specific characteristics of bird sounds, p. 214–252. In D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds. Vol. 1. Academic Press, New York.

BEHLE, W. H. 1956. A systematic review of the Mountain Chickadee. Condor 58:51–70.

BENT, A. C. 1912. A new subspecies of crossbill from Newfoundland. Smithsonian Misc. Coll. 60:1–3.

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237: 497–526.

BREHM, C. L. 1845. Drey neue deutche Vogelarten, nicht Subspecies, sondern Species, und ein Beschreibung der bindigen Kreuzschnäbel. Isis von Oken 2:243–269.

BROOKS, M., AND W. A. LUND. 1942. White-winged Crossbills and Sitka Crossbills summering in the West Virginia spruce belt. Auk 59:118–119.

CARTER, J. H., III. 1976. Probable breeding of the Red Crossbill in the North Carolina sandhills. Chat 40:100.

COUTLEE, E. L. 1971. Vocalizations in the genus Spinus. Anim. Behav. 19:556–565.

DICKERMAN, R. W. 1987. A review of the Red Crossbill in New York State. Part 2. Identification of

specimens from New York. Kingbird 36:127–134. 134.

GLOGER, C. L. 1834. Vollständiges Handbuch der Naturgeschichte der Vögel Europas, mit besonderer Rücksicht auf Deutschland. Vol. 1. August Schulz, Breslau.

GOETZ, E. J. 1981. Nesting of Red Crossbills in Rockingham County, West Virginia (sic). Redstart 48: 90–92.

GOLDSTEIN, R. B. 1978. Geographic variation in the "hoy" call of the Bobwhite. Auk 95:85–94.

GRANT, B. R., AND P. R. GRANT. 1979. Darwin's finches: population variation and sympatric speciation. Proc. Natl. Acad. Sci. 76:2359–2363.

GRANT, P. R. 1986. Ecology and evolution of Darwin's finches. Princeton Univ. Press, Princeton, NJ.

GRANT, P. R., I. ABBOTT, D. SCHLUTER,R. L. CURRY, AND L. K. ABBOTT. 1985. Variation in the size and shape of Darwin's finches. Biol. J. Linn. Soc. 25:1–39.

GRISCOM, L. 1937. A monographic study of the Red Crossbill. Proc. Boston Soc. Nat. Hist. 41:77–210.

GROTH, J. G. 1984. Vocalizations and morphology of the red crossbill (Loxia curvirostra, L.) in the southern Appalachians. M.S.thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.

HAGGERTY, T. 1982. Confirmation of breeding Red Crossbills in the mountains of North Carolina with notes on nesting behavior. Chat 53:83–86.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93:145–159.

HUXLEY, J. S. 1955. Morphism in birds. Proc. XI Int. Ornithol. Congr. (1954):309–328.

INTERNATIONAL TRUST FOR ZOOLOGICAL NOMENCLATURE. 1985. International Code of Zoological Nomenclature. 3rd ed. International Trust for Zoological Nomenclature, London.

JOHNSON, N. K. 1963. Biosystematics of sibling species of flycatchers in the Empidonax hammondii-oberholseri-wrightii complex. Univ. Calif. Publ. Zool. 66:79–238.

JOHNSON, N. K. 1980. Character variation and evolution of sibling species in the Empidonax difficilis-flavescens complex (Aves: Tyrannidae). Univ. Calif. Publ. Zool. 112:1–151.

JOHNSTON, D. W. 1963. Further evidence of Red Crossbills breeding in North Carolina. Chat 27: 81–82.

JOLLIE, M. 1953. Plumages, molts, and racial status of Red Crossbills in northern Idaho. Condor 55: 193–197.

JONES, F. M. 1932. Field notes from the Bristol area. Raven 3:3.

KEMPER, T. 1959. Notes on the breeding cycle of the Red Crossbill (Loxia curvirostra) in Montana. Auk 76:181–189.

KNOX, A. G. 1975. Crossbill taxonomy, p. 191–201. In D. Nethersole-Thompson [ed.], Pine crossbills. T. & A. D. Poyser, Berkhamsted.

KNOX, A. G. 1976. The taxonomic status of the Scottish Crossbill Loxia sp. Bull. Br. Ornithol. Soc. 96: 15–19.

LACK, D. 1944. Correlation between beak and food in the crossbill Loxia curvirostra Linneaus. Ibis 86:552–553.

LACK, D. 1947. Darwin's finches. Cambridge Univ. Press, Cambridge.

LACK, D. 1971. Ecological isolation in birds. Blackwell Sci. Publ., Oxford.

LANYON, W. E. 1969. Vocal characters and avian systematics, p. 291–310. In A. Hinde [ed.], Bird vocalizations. Cambridge Univ. Press, Cambridge.

LANYON, W. E. 1978. Revision of the Myiarchus of South America. Bull. Am. Mus. Nat. Hist. 161: 427–628.

LÖHRL, H. 1963. The use of bird calls in clarifying taxonomic relationship. Proc. XIII Int. Ornithol. Congr. (1962):544–552.

MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209–220.

MARLER, P., AND P. C. MUNDINGER. 1975. Vocalizations, social organization, and breeding biology of the Twite Acanthus flavirostris. Ibis 117:1–17.

MAYR, E. 1970. Populations, species, and evolution. Harvard Univ. Press, Cambridge, MA.

MAYR, E., G. E. LINSLEY, AND R. L. USINGER. 1953. Methods and principles of systematic zoology. McGraw-Hill, New York.

MCCABE, T. T., AND E. B. MCCABE. 1933. Notes on the anatomy and breeding habits of crossbills. Condor 35:136–147.

MILLER, A. H. 1941. Speciation in the avian genus Junco. Univ. Calif. Publ. Zool. 44:173–434.

MILLER, E. H. 1979. An approach to the analysis of graded vocalizations of birds. Behav. Neural Biol. 27:25–38.

MILLER, E. H. 1986. Components of variation in nuptial calls of the least sandpiper (Calidris minutilla; Aves, Scolopacidae). Syst. Zool. 35:400–413.

MONSON, G., AND A. R. PHILLIPS. 1981. The races of Red Crossbill, Loxia curvirostra, in Arizona, p. 223–230. In Annotated checklist of birds of Arizona. 2nd ed. Univ. Arizona Press, Tucson.

MORTON, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules, p. 183–212. In D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds. Vol. 1. Academic Press, New York.

MULLIGAN, J. A., AND K. C. OLSEN. 1969. Communication in Canary courtship calls, p. 165–184. In R. A. Hinde [ed.], Bird vocalizations. Cambridge Univ. Press, London.

MUNDINGER, P. C. 1970. Vocal imitation and individual recognition of finch calls. Science 168:480–482.

MUNDINGER, P. C. 1979. Call-learning in the Carduelinae: ethological and systematic implications. Syst. Zool. 28:270–283.

MURRAY, J. W. 1971. Notes on Red Crossbills near Blacksburg, Virginia. Raven 42:46–47.

NETHERSOLE-THOMPSON, D. 1975. Pine crossbills. T. & A. D. Poyser, Berkhamsted.

NEWTON, I. 1973. Finches. Taplinger, New York.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package

for the social sciences. 2nd ed. McGraw-Hill, New York.

NORRIS, R. A. 1958. Comparative biosystematics and life history of the nuthatches *Sitta pygmaea* and *S. pusilla*. Univ. Calif. Publ. Zool. 56:119–300.

PAYNE, R. B. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. Ornithol. Monogr. No. 11. American Ornithologists' Union, Washington, DC.

PAYNE, R. B. 1986. Bird songs and avian systematics, p. 87–126. *In* R. F. Johnston [ed.], Current ornithology. Vol. 3. Plenum Press, New York.

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.

PAYNE, R. B., AND P. BUDDE. 1979. Song differences and map distances in a population of Acadian Flycatchers. Wilson Bull. 91:29–41.

PHILLIPS, A. R. 1977. Sex and age determination of Red Crossbills (*Loxia curvirostra*). Bird-Banding 48:110–117.

POWER, D. M. 1983. Variability in island populations of the House Finch. Auk 100:180–187.

RATCLIFFE, L. M., AND P. R. GRANT. 1983. Species recognition in Darwin's finches (*Geospiza* Gould). I. Discrimination by morphological cues. Anim. Behav. 31:1139–1153.

RISING, J. D. 1970. Morphological variation and evolution in some North American orioles. Syst. Zool. 19:315–351.

ROBBINS, M. B., M. J. BRAUN, AND E. A. TOBEY. 1986. Morphological and vocal variation across a contact zone between the chickadees *Parus atricapillus* and *P. carolinensis*. Auk 103:655–666.

ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1980. NTSYS numerical taxonomy system of multivariate statistical programs. State Univ. of New York at Stony Brook, NY.

SAMSON, F. B. 1978. Vocalizations of Cassin's Finch in northern Utah. Condor 80:203–210.

SAS INSTITUTE. 1982. SAS user's guide: statistics. SAS Institute, Cary, NC.

SCHOENER, T. W. 1965. The evolution of bill size difference among sympatric congeneric species of birds. Evolution 19:189–213.

SCHNELL, G. D., D. J. WATT, AND M. E. DOUGLAS. 1985. Statistical comparison of proximity matrices: applications in animal behavior. Anim. Behav. 33:239–253.

SCIPLE, G. W. 1952. A collection of Newfoundland crossbills at Stone Mountain, Georgia. Oriole 17:6–7.

SCOTT, F. R. 1964. The 1963–64 crossbill flight in Virginia. Raven 35:35–41.

SCOTT, F. R. 1981. Evidence for a resident crossbill population on Shenandoah Mountain. Raven 52:61–64.

SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. Univ. Calif. Publ. Zool. 74:1–305.

SELANDER, R. K. 1971. Systematics and speciation in birds, p. 57–147. *In* D. S. Farner and J. R. King [eds.], Avian biology. Academic Press, New York.

SELANDER, R. K., AND R. F. JOHNSTON. 1967. Evolution in the House Sparrow. I. Intrapopulation variation in North America. Condor 69:217–258.

SELLERS, R. M. 1986. Biometrics of the Siskin *Carduelis spinus*. Ringing & Migr. 7:99–111.

SHAPIRO, S. S., AND M. B. WILKS. 1965. An analysis of variance test for normality. Biometrika 52:591–611.

SIMBERLOFF, D., AND W. BOECKLEN. 1981. Santa Rosalia reconsidered: size ratios and competition. Evolution 35:1206–1228.

SIMPSON, M. B. 1974. Red Crossbill observations in western North Carolina. Chat 38:44–45.

SIMPSON, M. B. 1987. Crossbills nesting at Linville Gorge, Burke Co., N. C. Chat 51:60–61.

SMITH, J.N.M., AND R. ZACH. 1979. Heritability of some morphological characters in a song sparrow population. Evolution 33:460–467.

SMITH, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. Nature 329:717–719.

SMITH, T. B., AND S. A. TEMPLE. 1982. Feeding habits and bill polymorphism in Hook-billed Kites. Auk 99:197–207.

SNEATH, P.H.A., AND R. R. SOKAL. 1973. Numerical taxonomy. Freeman, San Francisco.

SNEDECOR, G. W., AND W. G. COCHRAN. 1965. Statistical methods. State College Press, Ames, IA.

SPARLING, D. W., AND J. D. WILLIAMS. 1978. Multivariate analysis of avian vocalizations. J. Theor. Biol. 74:83–107.

STEIN, R. C. 1958. The behavioral, ecological, and morphological characteristics of two populations of the Alder Flycatcher, *Empidonax traillii* (Audubon). N.Y. State Mus. Bull. 37:1–63.

STEIN, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatchers. Proc. Am. Philos. Soc. 107:21–50.

STUPKA, A. 1963. Notes on the birds of the Great Smoky Mountains National Park. Univ. Tennessee Press, Knoxville.

SWINDELL, M. 1974. Fledgling Red Crossbills at Newfound Gap. Chat 38:43–44.

SYKES, P. W. 1974. Additional information on the Red Crossbill breeding in the lower Piedmont of North Carolina in 1967. Chat 38:42–43.

VAN ROSSEM, A. J. 1934. Notes on some types of North American birds. Trans. San Diego Soc. Nat. Hist. 7:347–362.

WARREN, R. C., JACKSON, J. A., AND T. L. DARDEN. 1977. Nesting of the Red Crossbill in Mississippi. Am. Birds 31:1100.

WIENS, J. A. 1982. On size ratios and sequences in ecological communities: are there no rules? Ann. Zool. Fenn. 19:297–308.

ZINK, R. M. 1986. Patterns and evolutionary significance of geographic variation in the Schistacea group of the Fox Sparrow (*Passerella iliaca*). Ornithol. Monogr. No. 40. American Ornithologists' Union, Washington, DC.