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POPULATIONS AND TYPE SPECIMENS OF A NOMADIC  
BIRD: COMMENTS ON THE NORTH AMERICAN  
CROSSBILLS *LOXIA PUSILLA* GLOGER 1834 AND  
*CRUCIROSTRA MINOR* BREHM 1845

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ABSTRACT.—Payne, Robert 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. Occ. Pap. Mus. Zool. Univ. Michigan, 714: 1-37, figs. 1-3.* The type specimens of *Loxia pusilla* and *Crucirostra minor* were compared with specimens of crossbills from northern and eastern North America. The type of *Loxia pusilla* is a large-billed bird resembling crossbills from the Appalachian region. It also falls within the range of variation of the western form *L. curvirostra bendirei* and its synonym *L. c. benti*. The forms *neogaea* and *benti* are here found to be indistinguishable from *bendirei* and are synonyms, but it is uncertain whether *bendirei* in turn is a synonym of *pusilla*. *L. c. percna* from Newfoundland is a distinct form, not a synonym of *pusilla*. The type of *Crucirostra minor* was taken in Michigan in 1834 and resembles the small-billed birds that have bred in the state during this century. It falls within the range of variation of birds from the Pacific northwest and from Idaho. *Loxia curvirostra sitchensis* and *L. c. reai* are indistinguishable synonyms of *L. c. minor*. Breeding crossbills of the eastern United States from Maine to Georgia are larger than the type of *minor*. Crossbills in Michigan vary considerably and significant differences were found both among counties and among years. These probably represent different populations or mixed populations, or both. Banding recovery data showed movements of individual crossbills between western, central, and eastern North America, but no direct evidence of movements from the Pacific northwest to the east. Breeding data in this region are inadequate to test

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whether the different forms represent genetic units, and biochemical and behavioral studies will be required to determine the biological distinctiveness of crossbill populations.

Key words: *Appalachia*, *crossbill*, *Loxia curvirostra*, *C. L. Brehm*, *A. C. Koch*, *North America*, *Michigan*, *dispersal*, *nomadism*, *banding recoveries*.

## INTRODUCTION

North American Red Crossbills (*Loxia curvirostra* Linnaeus 1758) are morphologically variable across the continent. They are highly dispersive and irruptive in certain years, particularly in northern and eastern parts of their range. Breeding crossbills in eastern North America have usually been identified as *L. c. pusilla* Gloger 1834 or *L. c. minor* (Brehm 1845). Although these names have been widely used over the past 80 years, the type specimens have never been compared with other crossbills in North America. The types were described and photographed in Berlin by van Rossem (1934), but he did not examine comparative material at the time and did not measure one of the two types (*minor*). With growing interest in crossbill biology in recent years (Nethersole-Thompson, 1975; Phillips, 1975, 1977; Knox, 1976, 1983; Monson and Phillips, 1981; Groth, 1984), it is appropriate to compare these type specimens so that names can be matched with populations. Some biologists have suggested that crossbills recognized as different populations or subspecies may in certain cases be distinct species (Groth, 1984). Monson and Phillips (1981:223) viewed them as "independent little semi-species wandering around." In the present note I review the history of *pusilla* and *minor* and compare their morphological characteristics with those of birds taken more recently in the same areas. I also describe the evidence from banding recoveries that shows their long distance movements, and discuss certain problems in systematics that follow from the crossbills' erratic seasons of breeding and movements.

## METHODS

The type specimens of *pusilla* and *minor* were borrowed from the Museum für Naturkunde der Humboldt-Universität zu Berlin (=Zoologisches Museum Berlin, here called the Berlin Museum). They were compared in several North American museums with the types of certain other forms as well as series of specimens taken in the same place as the type, and sometimes in the same year. A list of comparative material examined is provided in the Appendix. The following mea-

measurements were taken for all crossbills: (1) Wing arc (mm), wing with primaries straightened and flattened, bend of wing to tip of longest primary. (2) Wing chord (mm), length of wing without flattening the primaries. (3) Bill length (mm) from anterior edge of nostril to tip of upper mandible. (4) Bill length (mm) from posterior margin of rhamphotheca just anterior to base of feathers of forehead to tip of upper mandible. (5) Bill width (mm), lower mandible, measured across posterior margins of mandibular rami. (6) Bill width (mm), measured across cutting edge of upper mandible at point perpendicular to line drawn to edge of bill from anterior margin of nostril. (7) Bill depth (mm) measured on a line perpendicular to edge of mandible and drawn through anterior edge of nostril. (8) Tarsus (mm) measured from proximal edge of tarsometatarsus to distal edge of distalmost scale that overlies the three anterior toes. Bill depths were measured from some birds with incompletely closed bills—an artifact of specimen preparation not seen in live crossbills (see Fig. 1). In measuring, the calipers compressed the bill above and below the nostril so that the edges were approximated. The left tarsus was measured in most; however the tarsus tends to be shorter on the side of the bird to which the lower mandible crosses, perhaps in relation to the mechanics of opening pine cones (Knox, 1983). Color scores were determined by referring to the page, column, and row of the Methuen Colour Guide (Kornerup and Wanscher, 1967). The color terms used to describe the plumage are from this guide. As crossbills cannot be aged consistently into age classes by plumage (Phillips, 1977), no separation into age classes (other than by excluding the streaked juvenile specimens) was made. Birds in their first year (determined by skull pneumatization) tend to be slightly smaller (Tordoff, 1952); most specimens examined lacked any skull information, and no specimens were excluded from measurement on skull criteria alone.

Measurements were compared between the two types and reference populations. The populations used for comparison were those which the historical evidence indicated as the sources of the types, and populations from northern and eastern North America from which other named taxa have been described, as follows: southern Appalachian states (Georgia was the apparent type locality of *L. pusilla* Gloger 1834, but this is not well documented) (Georgia, South Carolina, North Carolina, Tennessee, and Virginia northwards through Montgomery County); Michigan (type locality of *L. minor* [Brehm 1845]); Newfoundland (type locality of *L. c. percna* Bent 1912); Lake Umbagog, Maine (type locality of *L. c. neogaea* Griscom 1937); Grafton, North Dakota (type locality of *L. c. benti* Griscom 1937);

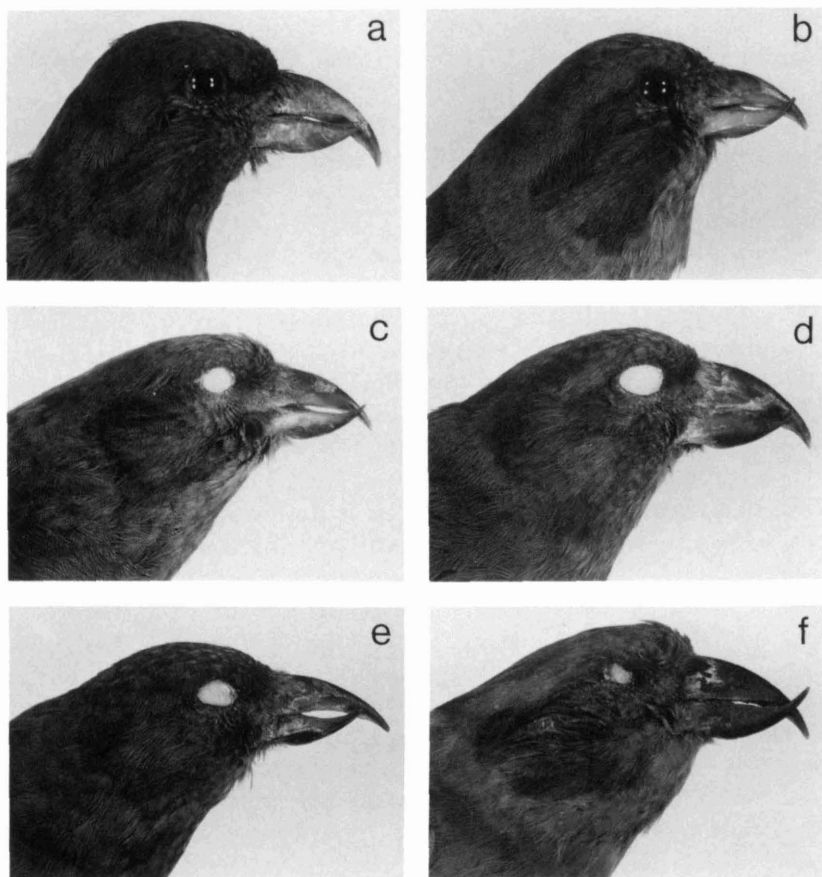


FIG. 1. Variation in bill size and shape in crossbills *Loxia curvirostra* in northern and eastern North America. a, Berlin Museum 6984, type of *Loxia pusilla* Gloger 1834. b, Berlin Museum 6982, type of *Crucirostra minor* Brehm 1845. c, UMMZ 110719, Huron Mountain Club, Marquette County, Michigan, 28 Jan. 1941. d, UMMZ 166116, Princeton, Newfoundland, 22 June 1942. e, UMMZ 166131, Mt. Mitchell, North Carolina, 2 May 1930. f, UMMZ 68340, Grafton, North Dakota, 8 Oct. 1931.

Dismal Lake, Shoshone County, Idaho (type locality of *L. c. reai* Monson and Phillips 1981); Fort Klamath, Oregon (type locality of *L. c. bendirei* Ridgway 1885); and coastal British Columbia and southern Alaska (Admiralty Island, Alaska, the type locality of *L. c. sitkensis* Grinnell 1909). No type series were ever collected for the other named taxa of North American *L. curvirostra*: *L. c. mesamericana* Griscom 1937, *L. c. stricklandi* Ridgway 1885, *L. c. grinnelli* Griscom 1937, and

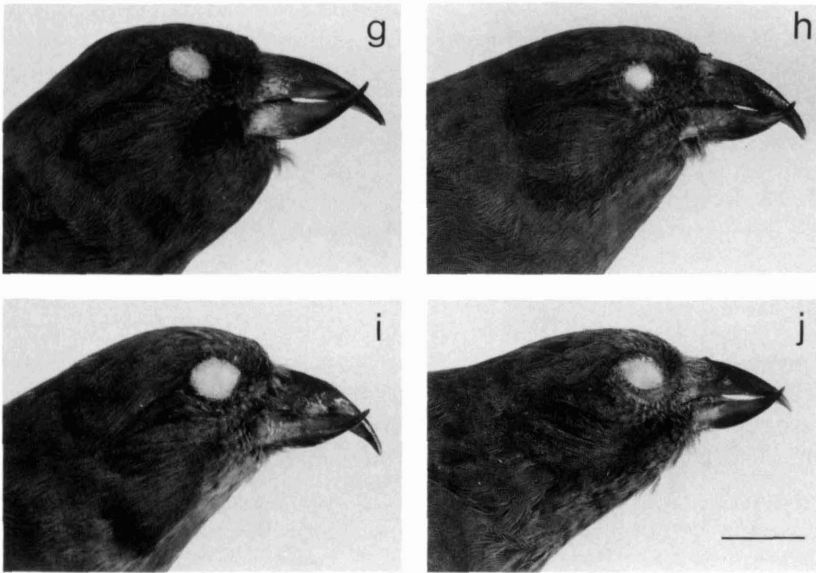


FIG. 1, cont. g, UMMZ 166117, Wolfville, Nova Scotia, 27 Feb. 1932. h, UMMZ 83057, Oxford Co., Maine, 21 March 1904. i, USNM 94873, Fort Klamath, Oregon, 5 Dec. 1882. j, CAS 60557, Wrangell Island, Alaska, 4 June 1946. Note: a, f, and g are printed in reverse for comparison so that the bills appear to cross in the same direction as in the other specimens.

*L. c. viridior* Monson and Phillips 1981. Type specimens of these named taxa were not compared with the types of *pusilla* and *minor* because of geographic distribution (the two Berlin types were not taken in southwestern North America) and because of the absence of type series. Large samples of ten or more birds were available from the time (within a year) and place of collection of the type of *benti* and *bendirei*; collections made locally over several years were used for *percna*. Collections over a larger area and a series of years were pooled for the remaining forms. Especially in these latter forms the samples may be heterogeneous, as more than one crossbill population may appear in an area in different years in irruptive or migratory movements. Also included are measurements from a large series taken in one locality in eastern North America (Algonquin National Park, Ontario) and a specimen from a nearby breeding population (Lawrence, 1949).

Specimens examined were in the American Museum of Natural History (AMNH), Museum of Northern Arizona (MNA), California Academy of Sciences (CAS), Carnegie Museum of Natural History (CM), Cornell University (CU), Central Michigan University (CMU),

Delaware Museum of Natural History (DEL), Field Museum of Natural History (FMNH), Grand Rapids Public Museum (GRPM), Kalamazoo College of Science (KCS) collection now at Kalamazoo Nature Center-Michigan Audubon Society (KNC), University of Kansas Museum of Natural History (KU), Louisiana State University Museum of Zoology (LSU), Michigan Technical University (MTECH), Michigan State University (MSU), University of Montana Zoology Museum (UMZM), Museum of Comparative Zoology (MCZ), Museum of Vertebrate Zoology, University of California (MVZ), National Museum of Canada (NMC), Royal Ontario Museum (ROM), San Diego Museum of Natural History (SDMNH; AMR collection of A.M. Rea), U. S. National Museum (USNM), University of Georgia Museum of Natural History (UGA), University of Michigan Biological Station (UMBS), University of Michigan Exhibits Museum (UMEM), University of Michigan Museum of Zoology (UMMZ), Virginia Polytechnic Institute and State University (VTECH, including JGG collection of J.G. Groth), and Yale University Peabody Museum (YALE). For certain geographic areas only the first museum sample or samples that I examined were measured (especially for western Canada and Alaska).

An objective of the study was to test whether the types of *pusilla* and *minor* fell within the range of variation of other samples taken in the same localities. The large sample areas of southern Appalachia and Michigan provide an outer limit of variation within which the types were expected to fall. The more local populations of other named taxa are useful for comparison both to the types and to other taxa in which they have sometimes been included. However, except for *L. c. neogaea*, none of the types or type series were known to be from breeding populations. Another objective was to compare the type series with each other, where type series were known. The present study does not test the nature of intergrading or distinctiveness among all included taxa. Few breeding crossbills have been collected from the northern and eastern parts of North America. Biological data such as song and biochemical genetic information are not generally available for North American crossbills. Nor is the nature of the reproductive interaction between different morphological extremes that may breed in a common area, or population data from the movements of individual birds.

Univariate and multivariate numerical techniques were carried out on the available population samples. A descriptive technique (principal components analysis) using a covariance matrix was used to compare samples and to compare the types with selected population samples. For the principal components analysis, five characters were selected: (1), (3), (4), (7), and (8). Character (2, wing chord) was nearly

identical to character (1, wing arc); the standard deviation was marginally greater for (2). Characters (5, bill width at base) and (6, bill width at nostril) were of low repeatability; the measured bill width in the same individual varied more than 10%. The measurements were transformed to natural logarithms in order to decrease the difference in scaling and variance among characters, while retaining an emphasis on size. The rationale for log transformation of measured data is discussed in Bookstein et al. (1985). Quantitative comparisons were made using programs available in MIDAS (Statistical Research Laboratory, University of Michigan). Because the types were unique, statistical inference was not attempted for these specimens. Graphic interpretation of the results was generally consistent with visual comparison of the specimens. The Ontario sample was not included in these analyses; separate analyses are available for the Ontario birds.

## HISTORICAL COMMENTS

### *Loxia curvirostra pusilla* Gloger 1834

*L[oxia] pusilla* Gloger 1834, Vollst. Handb. Naturg. Vögel Europa's, 1, p. 356. (Nordamerika).

Gloger (1834: 356) published the name *L. pusilla* Lcht. in a footnote to his account of *Loxia curvirostra* and compared the two in size and color: "Man sieht den Vogel bei uns nicht selten eben so klein, wie oft den amerikanischen, die ?*L. pusilla* Lcht. und *Curvirostra americana* Wls., der schwerlich von ihm verschieden, nur meist etwas röther ist." Gloger's reference to Lichtenstein was evidently to an unpublished manuscript name. Although two reviewers suggested to me that the name may be a nomen nudum, the publication by Gloger constitutes a description, even though it is not as detailed as in certain other taxonomic descriptions or in current practice. The publication is available insofar as it meets the 1985 Code's Article 12 (Names published before 1931.—(a) Requirements). Gloger did not designate a type specimen, so there is no holotype: Stresemann's (1922:42) publication of Berlin specimen 6984 as "Der Typus" designated a lectotype.

The type specimen was acquired from the naturalist-dealer C. H. Bescke in Hamburg, and according to Stresemann (1922) came from Georgia. Its plumage is Methuen "orange-red" (8B7). The measurements are recorded in Table 1; the bill is illustrated in Fig. 1. It was accompanied by another specimen in female plumage (no. 6985), also seen by van Rossem (1934); this is being remade into a study skin (G.

Mauersberger, in litt.). When van Rossem (1934) saw the male specimen it was mounted as a display; it has since been remade as a study skin. The label on the mount seen in van Rossem's photograph is now attached to the specimen; the only difference is the addition of register number 6984. The history of the specimen was summarized by van Rossem, presumably with information provided by Stresemann. The date "Nov. 1823" on the label indicates not the date of collection but of acquisition ("Eingang") by the Berlin Museum. The specimen was collected by Bescke's son who sent his father bird skins from several eastern states including Georgia. Possibly Stresemann (1922) designated Georgia as the type locality on the basis of correspondence concerning the similar, large-billed birds (USNM 10535, 32400) collected by J. L. Le Conte at Midway, Liberty County, Georgia, in 1846 and 1850. Through R. L. Zusi, the Smithsonian Archives searched for correspondence between Stresemann and the USNM staff concerning crossbills, without success.

TABLE 1  
MEASUREMENTS (MM) OF TWO EARLY TYPE SPECIMENS OF *Loxia curvirostra*

Character	<i>L. pusilla</i>	<i>C. minor</i>
wing length, arc	91.	86.
wing length, chord	90.	86.
bill from nostril	16.0	12.5
bill from head	18.3	14.4
bill width at lower mandible	10.1	8.3
bill width at nostril	6.7	6.0
bill depth	9.8	8.3
tarsus	16.8	16.0 <sup>a</sup>

<sup>a</sup> estimated; the tarsi were broken and reglued when the specimen was converted from a mount to a study skin

Alexander Wilson (1811) was the first to describe a crossbill from North America. His *Curvirostra americana*, recognized by Bonaparte (1838) as the species *Loxia americana*, is a junior secondary homonym of *Loxia americana* Gmelin 1789 (= *Sporophila americana* [Gmelin]) and therefore invalid (International Trust for Zoological Nomenclature, 1985, referred to here as "Code, 1985": Articles 57c (i), 59b). Hellmayr (1938) pointed out these two uses of the name *Loxia americana*, and he replaced Wilson's name with *Crucirostra minor* Brehm. Whether the specimens illustrated by Wilson refer to *minor* or to *pusilla* is uncertain; the bill is shorter than the tarsus, as in *minor* (see Tables 1 and 2), but disproportionately so and unlike specimens



that I have measured. Wilson's types were in Peale's Museum in Philadelphia and apparently have been lost (Hellmayr, 1938).

*Loxia curvirostra minor* (Brehm 1845)

*Crucirostra minor* Brehm, 1845, Isis von Oken, Leipzig, II: col. 267: Nord Amerika.

At the time of van Rossem's visit to the Berlin Museum, the type specimen of *Crucirostra minor* was known only to have come from "Nord Amerika." Subsequently Stresemann determined that it was collected in Michigan. The specimen label, in Stresemann's handwriting, bears the information "Black River 50 engl. Meilen oberh. [=oberhalb] Mündung in Michigan," and "Jan./März 1834 Franz Schumann & Albert Koch leg.," as noted by Eck (1981). Koch was a naturalist and collector from Germany who resided for a few years in St. Clair, St. Clair County, southeastern Michigan. His life there has not been recorded in detail. He visited a sawmill on the Black River near Lake Huron in 1832 (Koch, 1850: 351). This river is the only Black River in the area of St. Clair, so it is probably the one that is the type locality. At the present time, 50 miles above the mouth of the Black River is near Deckerville in Sanilac County. Contemporary historical maps of Michigan in the early 1800's showed a "Black River" running eastward from the thumb region of Michigan into Lake Huron south of Saginaw Bay but no such river exists today. Koch left Michigan for St. Louis, Missouri, where his name appeared in September 1836 as the proprietor of the St. Louis Museum (Koch, 1972: xix, 153). He remained in St. Louis for a few years, then travelled in Europe from 1841 to 1843, where he sold specimens to the Royal Museum in Berlin (Koch, 1972: xxvii). The following year he returned to the United States. Descriptions of his later expeditions in fossil hunting were published (Koch, 1972), but his earlier diaries were lost. The history of Koch is consistent with his having taken the type specimen of *minor* in southeastern Michigan in early 1834. I have not located any information about Schumann.

Although publication of the name *Crucirostra minor* is usually cited (e.g. Griscom, 1937; Paynter, 1968) as Brehm 1846, that work was published later than Brehm's brief description of the taxon in his review in Isis 1845, so the correct citation is Brehm 1845.

*Crucirostra minor* was described by Brehm (1845) in no more detail than as a small crossbill from North America. He later implicitly designated a specimen as a type when he illustrated and labelled it (Brehm, 1853; reprinted by Mauersberger, 1976). Berlin specimen 6982

TABLE 2  
 VARIATION IN MEASUREMENTS (MM) OF GEOGRAPHIC SAMPLES OF *Loxia curvirostra*<sup>a</sup>

Character	Male					Female				
	<i>N</i>	min	max	mean	SD	<i>N</i>	min	max	mean	SD
	S. Appalachians									
wing length, arc	44	83.	98.	89.46	3.38	24	82.	96.	87.86	3.52
wing length, chord	44	82.	97.	88.89	3.34	24	81.	96.	87.46	3.65
bill, nostril	44	12.8	18.0	14.64	1.02	24	13.0	17.3	14.84	1.20
bill, head	44	15.2	20.5	17.27	1.15	24	15.5	19.9	17.38	1.19
bill width, mandible	45	7.8	10.8	9.19	0.61	24	8.1	10.5	9.15	0.67
bill width, nostril	45	5.9	7.3	6.59	0.40	24	6.0	7.5	6.72	0.40
bill depth	44	8.3	10.4	9.29	0.44	24	8.9	10.2	9.48	0.35
tarsus	45	14.9	17.5	16.10	0.68	24	15.5	17.7	16.44	0.63
	Maine: Lake Umbagog									
wing length, arc	23	85.	94.	89.04	2.44	12	85.	89.	86.25	1.54
wing length, chord	23	85.	94.	88.65	2.50	12	84.	88.	85.58	1.38
bill, nostril	23	12.2	16.6	14.26	0.95	12	13.1	15.2	14.08	0.57
bill, head	23	15.1	19.5	16.87	0.93	12	15.7	17.5	16.44	0.48
bill width, mandible	23	5.9	10.4	8.94	0.91	12	7.5	9.6	8.79	0.60
bill width, nostril	23	5.7	7.7	6.78	0.58	12	6.0	7.4	6.64	0.42
bill depth	23	8.0	10.4	9.40	0.60	12	5.3	9.7	8.82	1.17
tarsus	22	14.8	17.0	15.99	0.54	12	15.3	16.8	15.98	0.47
	Newfoundland									
wing length, arc	43	90.	98.	92.70	1.70	21	84.	94.	90.14	2.31
wing length, chord	43	89.	98.	92.02	1.70	21	84.	93.	89.48	2.11
bill, nostril	42	13.9	16.4	15.16	0.52	22	13.5	16.4	15.05	0.74
bill, head	42	16.6	19.4	17.91	0.57	22	16.5	19.5	17.76	0.93

bill width, mandible	42	8.7	11.2	10.01	0.60	21	9.0	10.5	9.69	0.45
bill width, nostril	42	6.5	8.3	7.23	0.33	22	6.4	7.8	7.23	0.33
bill depth	41	9.8	11.4	10.54	0.35	21	9.6	11.4	10.49	0.43
tarsus	43	15.3	18.3	16.52	0.62	22	14.6	17.6	16.47	0.76
Michigan										
wing length, arc	177	80.	99.	88.01	4.14	129	77.	94.	85.22	3.79
wing length, chord	177	80.	98.	87.32	4.13	129	76.	93.	84.40	3.78
bill, nostril	177	10.8	17.1	13.76	1.42	128	10.6	16.3	13.41	1.38
bill, head	177	12.7	20.4	15.95	1.52	128	12.5	18.6	15.51	1.49
bill width, mandible	177	5.5	11.5	8.47	0.93	129	6.6	11.0	8.24	0.81
bill width, nostril	177	5.2	8.1	6.16	0.49	128	5.1	7.7	6.07	0.48
bill depth	177	7.4	11.0	8.83	0.71	125	6.8	10.2	8.69	0.23
tarsus	177	14.6	17.5	15.92	0.66	129	14.3	18.4	15.88	0.79
North Dakota: Grafton										
wing length, arc	10	89.	97.	94.10	2.08	7	89.	94.	91.86	1.86
wing length, chord	10	88.	96.	93.40	2.17	7	88.	94.	91.00	2.08
bill, nostril	10	15.	16.6	15.72	0.56	7	14.7	16.5	15.67	0.60
bill, head	10	17.4	19.1	18.09	0.52	7	17.0	18.6	17.90	0.56
bill width, mandible	10	8.7	9.6	9.22	0.23	7	7.8	9.8	8.87	0.66
bill width, nostril	10	6.4	7.3	6.69	0.27	7	6.4	7.2	6.74	0.28
bill depth	10	9.0	10.5	9.63	0.44	7	9.4	10.0	9.69	0.23
tarsus	10	16.2	17.8	16.86	0.62	7	15.7	16.7	16.33	0.35
Oregon: Fort Klamath										
wing length, arc	16	89.0	96.0	93.67	2.09	6	83.0	94.0	90.17	3.97
wing length, chord	16	89.0	95.0	92.88	2.09	6	83.0	93.0	89.67	3.72
bill, nostril	16	13.6	16.3	14.99	0.73	6	12.2	16.4	14.88	1.47
bill, head	16	16.0	18.9	17.28	0.84	6	15.8	17.9	16.97	0.79
bill width, mandible	16	7.7	9.8	8.56	0.51	6	7.6	9.5	8.18	0.67

TABLE 2 Continued

Character	Male					Female				
	<i>N</i>	min	max	mean	SD	<i>N</i>	min	max	mean	SD
bill width, nostril	16	5.9	7.2	6.55	0.37	6	5.8	6.7	6.32	0.32
bill depth	16	8.6	9.9	9.39	0.43	6	8.2	9.8	9.12	0.58
tarsus	16	14.8	17.6	16.27	0.73	6	15.7	16.5	16.10	0.34
Alaska										
wing length, arc	27	82.	88.	85.22	1.55	15	78.	88.	83.07	2.37
wing length, chord	27	82.	88.	84.63	1.60	15	78.	88.	82.60	2.32
bill, nostril	26	11.6	14.6	12.67	0.56	15	11.6	13.3	12.25	0.44
bill, head	26	13.6	17.3	14.86	0.72	15	12.9	15.6	14.27	0.63
bill width, mandible	27	5.5	9.6	7.68	1.30	15	5.3	9.4	7.42	1.56
bill width, nostril	27	5.2	8.4	6.34	1.07	15	5.2	7.8	6.69	0.97
bill depth	26	7.7	9.5	8.46	0.36	15	7.7	8.8	8.27	0.32
tarsus	27	14.6	16.8	15.49	0.64	15	14.2	16.1	15.01	0.65
British Columbia: coastal										
wing length, arc	36	82.	90.	85.50	2.16	20	79.	90.	83.60	3.10
wing length, chord	36	82.	89.	84.69	2.11	20	78.	90.	82.80	3.21
bill, nostril	34	11.9	14.7	12.96	0.72	21	11.2	15.	12.99	1.01
bill, head	34	13.7	17.2	15.01	0.88	21	13.2	17.4	15.00	1.01
bill width, mandible	36	5.5	10.0	8.01	1.24	21	5.6	9.7	8.01	1.02
bill width, nostril	36	5.4	7.7	6.29	0.73	21	5.1	8.2	6.05	0.83
bill depth	36	7.8	10.0	8.64	0.44	21	7.6	9.4	8.57	0.42
tarsus	36	14.3	18.0	15.56	0.75	21	14.7	16.4	15.67	0.53

Ontario: Algonquin National Park										
wing length, arc	33	82.	96.	87.21	3.84	21	79.	91.	84.76	3.36
wing length, chord	33	82.	95.	86.52	3.81	21	79.	91.	84.14	3.31
bill, nostril	33	11.9	16.5	13.34	1.27	21	11.5	16.2	13.04	1.26
bill, head	33	13.7	18.7	15.43	1.40	21	12.4	18.8	15.03	1.52
bill width, mandible	33	7.0	9.6	7.86	0.69	21	6.6	9.3	7.50	0.75
bill width, nostril	33	5.2	8.4	6.25	0.62	21	5.2	7.1	6.07	0.58
bill depth	33	7.9	9.8	8.62	0.55	21	7.8	9.9	8.41	0.65
tarsus	33	14.2	18.9	15.79	0.92	21	14.0	17.1	15.74	0.88
Idaho: Shoshone County										
wing length, arc	10	81.	87.	83.50	1.71	2	81.	85.	83.0	
wing length, chord	10	81.	86.	83.00	1.56	2	81.	84.	82.5	
bill, nostril	10	12.4	13.7	12.80	0.37	2	12.1	13.0	12.6	
bill, head	10	14.4	16.2	15.00	0.52	2	14.4	15.6	15.0	
bill width, mandible	10	6.8	8.0	7.51	0.42	2	7.0	7.8	7.4	
bill width, nostril	10	5.8	6.6	6.18	0.29	2	6.2	6.5	6.4	
bill depth	10	8.1	8.8	8.45	0.21	2	8.0	8.2	8.1	
tarsus	10	15.0	16.7	15.98	0.42	2	14.9	16.8	15.9	

<sup>a</sup> See Methods section for descriptions of measurement technique.

closely resembles Brehm's (1853) published illustration of *minor*, and van Rossem regarded it as the type. Because Brehm did not designate the specimen as a type at the time of his original description, however, it is not a holotype. Schumann and Koch also collected a second specimen, a female (Berlin Museum no. 6983) (van Rossem, 1934; G. Mauersberger, in litt.). Other birds known from the Brehm collection include three females with no locality more specific than "North America" (AMNH 457078, 457079, and 457053); the first two were collected in 1833 and 1842; the third is not dated. A. R. Phillips has written "cotypes" on the labels of the first two. Hartert (1918) reviewed the types in the Brehm collection and did not consider any of these to be nomenclatural types. Brehm may have had these before him for his review insofar as they are in female plumage and he referred in the plural to the plumage of females ("die Weibchen haben . . .") (Brehm, 1853). However, he also referred to males in the plural form ("Die alten Männchen . . ."), yet only one currently exists. The original description (Brehm, 1845) did not refer to females, and no series was explicitly indicated. He may have had available as syntypes both the specimens now in the Berlin Museum (van Rossem, 1934) and the specimens from the Brehm collection now at AMNH. Other Brehm specimens at the Museum Alexander Koenig in Bonn (cf. Niethammer, 1964a,b) do not include any North American *L. curvirostra* (S. Conrad, in litt.). Because "it cannot be determined that a nominal species-group taxon was established on a single specimen, and . . . a holotype was not designated, the first subsequent author to have published the inference . . . that one original specimen is the "holotype," or "the type," is deemed . . . to have designated a lectotype" (Code, 1985, Art. 74(b)). By describing and illustrating the Berlin specimen, van Rossem (1934) designated a lectotype: "it seems proper to designate adult male number 6982 as the type." Specimens Berlin 6983 and AMNH 457078, 457079, and 457053 may be paralectotypes (Code, 1985, Rec. 74F), but their status is uncertain. Neither Brehm (1845, 1846, 1853) nor Hartert (1918) mentioned them in their discussion of types.

#### COMPARISON OF THE TYPE SPECIMENS WITH CERTAIN NORTH AMERICAN POPULATIONS

##### *Loxia curvirostra pusilla* Gloger 1834

The type of *L. pusilla* was compared with birds of the southern Appalachian states, as historical evidence available to Stresemann

indicated that the specimen was taken in Georgia. The only known breeding specimens in Georgia were large-billed birds identified as *L. c. pusilla* by comparison with identified specimens at USNM (Sciple, 1952; Burleigh, 1958). The two birds taken in 1951 (UGA 895 and 896) were a male and a female. Bill lengths from the nostril were 15.7 and 16.0 mm, bill lengths from the head were 18.6 and 18.0 mm, and wing lengths (flat) were 97 and 95 mm, so the bills were similar to that of the type of *pusilla* but the wings were longer. These birds were singing, a male flew to a female and presented a straw, and the gonads were sufficiently large (testes 4 mm) to have sperm (cf. Tordoff and Dawson, 1965). Other breeding records of crossbills are known from the southern Appalachians (Virginia Society of Ornithology, 1979; Haggerty, 1982), but morphological details are lacking.

In a principal components comparison of the size and shape of male crossbills, the type of *pusilla* falls within the range of variation of birds from the southern Appalachian states. It falls outside the range of variation of birds from Newfoundland. The type of *pusilla* has a long bill, less deep and without the swollen base of specimens from Newfoundland (Tables 1, 2; Figs. 1-3). Its plumage is less deep red (more pink) than in most Newfoundland specimens (9B8, "red") though a close match ("orange-red," 8B7) to UMMZ 166116 from Princeton, Newfoundland. The type of *pusilla* is marginally outside the range of variation of birds from Lake Umbagog, Maine. It falls within the range of variation of birds from Michigan, of the type series of *benti* from North Dakota, and of the type series of *bendirei* from Oregon. It falls outside the range of variation of crossbills from Alaska and coastal British Columbia. The bill is less deep in birds from the southern Appalachians and from Maine than in birds from Newfoundland. When bill depth is plotted against bill length, little overlap is seen between Newfoundland birds and these other populations (Fig. 3). The type of *pusilla* has a bill that is proportionally less deep than in any Newfoundland bird and longer than in all but one bird in the Maine sample. The size and shape of the bill of the type fall outside the range of variation of that of birds from Maine and Newfoundland, but within the range of variation of that of the southern Appalachian birds. The results are consistent with it having been collected in Georgia as stated by Stresemann (1922).

Newfoundland crossbills were named *L. c. percna* by Bent in 1912. When van Rossem (1934) examined the type of *L. c. pusilla*, he regarded *percna* as a synonym of *pusilla*. He did not directly compare the type specimen of *pusilla* with specimens from Newfoundland, however. His opinion was followed by Griscom (1937), Paynter (1968),

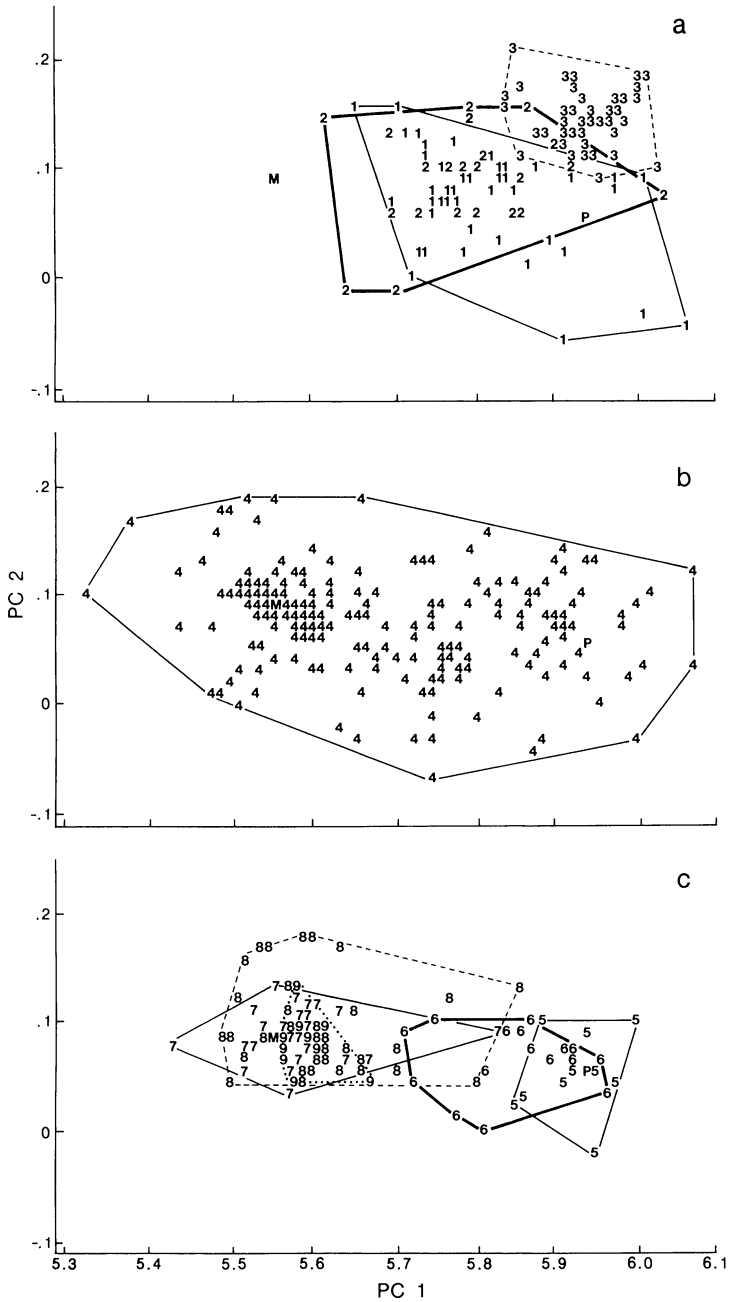


FIG. 2. Principal components analysis of morphological variation in adult male *Loxia curvirostra* in selected areas of North America. a: 1, Southern Appalachians (central →



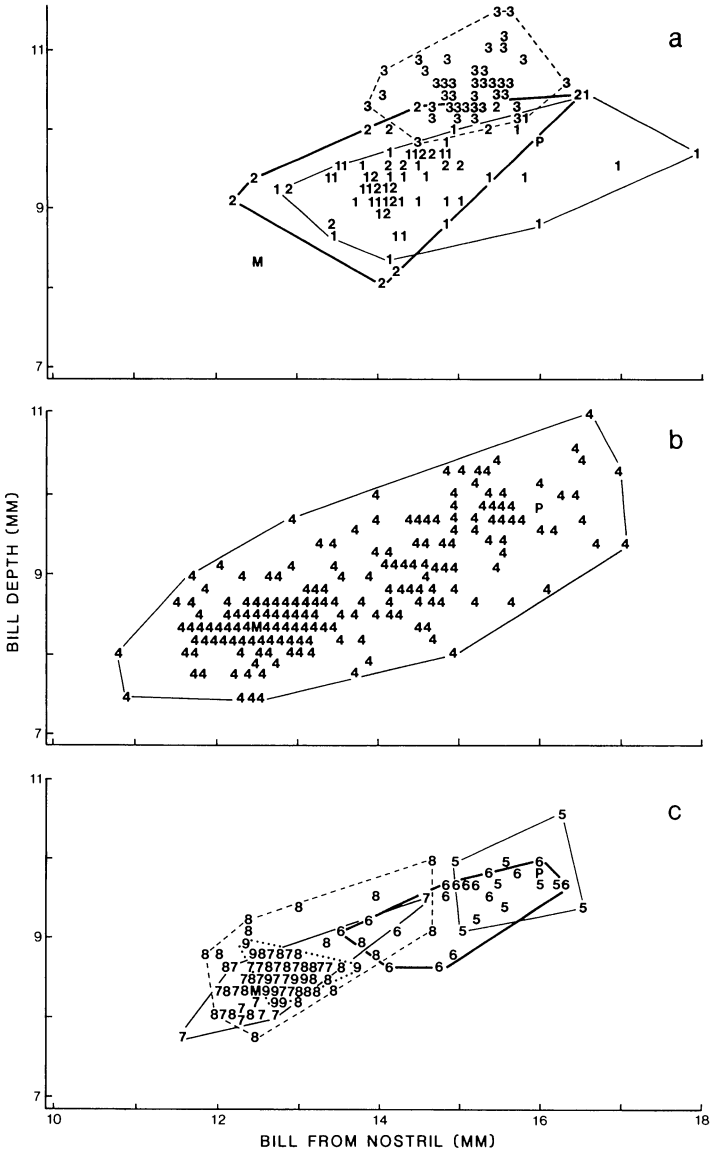


FIG. 3. Bill length (measured from nostril) and bill depth in adult male *Loxia curvirostra* in selected sample areas in North America. Symbols as in Fig. 2.

Virginia to Georgia); 2, Lake Umbagog, Maine; 3, Newfoundland. b: 4, Michigan. c: 5, Grafton, North Dakota; 6, Fort Klamath, Oregon; 7, Alaska; 8, coastal British Columbia (Queen Charlotte Islands, Vancouver Island, mouth of Oyster River); 9, Dismal Lake, Idaho. M, type specimen of *Crucirostra minor*. P, type specimen of *Loxia pusilla*.

and Austin (in Bent, 1968: 498), none of whom compared the specimens. Monson and Phillips (1981) realized that the birds of the southern Appalachians differed in male plumage color and were narrower-billed than the Newfoundland birds, and Phillips annotated many museum specimen labels accordingly. Most museum specimens differ in color; Newfoundland males are a darker "red" (9B8) whereas the large-billed males of the Appalachians are more "red-orange" (8B7). Some variation in plumage color may be due to seasonal wear and stain (months after the molt is completed the birds are often blackened from resin of the conifers on which the crossbills feed). The Newfoundland birds were collected mainly in summer, the Appalachian birds mainly in other seasons. Nevertheless, the observation that bill widths and depths are nearly all greater in the Newfoundland birds than in the birds of southern Appalachia (Tables 1, 2) indicates that *L. c. percna* is not a synonym of *L. c. pusilla*. On the basis of specimens available it is reasonable to recognize *L. c. percna* as distinct from *L. c. pusilla*.

Crossbills from southern Appalachia are heterogeneous in morphology and behavior. Groth (1984) discovered that large and medium-sized crossbills near Blacksburg in Montgomery County, Virginia, both bred there, mated assortatively, and had different call notes. In a preliminary attempt to determine whether the type of *pusilla* was associated with one of these two forms, I compared it with Groth's VTECH specimens collected in June and July 1983 in Virginia. The type of *pusilla* proved to be intermediate in size and unlike either of Groth's series in bill shape. At present it is not possible to determine with which of the Appalachian populations the type of *pusilla* is associated. For this reason it may not be appropriate to regard *bendirei* (or *benti*, or *neogaea*) as a synonym of *pusilla*. Resolution of this question awaits further analysis of the known breeding birds in the Appalachians.

#### *Loxia curvirostra minor* (Brehm 1845)

The type specimen of *L. minor* falls within the range of variation of crossbills taken in Michigan (Figs. 2, 3). The variation among crossbills in Michigan coincides with the range of variation among all populations considered in this study except Newfoundland (i.e., excluding those from southwestern United States and Mexico). The smaller birds (low values on PCI, which is determined by size, particularly bill length, Table 3) from Michigan are morphologically similar to the northwestern populations from Alaska and coastal

British Columbia, including the type series of *L. c. sitkensis* Grinnell 1909 from Admiralty Island, Alaska (Figs. 2, 3). The type of *minor* falls within this range of variation. On the other hand, the type of *minor* falls outside the observed variation among birds of (1) the southern Appalachian region, (2) Lake Umbagog, Maine, (3) Newfoundland, (5) Grafton, North Dakota, and (6) Fort Klamath, Oregon (Figs. 2, 3).

The five specimens available from the eastern thumb region of southeastern Michigan between Saginaw Bay and Lake St. Clair are small and resemble the type of *minor*. The five were collected between November 1950 and March 1951 in St. Clair and Lapeer counties; the three males had wing lengths (chord) of 87 mm, bill lengths from nostril of 11.8-12.5 mm, and small gonads (testes no larger than 2 mm). Small crossbills were numerous in the western Great Lakes region in that season (Dickerman, 1957). The locality, size, shape, and (for males) plumage color of these birds is similar to that of the type taken in January-March 1834 and may represent local invasion by the same population.

TABLE 3

CHARACTER SCORES AND CORRELATIONS OF MALE *Loxia curvirostra* IN A PRINCIPAL COMPONENTS ANALYSIS<sup>a,b</sup>

Character <sup>c</sup>	Loading			Correlation		
	PC1	PC2	PC3	PC1	PC2	PC3
wing length, arc	.24	.02	-.16	.83	.03	-.13
bill from nostril	.59	-.44	.04	.96	-.22	.02
bill from head	.58	-.29	.18	.97	-.14	.07
bill depth	.49	.85	.12	.88	.47	.05
tarsus	.15	.03	-.96	.55	.03	-.82

<sup>a</sup> Total cumulative variance, % PC1=84.1, PC2=91.7, PC3=96.5

<sup>b</sup> Correlation  $R_{\alpha.05} = 0.10$ ,  $R_{\alpha.01} = 0.13$

<sup>c</sup> Character values were transformed to natural logarithms for the PC scores. The correlation scores given are for the untransformed characters.

Griscom (1937) regarded *L. c. sitkensis* Grinnell 1909 as a synonym of *L. c. minor*. Although he did not examine the type of *minor*, he noted that the short bill as illustrated in Brehm (1853) resembled the short bills of crossbills of the northwestern coast of North America. Small-billed birds are seen in large numbers through much of North America only in occasional years. They are more regularly found in the northwest, and Griscom thought that the sporadic occurrences of small birds in the east resulted from long-distance movements from there.

Grinnell (1909) noted that plumage color of males from the Pacific northwest tended to be more orange (less red) than in eastern males. In fact, many small-billed eastern males have much yellow and orange in the plumage. This is seen not only in UMMZ specimens collected in northern Michigan and Ontario, but also in a series of captive crossbills captured in northern Michigan and Kansas by H. B. Tordoff and held alive for various periods before they were skinned. The longer the birds were held, the less reddish their plumage became, due to decreasing amounts of red carotenoids in feathers grown in captivity (KU and UMMZ series). \* Change in the color of growing feathers is also evident through late winter and early spring in Kansas birds. New feathers were yellowish, not reddish (Tordoff, 1952; KU series). It is well known that captive crossbills become yellow (Wilson, 1811; Völker, 1957; Phillips, 1977; UMMZ series). As plumage color of the developing feathers is so labile, the variation among geographic samples may be partly environmental rather than genetic in origin. The differences in plumage before and after molt in captivity can be considered a successful experimental test of this hypothesis. Phillips (1977) proposed that female Alaskan birds differ from other crossbills in having a narrow but distinct region of yellow on the throat and this was used as a field mark for the "Alaska form" in the National Geographic Society (1983) field guide. As pointed out by Monson and Phillips (1981), not all females in Alaska have yellow throats, and some females in other parts of the range have yellow throats. Throat color does not consistently differentiate females of Alaskan populations from any others.

As indicated also by Monson and Phillips (1981), it appears to be impossible to separate *L. c. sitkensis* Grinnell 1909 from *L. c. minor* (Brehm 1845). That is, *L. c. sitkensis* is a synonym of *L. c. minor*. Small crossbills occur with some regularity in certain areas of the boreal forests in eastern North America. Breeding specimens from the Huron Mountains, Marquette County, Michigan, in 1921 (a fledged juvenile with the bill not yet crossed, UMMZ 208831; two adults with no gonad size indication, UMMZ 208830, YALE 70433) and in 1941 (seven UMMZ adults, all with large gonads or large oviducts) were small-billed birds indistinguishable in size and plumage from birds of the Pacific northwest (Manville, 1941; Payne, 1983). Similar small birds were present in all other years when the species was collected there (specimens in Appendix). In certain other years in the 1960's, no crossbills were found (H. B. Tordoff, pers. comm.). Small crossbills have occurred over many years and bred in Marquette County, and small crossbills have been taken elsewhere in Michigan (Fig. 2), so it seems unlikely that the form is restricted in any biological sense to the

\*See Note Added in Proof, p. 33.

Pacific northwest. Crossbills taken in the winters of 1960-61 and 1972-73 along highway 60 in Algonquin National Park, Ontario and from a breeding population at Pimisi Bay, Ontario (Lawrence, 1949) are similar in size to these small Michigan birds.

Monson and Phillips (1981) described a new subspecies, *L. c. reai*, from a sample of crossbills collected at Dismal Lake, SE Avery, Shoshone County, Idaho. Most males were taken in molt and were mainly in greenish not reddish plumage. I include two specimens in about 20% juvenile plumage; these are no smaller than the others in the series. Two females were named as "types" (Monson and Phillips, 1981:228), so there is no holotype (Code, 1985: Articles 73, 74). I designate specimen AMR 3627, a male, as the lectotype: the label is annotated "paratype *reai*" by A. R. Phillips. The other 12 specimens from the same locality and taken in September 1971 are paralectotypes. The birds are morphologically indistinguishable from *L. c. minor* and fall within the range of variation in size and shape of birds from Alaska, coastal British Columbia, Michigan, and Ontario (Tables 1, 2; Figs. 2, 3). *L. c. reai* is a synonym of *L. c. minor*.

Griscom (1937) described *L. c. neogaea* as a new subspecies from Lake Umbagog, Maine. He considered these birds to represent the crossbill common in eastern North America, but he did not examine the type of *minor*. Peters (1943) and Mengel (1965) regarded *neogaea* as an unnecessary renaming of a well-known eastern population. Parkes (1954) stated that the photograph of the type of *minor* resembled the birds of the northeast in bill shape rather than birds of the northwest (he called these *sitkensis*). In measurements the type of *minor* does not fall within the range of variation of crossbills taken at Lake Umbagog (Fig. 2). The bill of the type of *minor* is smaller in all dimensions than that of most birds from Lake Umbagog (Tables 1, 2). It is also shorter and less deep in proportion than in any males in that sample (Fig. 3). It is unlikely that the type of *minor* came from the same population as the Lake Umbagog birds. These birds overlap considerably in size and bill shape with birds from the southern Appalachians. They also are not separable in size and shape from the type series of *L. c. bendirei* and *L. c. benti* (Figs. 2, 3) from western North America. All males in the type series of *benti* have a pale, rosy plumage—a characteristic emphasized by Griscom (1937) as differing from *bendirei*. The *benti* specimens were taken in fresh plumage in October; most *bendirei* were taken later in the year after molting but the birds closest in date are not consistently different in plumage color from the October birds in the type series of *benti*. In describing the form *neogaea*, Griscom admitted that birds in the type series from Maine were not morphologically

distinct from birds of the montane northwestern United States. Measurements suggest that *benti* and *neogaea* may not be distinguishable from *L. c. bendirei* and are synonyms of that form.

The type series of *L. c. bendirei* is variable but no more so than the type series of *benti* and *neogaea* (Table 2, Fig. 2), and I see no reason to suspect that more than one population is represented in the 1882-1883 series from Fort Klamath, Oregon. Confusion has surrounded the type of *L. c. bendirei*. Ridgway (1885) did not designate a holotype. Deignan (1961:624) designated two "cotypes" based on Ridgway's red specimen labels. Griscom (1937:108, 127) and Phillips (in Phillips et al., 1964:183) referred to the "lectotype" of *bendirei* but did not specify which specimen was so considered. I here designate the male, USNM 94881, as the lectotype. The other specimens are paralectotypes.

#### MOVEMENTS AND DISPERSAL OF CROSSBILLS IN NORTH AMERICA

Crossbills wander erratically. They are locally common in some areas in one year but are not seen in others, and they may be absent for several years in succession. Palearctic populations have been observed to move thousands of kilometers, and direct observations of moving flocks have been reported from strategically placed field observatories (Newton, 1970). Recoveries of crossbills banded in 1959 and 1963 in Switzerland were made in Spain in the following year, and in northern Russia in subsequent years; the distances involved were as great as 4000 km (Newton, 1970, 1973). Crossbills banded on the Baltic Sea, USSR, have been recovered as far as 1500 km south and southwest on the coast of the Mediterranean Sea (Paevskii, 1973). Crossbills may occur beyond their usual breeding range as rare winter visitors over a period of decades and then start to nest in these areas, as they have in Israel, where they have nested at progressively more southern localities since their arrival in 1972 (Ilani and Shalmon, 1984).

The evidence for movements in North America has been less direct. It is based mainly on the irregular seasons and years of occurrence of crossbills in any one area (Griscom, 1937; Bent, 1968). Crossbill movements are irruptive and associated with the abundance of the local seed crops of northern conifers (Bock and Lepthien, 1976). In autumn of certain years they appear hundreds of km southwards of any sightings in previous years, then remain for a winter or longer and sometimes breed. Different populations may move into the same areas in different years, or even in the same year, confounding attempts to understand variation in terms of the geographic subspecies concept.

Direct evidence for long-distance movement in North America is available in the banding recovery file of the Bird Banding Laboratory, U. S. Fish and Wildlife Service. Through March 1983, 76 recoveries of banded crossbills were reported. Ten involved movements between provinces and states (Table 4). The greatest distance moved was more than 2000 km. If these represent segments of movements of individual birds, then birds from western Canada may disperse more than 3000 km into the eastern United States. There are no banding recoveries from the Pacific northwest to the northeastern United States, however. None of the 76 recoveries involved birds of known site of birth, or were known breeding birds; all were banded as independent grown juveniles or adults. The banding recoveries do not indicate that movements from the northwest to eastern North America are more common than north-south movements from the boreal coniferous forests: few birds are banded in the northern forests.

#### VARIATION OF POPULATIONS IN SPACE AND TIME

The variation among crossbill populations in space is complicated by the episodic widescale movements of the populations in time. Certain areas retain their population identity across years of sampling, such as the thick-billed birds from Newfoundland, and to a lesser degree the small birds from Marquette County, Michigan, and the larger birds from southern Appalachia. Other samples were likely to have been from populations that generally breed in other areas. Crossbills taken in the winters of 1960, 1961, and 1963 near Ann Arbor, Washtenaw County, Michigan, (UMMZ) all had small gonads and resemble closely the type series of *benti* taken at Fargo, North Dakota, in 1930 (UMMZ). The number of birds sampled in any one locality is small (32 males were collected in the largest sample in Michigan, Marquette County) and usually these were taken over more than a year.

The local samples in Michigan with 10 or more males from a county or a year were subjected to analyses of variance (anova). County populations varied significantly, but so did birds in different years (Tables 5 and 6). The samples are too small to allow statistical comparison of variation among years within a single local area, or variation among areas within a year. It is not possible to compare the local variation with the annual variation that may represent influxes of different populations into Michigan. The variances among samples were unequal for most characters in which the means were unequal

TABLE 4  
BANDING RECOVERIES OF *Loxia curvirostra* BETWEEN STATES AND PROVINCES IN NORTH AMERICA

band no.	sex	age <sup>a</sup>	banding location <sup>a</sup>	banding date day-mo-yr	recovery location <sup>a</sup>	recovery date day-mo-yr	minimum distance travelled (km)
030160421	male	ad	ME 46.0°N, 68.4°W	31-03-67	NY 41.5°N, 73.5°W	01-04-70	657
003168051	male	-	MA 42.1°N, 71.4°W	12-05-32	MN 47.2°N, 94.5°W	09-04-34	2284
102106076	-	ad	NJ 40.3°N, 75.0°W	25-02-70	PA 40.0°N, 75.0°W	31-03-70	29
108153988	-	ad	PA 39.5°N, 75.1°W	31-01-70	NY 42.0°N, 73.5°W	05-70	287
022182821	male	ad	MN 46.4°N, 95.5°W	11-03-64	ND 46.5°N, 96.4°W	05-05-64	87
104152656	female	ad	MN 47.2°N, 94.5°W	11-03-70	ND 46.5°N, 96.4°W	16-06-70	196
027156761	male	ad	WI 42.4°N, 88.5°W	18-01-60	MI 43.2°N, 86.0°W	19-03-61	253
061198293	female	ad	ND 46.5°N, 96.4°W	10-02-64	MN 46.4°N, 95.5°W	12-03-64	29
101188857	-	-	ND 46.4°N, 100.4°W	09-11-69	BC 49.3°N, 117.3°W	10-71	1654
110144479	male	ad	MB 49.5°N, 97.0°W	16-01-73	MN 47.1°N, 95.3°W	26-02-73	169

<sup>a</sup> BC = British Columbia, MA = Massachusetts, MB = Manitoba, ME = Maine, MI = Michigan, MN = Minnesota, ND = North Dakota, NJ = New Jersey, NY = New York, PA = Pennsylvania, WI = Wisconsin, ad = adult.



among years. The inequality of variances cautions against interpreting the differences among counties as geographic variation and the differences among years as immigration of different populations. This unequal variance may be due to certain samples being single populations and others being mixes of two or more populations immigrating into Michigan. Different kinds of *L. curvirostra* may occur together in the same forests in winter. Near the University of Michigan Biological Station in Cheboygan County during the winter of 1950-1951, 21 specimens of two kinds of *L. curvirostra* were taken (DEL, UMBS, UMEM, UMMZ). The large birds were scattered in white pines (*Pinus strobus*) on a hill south of the station and the small birds flocked together and fed in hemlock (*Tsuga canadensis*) near Douglas Lake east of the station (R. S. Butsch, pers. comm.). Perhaps the birds from one flock sorted into different habitats depending on their bill size, or perhaps two populations invaded.

The occurrence of small birds from Marquette County over several years and the scarcity of large birds in the same years suggest that there may be a relatively regular breeding population of small crossbills in the boreal forest of the Upper Peninsula. The conifers of the Huron Mountains include hemlock (*Tsuga canadensis*) and pines (*P. strobus* and *P. resinosa*); hemlocks predominate (Hebard, 1929), but crossbills of the area feed on several kinds of conifers (Manville, 1941). Conifers of the Black River area in southeastern Michigan include tamarack (*Larix laricina*) (Shelton, 1970) and white pine (*Pinus strobus*); the crossbills taken in 1950 and 1951 were feeding on hemlock cones (UMMZ). The crossbills taken at the Huron Mountain Club, Marquette County, in 1960 and 1961 were all smaller in bill length than crossbills that I found feeding in a plantation of ponderosa pine (*P. ponderosa*) near Ann Arbor during the same two winters. Apparently certain populations that irrupt may occur in the same area (Michigan) as relatively regular local populations.

Variation within local collections may also involve birds from more than one population. Crossbills captured near Lawrence, Kansas, in the winter of 1951 mainly had long, thin bills and were identified as *L. c. benti*, but one had a different plumage color and a thicker bill and was identified as *L. c. stricklandi*. The odd bird had a call different from the others (Tordoff, 1954). These nonbreeding birds may have arrived independently from different breeding populations; their history was unknown. Groth's (1984) observation of social pairing of two kinds of crossbills that differed in call-types and morphology near Blacksburg, Virginia, at a time when both kinds were breeding locally, suggests two populations behaving as two distinct species. Without

TABLE 5  
ANALYSIS OF VARIANCE OF MALE *Loxia curvirostra*: COMPARISON OF MICHIGAN COUNTY  
SAMPLES WITH AT LEAST 10 MALES IN EACH COUNTY<sup>a</sup>

Character	N males	grand mean	equality of means		equality of variances	
			F-statistic	P	F-statistic	P
wing, arc	114	87.60	2.86	<.05	.79	ns
wing, chord	114	86.90	2.44	<.05	.68	ns
bill from nostril	114	13.56	2.70	<.05	.34	ns
bill from head	114	15.76	2.32	<.05	.19	ns
bill width, mandible	114	8.46	3.33	<.01	2.71	<.05
bill width, nostril	114	6.14	.93	ns	1.37	ns
tarsus	114	15.94	3.64	<.01	.50	ns
bill depth	114	8.81	1.33	ns	.82	ns

<sup>a</sup> Chippewa, Jackson, Kalamazoo, Marquette, Schoolcraft, and Washtenaw counties.

TABLE 6  
ANALYSIS OF VARIANCE OF MALE *Loxia curvirostra*: COMPARISON OF MICHIGAN YEAR  
SAMPLES WITH AT LEAST 10 MALES IN EACH YEAR<sup>a</sup>

Character	N males	grand mean	equality of means		equality of variances	
			F-statistic	P	F-statistic	P
wing, arc	76	87.70	4.83	<.01	4.34	<.01
wing, chord	76	86.12	5.17	<.01	4.21	<.01
bill from nostril	76	13.63	4.80	<.01	6.22	<.001
bill from head	76	15.78	2.93	<.05	5.97	<.001
bill width, mandible	76	8.39	1.06	ns	1.31	ns
bill width, nostril	76	6.09	3.04	<.05	4.14	<.01
tarsus	76	15.98	2.05	ns	.28	ns
bill depth	76	8.79	3.01	<.05	5.59	<.01

<sup>a</sup> 1883, 1941, 1950, 1951, and 1960.

biological data on breeding and behavior such as in these studies, it is not known whether a local sample represents a single population.

The relationships among crossbills are also obscure because of their "breeding seasons." In some areas (the Colorado Rocky Mountains), *L. curvirostra* breeds in all months (Bailey et al., 1953). In others, crossbills are more seasonal. After they arrive in early winter they may breed into the following spring, then disappear to higher latitudes or higher altitudes. In Minnesota, Michigan, and southern Ontario the breeding records are nearly all in winter and spring (Green and Janssen, 1975; Payne, 1983; Peck and James, 1986). Some crossbills have small gonads in winter (Washtenaw County, Michigan, in 1960, 1961, and 1963) while others breed in the same months (Marquette

County, Michigan, in 1941; Algonquin National Park and Rutherglen area, Ontario, in 1948 and 1973) (Manville, 1941; Lawrence, 1949; specimens in Appendix). Crossbills sometimes molt when they breed (Kemper, 1959; Newton, 1973), and in European populations the post-juvenile molt may be arrested before the adult plumage has completely grown (A.G. Knox, pers. comm.), so birds in partial juvenile plumage or in molt are not necessarily nonbreeding. Finally, juveniles in completely streaky brown plumage in Michigan may have gonads as large as breeding adults (UMMZ 155580) and birds in juvenile plumage in Maine have been seen to sing, incubate, and turn eggs in the nest (Tingley, 1984). It is unknown how long juveniles remain in their natal area. Lawrence (1949: 159) watched a mated pair, recognizable by their plumage, feeding at salt over several weeks during the nesting season, then reappearing with their fledged young, which begged and was fed by the pair. The young bird was nearly fully grown, its bill slightly crossed. The observation suggests that birds may not disperse while their young are still dependent on parental care and their bills have not yet crossed, and juvenile crossbills with uncrossed bills were probably born in the same area.

There is no evidence that crossbills in local populations are generally composed of different kinds of birds, though sometimes they are (Tordoff, 1954; Groth, 1984; R. S. Butsch observations). Crossbills are social and group together in flocks for much of their lives (Tordoff, 1954; Bent, 1968; Newton, 1970, 1973). It is unjustified to conclude simply on the basis of variable morphology within a sample that subspecies of crossbills live and may breed sympatrically as separate populations, as Griscom (1937), Kemper (1959), and Monson and Phillips (1981) have proposed. Griscom (1937: 109) stated that Bendire's sample from Fort Klamath consisted of three subspecies (*bendirei*, *benti*, *sitkensis*) even though the specimens are morphologically similar and were taken within a well-defined period (September 1882 to December 1883) (Figs. 2, 3). No specimens from Fort Klamath, Oregon, that I found were small-billed "*sitkensis*," and Griscom (1937:165-166) did not mention any in his account of Oregon specimens. Kemper (1959) identified two subspecies of crossbills in a single flock in Montana with both apparently breeding at the same time and place. His identifications were based on wing measurements compared with those in Griscom (1937). Kemper's table of the frequency distributions of wing lengths does not show bimodality, however. My examinations of Kemper's specimens (UMMZ, UMZM) indicate a single "kind" of crossbill in the sample. The variation described in a single breeding population may simply indicate an inadequacy of Griscom's account

of crossbill variation (Tordoff, 1952, and Parker, 1970, commented similarly on Griscom's analysis). Monson and Phillips (1981), describing a new subspecies *L. c. reai*, identified as such a crossbill from Manville's 1941 breeding population at the Huron Mountains, Marquette County, Michigan, taken within 0.5 km of other specimens that they (i.e., A. R. Phillips) identified as *minor* (and *sitkensis*). It appears unlikely in this instance that two forms bred sympatrically, for the sample is morphologically homogeneous by crossbill standards, and the type series of *reai* itself does not merit subspecific recognition. Other evidence of variability within local breeding populations includes a series of three crossbills taken in the Canadian Rocky Mountains north of Revelstoke, British Columbia, on 26 August and 1 September 1955 (Appendix). Both females had a brood patch, one (the larger, wing 90 mm, bill from nostril 14.8 mm) labelled *bendirei*, the other (wing 83 mm, bill from nostril 12.8 mm, ova about 4 mm) labelled *sitkensis* and taken with a small male (wing 85 mm, bill 12.6 mm, testes 5x4 mm). The record shows that large and small individual crossbills sometimes breed in the same time and place, but not necessarily that two distinct populations do so. Other records of large and small crossbills occurring together in the Rocky Mountains include those of Jollie (1953) in northern Idaho (near the type locality of *L. c. reai*) and Selander (1953) in northern Utah. The small crossbills were not noted to breed in either instance. Jollie noted that the large and the small crossbills lived in separate flocks in one locality. No other behavioral observations are available for the coexistence and lack of interbreeding of distinct populations in the Rockies.

In writing subspecies names on specimen labels in most North American museums, Phillips (like Griscom, 1937) has idiosyncratically distinguished among morphological extremes (including combinations of size, bill shape, and plumage color) within many samples of crossbills taken at one time and place. As these occur without apparent regard to geographic differences, it is not possible to say that different subspecies are involved. The situation differs from that of distinct subspecies migrating through an area at different times in a season as in certain other species; in these cases, the morphological forms are known to breed in different areas (Phillips et al., 1964).

## RETROSPECTIVE

The present study was limited mainly to a comparison of the types of *pusilla* and *minor* with other named types and type series taken in

areas where *pusilla* and *minor* may have been taken, or in areas where similar birds occur. A comprehensive revision of the relationships among populations of *Loxia curvirostra* is impractical at this time because of the lack of critical information for most museum specimens. The species is highly irruptive, with birds moving long distances partly on a seasonal basis and with irregular occurrence in many areas as breeding birds. Flocks sometimes move into the areas where other kinds of crossbills occur, and breeding outside the "usual" range of a population (and in the range of another population, if it is distinct) may take place after long-distance movements. Nearly all museum specimens in northern and eastern North America were nonbreeding. Even for the type specimens there is no assurance that the birds were breeding in the localities where they were collected. In general the small-billed *L. c. minor* are often found in most of the boreal forests and the larger-billed *L. c. bendirei* (?=*L. c. pusilla*) in the mountains of the east and west. Because crossbills sometimes undergo irruptive population movements over long distances and individuals from more than one breeding population may appear at the same time and place, the degree to which crossbill populations are distinct geographic races is uncertain. The present work is a prolegomenon to further studies. Field observations on breeding birds and experimental tests of behavior will be necessary before the nature of gene flow and population differentiation is understood in these birds.

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#### NOTE ADDED IN PROOF

The color of the new growing feathers of male crossbills varies with the time of molt, which may occur in nearly any season. Males tend to grow yellow feathers in late winter and spring, and red feathers in the autumn (Weber, 1953; Newton, 1973). The mechanism underlying the development of feather color may involve seasonal change in diet, as crossbills switch from feeding on old cones to new cones of the year at about the same time of year that the plumage again grows in red (Newton, 1973).

## APPENDIX

*Loxia curvirostra* SPECIMENS EXAMINED FROM NORTHERN AND EASTERN NORTH AMERICA

The following specimens were collected in areas in which named taxa of crossbills have been described or in known breeding populations east of the Rocky Mountains or north of 42°N latitude, or were otherwise mentioned in the text. The southwestern and Central American areas, where occur the forms *grinnelli*, *stricklandi*, *viridior*, and *mesamericana*, are not included. Calendar years are indicated, as different populations may be observed in different years depending on irregular movements.

## CANADA

ALBERTA: Cypress Hills 1945, NMC 30734-30741 (see also Rand, 1948, and Godfrey, 1950).

BRITISH COLUMBIA, coastal: Oyster River mouth 1934, CM 115950, 115959; Queen Charlotte Islands (including Graham Island and Langara Island) 1914, 1916, 1920, 1930, 1939, 1940, 1942, 1946, 1971, AMNH 761704, 761707-761709, 761712, 761714-761715, 803789-803790, FMNH 163447, 166291-166293, 166295-166296, 177771-177773, VPI 10143, UMMZ 166075-166085, 218039-218040; Vancouver Island (Comox, Merville) 1926, 1933, 1934, 1939, CM 115502-115503, 115563, 115578, 115600, 115875-115878, FMNH 163442-163446, 177762, 177766 (FMNH 163443, 11 September 1933, "brood patch bare"), UMMZ 166089-166090.

BRITISH COLUMBIA, inland: Lillooet District (Tattan Lake) 18 September 1939, ROM 90045, testes 5x3mm, "breeding patch;" Revelstoke 15 mi N, 1 September 1955, ROM 90070, female, "brood patch;" Revelstoke 17 mi N, 26 August 1955, ROM 90102, male, testes 5x4 mm, "brood patch," ROM 90035, female, ova about 4 mm, "brood patch" (all collected by J. A. Munro); Okanagan, 19 March 1918, CM (ex Cleveland Museum) uncataloged nestling collected F. S. Hersey; local adults collected in same year include AMNH 48811, 48813, 367829, 367831, 367834, CM (with Cleveland Museum registrations) 47496, 48036-48038, UMMZ 166091, 166135-166136; Okanagan, 1 March 1921, FMNH 177774, female, "egg in oviduct." Okanagan, 23 January 1897, MCZ 47872, male with testes ca. 6.8 mm, further suggests a prolonged breeding season.

NEWFOUNDLAND: Badger 1942, 1947, 1954, USNM 318741-318742, 318744-318745, 393462, 396106, 594047; Bay Bulls 1947, USNM 393754; Bay of Islands 1894, MCZ 191134, 191138, 191140-191142 (191134 and 191138, 16 May 1894, juveniles with bills short but crossed); Deer Pond 1894, MCZ 191134-191136; Doyles 1959, NMC 46023, 46025, 46027, 46029, 46043-46050, 46052, ROM 94956; Exploits Bay 1890, MCZ 191131-191132; Flatbay River 1912, type series of *L. c. percna*, 18-21 July, AMNH 761746, 761750-761751, MCZ 258829, USNM 233930; Fox Is. River 1912, AMNH 132882, 761748-761749, MCZ 258830; Grand Lake 1917, 1918, 1919, MCZ 258831-258834; Hobbly Hills 1915, MCZ 25720, 25721; Nicholville, 1915, MCZ 25723-25724; Placentia 1890, MCZ 191133; Princeton 1942, UMMZ 166116, USNM 381743, 381747; Rocky Brook 1894, MCZ 191137; Salmonier 1949, NMC 36042-36046; South Brook 1949, NMC 36040; St. Georges 1946, USNM 393312-

393314; Stephenville 1913, AMNH 761752-761755 (all on 26 June 1913, 761752 juvenile, bill not crossed; 761755 juvenile, bill crossed but short); Tomkins 1945, 1946, 1959, USNM 381750, 393318-393319, 393321, NMC 46032, 46034, 46041-46042, ROM 94957-94958. Juveniles taken from May to July; later months' young are molting to adult plumage.

ONTARIO: Algonquin National Park 1960, 1961, 1967, 1972, 1973, NMC 58794-58830, 59176-59190; Rutherglen 1948, NMC 34533, ROM 75250 (13 March and 27 February, both had large testes, 7x5 mm and 3.5 mm, in a breeding population, killed on road, see Lawrence, 1949).

QUEBEC (breeding specimens only): Riviere Eastmain, 3 June 1983, NMC 80402, 80409, male with testes 4x3, female ovary 5x4 mm; Riviere Obinaco, 7 June 1983, NMC 80397, 80401, male with testes 5x4 mm; Temiscamie 35 km N, 21 May 1983, juvenile, bill short and barely crossed.

SASKATCHEWAN: Cypress Hills 1939, 1948, ROM 33117-33120, NMC 33634-33637, 33639-33640, 33643-33645, 33647, 33649-33650, 33652, 33656 (33644, 5 June 1948, juvenile, bill crossed but short) (Godfrey, 1950, mentions singing); Fond-du-Lac 1945, ROM 72418-72426 (15 July 1945, family group, 72418 male, 72420 female, 72421 and 72422 juveniles with bill short and not crossed, a few days out of nest; 16 July 1945, family group, 72426 male, 72425 female, 72423 and 72424 juveniles with bill short but crossed at tip; see also Houston, 1960).

#### UNITED STATES

ALASKA: Admiralty Islands (Mole Harbor, Windfall Harbor, Killisnoo) 1907, MVZ 469, 470, 472-484 (MVZ 480 juvenile bill short, barely crossed; MVZ 484 bill short, not crossed), type series of *L. c. sitkensis*; Prince of Wales Island 1920, FMNH 177755; Seward 1919, AMNH 761739; Sitka 1894, 1896, 1919, CAS 47771, MVZ 34450, 34451, AMNH 761723-761727, 761729-761731, 761733-761735, 761737-761738; Wrangell Island 1946, CAS 60549-60560 (CAS 60559, 30 March 1946, female, "ovary 5 mm, had recently laid eggs, brood patch well developed"), other breeding records from February to April and in late summer (Willet, 1921; Swarth, 1922; Gabrielson and Lincoln, 1959).

GEORGIA: "Georgia," November, 1823, Berlin 6982 (type of *pusilla*); Camden County (Griffins Neck) 1907, USNM 565948 (juvenile but bill crossed); DeKalb County (Stone Mt.) 24 February and 10 March 1951, UGA 895-896, USNM 419171-419172, nestbuilding seen, two males had testes 4 mm and 5 mm; 28 March 1956, UGA 4137-4139, male testes 3x2 mm and singing but both females with ova less than 1 mm; Liberty County (Midway) 1846, 1850, USNM 32400, 10535.

IDAHO: Dismal Lake, Shoshone County, 4 September 1971, type series of *L. c. reai*, NMC 78910, "oviduct rather large, evidently used! Belly bare, not very thick," two accessioned 1980407, male molting from juvenile to adult plumage, testes 5.8x4.5 mm; female no notes on breeding condition. Other specimens same series DEL 39868, 39887; AMR (in SDMNH) 3624-3628, 3630-3633.

MAINE: Lake Umbagog, July 1885-March 1886, AMNH 29800-29803, 29805, 83106, 83115, 83157, 298114, 367752, MCZ 10948, 11082-11083, 11086, 11108-11109, 11113, 11118, 11122, 11206, 11208, 11209, 11225, 11228, 11230, 11234, 211094, 211112, 211117, 295983, 295988, 295992 (the above series includes some of Brewster's collection numbers where no separate MCZ numbers were written on the labels), USNM 122281-122283, 151880. Some specimens were taken from breeding populations; see Brewster (1937).

MICHIGAN: Alcona County (Glennie 8 mi NW) 1947, DEL 49925; Alger County (Au Train, Grand Marais 11 mi S, Shingleton 2 mi W, Laughing Whitefish River) 1947, 1968,

1985, DEL 49925, UMMZ 114682-114683, 214118, 207623-207624, 207628, 207629; Antrim County (Elk Rapids) 1954, CMU 62.169; Charlevoix County (Petoskey) 1876, GRPM 23171; Cheboygan County (Burt Lake, Douglas Lake, Indian River) 1950, 1951, 1959, CMU 59.36, DEL 49923-49924, UMBS 1681-1683, 1685, UMEM 735-737, 744, 746, UMMZ 119641-119649, 119748; Chippewa County (Caribou Lane, Eckerman, Goetzville, Hulbert, Paradise, Sault Ste. Marie, Sugar Island, Vermillion, Whitefish Point) 1914, 1925, 1937, 1951, 1960, 1968, 1984, 1985, CMU 68.95, 68325, MSU 2984, UMMZ 46245, 55433, 91347, 91373, 91375, 119747, 207581-207585, 214119-214120, KNC unnumbered; Crawford County (Lovells) 1930, 1961, CMU 61.49, UMMZ 65975; Delta County (Escanaba) 1883, USNM 106627-106629, 163872; Emmet County (Cecil Bay, Wilderness State Park) 1947, UMBS 1372-1375; Genesee County (Brent Creek, Flushing) 1888, 1889, 1891, AMNH 99842, FMNH 309766, 309793, MCZ 99842, MVZ 34432-34433, ROM 20581, 20583, USNM 441880-441881; Gogebic County (Ironwood, Little Girls Point) 1932, 1940, UMMZ 69412-69413, 104893-104896, 106734-106737, 113874-113875, 115588; Grand Traverse County (East Bay Twp.) 1960, 1961, CMU 60126, 61244, 61.1, 61.2, 61308, 62377, 62379, 67.22; Houghton County (McLain Park) 1950, MTECH 711; Iron County (Iron Mt.) 1888, 1889, MSU 1171-1176; Isabella County (Clare 17 mi W) 1975, CMU 76.24, 76.27, 77.06; Jackson County (Jackson, Norrell Twp., Waterloo) 1888, 1892, 1923, 1925, DEL 9521, 9523, MCZ 40843, MVZ 11623-11625, UMBS 848, UMMZ 91097, 131957-131958, 166111-166115; Kalamazoo County (Kalamazoo, Kellogg Biological Station, Todds on M43, Wintergreen Lake) 1879, 1883, 1885, 1888, 1941, 1951, 1954, KCS 349, UMBS 1287-1288, UMEM 745, UMMZ 106327-106335, 110727, 119423-119424, 119984-119989, 119992-119993; Kent County (Grand Rapids) 1861, 1878, 1883, 1897, GRPM 23172, 28262, MCZ 5274, MSU 1162-1164, 1167-1168; Lapeer County 1951, UMMZ 134173, 151562-151564; Livingston County (Unadilla) 1896, UMMZ 38581-38582; Luce County (McMillan, Newberry) 1932, 1940, CM 55275-55276, UMMZ 68573-68574; Mackinac County (St. Ignace) 1985, UMMZ 207626; Marquette County (Big Bay, Huron Mts., Marquette, Pine River mouth) 1887, 1920, 1921, 1922, 1923, 1924, 1925, 1928, 1936, 1941, 1948, 1950, 1960, 1961, CAS 35827-35830, DEL 49916-49926, FMNH 97701-97702, KCS 1131-1132, MSU 7572, UMEM 1158-1159, UMMZ 83383-83384, 110719-110725 (UMMZ 110721, 30 January 1941, female, ova 5.2 mm; 110722, 4 February 1941, female, ova 9.0 mm; 110725, 9 February 1941, female, ova 2.7 mm; four males 28 January to 9 February 1941, testes 2.6, 3.4, 3.8, 4.2 mm measured from drawings on labels, differ from published approximations of Manville, 1941), 155579-155594, 156262-156264, 156288, 208824-208834 (see p. 000 for breeding details), YALE 70433; Oakland County (Birmingham) 1961, CMU 66210; Ontonagon County (Carp River, Ontonagon) 1904, 1921, MCZ 258837, UMMZ 224571-224572; Oscoda County (Luzerne, Mio, Red Oak) 1948, UMMZ 116257-116261, 116263-116264, 116278-116283 (UMMZ 116280, 15 June 1948, juvenile with short bill barely crossed; birds with testes 4-6 mm in length in February, March, and June); Presque Isle County (North Allis, T33N R8W) 1982, 1985, CMU 82.26, 82.33-82.35, UMMZ 207625, 207627; Roscommon County (Eddy Bros. Camp) 1889, YALE 3621, 3997, 23263; Sanilac County (Black River) 1834, Berlin 6982, type of *C. minor*; Schoolcraft County (Creighton, Cusino, Manistique, Seney, Shingleton, T47N R16W, Walsh) 1938, 1939, 1940, 1941, 1959, 1960, 1976, 1982, 1984, CMU 80.98, KCS 81, 1112-1116, 1118, 1124, MTECH 745, UMMZ 93920-93925, 130139-131043, 155601-155602, 166094-166110, 205492, 207586-207588, 224573; St. Clair County (Burtchville Twp.) 1950, UMMZ 119425; Washtenaw County (Ann Arbor, Ypsilanti) 1883, 1885, 1960, 1961, 1963, AMNH 19627, 113298, UMMZ 1004a, 119425, 155168-155175, 155595-155596, 156232, 156289, 156645, 157419, 159335-159338, 166118-166125; Wexford County (Cadillac) 1968, CMU 68.33, 68.40-68.41, 68161-68162.

MONTANA: Lake County, Yellow Bay, 1954, UMMZ 155658-155663, UMZM 4323, 4328, 4330, 4332-4335, 4337-4339.

NEW JERSEY: Burlington County (Quaker Bridge) 21 June 1963, adult male accompanying two juveniles with bills somewhat crossed but short, UMMZ 159778, 159779, 159863 (see Murray, 1972).

NORTH CAROLINA: Asheville 1889, MCZ 28304-28305; Buncomb County (Weaverville) 1887, MCZ 219692-219693; Great Smoky Mts. (Mt. Guyot, Three Forks) 1931, USNM 301779, 378234, UMMZ 166134; Mitchell County 1886, AMNH 83158; Mt. Mitchell 1930, 1932, UMMZ 166131-166133, USNM 301776-301778, 338119, 379142, 339854; Raleigh 1887, 1967, MCZ 13836 (5 June 1887, juvenile, bill crossed but short), USNM 565197 (6 May 1967, juvenile, bill barely crossed, some primaries in sheath, "age ca 5 weeks" H. B. Tordoff), USNM 565198-565199 (male and female adults, same day, taken with the juvenile).

NORTH DAKOTA: Grafton 2-8 October 1931, type series of *L. c. bentii*, UMMZ 68332-68348.

OREGON: Fort Klamath 7 September 1882 to 11 December 1883, all but three birds 5 December 1882 to 8 February 1883, types series of *L. c. bendirei*, USNM 94873-94894.

SOUTH CAROLINA: Charleston 1887, 1888, MCZ 13760-13766, 13768-13770, 18822; Chester 1887, AMNH 55392-55393; McPhersonville 1887, MCZ 258841, USNM 115432-115435, 115437-115444; Yemassee 1888, MCZ 14240.

SOUTH DAKOTA: Pennington County (Rapid City, Spring Creek Canyon) 1971, 1974, 1975, 1977, 1978, 1983, USNM 573578, 574894, 575373, 575755, 576032-576035, 576060-576064, 576072-576073, 576960, 577137, 599158, 599651-599654 (several juveniles with bills short but crossed at the tips, and adults with enlarged gonads).

TENNESSEE: Carter County (Road Mountain) 1886, AMNH 83159; Great Smoky Mtns. 1889, UMMZ 38583; Sullivan County (S of Bristol) 1965, LSU 82372.

VIRGINIA: Montgomery County (Blacksburg), 1983, JGG (in VTECH) K1, K2, K3, K4, 47, 54, 55, 56, 88, 125, 126, L5=112, 50=017, 51=018 (part of a series of adults of known call type taken with free-flying juveniles; some females with brood patch or enlarged ova, and several of known mates, Groth, 1984).





