

VOCALIZATIONS AND MORPHOLOGY
OF THE RED CROSSBILL (Loxia curvirostra L.)
IN THE SOUTHERN APPALACHIANS

by
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(ABSTRACT)

Two distinct forms of Red Crossbill (Loxia curvirostra) bred sympatrically in the southern Appalachians in 1983. The forms differed significantly in vocalizations and bill and body size, and the members of each of 20 male-female pairs were of the same size class. One of the forms from Virginia has been tape recorded in western North America in 1983 and in previous years, showing that vocal classes are not local dialects. Evidence presented here suggests that forms of Red Crossbill are not subspecies as is currently recognized, and that they behave as biological sibling species.

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INTRODUCTION

Red Crossbills (Loxia curvirostra) have several characteristics that are unusual among birds. Their asymmetrical bill structure is thought to be a specialization for feeding on conifer seeds. Because cone crops fluctuate, the birds are inconsistent in their distribution and breed in most areas on an irregular basis (Bent 1968, Lawrence 1949, Newton 1973). The details of the breeding biology are equally unusual. Although photoperiod may affect gonadal size (Tordoff and Dawson 1965), nesting has been observed in all months (McCabe and McCabe 1933, Bailey et al. 1953, Newton 1973) largely because the young can be raised on a diet of seeds (Bailey et al. 1953, Bent 1968, Newton 1973). Birds in streaked juvenile plumage may be capable of breeding (McCabe and McCabe 1933, Phillips 1977), and crossbills sometimes nest during molt (Newton 1973).

Because of this irregular breeding schedule, specimens of Red Crossbills taken in spring and summer cannot always be considered local breeders, limiting the usefulness of museum skins in systematic studies. The problem becomes more complicated in that more than one distinct size class may breed in the same area in North America (Griscom 1937,

Phillips 1981), and there are other examples of co-occurrence of more than one size class (Jollie 1953, Kemper 1959, Howell 1972). Thus, the morphological, temporal, and geographical data which systematists have long used in determining the subspecific status of specimens are not always concordant in North American Red Crossbills. There are now twelve subspecific names proposed for the Red Crossbill in North America: pusilla Gloger, 1834; minor (Brehm), 1853; stricklandi Ridgway, 1853; bendirei Ridgway, 1884; sitkensis Grinnell, 1909; percna Bent, 1912; neogaea Griscom, 1937; mesamericana Griscom, 1937; grinnelli Griscom, 1937; benti Griscom, 1937; reai Phillips, 1981; and vividior Phillips, 1981. The nomenclature has never been widely agreed upon (Griscom 1937, A.O.U. 1957, Phillips 1981).

The persistence of variation in bill and body size among populations of the Red Crossbill (see Griscom 1937, Phillips 1981) is puzzling because the potential for gene flow should be very large. It is thought that few other North American birds show so little fidelity to their natal area for breeding. One would expect that continental Red Crossbills would be monotypic, or nearly so, as are their close relatives, the White-winged Crossbill (Loxia leucoptera) and Pine Siskin (Carduelis pinus) (Bent 1968,

Mayr and Short 1970). This paradox has not been explained, nor have the mechanisms for maintenance of bill and body size variation in North American Red Crossbills been explored, although Phillips (1981) suggested that size classes may be reproductively isolated.

Little is known of variation in vocalizations of North American Red Crossbills. It may be difficult to demonstrate the existence of dialects or other patterns of geographic variation (Lemon 1975, Baker 1982, Mundinger 1982) in the Red Crossbill since it cannot be assumed, as for most passerines, that its populations are geographically fixed. Despite this difficulty, I introduce here a means of analysis that incorporates both morphological and vocal data in an approach to the problem of crossbill systematics.

METHODS

I observed, tape recorded and captured Red Crossbills in the southern Appalachians from January, 1983, through December, 1983. Most of the fieldwork was done in the Jefferson National Forest of southwestern Virginia near Blacksburg along a series of SW-NE ridges of approximately 800 m elevation. The habitat near Blacksburg is of mixed conifer and hardwoods, with pines listed in decreasing order of abundance: table mountain pine (Pinus pungens), pitch pine (P. rigida), Virginia pine (P. virginiana), and eastern white pine (P. strobus), but none were seen foraging on hemlock (Tsuga spp.) although it is common in the area. In early 1983, an average crop of cones of all conifer species was available in the forests near Blacksburg, but later in the year the white pine cone crop failed. Additional fieldwork was done in Highlands, North Carolina (elev. 1300 m), during October and November, 1983. White pine is the dominant conifer at Highlands, and in the late summer and autumn of 1983 it produced a large cone crop which attracted a number of Red Crossbills. No fieldwork was conducted in the spruce-fir forests at higher elevations.

An average of 25 h was spent weekly in the field throughout 1983. Few crossbills were found near Blacksburg in January through early February and from August through November, with the birds being most easily found in March through July. None of the birds appeared to be territorial or nesting, but the presence of dependent juveniles and females with old brood patches indicated that crossbills bred somewhere in the Appalachians in late winter and spring of 1983. Not one of the early summer crossbills was molting. Juveniles, molting immatures, and molting adults were very common at Highlands in the autumn of 1983.

Birds were captured using mist nets and caged live decoys (Adkisson 1975). Caged birds usually vocalized when crossbills or other cardueline finches flew over the trapping area. At least 60% of the wild crossbills seen at trapping stations were captured in 1983. This included 130 near Blacksburg and 53 at Highlands. I recorded the vocalizations of many of the birds before capture, and, where possible, mate associations were recorded.

Birds were classified as juveniles (in the streaked juvenal plumage and not yet into the postjuvenal molt), immatures (in the process of postjuvenal molt or possessing some traces of streaked plumage), or adults (no traces of

streaked plumage). Sex was determined by the descriptions of Phillips (1977). The samples included 66 adult males, 48 adult females, 35 immatures, and 34 juveniles. As birds were captured they were assigned a number, the first being 001.

Field and laboratory recordings were made with a Uher 4000 Report IC tape recorder with a Uher M 139 microphone mounted in a Sony PBR-330 parabola at a tape speed of 9.5 cms. Recordings were analyzed with a Kay Elemetrics Sonagraph model 7029A at the wide band (300 Hz) setting at the 160-16000 Hz frequency range.

Within 48 h of capture, each individual was placed outdoors in a small cage and its flight call was recorded. The flight call is the most frequent vocalization in the repertoire of wild Red Crossbills and the call most easily elicited from caged birds. Flight calls were often delivered at a fast rate (up to 6 per sec), making it possible to obtain samples of hundreds of notes from a single bird in a short time, although individuals varied greatly in their delivery rate. At least 15 flight call notes were obtained from 173 individuals. In most cases, however, the number of call notes exceeded 50. Nine birds were juveniles which gave only begging calls, and one bird

died before recording. Three juveniles gave both begging calls and adult calls, and 22 juveniles gave only adult calls during the recording sessions. Some of the birds were kept for extended periods to obtain additional recordings, but most were banded and released. Additionally, I obtained tape recordings of Red Crossbills from Arizona, California, Colorado, Illinois, Indiana, Maine, New Mexico, New York, North Dakota, South Dakota, Tennessee, and Utah (see Appendix A).

Visual inspection of sonograms showed that variation in the flight call of an individual is much less than the variation among individuals (see Fig. 1). Accordingly, one well-recorded call note from each individual was selected for data used in statistical analyses. The data consisted of ten separate measurements from each note made directly from the sonograms (Fig. 2): HI, highest frequency of the main component; LO, lowest frequency of the main component; FR, frequency range of the main component; FE, the frequency of greatest energy concentration; ICL, the length (mm) of the initial component; MCD, main component duration; DCD, downward component duration; A1, the angle through the high-energy part of the note; A2, the angle through the highest and lowest parts of the note; and EC, ending component score. Frequency measurements were made to the nearest 0.1

kHz, duration measurements were taken to the nearest 0.1 mm (converted to msec after statistical computations), angles were measured to the nearest 1°, and EC was scored on a scale ranging from 0 (no ending component) to 5 (large ending component).

Since classification of individuals on the basis of vocalizations was an important step in this study, a call note classification that did not assume group membership was necessary. This requirement was met by principal component analysis (PCA) since it can be used as an ordination procedure which allows one to examine the range of variation in a multidimensional space and to divide observations into groups (Blackith and Reyment 1971, Sparling and Williams 1978). PCA also identifies those features of the data which are most effective in group discrimination by examination of the variable loadings on those principal components along which the groups are segregated. Only the data for the 114 adults were used in the PCA, since some young birds were more variable than adults in their flight call structure.

To reduce the amount of irrelevant variation and avoid singular dispersion matrices, five of the original ten variables were not used in the analysis: A2 was omitted because of its dependency on the relationship of FR and DCD;

MCD was omitted because of its dependency on the values of ICL and DCD; and the three absolute frequency measures (HI, FF, LO) were omitted because there was generally little variation among the individuals in absolute frequency. The five remaining variables (FR, ICL, DCD, A1, EC) are all measures of call note shape that are independent of one another. Some variation in call note structure was not included in the analysis, such as other angles within the call note, fine structural artifacts, and amplitude modulation within a note, because of a lack of reliable means for measuring this variation. Since the variables used in the PCA were not measured in the same units, the principal components were derived from a correlation matrix which standardizes each variable with a variance of 1.0. The PCA computer program used was the SAS PROC PRINCOMP (SAS Institute, Inc., 1982). After grouping, univariate and multivariate statistics were used to assess the features of flight calls that were most effective in distinguishing among call types.

Within 24 h of capture the following morphological characters were measured: live body weight (WT) to the nearest 0.1 g (Blacksburg birds) or 0.5 g (Highlands birds), usually after the bird had defecated and before it had eaten: unflattened wing (WG); tarsus length (TR) from the

posterior surface of the tibiotarsus to the last undivided scale on the tarsometatarsus; upper mandible length (LU) from the anterior edge of the nostril to the tip; lower mandible length (LL) from the midline juncture of the lateral rami to the tip; total bill depth (BD) in a line perpendicular to the nostrils with the mandibles totally occluded; upper mandible depth (DU) in a line through the nostril; upper mandible width (WU) at the anterior edge of the nostrils; and lower mandible width (WL) at its widest point where the skin meets the two rami. Length measurements were made with dial calipers to the nearest 0.1 mm.

Resulting vocal classes (call types) obtained from the PCA classification were compared in morphology using univariate and multivariate statistics. Mean, standard deviation (SD), range, and coefficient of variability (CV) for each variable, and performed an ANOVA between call types. In addition, the coefficient of difference (CD) (Mayr, et al. 1953) was used for comparisons among groups. Because no single measurement was a good indicator of overall bill size (see Tables 9 through 14 for correlation matrices), an index of total bill size was obtained where:

$$\text{Bill Size Index (BSI)} = (\text{BD}) \left(\frac{\text{WU} + \text{WL}}{2} \right) \left(\frac{\text{LU} + \text{LL}}{2} \right)$$

As the bill is roughly conical, BSI is closely proportional to bill volume.

A discriminant function analysis (DFA) was used to determine the probability of classifying individuals to call type on a purely morphological basis. The discriminant analysis chosen was the SPSS method=DIRECT (Nie et al. 1975) which considers all of the variables simultaneously. This program computes unstandardized discriminant function coefficients for each variable with values relative to its contribution to group discrimination, as well as correlation coefficients for each variable and the discriminant function. Separate discriminant functions were derived for males and females because of significant sexual dimorphism in some traits. Plumage color was excluded from the analysis.

RESULTS AND DISCUSSION

Vocal Variation

Flight calls of Red Crossbills are loud, discrete vocalizations given in flight and in long distance calling bouts. They are by far the most frequently used vocalization in the repertoire of both sexes. All individuals in this study gave simple calls that modulated downward in frequency. Flight calls conform well to the theory that vocalizations used over long distances tend to be discrete (Morton 1982), and are in the same range of frequencies reported in long range communication for the Red-winged Blackbird (Brenowitz 1982). Individuals are remarkably consistent in their delivery of a call note of a particular structure, and each individual had its own recognizable signature call (see Fig. 1). One individual (bird 024, an adult female) alternated between two different flight calls, but one of these calls was unlike that of any other bird I heard or recorded, being modulated up in frequency. Her other primary call was used in the statistical analysis.

The correlation matrix used to derive the principal components of interindividual flight call note variation among the 114 adults is presented in Table 1. The strongest correlation is an inverse one between ICL and DCD at -0.801 . DCD is also negatively correlated with each of the other variables, indicating that birds with shorter downward components also tend to have greater frequency ranges, longer initial components, steeper angles, and stronger ending components. These inverse relationships provide most of the basis for the first principal component (PC1), which accounts for 46.3% of the total measured variation (see Table 2). All other correlations between variables are positive. A1 is by far the variable with the highest loading on the PC2 vector, with a value of 0.95.

An ordination of the data points for the first two principal components of the variation in call note shape is presented in Figure 3. The principal components can be interpreted easily since they can be described as functions of relatively few variables, and plotting the call notes as data points aids in visual examination of the ordination. Birds that are similar in the measured variables of note shape tend to fall near one another in the ordination, although 34.3% of the measured variation and all of the unmeasured variation in call note structure is not accounted for by the first two principal components.

In general, adults with high values for ICL, EC, and FR, and low values for DCD have higher values for PC1, and fall to the right on the ordination. Birds with higher values of A1, that is, birds with steeper angles, fall near the top of the ordination, while birds that give call notes in which the main sound energy is more horizontal (purer on tone) are near the bottom. There are two major clouds of points in the ordination, separated largely along PC1, with the cloud on the left more concentrated (less variable in the measured characters) than the cloud on the right. The cloud on the right, designated Call Type 1, contains the call notes of 30 males and 27 females. Call Type 2, the cloud on the left, has the call notes of 36 males and 21 females.

There was no significant sexual dimorphism in call note structure within a call type. Univariate statistics comparing the two call types with sexes pooled for all ten measured variables are shown in Table 3. Call types 1 and 2 differ significantly in nine of the ten measured variables at values of $P < .001$. A1 did not significantly differ between call types ($P = .11$), but Call Type 1 had a greater range in this character (see Table 4 for a comparison of variabilities). In addition there is no overlap between the

call types in the variable A2, and the ranges of DCD only barely overlap. The main difference between the call types is in call duration (providing a basis for the difference that I have learned to distinguish in the field). No birds in Call Type 2 possessed an initial component, while the size of the initial component of Type 1 birds varied considerably, with only two Type 1 birds lacking an initial component (see Fig. 8, pair A). The large range of overlap between call types in FR, A1, and EC, as well as in absolute frequency measures, indicates that durational differences and presence or absence of an initial component are the most important distinguishing features. Idealized call notes for both call types are reconstructed in Fig. 4 using the mean values for each of the ten measured variables. Rectilinear measurements are shown here to be adequate for quantifying the relevant variation, although grid overlay techniques (Miller 1979) or digitization (Field 1976) would probably retain more of the fine structural peculiarities in a call note which is likely to be important at the level of individual variation.

Two other calls in Red Crossbills were discrete and produced by the birds often enough for systematic comparison. The "toop" (using the terminology of Nethersole-Thompson (1975) for a similar vocalization in the

Scottish Crossbill), differs strikingly between the two call types (Fig. 5). Type 1 toops consist of single chevron-shaped notes at approximately 3.0 kHz with usually weak or no overlying harmonics. Type 2 birds give toops with two distinct elements, one at approximately 4.0 kHz and the other at 2.2 kHz. The toops of the two forms are quite easily distinguished by human listeners. I was not able to record the toops of each individual since tooping seems to occur only under conditions of social excitement, such as at the meeting of non-flockmates or after a bout of gaping or threatening. In my experience, birds of known flight call always gave only their own call type's stereotyped toop. The observed spectrographic structures and behavioral contexts of the toops of both call types conform well to the motivational-structural rules of Morton (1982) for "barking" calls.

The "alarm calls" of the two call types were different and could be recognized by ear. Type 1 birds give a higher pitched alarm note (approx. 2.8 kHz) very pure in tone, while Type 2 birds give a lower-pitched (approx. 2.1 kHz) note which is chevron-shaped (Fig. 6). Although Type 2 alarm calls superficially resemble to Type 1 toops, but the two kinds of calls were given in different contexts and Type 2 alarm calls were approximately 0.9 kHz lower in pitch than

Type 1 toops. Alarm calls for North American Red Crossbills have been described previously by Lawrence (1949) as "lu-lu-lu" and by Tordoff (1954) as "tuck-tuck-tuck". It is possible that these two observers were describing alarm calls of crossbill populations with different call characteristics. In my observations, no bird of known flight call ever gave the "wrong" alarm call.

Songs of the two call types are similar in the sense that they are long and consist of many discrete phrases. However, the structure of the notes and phrases within the songs of the two call types are dramatically different, without much interindividual variation within a call type (Groth unpubl. data). Because of the discreteness of the song phrases in crossbills, the cataloging of song phrases of the call types should prove useful, but due to the complexity of song in crossbills it not considered here. Red Crossbills also have other categories of calls (Groth unpubl. data).

Considering that captive adult cardueline finches have been shown to have vocal imitative (Mundinger 1970, 1979) it might be expected that some individual crossbills would give both call types, but none were encountered. Captive individuals generally do not imitate during months of

contact with birds of differing call type or differing flight call structure of the same call type (Groth and Adkisson, unpubl. data).

Morphological Variation

Females were significantly smaller ($p < 0.05$) than males in some measurements, so the sexes were considered separately. Univariate statistics comparing the two call types in each of the nine morphological characters is shown in Table 5 (males) and Table 6 (females). There is some overlap in the distributions of the call types, although differences in means for all nine variables are significant ($P < 0.00001$) for both sexes. The coefficients of difference (CD's) in bill and body size are approximately equal to, or beyond the level of, the conventional subspecific difference of 1.28 (Mayr et al. 1953). Both forms are about equally variable in the morphometric characters (Table 7).

Calculation of the bill size indices (BSI's) of the individuals, and comparison of the distributions of the two call types produced non-overlapping distributions between call types of a given sex (Tables 5 and 6). The largest-billed Type 1 males only barely overlap the smallest-billed Type 2 females using this index. Interestingly, the two call types are adjacent in this respect, and together they completely cover an entire range of bill sizes.

A discriminant function analysis of all nine of the measurements produced an even greater degree of difference between the call types than univariate or BSI comparisons (Fig. 7). All of the variables were positively correlated with the discriminant functions (Table 8), indicating that the functions are measures of overall size. The two discriminant functions (one for each sex) differed somewhat in their coefficients, but in general, bill size measurements had larger discriminant function coefficients and correlated more highly with the discriminant function vectors than did tarsus, wing, or body weight for both sexes. This, combined with the CD values (Tables 5 and 6), indicates that the difference between these two call types is slightly greater for bill size than for body size.

Males of yellow, orange, mottled, and all-red plumage coloration were found in each call type. Plumage colors of females of both call types varied from grayish-olive to bright yellow-green on the head and rump, and some had traces of orange on the rump, head, or flanks. Much of this variation could be due to diet (Brush and Power 1976). In addition, red males in fresh plumage appeared to be pinker than the more scarlet males found in spring and summer, indicating that feather wear contributes further to the variation. These results show that color is not a reliable systematic character in Red Crossbills.

Patterns of Mating.

Male-female pairs on the basis of field observations and the phenomenon of call matching in mated pairs of other cardueline finches (see Mundinger 1970, Marler and Mundinger 1975, Samson 1978). A total of 20 such pairs were identified. Twelve pairs were travelling together with no other adult crossbills (Fig. 8), and the eight other pairs were captured together but were associated with other adults (Fig. 9). As pairs were captured they were assigned a letter (the first being A, birds 005 and 006). Pair T was associated with a juvenile and a molting immature, and all four closely matched in flight call structure.

The BSI's of all 20 pairs are strongly correlated ($r = .83$, $p = 0.0001$) (see Figure 10). A similar analysis using discriminant function scores for the 20 pairs, which takes into account body weight, wing, and tarsus length, shows an even stronger correlation ($r = .90$, $p = 0.0001$). There was no significant correlation in either BSI or DF scores within only the Type 1 pairs ($n=8$) or the Type 2 pairs ($n=12$), although the largest male was paired with the largest female for each call type. It is not known whether crossbills visually assess one another as has been shown in mating Darwin's finches (Ratcliffe and Grant 1983) or whether vocalizations or other behavioral factors are involved.

In the Carduelinae, both members of a pair put a large investment into raising the young. Typically the male provides all or almost all of the food for the incubating female and later divides the responsibility of feeding the young with the female (Newton 1972). Thus, mate selection could be crucial for both sexes. In crossbills, there could be immediate and long-term adversity in matings across size classes. In the short term, it is possible that a pair of mixed bill size could have different conifer preferences and foraging efficiencies, making their integration as a foraging unit less than optimal; and, if bill size is coded for by many genes, their progeny would have bills intermediate in size and might not fit into an established size class system. In the evolutionary sense, matings across size classes would cause the size class phenomenon to break down, perhaps lessening the effective range of niche-space available to crossbills.

Taxonomic Considerations

In this study, analyses of vocal and morphological data lead to the same conclusion regarding the population structure of the Red Crossbills in the southern Appalachians in 1983; namely, that the entire sample is composed of two distinct groups. One group has larger bill and body size, and the two size classes differ in vocalizations. This evidence supports splitting of the Red Crossbill into biological units, but unlike previous systematic studies of crossbills, the taxonomic divisions envisioned here are not arbitrarily drawn on the basis of morphology or geographic locality. I will discuss separately four generally recognized categories for taxa at the near species level to which these groups might most appropriately be assigned: 1) morphs, 2) populations, 3) subspecies or semispecies, and 4) species.

Are size classes morphs? If size classes exist as a polymorphism in bill size, as has been suggested for the Hook-billed Kite (Chondrohierax uncinatus) (Smith and Temple 1982), we should not expect morphs to have different vocalizations unless vocal variation is genetically linked to bill size variation. In color morphs of the Common Bushtit (Psaltriparus minimus) (Raitt 1967) and the Brown

Jay (Cyanocorax morio) (Selander 1959), morphs have similar vocalizations. It would be expected that there should be at least some pairing between males and females of different morphs; however, no mixed pairs were observed in this study. Clearly the forms described here are not morphs.

Are call types different populations? Actual nesting areas were not discovered in this study. Thus, it might be argued that the two call types are dialects of different local populations in the southern Appalachians which happened to mix only after juveniles were fledged. If this was the case, these dialects should not exist in distant localities. Recordings made by others in Arizona, California, Colorado, Illinois, Indiana, New Mexico, New York, North Dakota, and South Dakota match Call Type 2 from Virginia, indicating that call types are not dialects, and that the taxa are not populations in the usual sense. The recorded calls from the Great Smoky Mountains of Tennessee match those of Type 1. I have knowledge of two additional call types: one in Maine which matches the upward modulated alternate call of bird 024; the other recorded in Utah (1970) and Colorado (1983). The number of call types in North America is unknown. These two call types cannot be considered dialect populations because of the significant size difference and the broad geographic range of Call Type 2.

Are call types subspecies or semispecies? According to Mayr (1970), both subspecies and semispecies are defined on the basis of geography, with semispecies (=allospecies) being geographically isolated species of a superspecies complex. Since the two forms described here were found in same place which is at the periphery of the total range of Red Crossbills, neither term is appropriate. However, using currently available descriptive literature, these two groups would be classified as subspecies; yet, despite the many subspecies names available, no separate subspecies has been described that represents this corner of the total range.

Call Type 1 falls within the range of Phillips' (1977, 1981) "Class II" and matches Griscom's (1937) neogaea. According to the A.O.U. (1957) the subspecies in the East should be called minor, but I have seen the type specimen of minor and it is smaller than any birds examined in this study. In my opinion the type specimen of pusilla, (which possibly came from Georgia in 1823 according to van Rossem, cited in Griscom 1937) is approximately intermediate between Call Types 1 and 2. Call Type 2 matches Phillips' (1977, 1981) "Class III", and the type specimens of bendirei and benti (which I have examined), and possibly also grinnelli, fall within the size range of Type 2. Newfoundland birds, termed pusilla (Griscom 1937 and A.O.U. 1957) which I have

examined in the U.S. National Museum (including the type of percna) have short, deep bills and are clearly unlike either call type examined here and unlike the type of pusilla. Because of this nomenclatural confusion, it is not certain which names best fit either call type.

Are call types of Red Crossbill biological species? If there is no gene flow between forms of Red Crossbill they are best termed sibling species, which are defined by Mayr (1970) as biological species that are difficult to distinguish from one another. There are several studies in which field work showing differences in vocalizations, combined with comparisons of morphology of vocal classes, have led to the elucidation of species limits within avian sibling species complexes. Examples include work on parasitic indigobirds (Vidua) (Payne 1973), Empidonax flycatchers (Kellogg and Stein 1953, Stein 1963), and Myiarchus flycatchers (Lanyon 1978). In other cases in which sibling species were already known by slight morphological differences, vocalizations have been shown to differ, as in Empidonax flycatchers (Johnson 1963, 1980), Catharus thrushes (Raitt and Hardy 1970), Cassidix grackles (Selander and Giller 1961), and Aechmophorus grebes (Nuechterlein 1981). In Europe, there is considerable overlap in measurements between the Common Crossbill (L.

curvirostra) and the Scottish Crossbill (L. scotica) (Knox 1975, 1976). Although once considered conspecific, these two forms have bred sympatrically in at least ten of the past eleven years (Knox in litt.), and their vocalizations have been shown to be different (Nethersole-Thompson 1975). They are now considered to be separate species (Voous 1978). These studies show the usefulness of the integration of both morphological and vocal data in studies at the near-species level, without which the status of the taxa involved would be more obscure.

According to Lack (1971), closely related sympatric species should exhibit ecological differences that allow their coexistence. Because the two call types found here differ in bill size, an interesting question is whether this corresponds to an ecological difference. During late May and June, when the greatest numbers of the birds were found, pine cones were generally without seeds and crossbills were foraging on other items including insects, tree flowers, leaf buds, and the seeds of serviceberry (Amelanchier sp.). I once observed a Type 1 female forage on serviceberry for 20 min and feed the regurgitated seeds to two begging young. The exception during this period was table mountain pine, which has large, spiked, serotinous cones and generally has a few seeds available throughout the year. In every case

where the call type of the crossbills foraging on table mountain pine was identified, it was Type 2. In Highlands, North Carolina, white pine was almost the only available conifer, and it had a good crop of cones in late summer of 1983. White pine cones have thinner and more flexible cone scales than other available local species, and this monotypic cone crop attracted practically only Type 1, the smaller billed form. Only 1 of the 53 birds captured in Highlands (an immature male) was of Type 2, and no other Type 2 birds were heard or recorded there. This evidence weakly supports the view that there may be some partitioning of available conifers by crossbill size class, although it is likely that there is some ecological overlap. Further work is needed on ecological relationships among the call types of Red Crossbills and the conifers on which they feed.

Because of the unusual shape of the beak, the genus Loxia is a good example of ecological specialization. Further evidence for specialization at an even finer level is that sedentary crossbills, such as the Scottish crossbill (L. scotica) and races of the Common Crossbill (L. c. guillemardi, L. c. balearica, L. c. meridionalis, L. c. luzonensis, and L. c. himalayensis) as well as the Haitian race of the White-winged Crossbill (L. leucoptera megaplaga) have beaks distinct in shape and/or size from their nearest

counterparts, perhaps indicating adaptation to local conifers. In addition, the degree of ecological specialization among crossbills may not only be a specialization on conifer cones, but sympatric species of crossbill in Europe may divide the available conifers (Lack 1944, 1971). If, as according to Futuyma (1979), ecologically specialized species should show a tendency toward speciation and should respond to different environmental conditions by genetic change, and considering the wide range of conifer cone types, crossbills may be in the position to undergo speciation. Ecological isolation is not the cause of speciation, but is essential after species formation and is a logical consequence of competition between differently-adapted species (Lack 1971). In sympatry, it may be possible that call types are subjecting themselves to the forces of character displacement in both vocal patterns (see Miller 1982) and morphology. Additional studies are needed on the extent of actual genetic divergence between Red Crossbill call types and the amount of gene flow between them, if any.

Flight calls are known to be used in species (Newton 1972), and individual (Mundinger 1970, Marler and Mundinger 1975, Samson 1978) recognition in cardueline finches, and also possibly population or subspecies recognition in Pine

Grosbeaks (*Pinicola enucleator*) (Adkisson 1981). In addition, incubating female crossbills call only in response to the calls of their mates and not to the calls of other crossbills (Lawrence 1949, Nethersole-Thompson 1975). As the flight call is relatively invariable within individuals, and since individuals differ to a measurable degree, and since male-female pairs share a flight call structure, it is highly likely that this vocalization is used by Red Crossbills in individual recognition. Thus, if birds can discriminate at this fine level, it is also probable that they have the ability to perceive call type differences described in this paper. Since vocal and morphological data sets are concordant, calls in Red Crossbills could convey information regarding approximate morphological state, such as bill size. An ecological implication is that call types could facilitate flocking of like-sounding birds with bills of approximately the same size. It may be adaptive for an individual crossbill to associate more closely with its own call type and size class if the latter have different foraging efficiencies and conifer preferences.

I propose that the two forms of Red Crossbill described here are biological species. That size classes are reproductively isolated solves the paradox of observed morphological variation in North American Red Crossbills.

Previous taxonomic confusion and inability of previous revisors to satisfactorily divide the Red Crossbill into subspecies is explained by the fact that taxonomic units of Red Crossbill are not subspecies. Vocalizations are probably the most important isolating mechanisms in the Red Crossbill complex.

SUMMARY

The vocalizations and morphology of Red Crossbills (Loxia curvirostra) were studied in the southern Appalachians in 1983. A total of 183 Red Crossbills were captured during the year, including 66 adult males, 48 adult females, 34 juveniles, and 35 immatures undergoing postjuvinal molt.

Each individual was tape recorded for the flight call, and one representative call note from each individual was measured for ten characters directly on the sonograms. Two groups were resolved out of the entire sample using principal component analysis (PCA) as an ordination and classificatory procedure based on the shape of call notes. Each individual was also measured for nine morphometric characters. Using data from adults, comparisons between groups differing in call note shape (call types) were compared in morphology revealed significant differences in bill and body size with little overlap between call types in univariate measures. A direct discriminant function analysis (DEA) using nine morphometric characters was able to classify correctly 100% of the individuals to call type on the basis of morphology, suggesting genetic distinctiveness of the groups. Other vocalizations were also found to differ between the call types.

Evidence for positive assortative mating between the two call types is provided on the basis of 20 male-female pairs that were identified as pairs on the basis of behavioral observations. Each of the pairs contained members of the same size class, indicating that the two call types may be reproductively isolated. The possibility that call types of Red Crossbill are sibling species is considered.

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Table 1. Correlation matrix of the five variables of flight call note shape used to derive the principal components.

	FR	ICL	DCD	A1	EC
ICL	0.327	-----			
DCD	-0.263	-0.801	-----		
A1	0.094	0.061	-0.236	-----	
EC	0.318	0.358	-0.357	0.154	-----

Table 2. Variable loadings and contributions to total measured variance for the five principal components of flight call note shape.

variable	Variable loading				
	PC1	PC2	PC3	PC4	PC5
FR	0.371	-0.075	0.722	-0.575	-0.071
ICL	0.564	-0.286	-0.327	-0.095	0.696
DCD	-0.569	0.064	0.424	0.071	0.698
A1	0.204	0.950	-0.103	-0.141	0.156
EC	0.422	0.074	0.425	0.797	-0.002
Cumulative Measured Variance	46.3%	65.7%	83.1%	96.5%	100%

Table 3. Comparisons of the univariate statistics of the measurements from the flight call notes of the 114 adults of Call Types 1 and 2.

var	Type 1 (n=57)			Type 2 (n=57)		
	mean	SD	range	mean	SD	range
FR	3.19	0.34	2.4-4.1	2.89	0.37	2.2-3.7 ¹
HI	5.12	0.33	4.6-6.0	4.60	0.29	4.1-5.6 ¹
FF	3.72	0.23	3.2-4.2	3.58	0.18	3.1-4.1 ¹
LO	1.92	0.26	1.1-2.3	1.74	0.29	1.3-2.6 ¹
ICL	9.51	3.70	0 - 17	0.00	0.00	0 - 0 ¹
DCD	31.83	3.28	26 - 39	48.45	4.29	39 - 59 ¹
MCD	37.16	3.54	31 - 44	48.45	4.29	39 - 59 ¹
A1	36.14	15.25	3 - 69	32.46	8.48	9 - 47 ²
A2	66.37	3.22	61 - 74	53.71	2.62	48 - 60 ¹
EC	1.47	1.02	0 - 5	0.68	0.66	0 - 2 ¹

¹Significant; $P < 0.001$.

²Not significant; $P = .11$.

Table 4. Coefficients of variability (CV's) for the measured variables of flight call note structure.

Coefficients of variability (CV's)		
var	Type 1 (n=57)	Type 2 (n=57)
DCD	10.31	8.85
MCD	9.54	8.85
ICL	38.90	0.00
A1	42.20	26.12
A2	4.85	4.87
FR	10.61	12.00
HI	6.43	6.22
LO	13.56	16.82
FF	6.00	5.16
EC	69.18	96.31

Table 5. Univariate morphological statistics on adult males.

var	Type 1 (n=30)			Type 2 (n=36)			C.D.
	mean	sd	range	mean	SD	range	
WT	30.36	1.94	25.8-34.5	32.89	1.74	29.0-35.6	0.688
WG	89.17	2.15	83.8-93.0	93.36	2.10	89.5-97.5	0.986
TR	19.24	0.56	18.0-20.4	20.12	0.56	18.8-21.3	0.786
LU	14.39	0.63	13.3-15.6	16.06	0.53	14.9-17.4	1.440
LL	11.37	0.59	10.5-12.9	12.49	0.52	11.5-13.5	1.009
BD	8.80	0.26	8.3- 9.4	9.58	0.25	9.2-10.0	1.529
DU	5.08	0.13	4.8- 5.4	5.51	0.15	5.2- 5.8	1.536
WU	6.47	0.25	6.0- 7.0	7.15	0.27	6.7- 7.8	1.308
WL	9.83	0.31	9.1-10.4	10.83	0.33	10.2-11.6	1.563
BSI	925	72	794-1053	1232	76	1126-1394	2.074

Table 6. Univariate morphological statistics on adult females.

var	Type 1 (n=27)			Type 2 (n=21)			C.D.
	mean	sd	range	mean	SD	range	
WT	29.01	2.01	24.5-32.5	32.56	1.88	30.2-36.2	0.915
WG	86.64	2.21	82.1-90.3	89.96	1.66	85.8-92.2	0.858
TR	18.92	0.60	17.3-20.3	20.07	0.66	18.0-21.0	0.913
LU	14.20	0.49	13.5-15.0	15.46	0.48	14.6-16.3	1.299
LL	11.16	0.46	10.3-12.4	12.10	0.47	11.3-13.2	1.011
BD	8.74	0.23	8.4- 9.2	9.40	0.27	8.8- 9.9	1.320
DU	5.07	0.11	4.8- 5.3	5.44	0.17	5.1- 5.7	1.321
WU	6.43	0.19	6.0- 6.8	7.15	0.20	6.8- 7.6	1.846
WL	9.80	0.28	9.3-10.3	10.67	0.36	9.8-11.5	1.359
BSI	899	49	802-1033	1156	72	1035-1259	2.124

Table 7. Coefficients of variability in the morphological measurements of the 114 adults.

Coefficients of Variability (CV's)						
var	Males			Females		
	Entire Sample (n=66)	Type 1 (n=30)	Type 2 (n=36)	Entire Sample (n=48)	Type 1 (n=27)	Type 2 (n=21)
WT	7.00	6.40	5.32	8.60	6.93	5.76
WG	3.26	2.41	2.25	2.92	2.55	1.85
TR	3.62	2.94	2.79	4.35	3.16	3.28
LL	6.56	5.15	4.17	5.66	4.08	3.92
LU	6.34	4.38	3.32	5.38	3.44	5.08
BD	5.08	2.99	2.64	4.59	2.60	2.86
DU	5.82	2.59	2.81	4.43	2.12	3.16
WU	6.17	3.80	3.58	6.07	2.78	2.82
WL	5.75	3.19	3.07	5.27	2.85	3.37
BSI	15.58	7.74	6.17	14.00	5.44	6.19

Table 8. Multivariate statistics for the two (male and female) discriminant functions. Unstandardized discriminant function coefficients and correlation coefficients are presented for each variable.

var	Males (n=66)		Females (n=48)	
	D.F.C.	Corr.	D.F.C.	Corr.
WT	-0.076	0.294	-0.066	0.344
WG	0.192	0.422	0.192	0.314
TR	0.039	0.336	0.251	0.347
UML	0.631	0.615	0.386	0.493
LML	0.117	0.437	0.018	0.379
BD	0.830	0.649	0.471	0.512
DU	1.268	0.624	0.517	0.504
WU	0.487	0.578	3.332	0.725
WL	1.328	0.660	1.347	0.526
(constant)	-58.494		-68.865	

Table 9. Correlation matrix of the morphological data for the entire sample (n=66) of adult males.

	WT	WG	TR	LU	LL	BD	DU	WU	WL
WG	.52	---							
TR	.63	.58	---						
LU	.57	.61	.61	---					
LL	.54	.60	.62	.82	---				
BD	.66	.56	.63	.79	.67	---			
DU	.67	.58	.62	.77	.64	.95	---		
WU	.59	.63	.59	.78	.60	.85	.83	---	
WL	.53	.60	.58	.73	.65	.83	.81	.75	---
BSI	.65	.65	.67	.91	.82	.94	.91	.88	.89

Table 10. Correlation matrix of the morphological data for the sample of adult males of Call Type 1 (n=30).

	WT	WG	TR	LU	LL	BD	DU	WU	WL
WG	.27	---							
TR	.32	.29	---						
LU	.17	.09	.34	---					
LL	.32	.41	.53	.66	---				
BD	.34	.01	.24	.33	.17	---			
DU	.15	-.07	.13	.22	.13	.84	---		
WU	.29	.22	.38	.36	.27	.67	.58	---	
WL	.13	.30	.19	.20	.10	.40	.35	.29	---
BSI	.37	.26	.48	.76	.64	.77	.63	.72	.54

Table 11. Correlation matrix of the morphological data for the sample of adult males of Call Type 2 (n=36).

	WT	WG	TR	LU	LL	BD	DU	WU	WL
WG	.15	---							
TR	.54	.21	---						
LU	.27	.06	.09	---					
LL	.12	-.02	.11	.46	---				
BD	.46	-.17	.28	.23	.19	---			
DU	.65	.01	.30	.30	.10	.85	---		
WU	.26	.08	.06	.35	-.16	.43	.40	---	
WL	.10	-.23	.07	.06	.13	.46	.40	.17	---
BSI	.41	-.11	.21	.64	.52	.80	.71	.53	.60

Table 12. Correlation matrix of the morphological data for the entire sample (n=48) of adult females.

	WT	WG	TR	LU	LL	BD	DU	WU	WL
WG	.64	---							
TR	.67	.54	---						
LU	.58	.63	.56	---					
LL	.53	.66	.45	.74	---				
BD	.66	.54	.64	.74	.66	---			
DU	.64	.48	.63	.76	.61	.91	---		
WU	.68	.53	.70	.75	.66	.80	.80	---	
WL	.61	.51	.51	.70	.67	.73	.75	.75	---
BSI	.70	.64	.65	.89	.83	.92	.89	.89	.87

Table 13. Correlation matrix of the morphological data for the sample of adult females of Call Type 1 (n=27).

	WT	WG	TR	LU	LL	BD	DU	WU	WL
WG	.36	---							
TR	.41	.17	---						
LU	.18	.32	-.06	---					
LL	.01	.57	-.27	.41	---				
BD	.23	-.03	.17	.16	.10	---			
DU	.06	-.20	.00	.20	-.14	.65	---		
WU	.39	-.19	.22	.03	.03	.28	.15	---	
WL	.07	.01	-.11	.25	.11	.11	.25	.28	---
BSI	.28	.25	-.02	.65	.56	.66	.44	.45	.54

Table 14. Correlation matrix of the morphological data for the sample of adult females of Call Type 2 (n=21).

	WT	WG	TR	LU	LL	BD	DU	WU	WL
WG	.35	---							
TR	.36	.19	---						
LU	-.01	.14	.15	---					
LL	.20	.04	.14	.40	---				
BD	.27	.13	.25	.42	.32	---			
DU	.35	.03	.32	.44	.25	.84	---		
WU	.06	-.05	.32	.29	.15	.32	.43	---	
WL	.23	-.09	-.08	.04	.33	.28	.30	-.30	---
BSI	.25	.07	.23	.65	.67	.81	.75	.44	.55

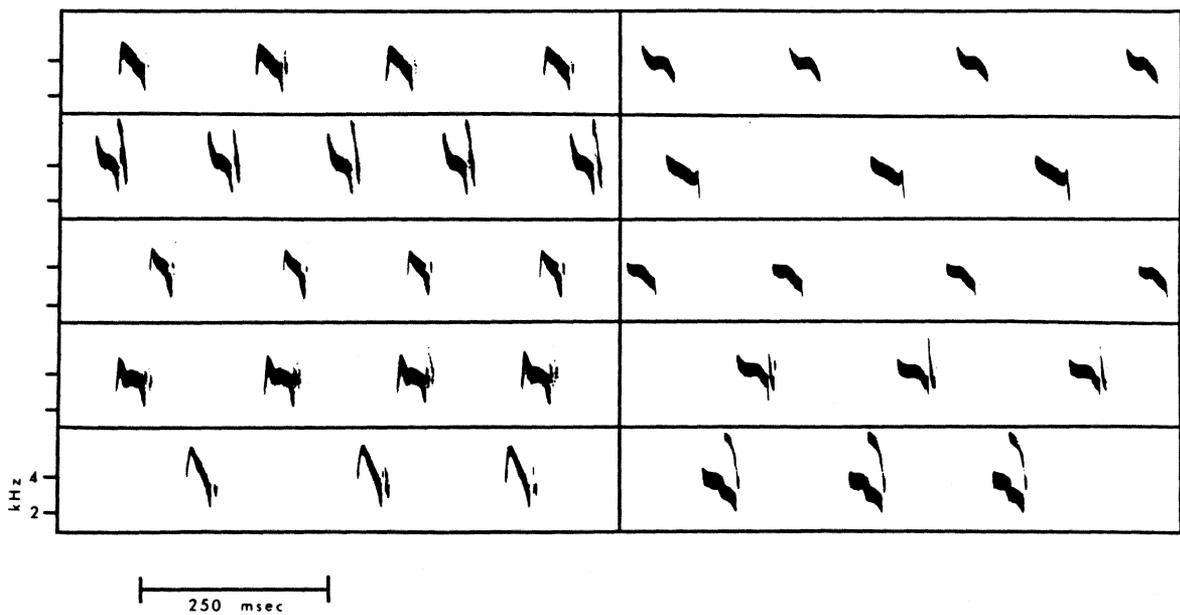


Figure 1. Examples of calling bouts of ten different individuals. Note the consistency in note structure within an individual.

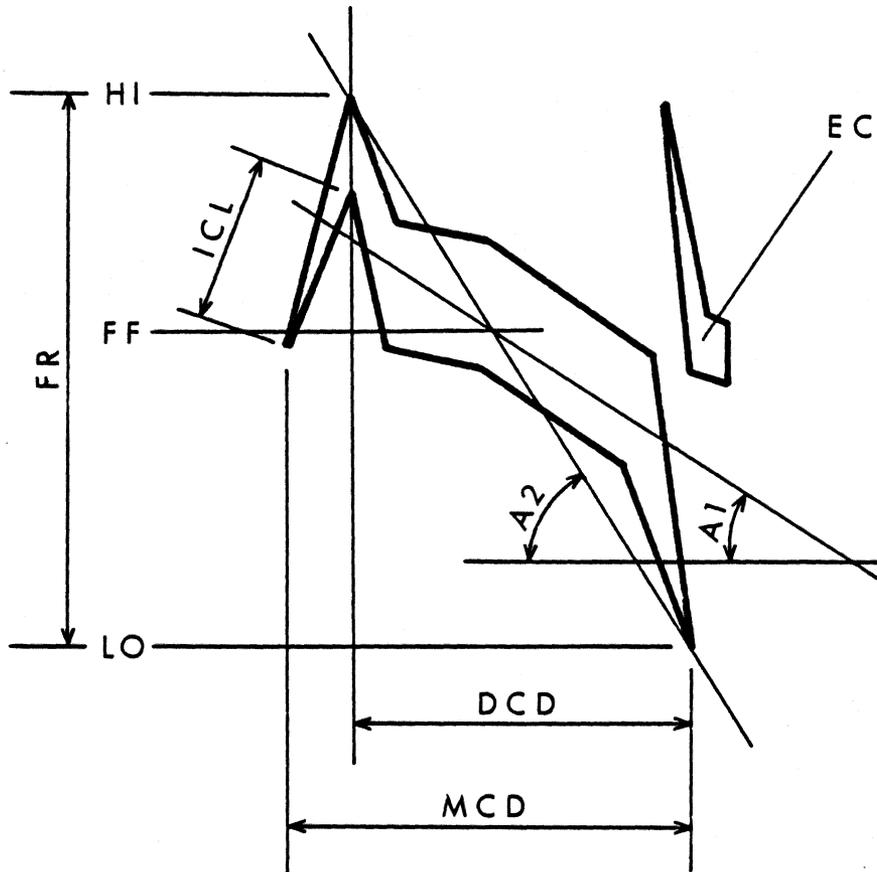


Figure 2. Methods of sonogram measurement.

Figure 3. Principal component ordination of the first two principal components of call note shape. One (randomly picked) data point is illustrated as a tracing of the call note for each 1X1 quadrant of the ordination space. Other data points are shown as dots, and 19 data points are not shown because they were behind other data points. Note the two groups divided along PC1.

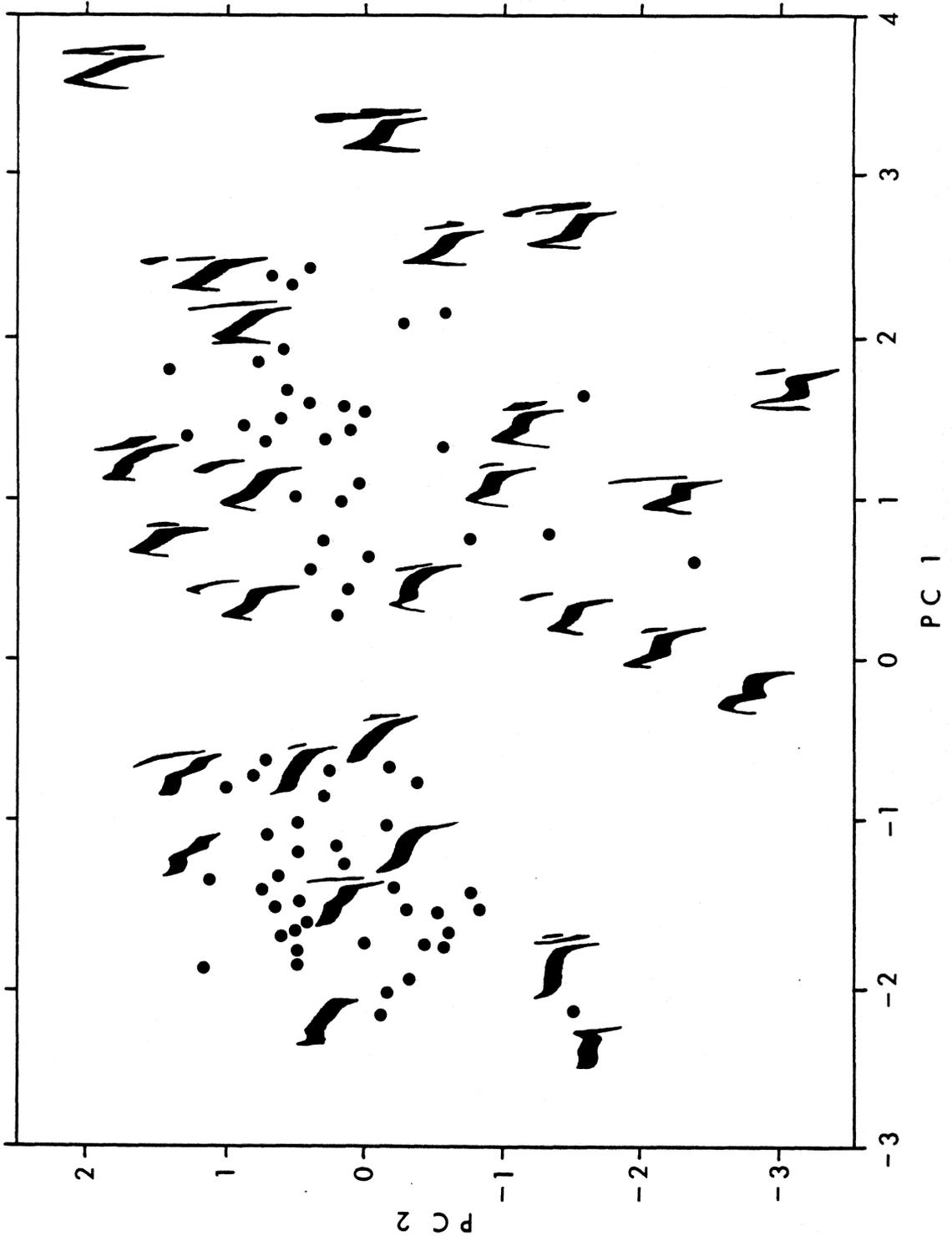
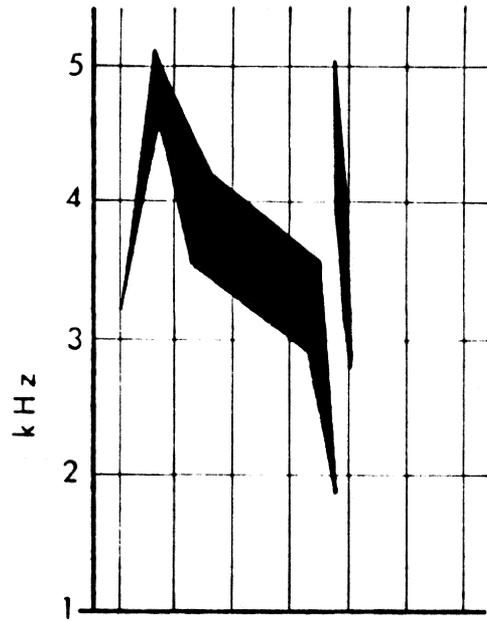
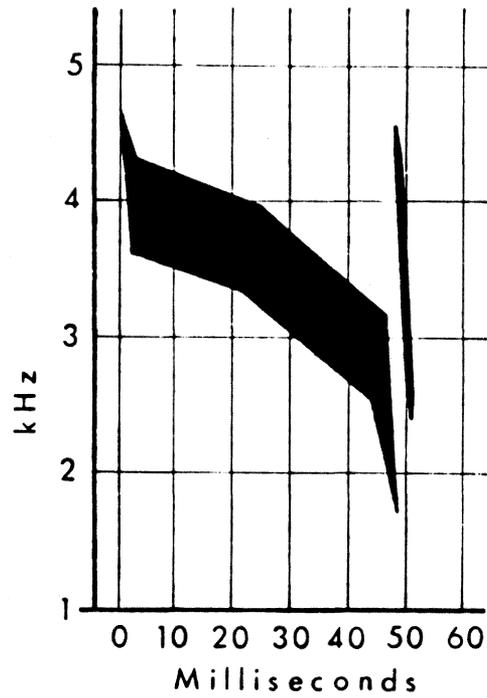


Figure 4. Reconstructed representations of Call Types 1 and 2 based upon the group averages of the ten measured variables from the sonograms of 57 adult Type 1 and 57 adult Type 2 birds.



Type 1



Type 2

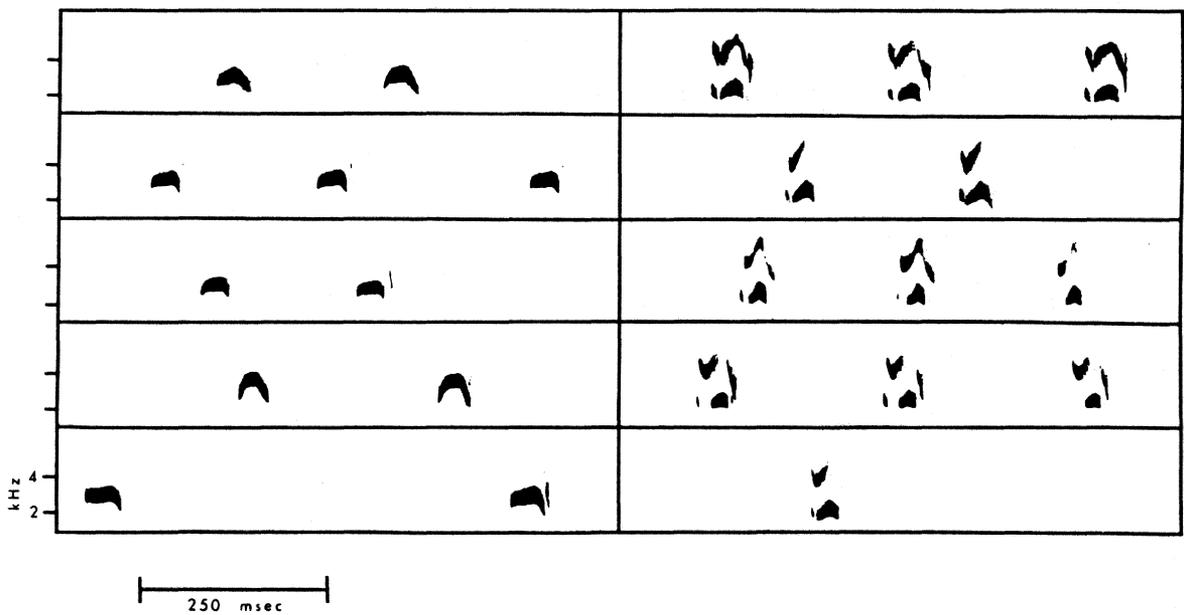


Figure 5. Toop calls. Series of toops from five different individuals of each call type. Type 1 on the left and Type 2 on the right.

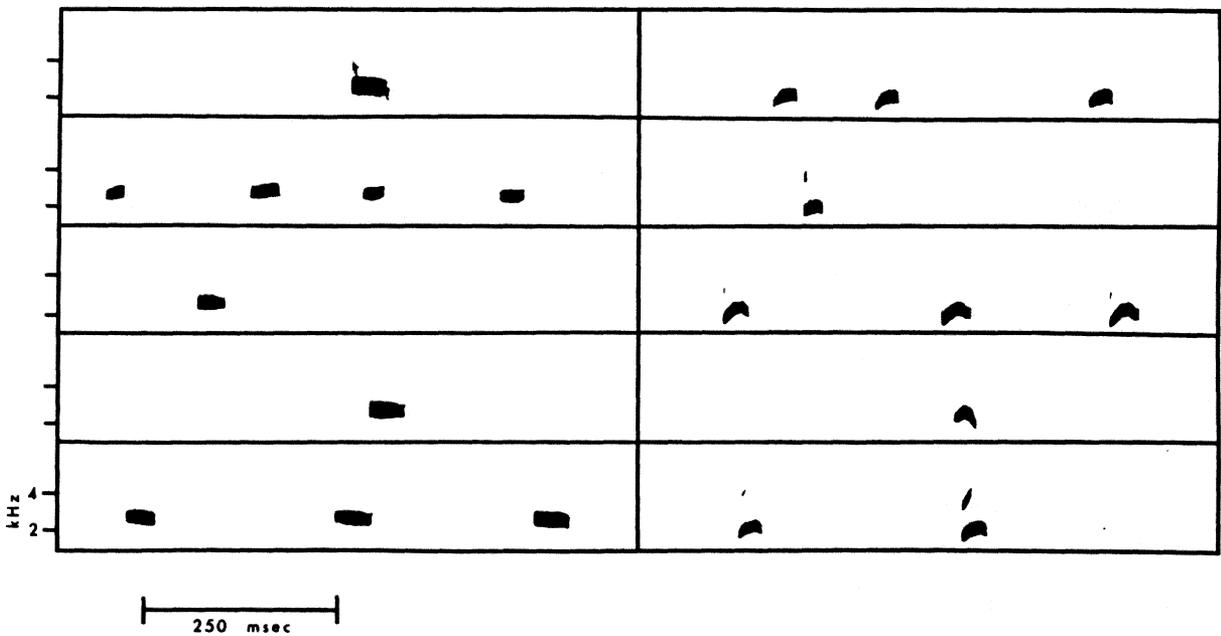


Figure 6. Alarm calls. Series of alarm calls from five different individuals of each call type. Type 1 on the left and Type 2 on the right.

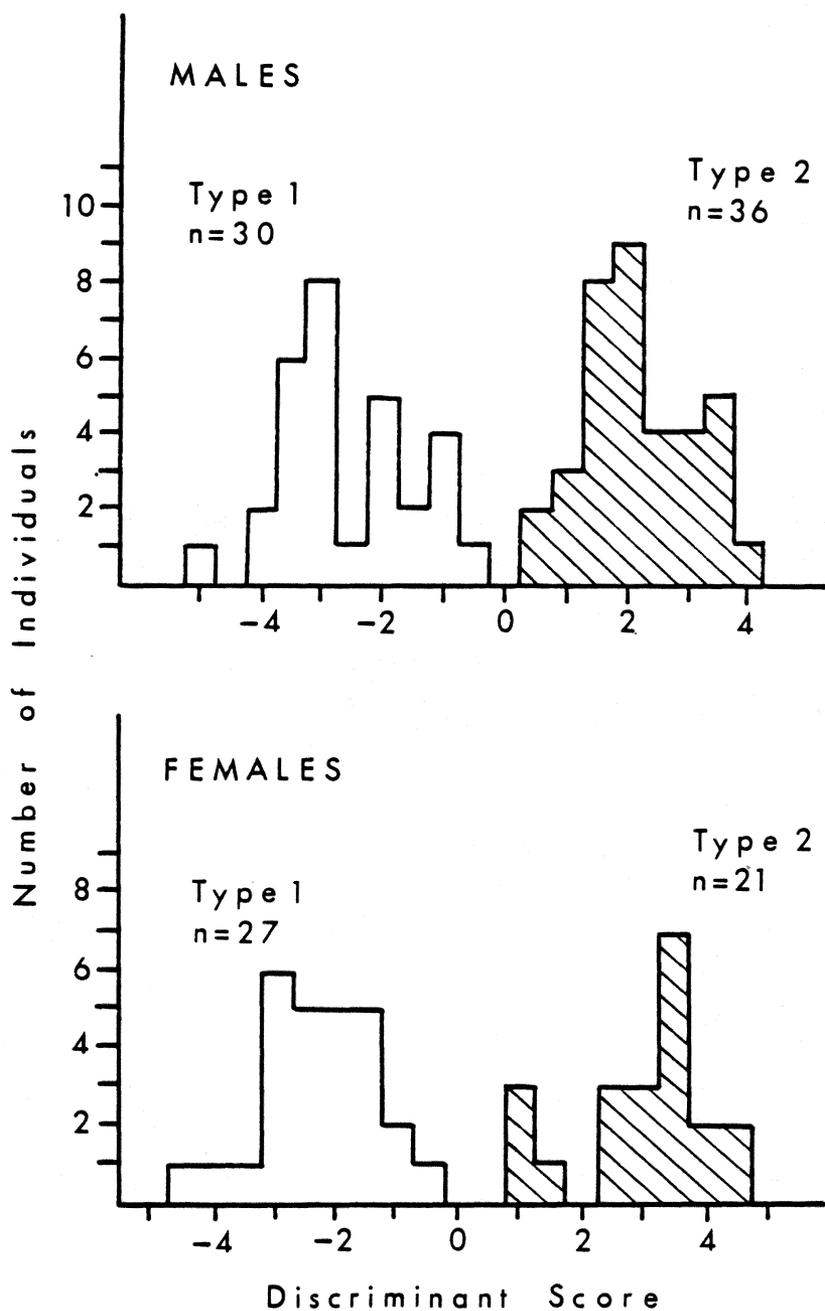


Figure 7. Ranges of discriminant scores for males and females of Call Types 1 and 2.

Figure 8. Sharing of flight call structure among the twelve male-female pairs that were travelling alone. Pairs A, B, D, and E are Type 1; pairs K, L, M, O, P, Q, S, and T are Type 2. Males on the left and females on the right.

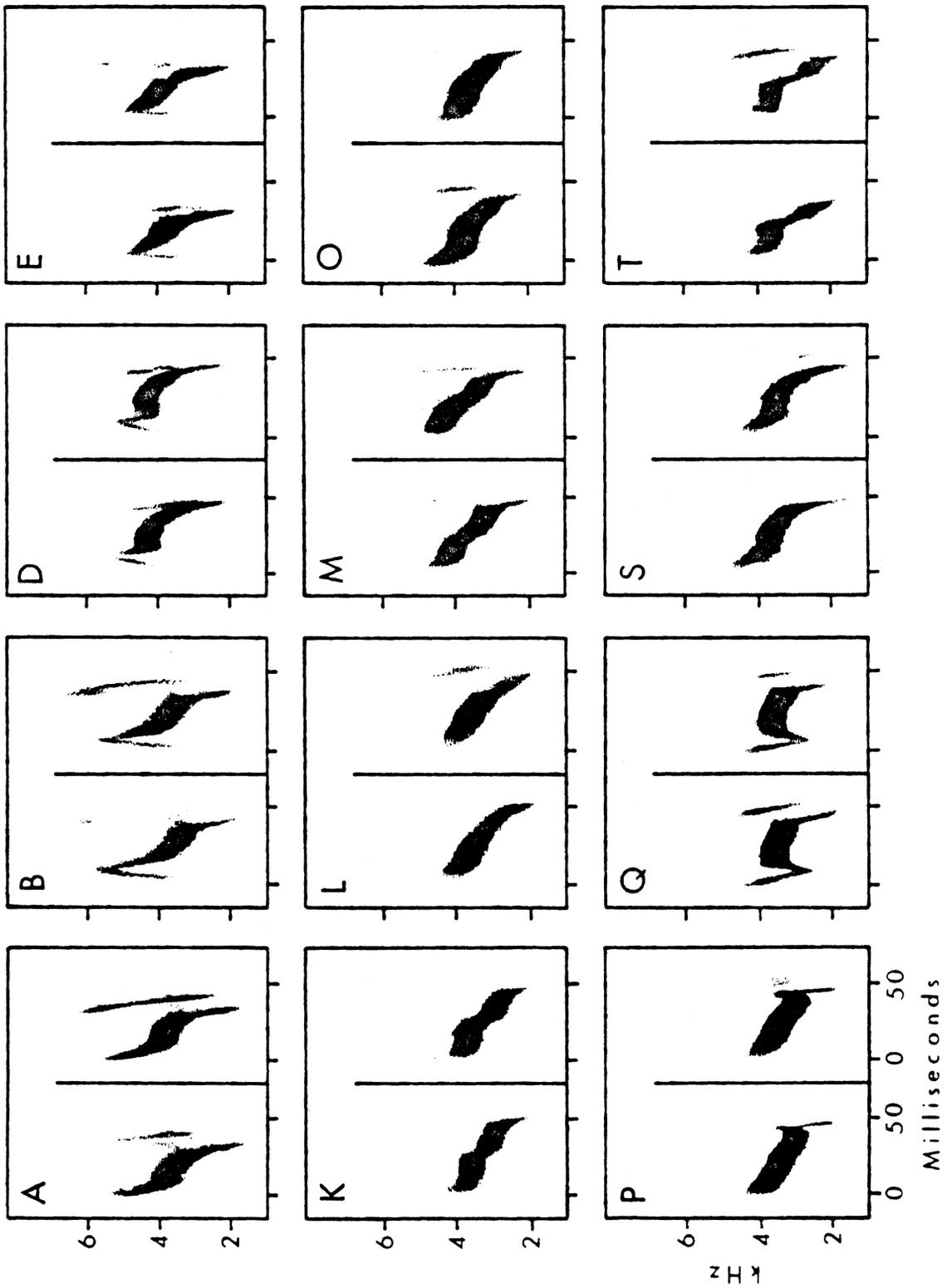


Figure 9. Sharing of flight call structure among the eight male-female pairs that were associated with other adults. Pairs C, H, I, and N are Type 1; pairs F, G, J, and R are Type 2. Males on the left and females on the right.

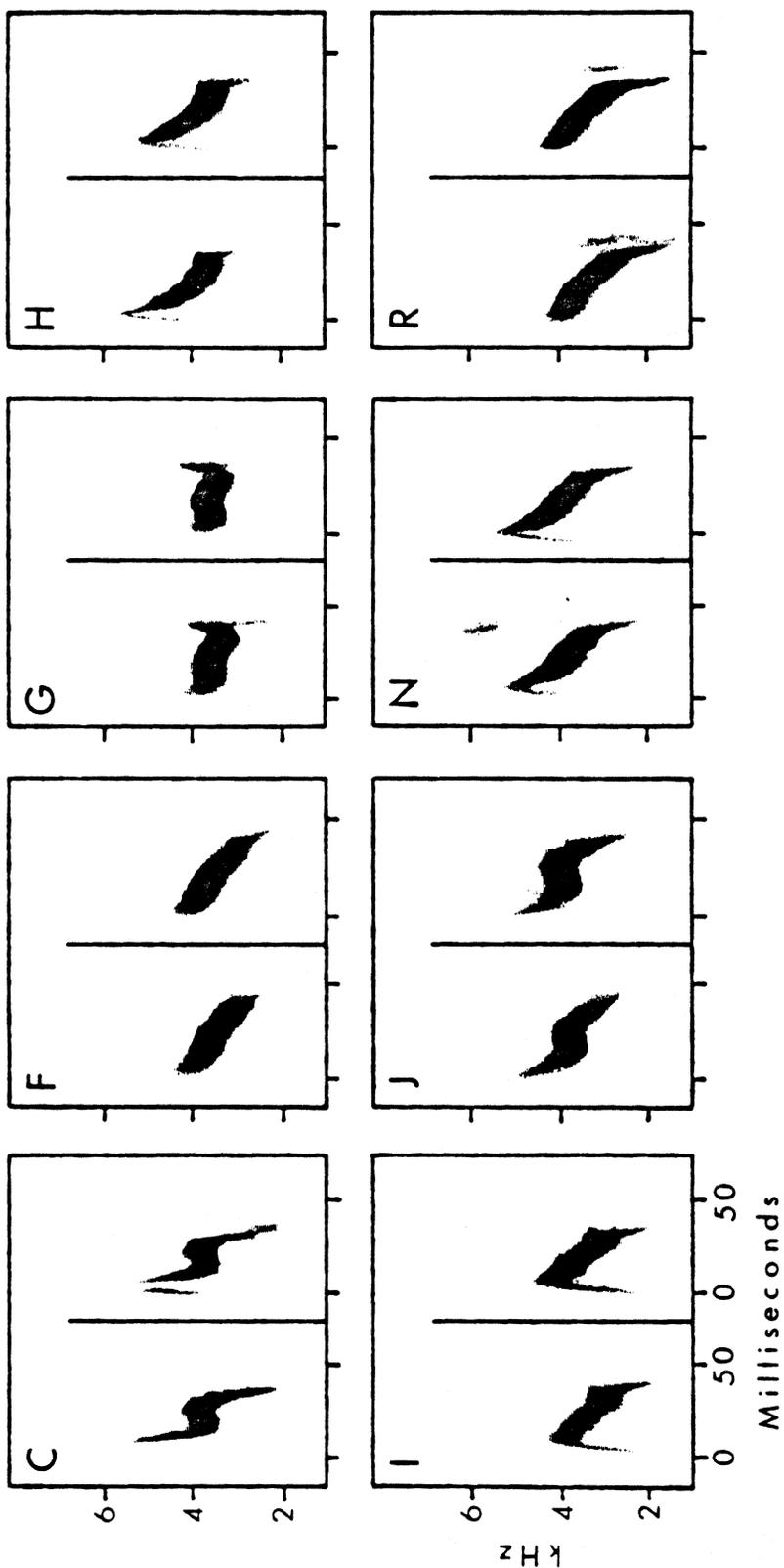
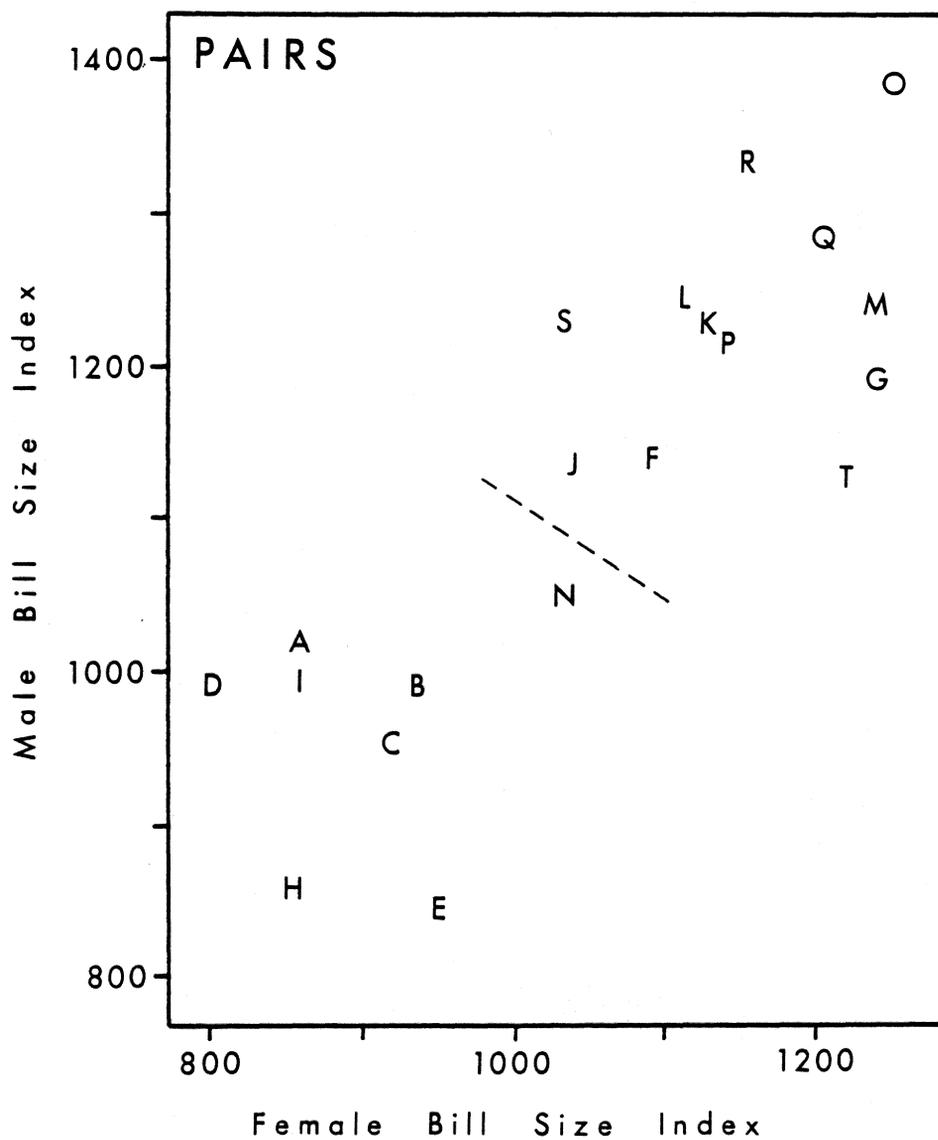


Figure 10. Correlation of bill sizes of presumed mated pairs. The dashed line separates Call Type 1 birds (lower left) from Call Type 2 birds (upper right). Letters follow Figures 8 and 9.



APPENDIX A

List of tape recordings obtained from others

Place	Year	Tape Owner
Oregon	1959	Cornell Laboratory of Ornithology
California	1979	
California	1981	
Arizona	1983	
New Mexico	1983	
Utah	1970	Curtis S. Adkisson
Colorado	1983	Curtis S. Adkisson
South Dakota	1961	Cornell Laboratory of Ornithology
North Dakota	1973	
Illinois	1970	
Indiana	1967	Curtis S. Adkisson
Tennessee	1981	
New York	1982	
Maine	1962	Cornell Laboratory of Ornithology

APPENDIX B

List of Individual Red Crossbills

Column 1 - Bird Number

Column 2 - Age and Sex

Column 3 - Date of Capture (all year 1983)

Column 4 - Place of Capture (B = Blacksburg, Virginia;
H = Highlands, North Carolina)

Column 5 - Flock Associations (| indicates association with adjacent individuals with |.) (Because of the large number of birds in Highlands, flock associations were difficult to observe. Here the entire sample is labelled as associated.)

Column 6 - Call Type (For the ten individuals that did not give adult calls, call type assignment was made on the basis of size.).

001	ad. fem.	22 Feb.	B	002, 003	1
002	ad. fem.	22 Feb.	B	001, 003	1
003	ad. fem.	22 Feb.	B	001, 002	1
004	ad. fem.	24 Feb.	B	005	1
005	ad. male	24 Feb.	B	004	1
006	ad. fem.	24 Feb.	B	alone	1
007	ad. male	24 Feb.	B	alone	2
008	ad. male	27 Feb.	B	009	1
009	ad. fem.	27 Feb.	B	008	1
010	ad. male	1 Mar.	B	011, 012	2
011	ad. male	1 Mar.	B	010, 012	1
012	ad. male	1 Mar.	B	010, 011	2
013	ad. male	3 Mar.	B	alone	1
014	ad. fem.	3 Mar.	B	alone	2
015	ad. male	5 Mar.	B	alone	1
016	ad. male	5 Mar.	B	alone	2
017	im. fem.	7 Mar.	B	018	1
018	ad. male	7 Mar.	B	017	1
019	ad. male	23 Mar.	B	alone	1
020	ad. male	28 Mar.	B	021, 022	2
021	ad. male	28 Mar.	B	020, 022	2
022	ad. male	28 Mar.	B	020, 021	2
023	ad. male	12 Apr.	B	alone	2
024	ad. fem.	14 Apr.	B	025, 026, 027	1
025	ad. fem.	14 Apr.	B	024, 026, 027	1

026	ad. male	14 Apr.	B	024, 025, 027	1
027	ad. male	14 Apr.	B	024, 025, 025	1
028	ad. male	21 Apr.	B	029	2
029	ad. male	21 Apr.	B	028	2
030	ad. fem.	28 Apr.	B	031	1
031	ad. male	28 Apr.	B	030	1
032	ad. male	28 Apr.	B	alone	1
033	ad. male	13 May	B	034	1
034	ad. fem.	13 May	B	033	1
035	ad. male	15 May	B	alone	1
036	ad. male	17 May	B	alone	2
037	ad. male	18 May	B	038	2
038	ad. fem.	18 May	B	037	2
039	juv. male	27 May	B		2
040	ad. male	27 May	B		2
041	juv. fem.	27 May	B		2
042	ad. male	27 May	B		2
043	juv. male	27 May	B		2
044	ad. fem.	27 May	B		2
045	juv fem.	27 May	B		2
046	ad. fem.	27 May	B	alone	1
047	ad. fem.	30 May	B		2
048	ad. male	30 May	B		2
049	ad. male	30 May	B		2
050	ad. fem.	30 May	B		1

051	ad. fem.	30 May	B		2
052	ad. male	31 May	B	alone	1
053	ad. fem.	31 May	B	alone	1
054	juv. fem.	31 May	B	055	2
055	ad. male	31 May	B	054	2
056	ad. male	1 June	B		1
057	ad. male	1 June	B		1
058	ad. male	1 June	B		1
059	ad. fem.	1 June	B		1
060	ad. fem.	1 June	B		1
061	ad. fem.	1 June	B		2
062	ad. male	1 June	B		2
063	ad. fem.	1 June	B		1
064	juv.	1 June	B	065, 066	1
065	juv.	1 June	B	064, 066	1
066	juv.	1 June	B	064, 065	1
067	ad. male	2 June	B	alone	2
068	juv. fem.	2 June	B	alone	2
069	ad. fem.	2 June	B	070, 071, 072	2
070	ad. fem.	2 June	B	069, 071, 072	2
071	ad. male	2 June	B	069, 070, 072	2
072	ad. male	2 June	B	069, 070, 071	2
073	ad. fem.	3 June	B	alone	2
074	ad. male	3 June	B	075	1
075	ad. fem.	3 June	B	074	1

076	juv. male	3 June	B	alone	2
077	ad. male	5 June	B	078, 079, 080	2
078	ad. male	5 June	B	077, 079, 080	2
079	ad. male	5 June	B	077, 078, 080	2
080	juv. fem.	5 June	B	077, 078, 079	2
081	ad. male	5 June	B	082, 083, 084	2
082	ad. fem.	5 June	B	081, 083, 084	2
083	ad. male	5 June	B	081, 082, 084	2
084	ad. fem.	5 June	B	081, 082, 083	2
085	ad. male	9 June	B	alone	1
086	ad. male	9 June	B	087	2
087	ad. fem.	9 June	B	086	2
088	ad. male	9 June	B	alone	2
089	ad. fem.	10 June	B	090	1
090	ad. male	10 June	B	089	1
091	ad. male	11 June	B	alone	2
092	ad. male	11 June	B	093	2
093	ad. fem.	11 June	B	092	2
094	juv. male	14 June	B	alone	2
095	juv. male	16 June	B	096	2
096	juv. fem.	16 June	B	095	2
097	juv. male	16 June	B	alone	2
098	ad. fem.	18 June	B	099	2
099	ad. male	18 June	B	098	2
100	ad. fem.	19 June	B	101	2

101	ad. male	19 June	B	100	2
102	juv. male	24 June	B	103	2
103	juv. male	24 June	B	102	2
104	ad. male	25 June	B	alone	2
105	ad. fem.	27 June	B	alone	2
106	ad. fem.	27 June	B	alone	2
107	ad. male	27 June	B	alone	2
108	ad. male	29 June	B	109	2
109	juv. fem.	29 June	B	108	2
110	juv. male	29 June	B	111	2
111	juv. male	29 June	B	110	2
112	ad. fem.	4 July	B	113	2
113	ad. male	4 July	B	112	2
114	ad. fem.	7 July	B	alone	1
115	juv. male	8 July	B	116, 117	2
116	juv. fem.	8 July	B	115, 117	2
117	juv. fem.	8 July	B	115, 116	2
118	juv. male	18 July	B	119, 120	2
119	juv. male	18 July	B	118, 120	2
120	juv. male	18 July	B	118, 119	2
121	juv. male	26 July	B	122, 123	1
122	juv. fem.	26 July	B	121, 123	1
123	juv. male	26 July	B	121, 122	1
124	juv. fem.	31 July	B	alone	2
125	ad. fem.	2 Oct.	B	alone	2

126	ad. fem.	26 Oct.	B	alone	2
127	im. male	30 Oct.	H		1
128	im. fem.	30 Oct.	H		1
129	ad. male	30 Oct.	H		1
130	ad. fem.	30 Oct.	H		1
131	im. male	30 Oct.	H		1
132	im. male	30 Oct.	H		1
133	im. fem.	30 Oct.	H		1
134	ad. fem.	30 Oct.	H		1
135	ad. male	30 Oct.	H		1
136	im. fem.	30 Oct.	H		1
137	im. fem.	30 Oct.	H		1
138	im. male	30 Oct.	H		2
139	im. male	30 Oct.	H		1
140	im. fem.	30 Oct.	H		1
141	juv. male	30 Oct.	H		1
142	im. male	30 Oct.	H		1
143	ad. male	30 Oct.	H		1
144	im. fem.	30 Oct.	H		1
145	im. male	30 Oct.	H		1
146	im. fem.	30 Oct.	H		1
147	ad. fem.	30 Oct.	H		1
148	im. fem.	30 Oct.	H		1
149	im. male	30 Oct.	H		1
150	im. male	30 Oct.	H		1

151	im. male	30 Oct.	H		1
152	im. fem.	30 Oct.	H		1
153	im. fem.	31 Oct.	H		1
154	im. male	31 Oct.	H		1
155	juv. male	31 Oct.	H		1
156	juv. fem.	31 Oct.	H		1
157	im. fem.	31 Oct.	H		1
158	ad. male	31 Oct.	H		1
159	im. fem.	31 Oct.	H		1
160	ad. male	31 Oct.	H		1
161	im. male	31 Oct.	H		1
162	im. male	19 Nov.	H		1
163	im. male	19 Nov.	H		1
164	ad. fem.	19 Nov.	H		1
165	im. male	19 Nov.	H		1
166	ad. male	19 Nov.	H		1
167	im. male	19 Nov.	H		1
168	im. fem.	20 Nov.	H		1
169	ad. fem.	20 Nov.	H		1
170	ad. fem.	20 Nov.	H		1
171	ad. male	21 Nov.	H		1
172	ad. fem.	21 Nov.	H		1
173	ad. male	21 Nov.	H		1
174	im. male	21 Nov.	H		1
175	ad. male	21 Nov.	H		1

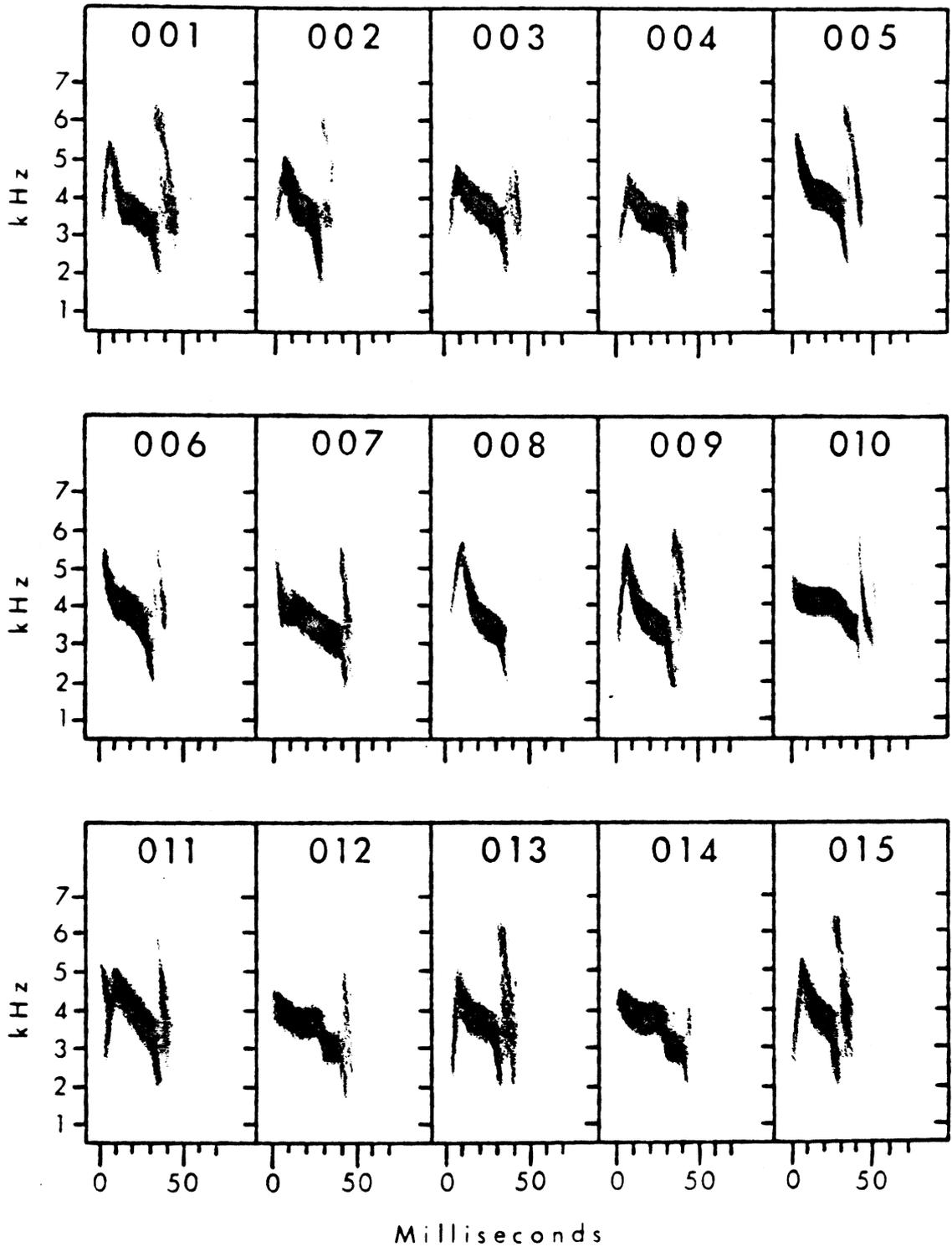
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178	im. male	21 Nov.	H		1
179	im. male	21 Nov.	H		1
180	ad. male	17 Dec.	B	181, 182, 183	2
181	ad. fem.	17 Dec.	B	180, 182, 183	2
182	juv. fem.	17 Dec.	B	180, 181, 183	2
183	im. male	17 Dec.	B	180, 181, 182	2

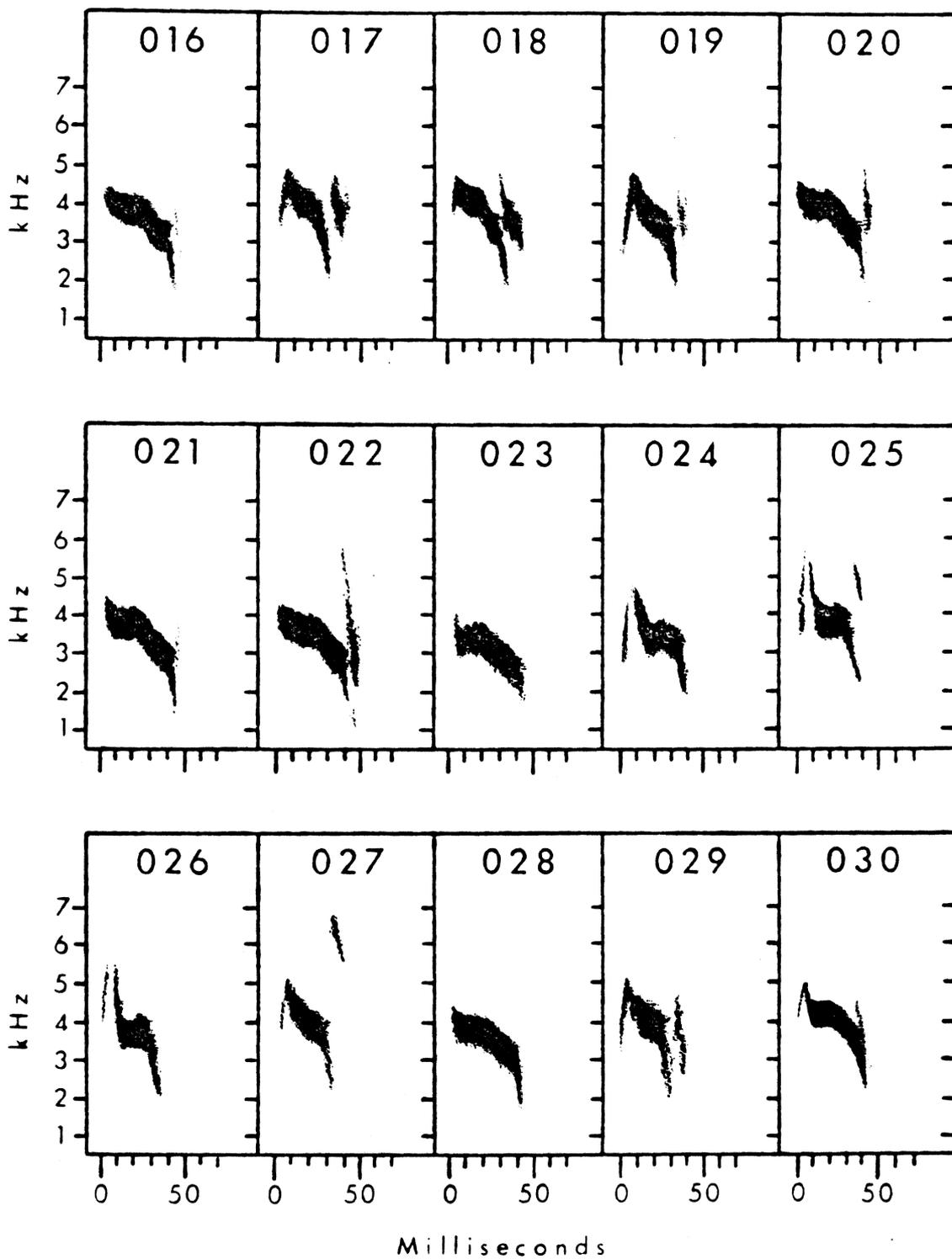
APPENDIX C

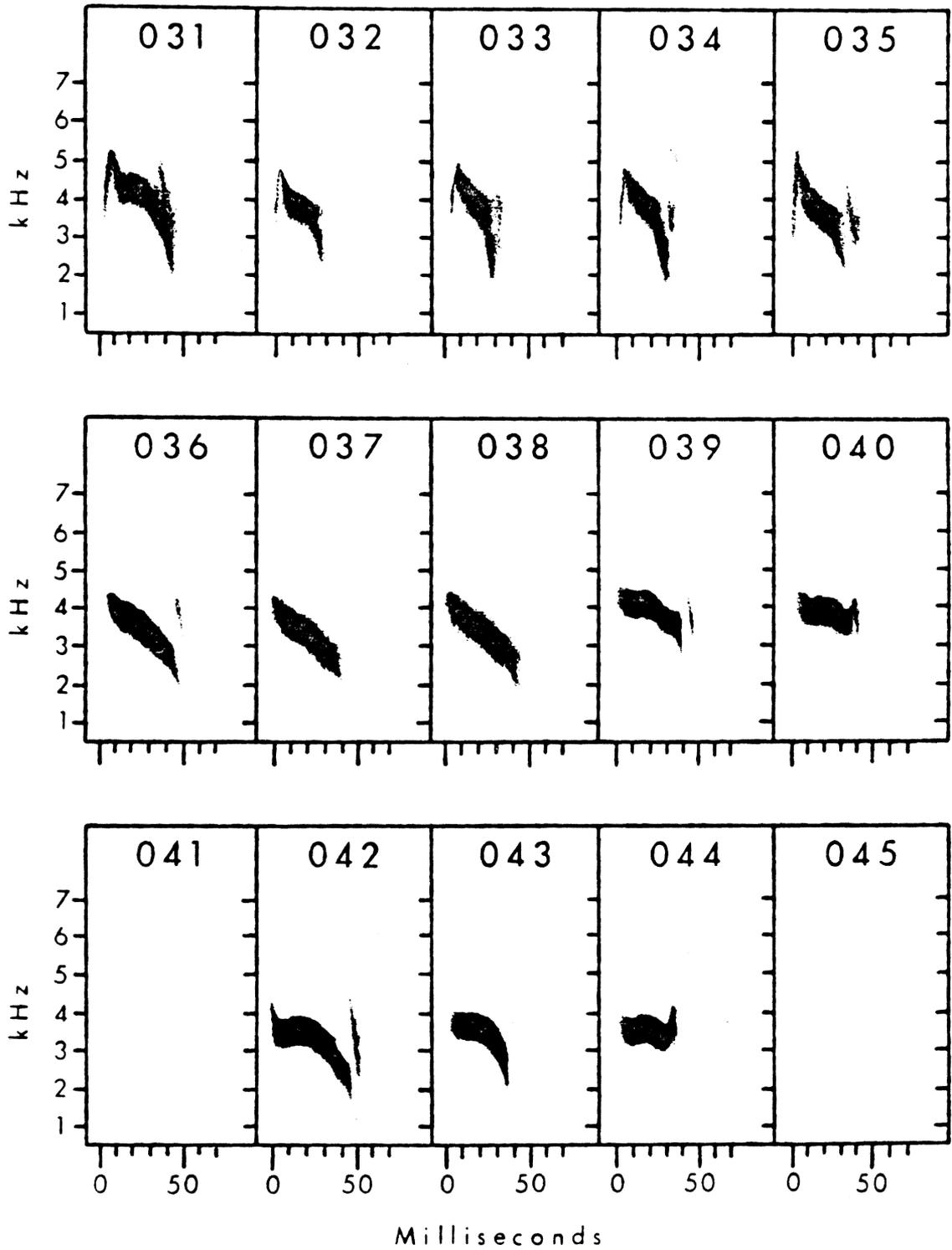
Representative Call Notes

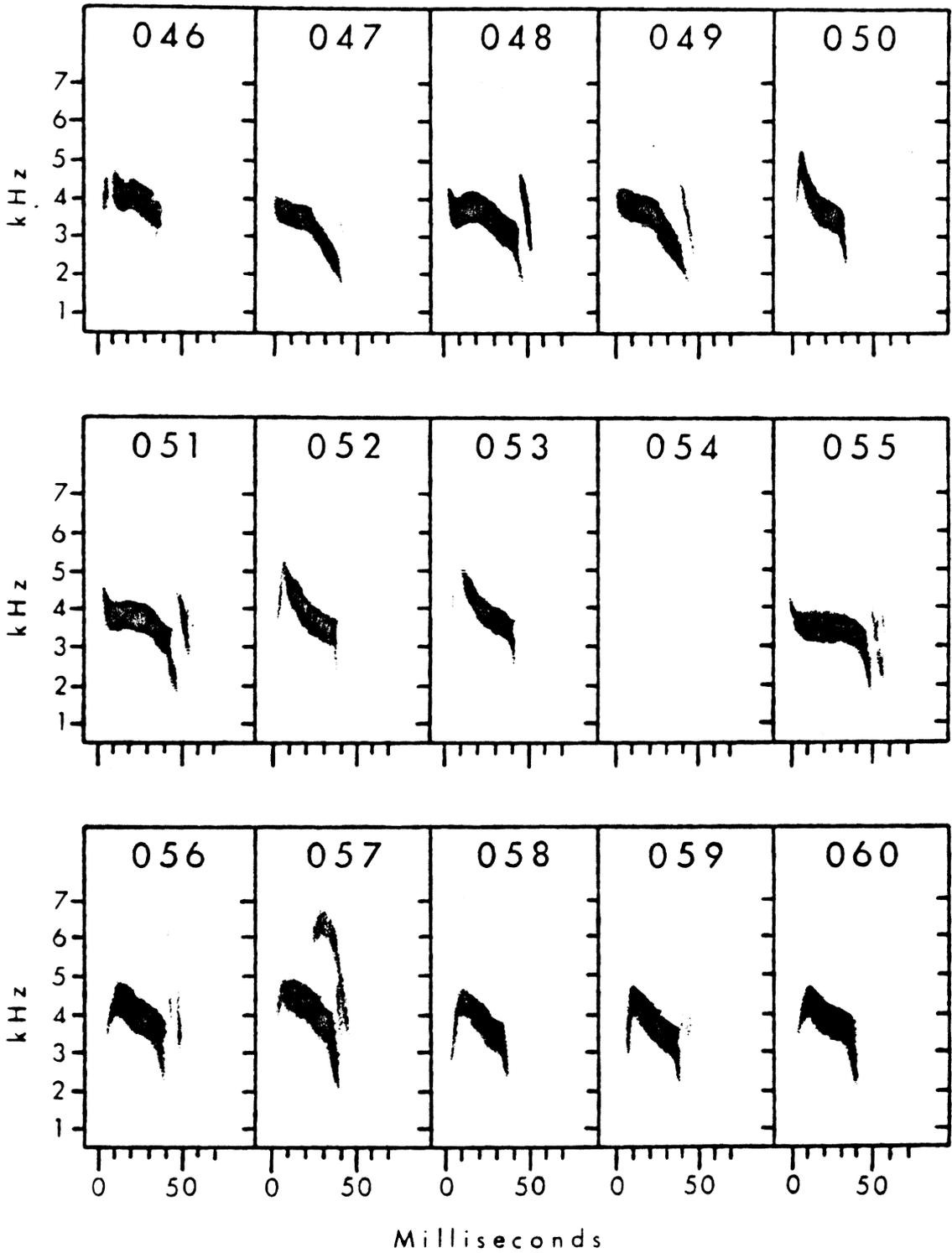
Individuals are listed in chronological order of capture as indicated in Appendix B.

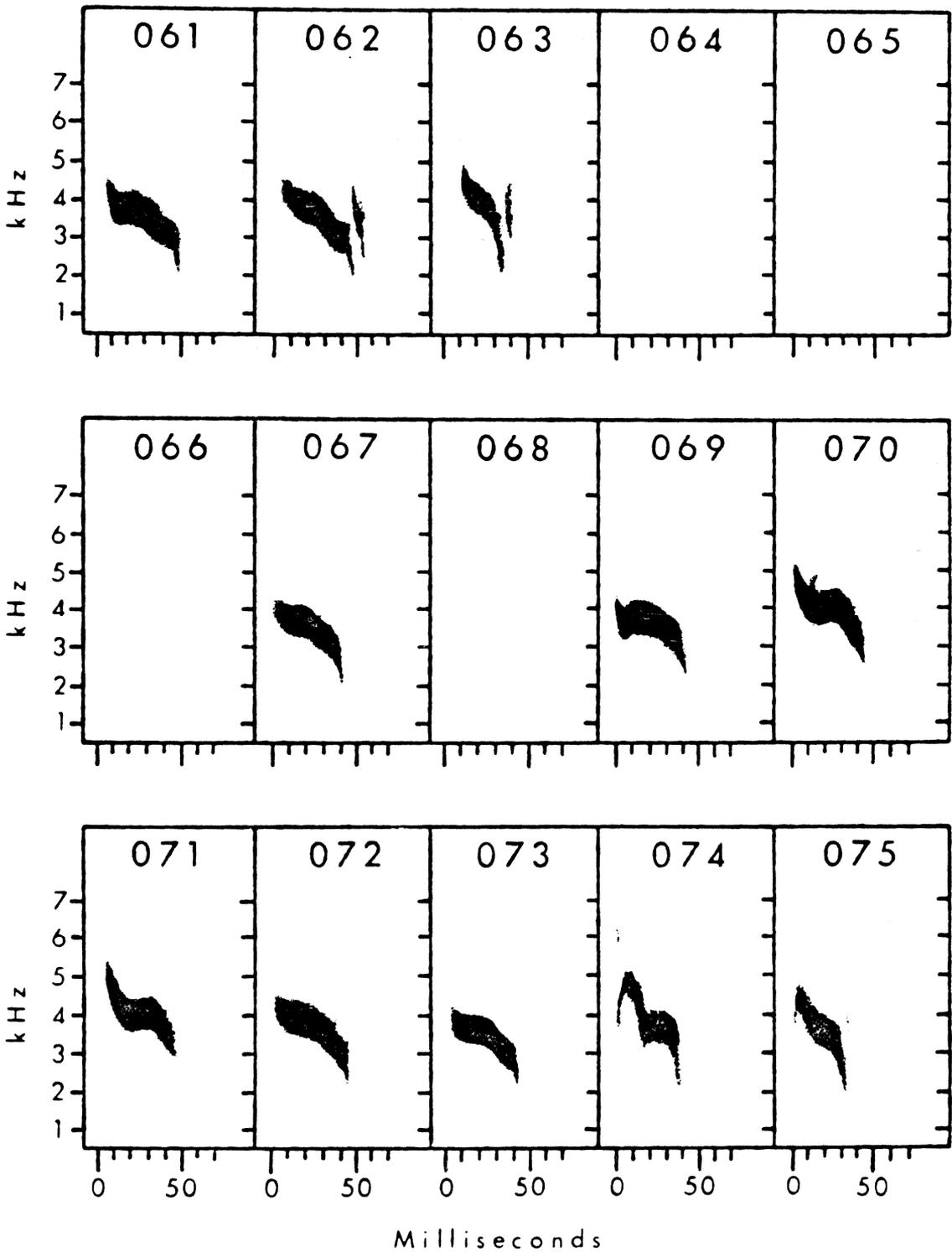
For each individual, one representative flight call note is presented. Those individuals that did not give adult calls are left blank.

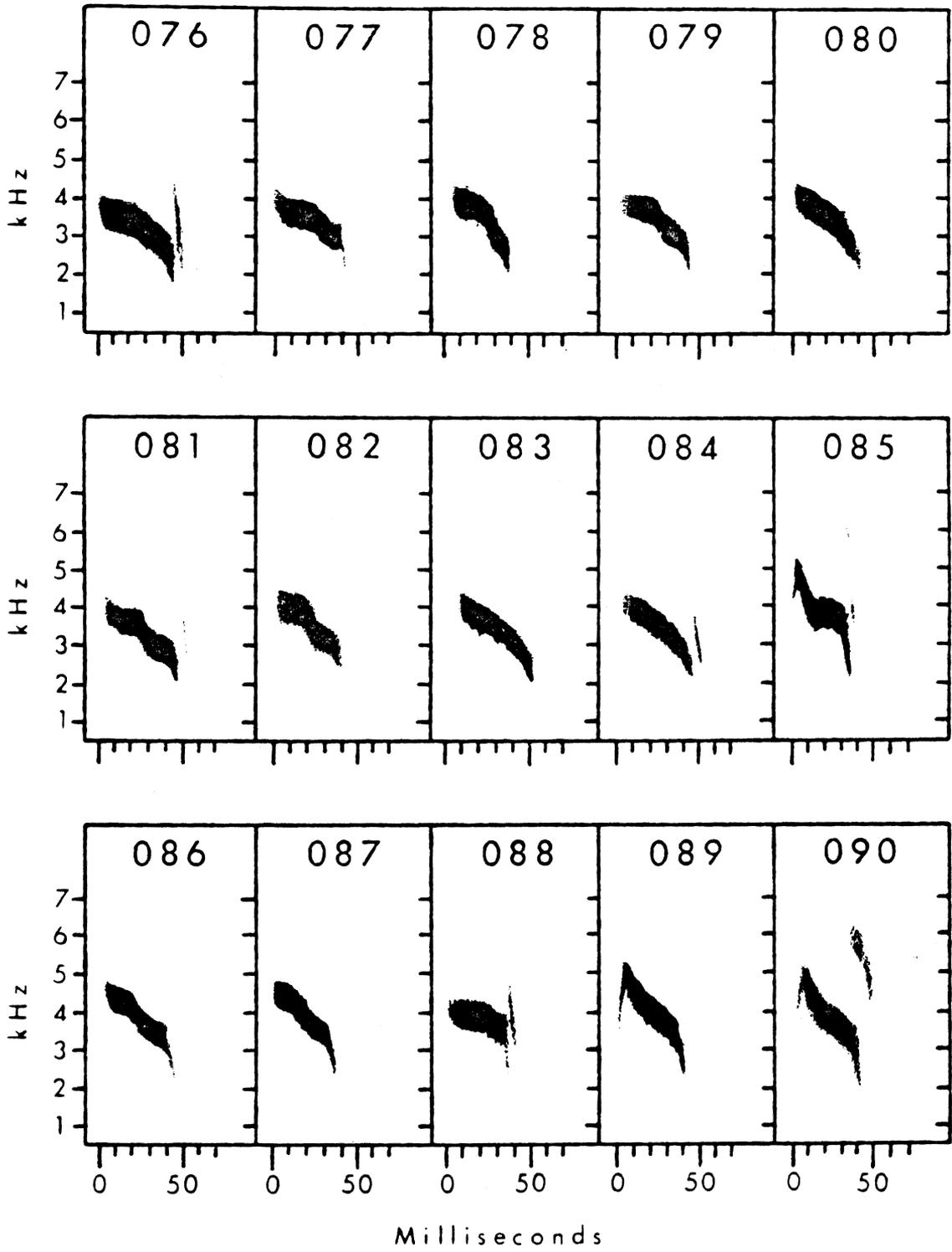


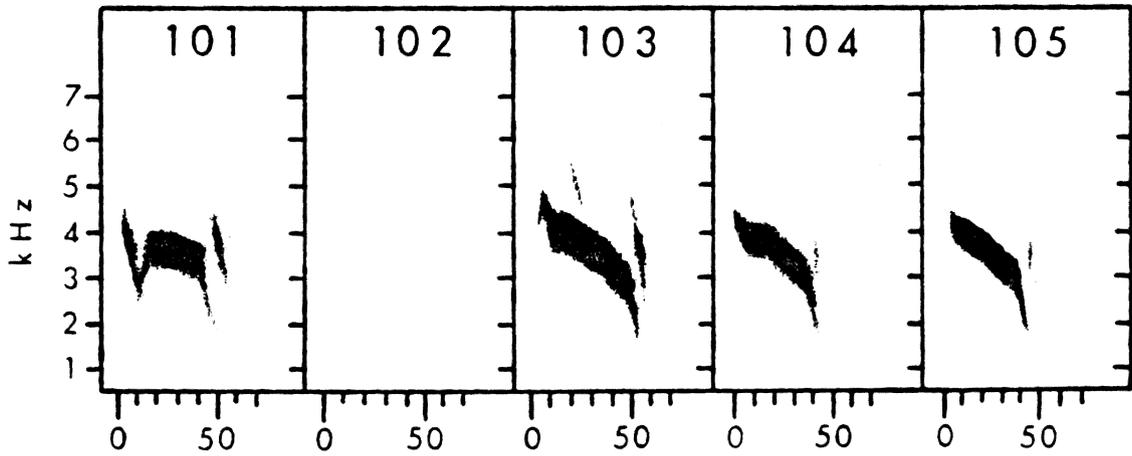
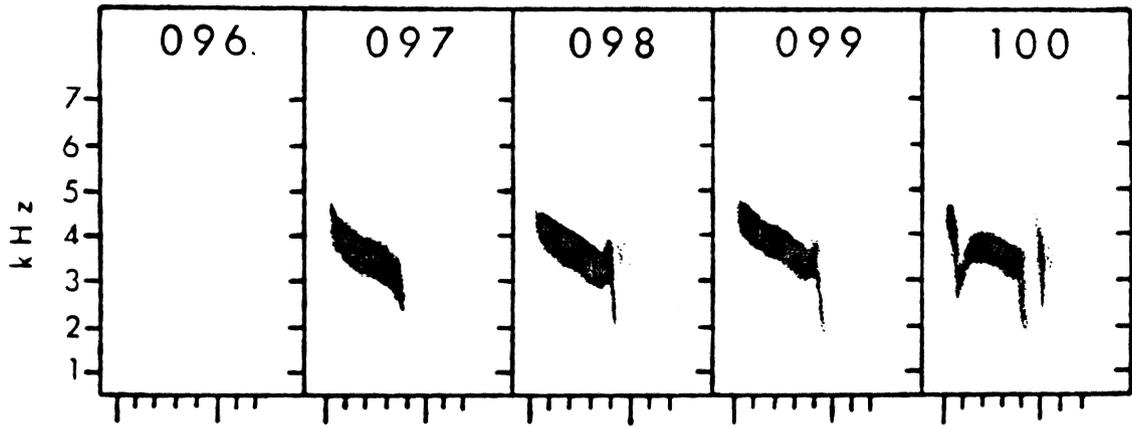
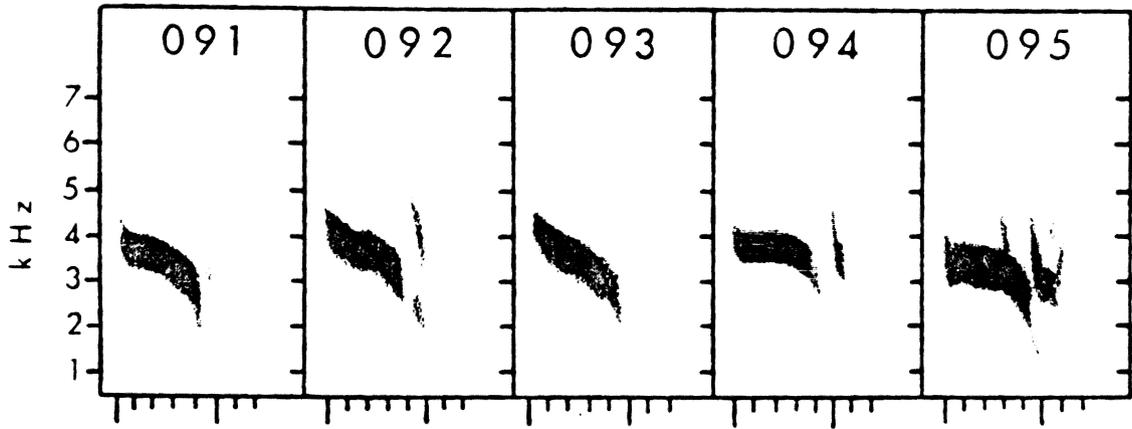




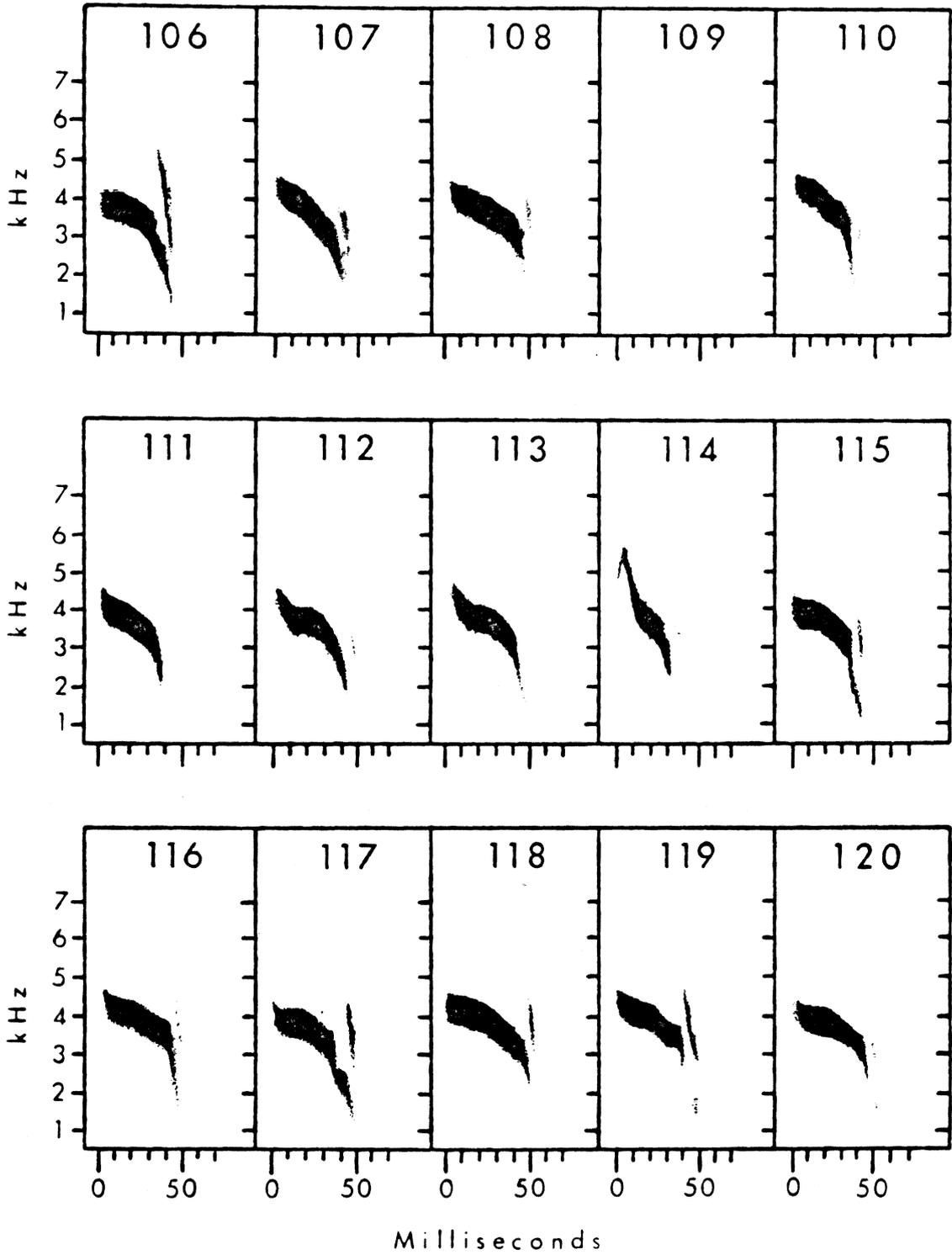


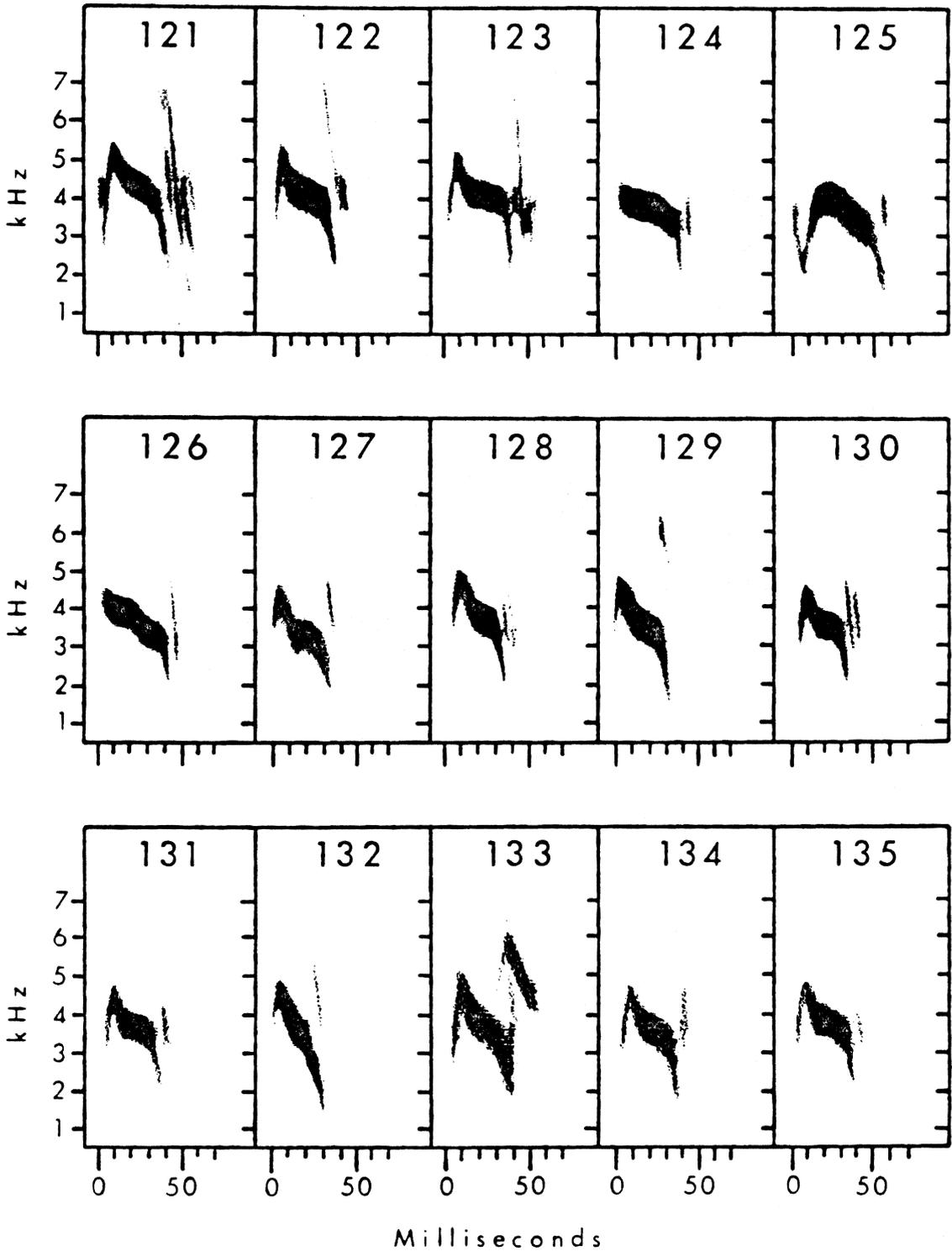


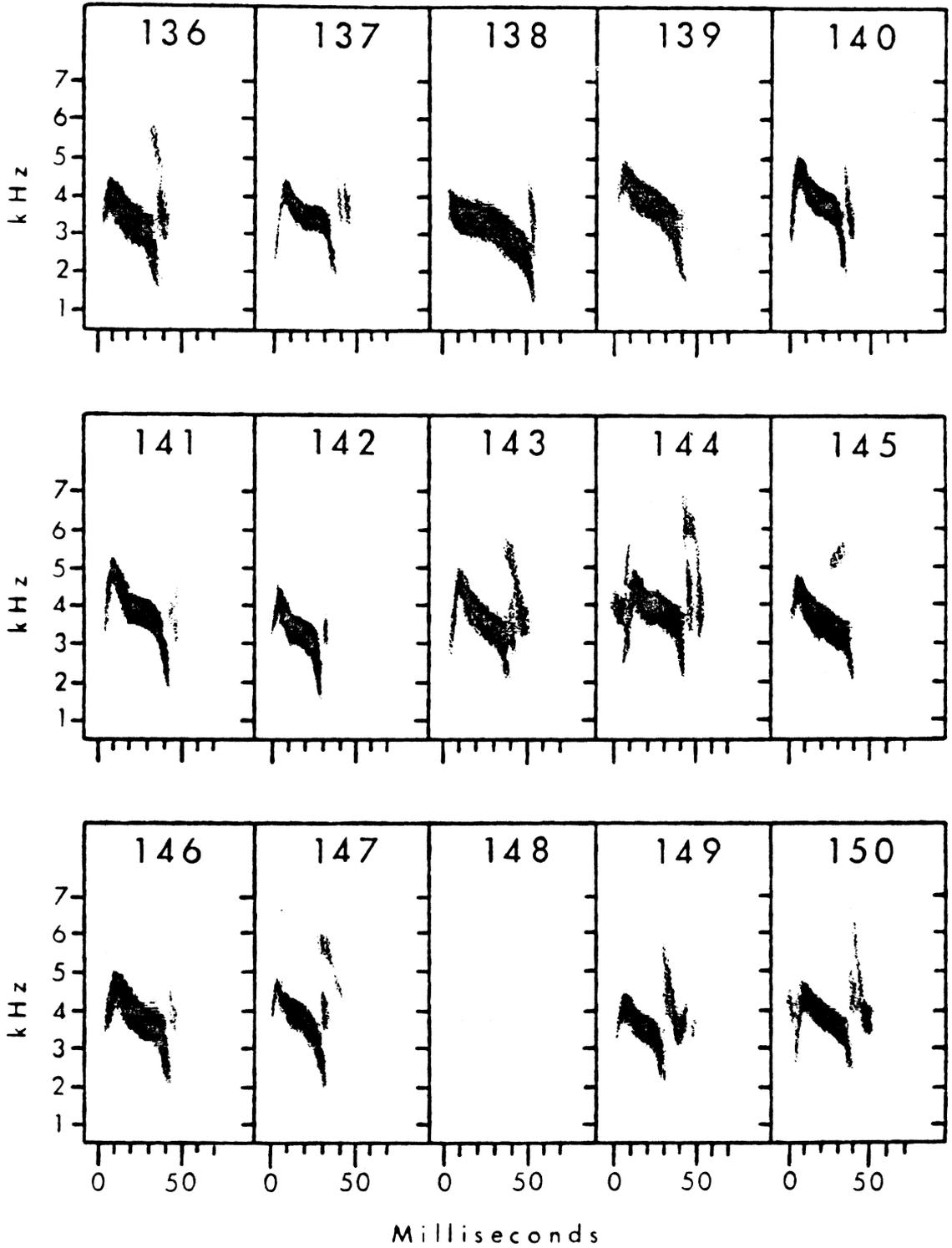


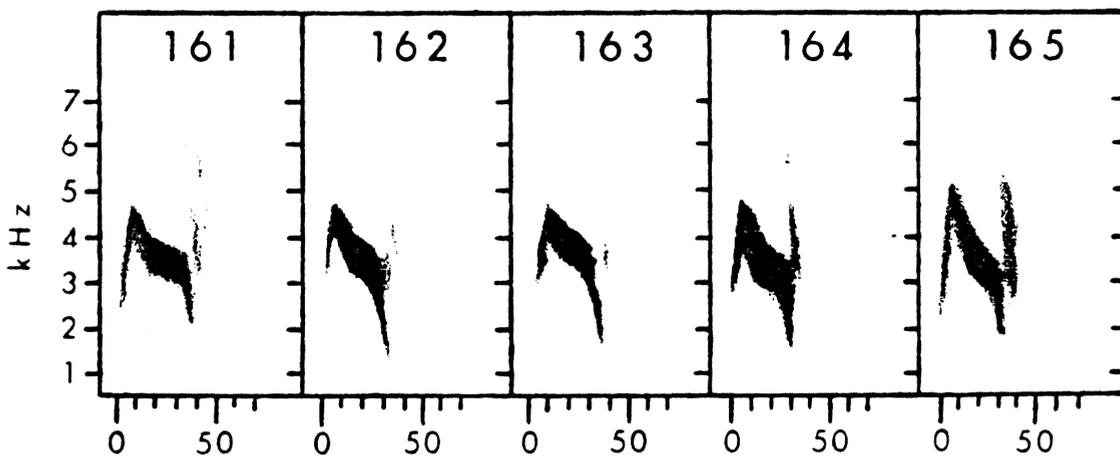
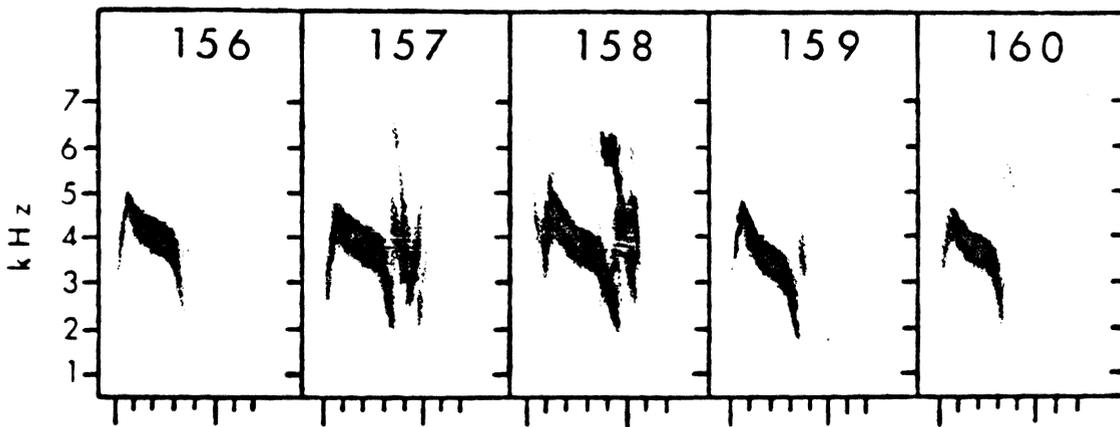
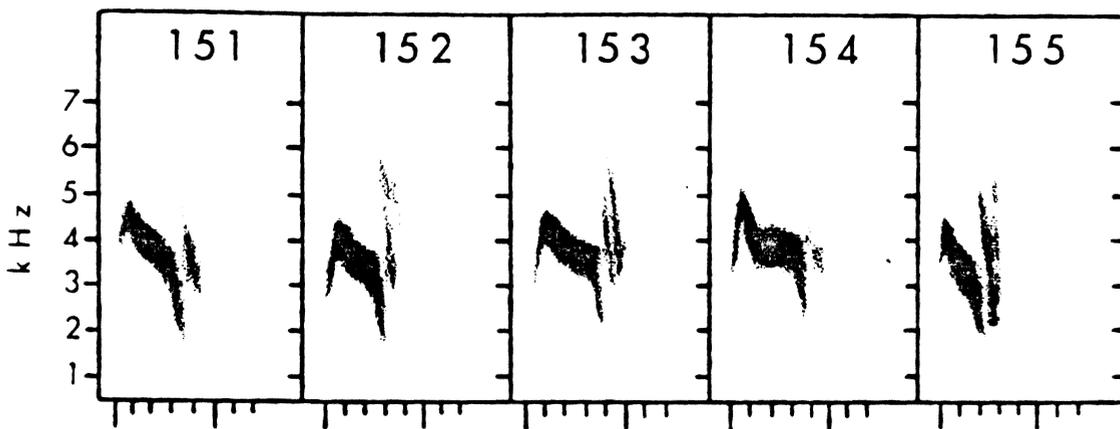


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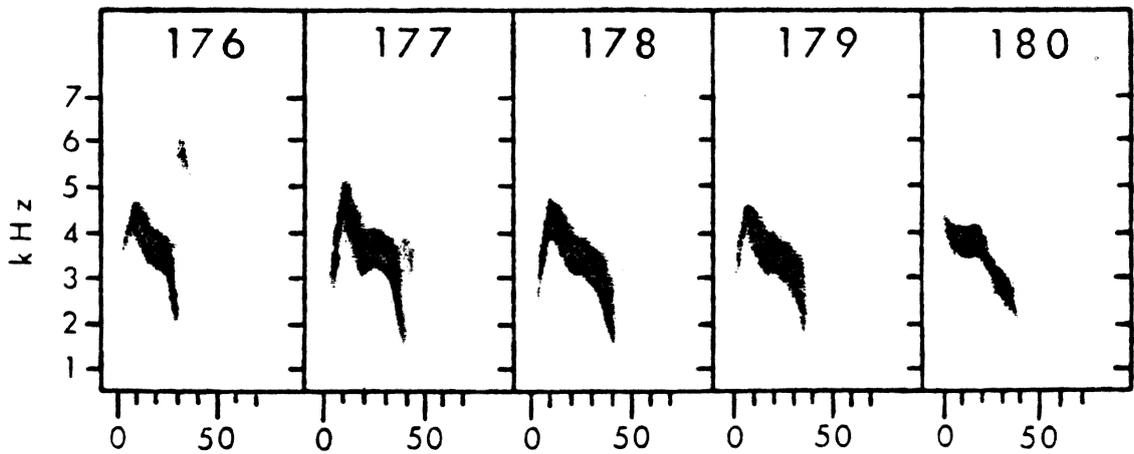
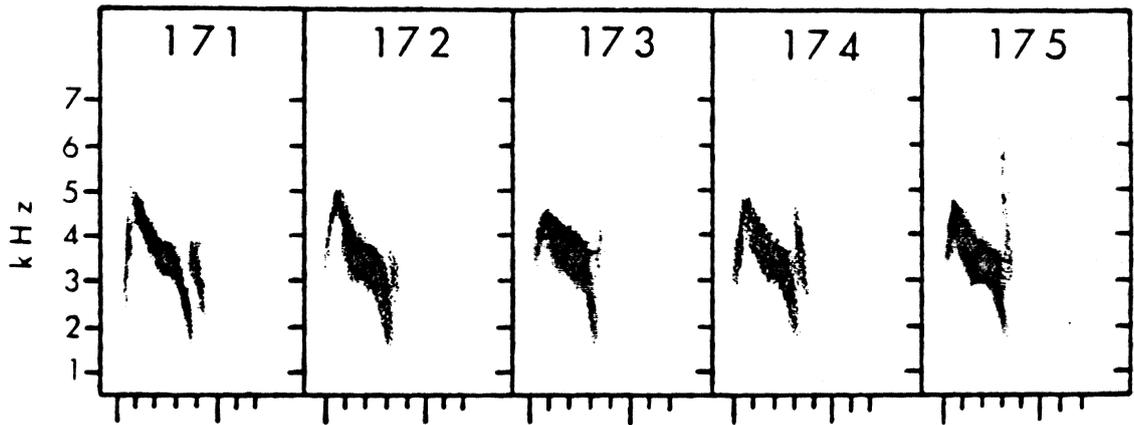
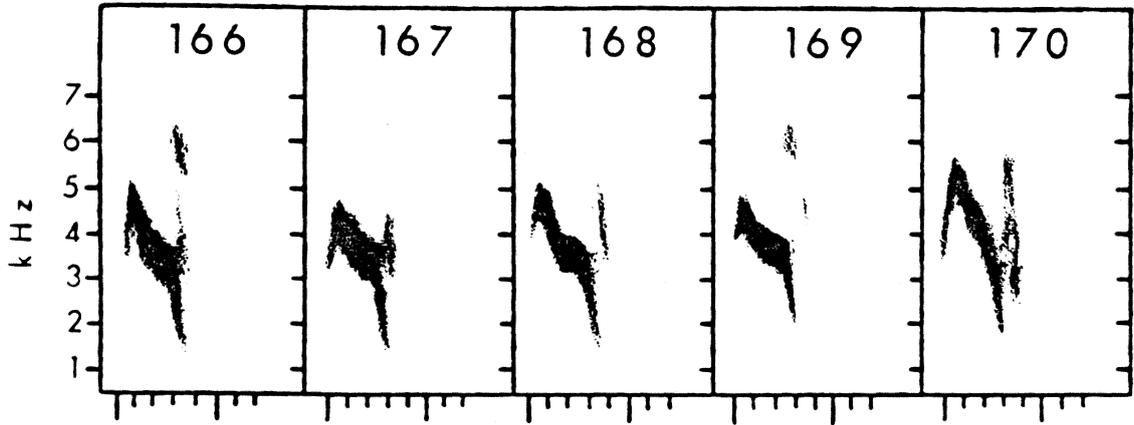




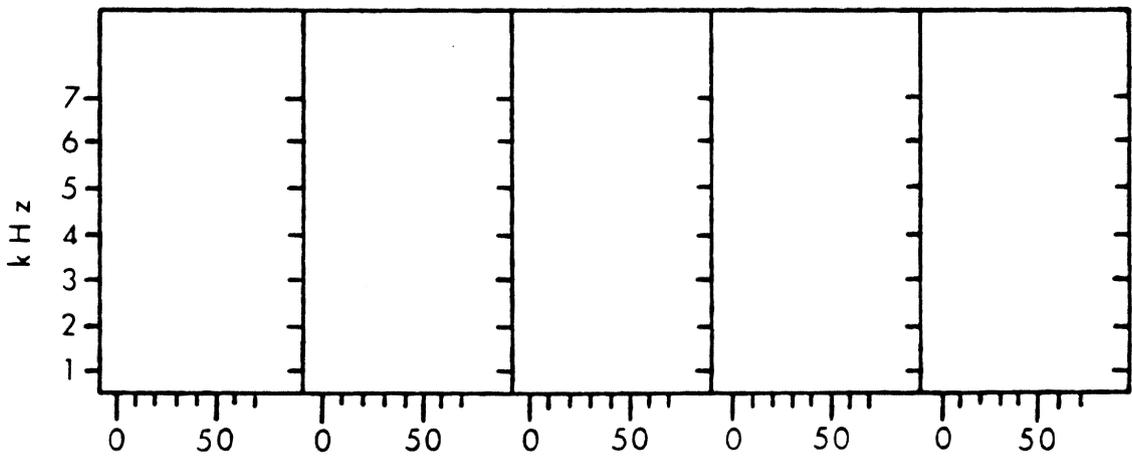
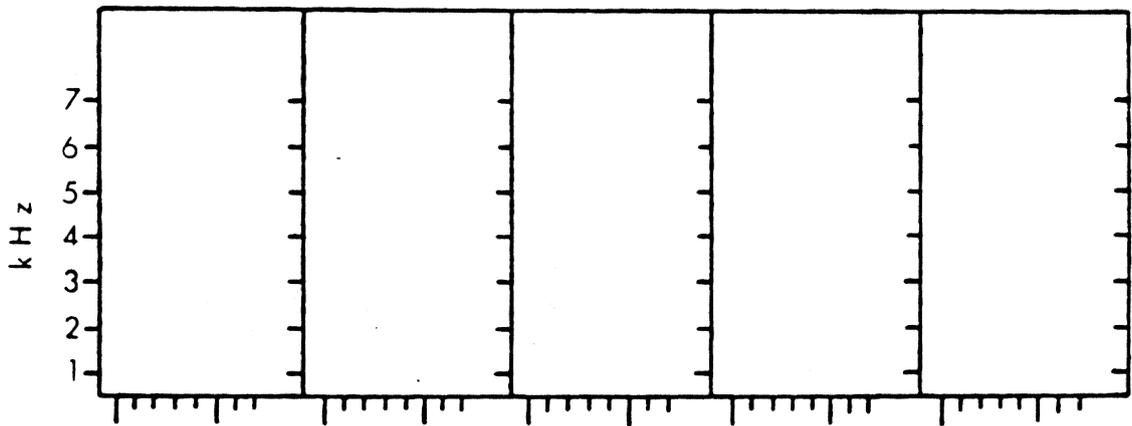
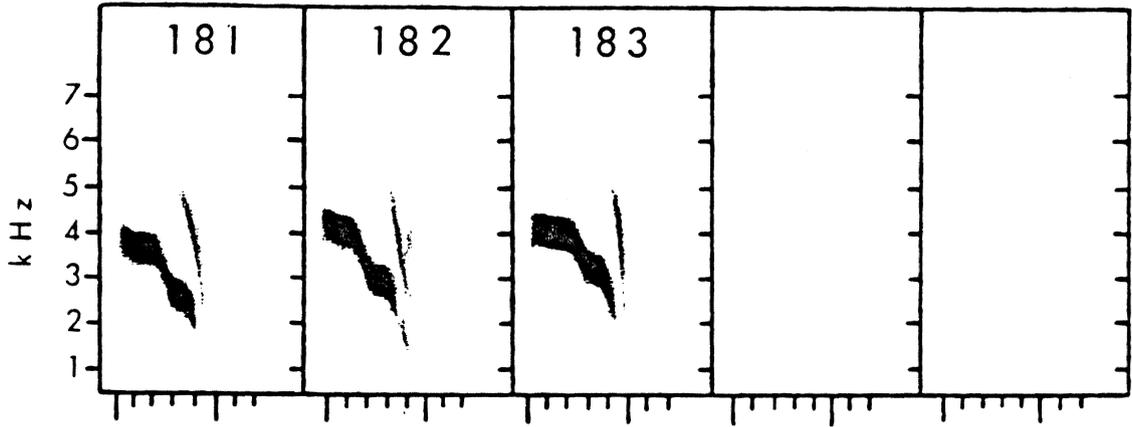




Milliseconds



Milliseconds



Milliseconds

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