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Geographic variation in song, morphology, and mitochondrial DNA in *Pardalotus striatus* in eastern Australia

Katz, Mary, Ph.D.

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U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

Geographic Variation In Song, Morphology, And Mitochondrial DNA In *Pardalotus striatus* In Eastern Australia

by

Mary Katz

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12/17/12
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Prof. D. Cooper, City College

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Prof F. Sheldon, Acad. Nat. Science Philadelphia

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The City University of New York

ABSTRACT

Geographic Variation In Song, Morphology, And Mitochondrial DNA In Pardalotus striatus In Eastern Australia

by

Mary Katz

Advisors: Dr. Robert F. Rockwell and Dr. Lester L. Short

Variation was investigated in this passerine species in a region where the ranges of three races (melanocephalus, substriatus, and ornatus) overlap. Birds were sampled at sites following a transect along the Great Dividing Range, between 17 and 32.5 degrees south latitude. Recordings were made of males singing near nest sites, and individuals were collected for analyses of plumage and mensural characters and mitochondrial DNA haplotype patterns.

Results of univariate analyses revealed general north-to-south clinal patterns for four song and four morphometric variables. Multivariate cluster analyses resulted in two major geographic clusters of localities by song, and three major clusters by morphology. Clustering of PC1 scores, derived from a principal components analysis of combined variables, resulted in three major geographic clusters. Analysis of mtDNA restriction fragment patterns revealed two geographically-distinct haplotype groups. All analyses

revealed two major clusters of localities, separated geographically by the McPherson Range.

Results suggested the following: 1) There was evidence for macrogeographic patterns in songs, based on the duration of the first song syllable. 2) Grouping of related mtDNA haplotypes indicated two mtDNA lineages, one southern and one northern, which probably diverged during a period of range disjunction and were now in secondary contact across approximately 450 km in southeastern Queensland. Differences in estimates of nucleotide diversity for these two lineages were comparable to differences in estimates for two forms of the Eastern Rosella (Platycercus adscitus and P. eximius), whose distributions overlap in approximately the same region. 3) Northern and southern stocks of P. striatus may have been isolated from each other due to fragmentation of eucalypt habitats during periods of severe aridity in the Plio-Pleistocene and earlier. 4) The McPherson Range and its rainforests have been a partial barrier to gene flow between northern and southern populations in this species. The contraction of the rainforest over the long term, and clearing and roadbuilding by humans in the surrounding eucalypt forests in this century, have presumably facilitated recontact.

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INTRODUCTION

Traditionally, studies of geographic variation in birds have been based on descriptions of external morphology in specimens from museum collections. However, existing collections have come to be considered inadequate for a thorough investigation of geographic variation (Baker 1985). Today, variation is often described from series freshly collected in the field and accompanied by tissues, song recordings, and behavioral and ecological data.

A goal of many early studies of geographic variation in birds was the identification and designation of subspecies. In recent analyses using multiple data sets, it has been shown that subspecies designations, based primarily on plumage characters, are not necessarily accurate descriptors of geographic variation (Ball et al. 1988; Barrowclough and Johnson 1988; Corbin and Wilkie 1988; Handford 1985; Zink 1983). However, many ornithologists believe that subspecies remain useful because they serve as markers of geographic forms that deserve further investigation (Gill 1982; Johnson 1982; Mayr 1982b; Zusi 1982).

This is the case for my study of geographic variation in Pardalotus striatus (Aves: Passeriformes) in eastern Australia, a region where three subspecies are known to breed and where hybrid zones among the subspecies have been identified by previous authors.

Forms of the Striated Pardalote are morphologically so distinct that they have been considered different species (Hindwood and Mayr 1946; Salomonsen 1961). However, the most recent classification considers these forms to be races of a single polytypic species (Schodde 1975, 1981). To date, taxonomic analysis has been based almost entirely on plumage characters and to a lesser extent on some mensural characters. Five forms have been distinguished by their plumages. Three of these forms (P. s. melanocephalus, P. s. substriatus, and P. s. ornatus) have distributions which overlap in eastern Australia. The map in Fig. 1 depicts this region of overlap, based on the range descriptions of Hindwood and Mayr (1946), Ford (1987b), and Pizzey (1980). (It should be noted that the complete ranges of these three forms have not been depicted.) Hybrid zones for ornatus and melanocephalus, ornatus and substriatus, and substriatus and melanocephalus have been described by Ford (1987). The major plumage differences among the three forms are summarized in Table 1. They are most readily distinguished from one another by their differences in degree of white striping on the crown and in the amount of white on the primaries (forming a broad patch or a narrow stripe, as illustrated in Fig. 2). P. s. melanocephalus has an all-black crown and a broad wing patch; substriatus has a striped crown and a broad wing patch; and ornatus has a striped crown and a narrow wing patch.

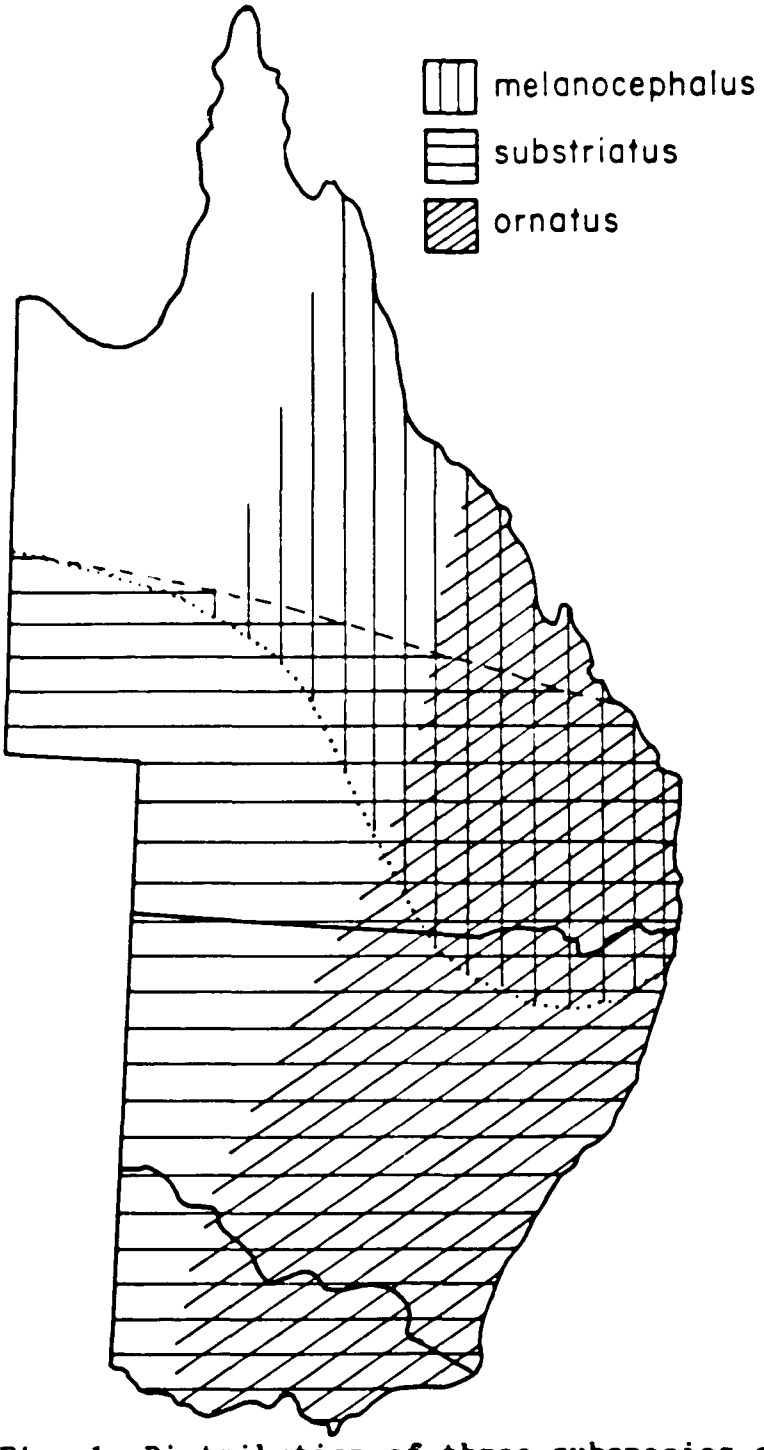


Fig. 1. Distribution of three subspecies of Pardalotus striatus in eastern Australia.

Table 1. Plumage differences among three forms of Pardalotus striatus found in eastern Australia.

Subspecies	Crown Striping	Wingspot	Primary edged in white								
			1	2	3	4	5	6	7	8	9
melanocephalus	-	crimson-red	+	+	+	+	+	+	+	-	+
			-	-							
substriatus	+	red-orange	+	+	+	+	+	+	+	-	+
			-	-							
ornatus	+	red-orange	-	-	-	-	-	+	+	-	+
							+	-			

Fig. 2. Museum skins of Pardalotus striatus from eastern Australia, illustrating two types of white pattern found on the primaries. The upper bird has a narrow stripe, typical of the form P. s. ornatus. The lower bird has a broad stripe or patch, typical of P. s. melanocephalus and P. s. substriatus.

Intergrades are known to exist for at least some of the plumage characters listed in Table 1. For example, in allopatric segments of their ranges, melanocephalus and substriatus are morphologically distinct. But some individuals from the zone of contact of these forms in Queensland have plumage patterns which are difficult to assess. The degree of crown striping can vary considerably, as illustrated by the series of specimens in Fig. 3. It is unclear whether individuals such as these represent hybridization among parental types or a cline in plumage pattern. A great degree of variation has been described, as well, for other plumage characters considered "diagnostic" for the three subspecies. For example, Woinarski et al. (1983) used six numerical indices simply to assess the amount of variation in the seven feathers of the wingspot. On the other hand, very few intergrades have been found for the character, white wing patch (Hindwood and Mayr 1946; Salomonsen 1961; Woinarski et al. 1983).

Based on plumage characters alone, the extent and pattern of intergredation, and the degree of introgression and hybridization (sensu Short 1969) in P. striatus, have remained unclear. In order to investigate variation in this species, in addition to plumage characters, I wanted to examine morphometric characters related to body size, and some patterns of variation in behavioral and genetic characters. Because differences in song among several

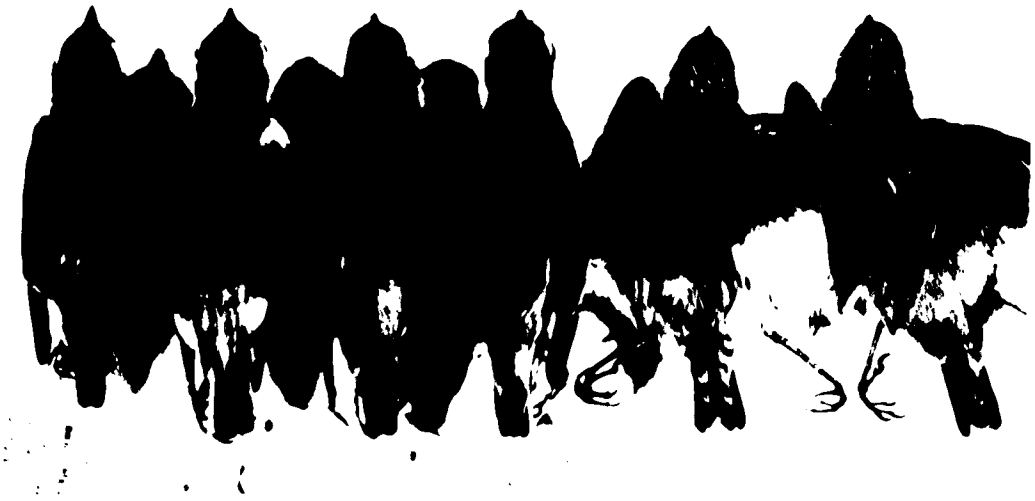


Fig. 3. Series of museum skins of Pardalotus striatus from eastern Australia, illustrating variation in the degree of white striping on the crown.

subspecies of P. striatus have been noted (Morse 1922; Hindwood and Mayr 1946)-- although this has been controversial (Serventy 1946; Cooper 1961; Sedgwick 1962; Nielsen 1962; Mees 1965)-- I decided to examine some characteristicss of the song for geographic variation. In addition, I decided to investigate patterns of variation in mitochondrial DNA (mtDNA) because mtDNA has appeared to offer greater resolving power than allozymes as a genetic marker at the species and subspecies level in birds (Avise and Zink 1988; Braun and Robbins 1986; Zink 1986; Zink 1991). To date, there have been only one or two studies of Australian species which have investigated geographic variation in song or which have utilized mtDNA. There have been no studies of Australian birds which have used three sets of characters in this manner.

There are numerous studies of macrogeographic variation in birdsong. Passerine species whose songs have been extensively studied include the White-crowned Sparrow (Zonotrichia leucophrys) (Marler and Tamura 1964; Baptista 1975; Baptista and King 1980; Baker 1975; Baker and Morton 1982; Baker et al. 1984); the Rufous-collared Sparrow (Zonotrichia capensis) (Nottebohm 1969, 1975); the House Finch (Carpodacus mexicanus) (Mundinger 1975, 1983; Bitterbaum and Baptista 1979); the Indigo Bunting (Passerina cyanea) (Thompson 1970; Shiovitz and Thompson 1970; Emlen 1971; Payne et al. 1981; Payne 1982, 1983); the Chaffinch

(Fringilla coelebs) (Slater and Ince 1979; Ince et al. 1980; Slater et al. 1980; Pickstock et al. 1980; Slater et al. 1984; Jenkins and Baker 1985); and the European Redwing (Turdus iliacis) (Bjerke 1982, 1984; Bjerke and Bjerke 1981). However, relatively few workers have compared patterns of geographic variation in song, with patterns of morphological or genetic variation (Baker 1975, 1982; Baker and Mewalt 1978; Baker et al. 1982; Handford and Nottebohm 1976; Johnson 1982; Balaban 1986; Miller 1986; Robbins et al. 1986; Pitocchelli 1990).

The American and European literature is extensive compared to the number of published studies of macrogeographic variation in the songs of Australian species. Although it is acknowledged that geographic variation in song exists for many Australian passerines, few scientific studies have been done (Pizzey 1980). A small number of authors has included descriptions of song in taxonomic studies (Zann 1976; Ford 1979, 1982; Short et al. 1983), while only one study has focussed on geographic variation (White 1987, in the Olive Whistler, Pachycephala olivacea).

With this in mind, in 1979 Short and Horne began an investigation of the songs of P. striatus, which included sampling in southeastern Queensland and northeastern New South Wales. They collected recordings of the songs of males at ten breeding sites in that region. I was able to

measure frequency and time components from sonagrams made from their recordings. Although samples were small ($n<4$) for each locality, the number of songs recorded per individual was relatively large (average $n=18$). Inspection of these sonagrams revealed three things. First, songs in this species were acoustically simple, compared to the songs of other species for which geographic variation had been analyzed. Second, the repertoires of individuals appeared to be restricted to single songs. And third, among repeats of single songs within individuals, variances were extremely low for the frequency and time variables measured; and the sonagrams appeared almost identical. I tested for stability of songs within individuals using a multivariate analysis of variance (SAS GLM/MANOVA) and Wilks' lambda as the test criterion on 74 songs from 6 individuals and 7 frequency and time variables. The variation among individuals was much greater than the variation within individuals ($F=84.31$, $p<0.001$). These three factors-- simplicity of the song, simplicity of individual repertoires, and stability of the song within individuals-- made *P. striatus* songs particularly suitable for quantitative analysis (Miller 1986).

The use of mtDNA as a tool in evolutionary studies has been reviewed by Avise *et al.* (1987), Moritz *et al.* (1987), and Quinn and White (1987). The molecular properties and rates of evolution of mtDNA have also been extensively

studied and reviewed (Avise and Lansman 1983; Lansman et al. 1983; Brown 1985; Brown et al. 1979; Wilson et al. 1985). The mtDNA molecule is considered a good marker for tracing genealogy because it is maternally inherited, does not undergo recombination, rarely exhibits heteroplasmy in vertebrates, and appears to be conservative in terms of gene content and arrangement (at least within taxonomic classes or phyla). In addition, although at times some mtDNA mutations must be considered to be subject to natural selection (Avise et al. 1987), most mtDNA variants are probably selectively neutral. Changes at certain nucleotide positions, presumed to be neutral and subject to random drift rather than selection, occur more often and become fixed in populations more rapidly in mtDNA than in nuclear DNA (Aquadro et al. 1984). Therefore, if population differentiation has occurred, it can be documented in terms of mtDNA sequence divergence. (This assumes low rates of dispersal in females. See Appendix II on dispersal and philopatry in P. striatus.)

As mentioned, intraspecific allozyme studies in birds have usually revealed little significant difference among populations or subspecies; while mtDNA has appeared to offer greater resolving power. Some species which have not exhibited geographic differentiation with respect to proteins, do show mtDNA differentiation. Differences in mtDNA haplotype patterns have been described for subspecies

of the Canada Goose (Shields and Wilson 1987b), Tufted Titmouse (Avise and Zink 1988), Seaside Sparrow (Avise and Nelson 1989, and Pacific Black Brant (Shields 1990); and for populations of the Fox Sparrow (Zink 1991). Surprisingly, some widespread species, such as the Red-winged Blackbird, the Common Grackle, and the Song Sparrow, which have morphologically-distinct subspecies, exhibit little allozyme or mtDNA differentiation (Ball et al. 1988; Zink 1991a; Zink et al. 1991b). However, mtDNA appears to be a good tool for discovering geographic partitioning when it exists.

One of the simplest methods used to assess mtDNA differences involves cleavage of purified mtDNA samples by restriction endonucleases, which recognize and cleave the molecule at particular base sequences, and resolution of the molecular fragments using gel electrophoresis (Lansman et al. 1981). Fragment profiles can then be compared among individuals and among populations. A variety of mathematical procedures, reviewed in Quinn and White (1987), have been devised which estimate nucleotide divergence from fragment patterns. The "fragment" method of Nei and Li (1979) involves pairwise comparisons of bands read directly from gels or autoradiographs. The greater the number of bands shared between samples, the more closely related the samples are taken to be. This particular version of the Nei-Li model is considered to be useful for intraspecific comparisons (Avise et al. 1987; Quinn and White 1987).

Without classifying individuals a priori as to subspecies designation or hybrid status, I tried to evaluate patterns of variation in plumage, morphometrics, song, and mitochondrial DNA in birds sampled across this region. I attempted to identify some of the important components of variation and to infer the evolutionary processes which might have shaped the observed geographic patterns.

In this study, I planned to examine the following questions:

Is there measurable geographic variation in song and morphology among populations of P. striatus? If geographic patterns are found, are these patterns congruent?

Can population structure in P. striatus be demonstrated using mtDNA? If so, how do the patterns of population differentiation relate to hypotheses concerning contact zones in this species?

Is there congruence or lack of congruence among the three sets of data, and what does this imply about the evolutionary processes that have shaped the patterns of variation?

Does subspecies classification, which has traditionally been based on plumage patterns, coincide with classification criteria based on song, morphometrics or mtDNA?

Can known contact (or hybrid) zones between forms of P. striatus be more clearly delineated? Can the patterns of

variation found in this zone help to explain the population dynamics there?

FORMAT OF THE THESIS

Some comments are given here on the format of the rest of the thesis. Appendix I and II contain information on the taxonomy and the ecology and behavior of P. striatus. These appendices are not comprehensive, but are intended to provide background information pertinent to this study. Interested readers might want to look at those sections first. The sections which follow are Materials and Methods and four Results sections. The Materials and Methods section contains a complete summary of methods. However, certain details of statistical methods have been included or reiterated in the Results sections, wherever I felt that this made for a more logical or readable presentation. The results are discussed together in a single Discussion section.

MATERIALS AND METHODS

Field work for this study was carried out in Australia in 1987, 1988, and 1989, during the breeding seasons for Striated Pardalotes. Songs of males were recorded in all three years. Collecting permits were obtained in 1988 and 1989 from both the Queensland and the New South Wales National Parks and Wildlife Services. In those years, songs were recorded and the males were then collected. The collecting limit was five birds per locality each year. If I was able to find more than five males at nest sites in a particular locality, I recorded their songs (in addition to the songs of the collected birds). During the 1989 field season, I also preserved soft tissues for mtDNA analysis.

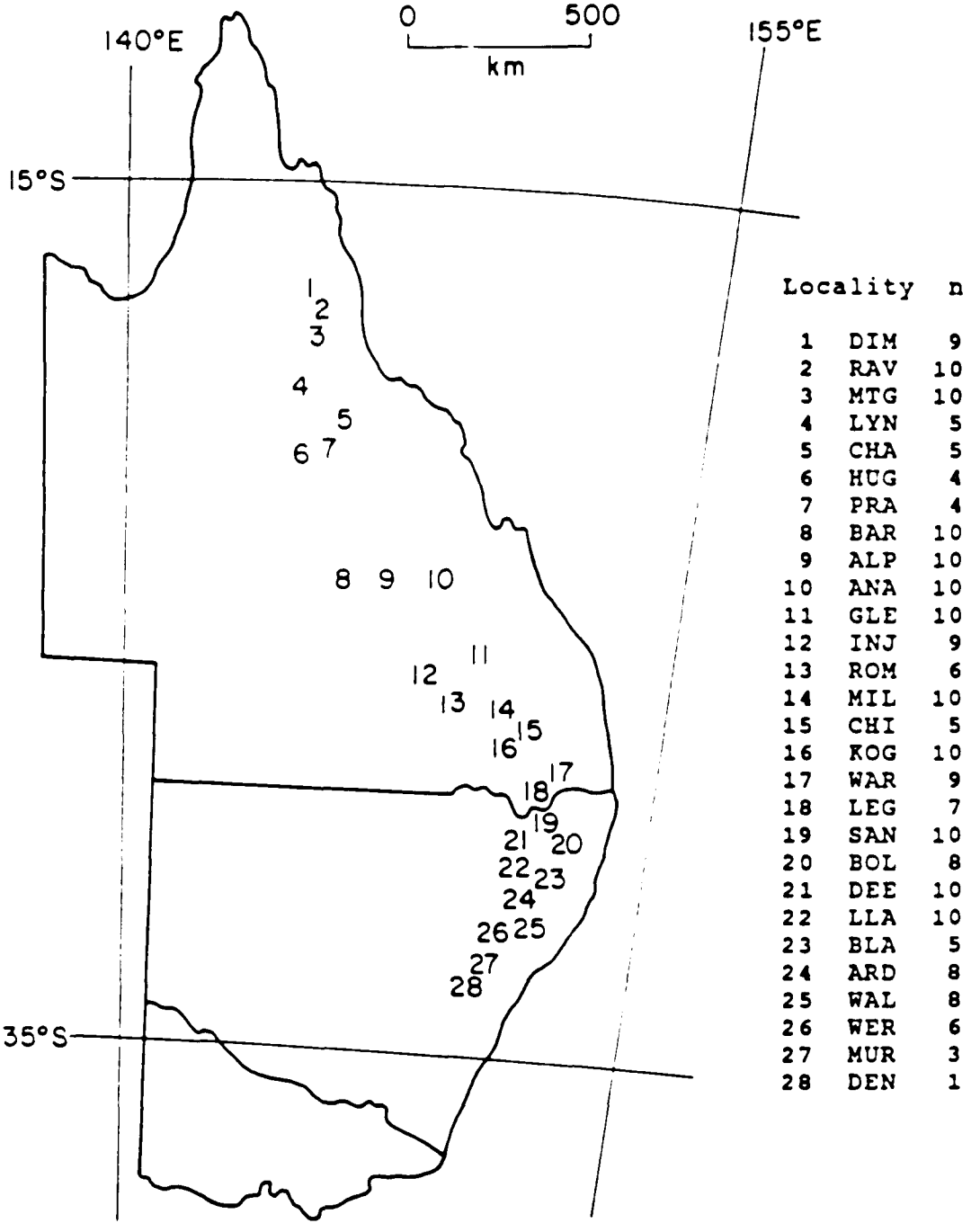
Localities were sampled along a north-south line roughly following the Great Dividing Range, for a distance of about 1800 kilometers, between 140-152 E longitude and 17-32.5 S latitude. The sampling area transects the eastern parts of the ranges of three subspecies of P. striatus and the region of their overlap (Fig. 1). Sample sites are listed in Table 2. In order to indicate to the reader as simply as possible the relative geographic positions of these sites, I have numbered them roughly from north to south. Thus, each locality is designated by a number, as well as by a three-letter abbreviation for its name. As an example, the northernmost locality, which is Dimbulah,

Table 2. Localities where specimens of Pardalotus striatus were recorded and collected. Each locality is designated by a number and a 3-letter code. An "s" included in the locality number indicates that songs were recorded there, but no birds were collected.

Locality	Number	Code	Latitude	Longitude
Dimbulah	1	DIM	17.1	145.8
Ravenshoe	2	RAV	17.4	146.0
Mt. Garnet	3	MTG	17.4	145.8
Innott Hot Springs	4s	INN	17.4	145.9
The Lynd	4	LYN	18.3	144.2
Charters Towers	5	CHA	20.0	146.7
Hughenden	6	HUG	21.5	144.0
Prairie	7	PRA	21.5	144.8
Barcaldine	8	BAR	23.5	145.3
Alpha	9	ALP	23.5	146.8
Anakie	10	ANA	23.5	148.2
Emerald	10s1	EME	23.5	148.4
Moura	10s2	MOU	24.1	150.0
Glebe Weir	11	GLE	25.2	150.0
Injune	12	INJ	25.4	147.4
Roma-Injune Road	12s	RNJ	25.9	148.0
Roma	13	ROM	26.7	148.6
Miles	14	MIL	26.8	150.0
Chinchilla	15	CHI	26.9	150.4
Riverside Station	15s1	RIV	27.0	150.5
Callitris Station	15s2	CAL	27.0	150.1
Condamine	15s3	CON	27.1	148.6
Kogan	16	KOG	27.1	150.7
Toowoomba	16s	TOO	27.6	151.9
Warwick	17	WAR	28.2	152.0
Lamington Ntl.Pk.	17s	LAM	28.5	152.3
Legume	18	LEG	28.5	152.1
Moorabinda Stn.	18s	MOO	29.0	151.4
Sandy Flat	19	SAN	29.2	152.0
Bolivia	20	BOL	29.3	152.0
Deepwater	21	DEE	29.4	151.7
Llangothlin	22	LLA	30.2	151.5
Black Mountain	23	BLA	30.3	151.3
Newholme Res. Stn.	24s	NEW	30.4	151.4
Arding	24	ARD	30.5	151.3
Walcha	25	WAL	30.8	151.2
Apsley Gorge N.P.	25s	APS	30.9	151.6
Werris Creek	26	WER	31.3	150.0
Murrurundi	27	MUR	31.8	150.2
Denman	28	DEN	32.5	149.9

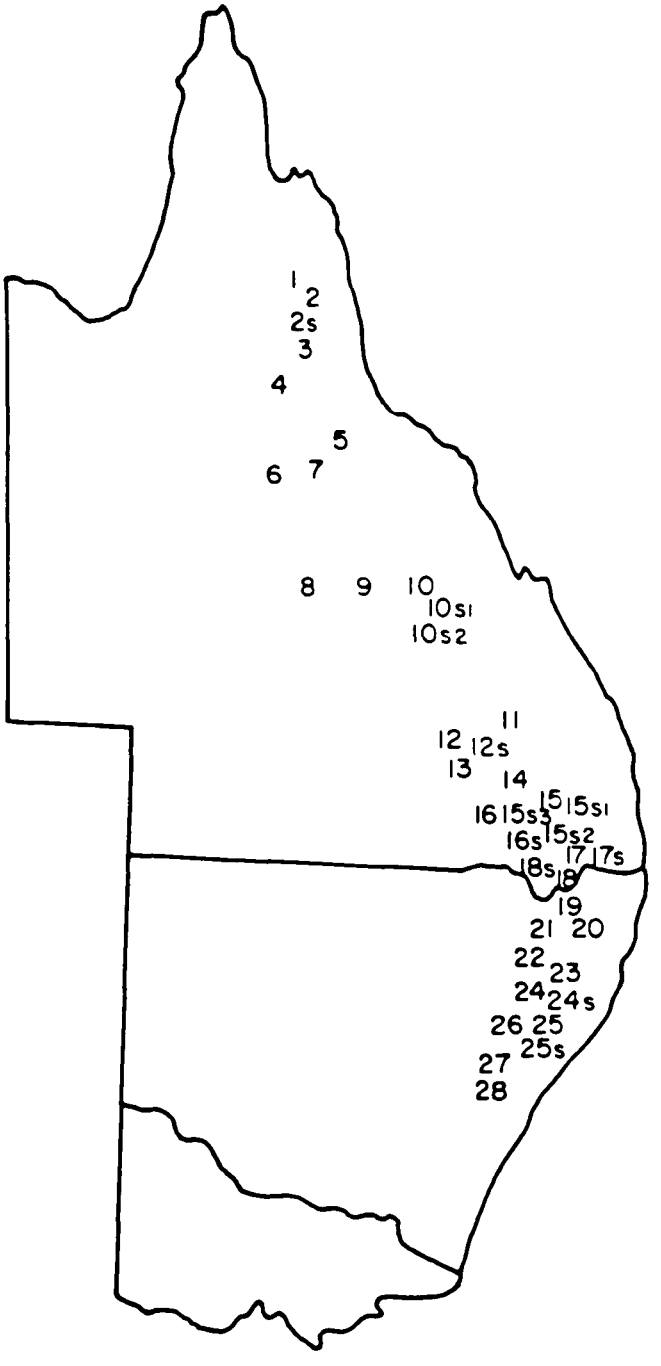
Queensland, is designated "1 DIM". When an "s" follows the locality number, it indicates that songs were recorded for birds in that locality but no specimens were collected there. For example, "25s APS" is the locality Apsley Gorge National Park, New South Wales, where I was permitted to record but not collect birds. The 28 localities shown on the map in Fig. 4 are localities where birds were *both* recorded and collected. The map in Fig. 5 depicts *all* localities where individuals were recorded (whether they were collected or not), and includes localities with "s" designations where specimens were not collected. Although the two maps obviously include some of the same localities, they are representative of two sets of data which I analyzed separately: 1) one set of 345 birds for which there is song data only; and 2) a subset of 210 of those birds, which were collected, and for which there is both song and morphological data.

Most of these localities are in uplands. In a line from north to south, they transect some of the major landform provinces reviewed by Wasson (1982). These are the southern part of the Peninsula Uplands, the Burdekin Uplands, the Fitzroy Uplands, New England, and the Moreton Uplands. A few localities in Queensland are situated in the eastern part of the Central Lowlands province. Before it was cleared for grazing and agriculture, much of this region was forest of some kind, and included patches of rainforest,



Locality		n
1	DIM	9
2	RAV	10
3	MTG	10
4	LYN	5
5	CHA	5
6	HUG	4
7	PRA	4
8	BAR	10
9	ALP	10
10	ANA	10
11	GLE	10
12	INJ	9
13	ROM	6
14	MIL	10
15	CHI	5
16	KOG	10
17	WAR	9
18	LEG	7
19	SAN	10
20	BOL	8
21	DEE	10
22	LLA	10
23	BLA	5
24	ARD	8
25	WAL	8
26	WER	6
27	MUR	3
28	DEN	1

Fig. 4. Localities in eastern Australia where Pardalotus striatus specimens were collected for this study. Each locality is designated by a number and 3-letter abbreviation, which is used throughout the text. The number of specimens collected at each locality is also shown.



Locality		n
1	DIM	17
2	RAV	16
2s	INN	3
3	MTG	12
4	LYN	5
5	CHA	6
6	HUG	4
7	PRA	4
8	BAR	22
9	ALP	11
10	ANA	9
10s1	EME	3
10s2	MOU	3
11	GLE	9
12	INJ	6
12s	RNJ	3
13	ROM	7
14	MIL	11
15	CHI	11
15s1	RIV	10
15s2	CAL	13
15s3	CON	4
16	KOG	16
16s	TOO	5
17	WAR	13
17s	LAM	12
18	LEG	14
18s	MOO	13
19	SAN	10
20	BOL	9
21	DEE	9
22	LLA	10
23	BLA	5
24	ARD	8
24s	NEW	5
25	WAL	11
25s	APS	5
26	WER	3
27	MUR	4
28	DEN	4

Fig. 5. Localities in eastern Australia where songs of Pardalotus striatus were recorded. Each locality is designated by a number and three-letter abbreviation. Localities where songs were recorded but no specimens were taken are indicated by an "s", "s1", etc.

open and closed types of Eucalyptus forest and woodland, and some semi-arid shrub woodland (Williams 1982). Almost all of the localities I sampled are nowadays sheep and cattle stations or farms, with strips of woodland remaining as hedgerows between fields and paddocks or as edges along water courses and roads.

In order to locate birds in the field, I looked first for nest sites which might be attractive to this species. These sites proved to be easy to find, and pardalotes were almost always immediately heard in the vicinity of these sites. Effort was made to identify breeding (or potentially-breeding) males by their behavior, which included singing from perches near nest holes, acting aggressively toward other males, and successfully attracting females to the nest sites.

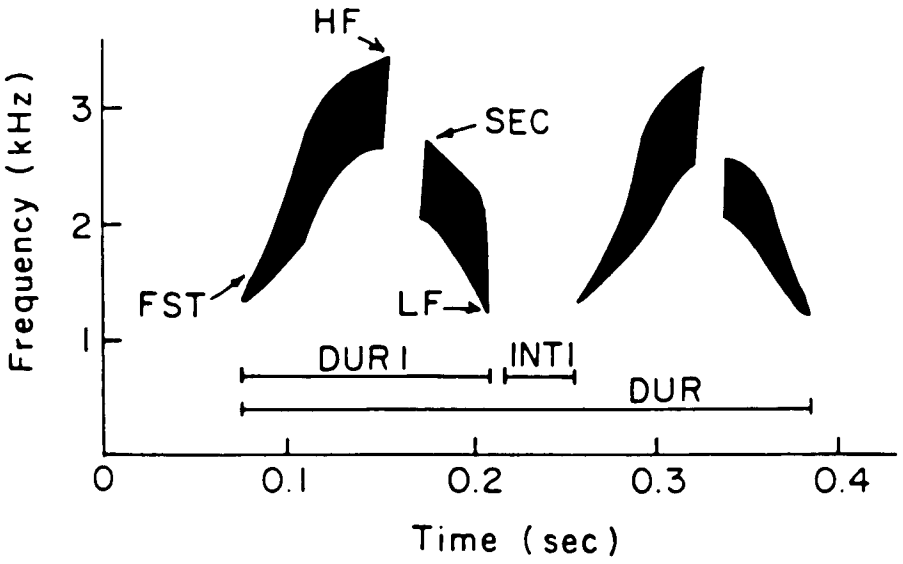
The songs of these males were recorded using a Marantz PMD-221 monaural cassette tape recorder, a Dan Gibson 24" parabola, and a Sennheiser ME80 electret microphone. All recordings were made on TDK high bias 70ms chrome oxide tapes, which were stored in a styrofoam cooler in the field. Several seconds of a 4 kHz tone from a pitchpipe were recorded on each tape, to allow for correction in the lab of any frequency distortion that can sometimes occur with cassette tapes.

Males were recorded as they sang from perches near nest holes. Recording distances varied from about 1 to 10

meters. An individual was recorded usually for a minimum of one singing "bout" -- that is, for as long as he sang continuously from the perch, before flying away. Thus, recordings for a few individuals contain only single songs, while some song samples are several minutes long and contain several hundred repeats of the songs. Playback was never used to elicit singing.

I attempted to determine whether an individual's song varied from year to year. In two localities in 1987, I trapped and color-banded 7 males. I was able to re-record 6 of these banded birds at the same localities in 1988.

From the field recordings, sound spectrograms were made on a Kay Elemetrics 6061 Sona-Graph machine at the American Museum of Natural History. Wide-band settings were used. Frequency and time variables were measured directly from the spectrograms of songs of 345 males. Fig. 6 illustrates these variables, which were: 1) the number of syllables in the song; 2) the highest frequncy of the first syllable; 3) the lowest frequency of the first syllable; 4) the frequency of the second highest peak in the first syllable, if there was a second peak; 5) whether the song began as an ascent from lower to higher frequency, or as a descent from higher to lower; 6) the duration of the first syllable; 7) the duration of the entire song; 8) the interval between the first and second syllable, if the song had more than one syllable; and 9) the interval between the second and third



SYLL	Number of syllables in the song
HF	Highest frequency of the first syllable
LF	Lowest frequency of the first syllable
FST	First sound ascending, or descending?
SEC	Frequency of the second highest peak in the first syllable (when it exists)
DUR1	Duration of the first syllable
INT1	Duration between the first and second syllables of the song
INT2	Duration between the second and third syllables of the song
DUR	Duration of the song

Fig. 6. Song variables which were measured for this study. For the particular song illustrated above, the variable SYLL = 2 and the variable INT2 has no value.

syllables, if the song had more than two syllables.

Fig. 7 illustrates the way in which the variable "syllable number" was interpreted. 1-, 2-, 3-, and 4-syllable songs of different males are shown. I considered a syllable to be comprised of a sound that was continuous to my ear. The tracing on the spectrogram did not have to look continuous for this to be the case. For example, the song of Male 0201 is classified as a 1-syllable song and sounds like a sliding "wheeo." The 2-syllable song of Male 0180 sounds like "tchoo tchoo." The 4-syllable song of Male 0152 is a clipped "chip-chip chip-chip."

Fig. 7 also illustrates how simple the songs of this species are. Each of the spectrograms shown is the full song, and the only song, of that male. These songs are often repeated for many minutes at a time.

All recordings from this study were transferred to high quality reel-to-reel tapes and deposited in the archive of The Library of Natural Sounds of The Laboratory of Ornithology of Cornell University in Ithaca, New York. The LNS catalog numbers are 46621-46823, 48377-48399, and 48427-48540.

Immediately after its song was recorded, a bird was collected and its skin was prepared in the field. Prior to preparation, the following measurements were taken within several hours of collection of the bird. Weight was taken using a Pesola scale. Other measurements were taken with

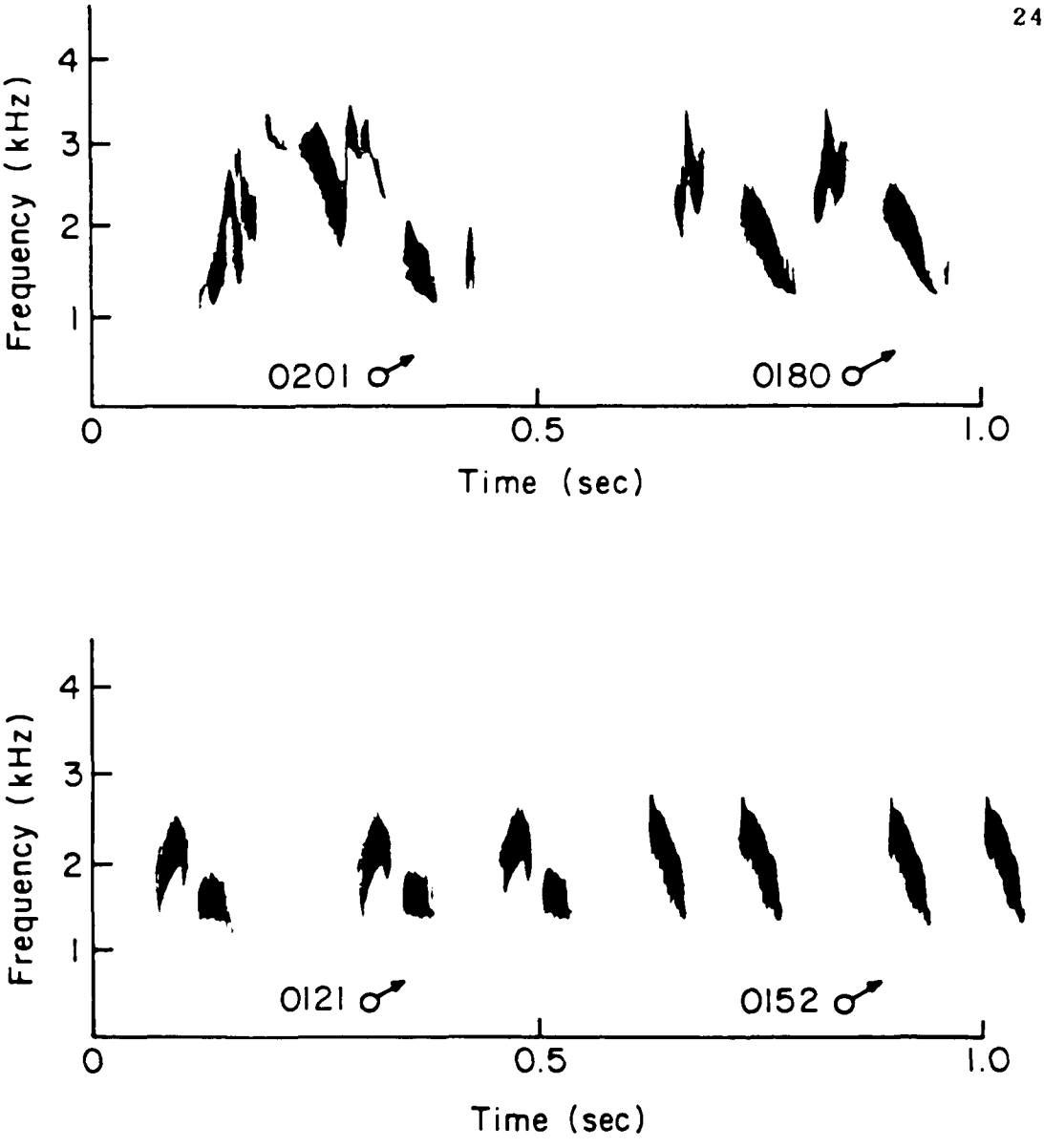


Fig. 7. Examples of 1-, 2-, 3-, and 4-syllable songs of Pardalotus striatus males.

either dial calipers or with a wing ruler. Wing length was measured as length of the unflattened chord. Wingspan was measured from tip to tip of the longest primary on each side, with the specimen on its back and with its wings spread naturally. Tail length was measured as the distance from the base between the insertions of the two center rectrices to the tip of the longest rectrix. Culmen length was measured as the distance from the base of feathers at the head to the tip of the upper mandible. Tarsus length was measured as the length of the tarsometatarsus from proximal joint with the tibiotarsus to the first scute of the middle toe.

The following additional characters were also recorded in the field, during preparation of the specimen: the colors of iris, gape, bill, legs, and plumages of rump, wingspot, lores, and edging on the secondaries; the extent of white striping on the crown feathers; and the number of primaries edged in white. An index was used to score individuals on four of the plumage characters (primary white, crown striping, wingspot color, and secondary-edge color). Degree of fat, state of molt, and size of testes were also noted.

Liver, heart, and muscle tissues were recovered from specimens collected in the third field season. Tissues were frozen in liquid nitrogen in the field and stored at -70C in the laboratory, until mitochondrial DNA (mtDNA) could be isolated from them. The biochemical work was completed in

1990 at The Philadelphia Academy of Natural Sciences. MtDNA was isolated, purified, and cleaved by restriction enzymes using procedures described by Lansman et al. (1981), Spolsky and Uzzell (1984) and Mack et al. (1986).

Briefly, the isolation and purification procedures involved homogenization and centrifugation of the tissue to produce a crude mtDNA extract; purification of the crude extract by a series of phenol and chloroform extractions; removal of RNA and proteins with RNAse and proteases; and final precipitation with ethanol. Digestions of purified mtDNA from a limited number of samples were performed using 13 commercially-prepared endonucleases, following specifications of the supplier (Bethesda Research Laboratories). It was determined that the enzymes Ava I and Hae II were good indicators of differences among samples, and subsequently all samples were treated with these two enzymes. Several samples from different geographic areas were treated with additional informative enzymes (BamH I, EcoR V, Hinc II, Hind III, Nde I, Pst I, and Pvu I). Restriction fragments were end-labelled with a ^{32}P nuclide and separated by electrophoresis on horizontal 1% agarose gels. A standard lambda phage 1kb ladder was included on each gel, so that fragment sizes could be determined. Autoradiographs were made from the gels; these were photographed.

The size of the mtDNA molecule for this species was

estimated by averaging the sums of fragment lengths obtained from different sample runs on the gels. Haplotypic diversity, average nucleotide diversity, and average nucleotide differences among populations were estimated, using the formulas of Upholt (1977), Nei and Li (1979), Nei and Tajima (1981), and Nei (1987). A summary of the mathematics involved is given in Appendix VII. The rate of evolution in mtDNA calculated by Shields and Wilson (1987a) was used to estimate the amount of time that two mtDNA clonal groups in P. striatus would have been isolated, prior to secondary contact.

I examined all specimens of P. striatus in the collections of the American Museum of Natural History, Australian National Wildlife Collection, Australian Museum, Queensland Museum, South Australian Museum, and Western Australia Museum. 182 of these specimens were adult males collected during likely breeding periods for this species. These birds were measured for wing, tail, tarsus, and culmen lengths, and assessed for degree of crown streaking, wingspot color, and number of primaries edged in white. Weight, body length, and wingspan were also recorded if these measurements were available from the specimen tag. An attempt was made to find geographic samples large enough to supplement samples collected for this study.

Prior to statistical analysis, an index was devised to score individual specimens for plumage characters. Colors

of leg, iris, bill, and gape were virtually the same for all specimens. I was unable to assess rump color consistently, so this character was not indexed. The following indices were used: wingspot color, 0-4 (0=crimson, 1=scarlet-crimson mix, 2=scarlet, 3=scarlet-orange mix, 4=orange); crown striping, 0-4 (0=all black crown, 1=hindcrown partly striped, 2=hindcrown completely striped, 3=midcrown partly striped, 4=completely striped crown); secondary edge color, 0-3 (0=white, 1=white-buff or white-chestnut with white predominant, 2=chestnut-white or chestnut-buff with chestnut predominant, 3=chestnut); primary white 0-1 (0=broad white patch, with primaries 1 to 6 or 7 edged in white; 1=intermediate, with primaries 1 to 3, 4, or 5 edged in white; 2=narrow white stripe, with primaries 1 or 1 and 2 only edged in white).

Statistical analyses of the data were performed using a variety of programs in SAS (1985, Version 5) and NTSYS-PC (1990, Version 1.60). Simple descriptive statistics were computed for morphological and song variables for each locality. Tests for multiple comparisons of means (SAS PROC GLM/GT2) were performed on all variables, and results were visualized on maps in the manner used by Sokal and Rinkel (1963).

Discriminant function analyses (SAS PROC DISCRIM) were used to determine whether classifications of specimens by song and morphological variables corresponded to subspecies

classifications based on traditional plumage characters.

Several methods were used to derive phenograms that clustered localities according to the similarity of means among samples. Distance matrices were derived for morphometric, plumage, and song variables and used to construct separate phenograms for these three data sets (Sneath and Sokal 1973). I ran both SAS PROC CLUSTER and NTSYS SIMINT and SAHN programs for constructing UPGMA phenograms. These programs use slightly different clustering algorithms, but each is based on agglomerative hierarchical clustering (Sneath and Sokal 1973). The programs NTSYS COPH and MXCOMPG were used to derive cophenetic correlation coefficients for each of these phenograms, to test the goodness of fit of the phenogram to the set of data (Rohlf and Sokal 1981).

Principal components analyses (SAS PROC PRINCOMP) were also applied to matrices of song variables, morphometric variables, and song and morphometric variables combined. Since it was found that the first principal component (PC1) accounted for a large proportion of the variance in each of these analyses, and since localities appeared to demonstrate a geographic pattern when ordered by standardized PC1 scores, a distance matrix and a phenogram based on the scores were derived for each of the three PCA's. In addition, localities were plotted by map distance (km) and mean PC1 score to look for geographic regions of steep

changes in scores, which would be an indication of increased variability in that region.

I described similarity among data sets in several ways. First, map distances among localities were compared with distances derived from the phenograms for song and morphological data. Second, Mantel's (1967) test was used to describe the similarity in overall structure between each pair of distance matrices (for plumage, morphometric, song, and PC1 matrices). Third, major geographic clusters were identified from the phenograms and compared qualitatively with each other and with geographic clusters inferred from the mtDNA data.

Possible interpretations of the observed geographic patterns are discussed.

SONG RESULTS

The results presented in this section are for the univariate and multivariate analyses of measurements made from the sonagrams of songs of 345 males recorded in 40 localities. In addition, the results of multivariate analyses of the songs of the subset of 210 collected males are presented, which will later be compared with the results of morphological analyses for those birds. Reproductions of the sonagrams of all songs used for these analyses are presented in Appendix V.

As in the preliminary analysis of the data of Short and Horne, I again tested for the stability of songs within individuals using the same multivariate analysis of variance (SAS GLM/MANOVA) and Wilks' lambda as the test criterion. I used a subsample of 100 songs of 10 males and the song variables SYLL, HF, LF, SEC, DUR1, and DUR. Variation among individuals was again shown to be significantly greater than within individuals ($F=59.6$, $p<0.001$).

Descriptive statistics, by locality, for each of the song variables measured are presented in Tables 3-10. Sample size, mean, standard deviation, minimum value, maximum value, variance, standard error, and coefficient of variation are given. The variables INT1, INT2, and SEC (intervals between first and second, or between second and third syllables, and highest frequency in second peak of first syllable) were not applicable to all songs; and the

sample sizes listed reflect this. Correlations of means with latitude were also tested.

The following observations can be made from these tables. Songs were comprised of from 1 to 4 syllables. The range for mean highest frequency in the first syllable was 2.2-3.6 kHz; for lowest frequency, 0.7-1.6 kHz; for duration of the first syllable, 0.03-0.46 sec; and for duration of the entire song, 0.13-0.57 sec. Mean number of syllables in the song (Table 3) decreased for samples from southern localities. Correlation of mean syllable number with latitude was significant (Pearson product-moment correlation coefficient $r=-0.543$, $p<.01$). Mean duration of the first syllable (Table 6) appeared to increase from north to south. Means of this variable were also significantly correlated with latitude (Pearson product-moment correlation coefficient $r=0.60$, $p<.01$).

Mean coefficients of variation (CV) for all song variables, computed over all localities, are given in Table 11. CV's were found to be of the same order of magnitude as CV's for song measurement variables in 17 of 23 species compiled by Miller (1986). Duration measures in the songs of all of these species had a greater degree of variability than frequency measures. Regressions of mean CV's of frequency and time variables on latitude were not significant ($p>.05$), indicating that there were no general increases or decreases in variability from north to south in

Table 3. Descriptive statistics for song variable SYLL, number of syllables in song.

LOC		N	MEAN	SD	MIN	MAX	VAR	SE	CV
1	DIM	17	3.18	0.39	3.00	4.00	0.15	0.10	12.37
2	RAV	16	2.00	0.00	2.00	2.00	0.00	0.00	0.00
2s	INN	3	2.00	0.00	2.00	2.00	0.00	0.00	0.00
3	MTG	12	2.92	0.29	2.00	3.00	0.08	0.08	9.90
4	LYN	5	1.80	0.45	1.00	2.00	0.20	0.20	24.85
5	CHA	6	3.50	0.84	2.00	4.00	0.70	0.34	23.90
6	HUG	4	3.50	1.00	2.00	4.00	1.00	0.50	28.57
7	PRA	4	2.50	1.00	2.00	4.00	1.00	0.50	40.00
8	BAR	22	2.36	0.79	2.00	4.00	0.62	0.17	33.40
9	ALP	11	2.00	0.00	2.00	2.00	0.00	0.00	0.00
10	ANA	9	2.78	0.83	1.00	4.00	0.69	0.28	30.00
10s1	EME	3	3.00	0.00	3.00	3.00	0.00	0.00	0.00
10s2	MOU	3	3.00	0.00	3.00	3.00	0.00	0.00	0.00
11	GLE	9	2.44	0.53	2.00	3.00	0.28	0.18	21.56
12	INJ	6	3.00	0.00	3.00	3.00	0.00	0.00	0.00
12s	RNJ	3	2.67	0.58	2.00	3.00	0.33	0.33	21.65
13	ROM	7	2.29	0.49	2.00	3.00	0.24	0.18	21.35
14	MIL	11	2.18	0.40	2.00	3.00	0.16	0.12	18.54
15	CHI	11	2.00	0.00	2.00	2.00	0.00	0.00	0.00
15s1	RIV	10	2.10	0.32	2.00	3.00	0.10	0.10	15.06
15s2	CAL	13	2.00	0.00	2.00	2.00	0.00	0.00	0.00
15s3	CON	4	2.25	0.50	2.00	3.00	0.25	0.25	22.22
16	KOG	16	2.00	0.00	2.00	2.00	0.00	0.00	0.00
16s	TOO	5	2.80	0.45	2.00	3.00	0.20	0.20	15.97
17	WAR	13	2.00	0.00	2.00	2.00	0.00	0.00	0.00
17s	LAM	12	3.00	0.00	3.00	3.00	0.00	0.00	0.00
18	LEG	14	1.79	0.80	1.00	3.00	0.64	0.21	44.90
18s	MOO	13	2.00	0.00	2.00	2.00	0.00	0.00	0.00
19	SAN	10	1.00	0.00	1.00	1.00	0.00	0.00	0.00
20	BOL	9	1.11	0.33	1.00	2.00	0.11	0.11	30.00
21	DEE	9	1.33	0.50	1.00	2.00	0.25	0.17	37.50
22	LLA	10	1.00	0.00	1.00	1.00	0.00	0.00	0.00
23	BLA	5	1.00	0.00	1.00	1.00	0.00	0.00	0.00
24	ARD	8	1.25	0.71	1.00	3.00	0.50	0.25	6.57
24s	NEW	5	1.00	0.00	1.00	1.00	0.00	0.00	0.00
25	WAL	11	1.55	0.93	1.00	3.00	0.87	0.28	60.45
25s	APS	5	1.20	0.45	1.00	2.00	0.20	0.20	7.27
26	WER	3	1.67	0.58	1.00	2.00	0.33	0.33	4.64
27	MUR	4	1.00	0.00	1.00	1.00	0.00	0.00	0.00
28	DEN	4	2.00	0.00	2.00	2.00	0.00	0.00	0.00

Table 4. Descriptive statistics for the song variable HF, highest frequency in first syllable of the song (kHz).

LOC		N	MEAN	SD	MIN	MAX	VAR	SE	CV
1	DIM	17	2.79	0.26	2.40	3.20	0.07	0.06	9.31
2	RAV	16	2.86	0.15	2.60	3.10	0.02	0.04	5.39
2s	INN	3	3.33	0.06	3.30	3.40	0.00	0.03	1.73
3	MTG	12	2.74	0.20	2.40	3.10	0.04	0.06	7.37
4	LYN	5	2.86	0.31	2.40	3.20	0.10	0.14	10.95
5	CHA	6	2.87	0.19	2.70	3.10	0.03	0.08	6.49
6	HUG	4	2.80	0.08	2.70	2.90	0.01	0.04	2.92
7	PRA	4	2.77	0.19	2.50	2.90	0.04	0.09	6.82
8	BAR	22	2.74	0.23	2.30	3.10	0.05	0.05	8.25
9	ALP	11	2.75	0.12	2.60	2.90	0.01	0.04	4.41
10	ANA	9	2.73	0.29	2.30	3.10	0.09	0.10	10.67
10s1	EME	3	2.57	0.06	2.50	2.60	0.00	0.03	2.25
10s2	MOU	3	2.63	0.23	2.50	2.90	0.05	0.13	8.77
11	GLE	9	2.91	0.31	2.50	3.30	0.10	0.10	10.79
12	INJ	6	2.93	0.24	2.50	3.20	0.06	0.10	8.26
12s	RNJ	3	2.63	0.23	2.50	2.90	0.05	0.13	8.77
13	ROM	7	2.80	0.20	2.50	3.00	0.04	0.08	7.14
14	MIL	11	2.94	0.25	2.50	3.20	0.06	0.07	8.38
15	CHI	11	2.86	0.23	2.40	3.20	0.05	0.07	8.00
15s1	RIV	10	2.70	0.34	2.40	3.40	0.12	0.11	12.59
15s2	CAL	13	2.86	0.27	2.50	3.20	0.07	0.07	9.30
15s3	CON	4	2.87	0.19	2.60	3.00	0.04	0.09	6.58
16	KOG	16	2.76	0.26	2.20	3.20	0.07	0.07	9.55
16s	TOO	5	2.74	0.11	2.60	2.90	0.01	0.05	4.16
17	WAR	13	3.07	0.33	2.50	3.50	0.11	0.09	10.84
17s	LAM	12	2.77	0.22	2.50	3.20	0.05	0.06	7.85
18	LEG	14	3.00	0.20	2.50	3.30	0.04	0.05	6.79
18s	MOO	13	3.05	0.33	2.60	3.60	0.11	0.09	10.75
19	SAN	10	3.13	0.29	2.50	3.40	0.08	0.09	9.17
20	BOL	9	3.13	0.21	2.90	3.50	0.05	0.07	6.77
21	DEE	9	3.04	0.24	2.50	3.30	0.06	0.08	7.90
22	LLA	10	3.16	0.20	2.90	3.50	0.04	0.06	6.36
23	BLA	5	3.16	0.23	2.90	3.40	0.05	0.10	7.29
24	ARD	8	3.06	0.20	2.90	3.30	0.04	0.07	6.52
24s	NEW	5	2.90	0.16	2.70	3.10	0.02	0.07	5.45
25	WAL	11	3.07	0.21	2.80	3.40	0.04	0.06	6.68
25s	APS	5	3.16	0.09	3.10	3.30	0.01	0.04	2.83
26	WER	3	2.77	0.21	2.60	3.00	0.04	0.12	7.52
27	MUR	4	3.00	0.12	2.90	3.10	0.01	0.06	3.85
28	DEN	4	2.90	0.22	2.60	3.10	0.05	0.11	7.45

Table 5. Descriptive statistics for song variable LF, lowest frequency of first song syllable (kHz).

LOC		N	MEAN	SD	MIN	MAX	VAR	SE	CV
1	DIM	17	1.08	0.08	0.90	1.20	0.01	0.02	7.72
2	RAV	16	1.13	0.10	1.00	1.40	0.01	0.03	8.97
2s	INN	3	1.37	0.06	1.30	1.40	0.00	0.03	4.22
3	MTG	12	1.07	0.07	1.00	1.20	0.00	0.02	6.11
4	LYN	5	1.18	0.18	1.10	1.50	0.03	0.08	15.16
5	CHA	6	1.25	0.10	1.10	1.40	0.01	0.04	8.39
6	HUG	4	1.10	0.00	1.10	1.10	0.00	0.00	0.00
7	PRA	4	1.02	0.05	1.00	1.10	0.00	0.02	4.88
8	BAR	22	1.06	0.11	0.80	1.20	0.01	0.02	10.28
9	ALP	11	1.14	0.08	1.00	1.20	0.01	0.02	7.12
10	ANA	9	1.09	0.11	1.00	1.30	0.01	0.04	9.68
10s1	EME	3	0.93	0.06	0.90	1.00	0.00	0.03	6.19
10s2	MOU	3	0.97	0.06	0.90	1.00	0.00	0.03	5.97
11	GLE	9	1.12	0.07	1.00	1.20	0.00	0.02	5.94
12	INJ	6	1.07	0.05	1.00	1.10	0.00	0.02	4.84
12s	RNJ	3	1.20	0.00	1.20	1.20	0.00	0.00	0.00
13	ROM	7	1.09	0.15	0.90	1.30	0.02	0.06	13.48
14	MIL	11	1.15	0.19	1.00	1.50	0.03	0.06	16.14
15	CHI	11	1.08	0.13	1.00	1.40	0.02	0.04	11.56
15s1	RIV	10	1.13	0.13	1.00	1.40	0.02	0.04	11.08
15s2	CAL	13	1.21	0.21	0.70	1.50	0.04	0.06	17.06
15s3	CON	4	1.30	0.08	1.20	1.40	0.01	0.04	6.28
16	KOG	16	1.14	0.13	1.00	1.50	0.02	0.03	11.50
16s	TOO	5	1.06	0.05	1.00	1.10	0.00	0.02	5.17
17	WAR	13	1.10	0.06	1.00	1.20	0.00	0.02	5.25
17s	LAM	12	1.12	0.14	0.90	1.40	0.02	0.04	12.57
18	LEG	14	1.08	0.07	1.00	1.20	0.00	0.02	6.48
18s	MOO	13	1.12	0.16	0.90	1.40	0.03	0.04	14.15
19	SAN	10	1.00	0.07	0.90	1.10	0.00	0.02	6.67
20	BOL	9	1.02	0.07	0.90	1.10	0.00	0.02	6.52
21	DEE	9	1.07	0.11	0.90	1.20	0.01	0.04	10.48
22	LLA	10	1.02	0.06	0.90	1.10	0.00	0.02	6.20
23	BLA	5	1.04	0.09	0.90	1.10	0.01	0.04	8.60
24	ARD	8	1.05	0.05	1.00	1.10	0.00	0.02	5.09
24s	NEW	5	1.26	0.05	1.20	1.30	0.00	0.02	4.35
25	WAL	11	1.12	0.10	1.00	1.30	0.01	0.03	8.78
25s	APS	5	1.02	0.04	1.00	1.10	0.00	0.02	4.38
26	WER	3	1.20	0.10	1.10	1.30	0.01	0.06	8.33
27	MUR	4	1.10	0.00	1.10	1.10	0.00	0.00	0.00
28	DEN	4	1.32	0.19	1.20	1.60	0.04	0.09	14.29

Table 6. Descriptive statistics for the song variable DUR1, duration (sec) of the first song syllable.

LOC		N	MEAN	SD	MIN	MAX	VAR	SD	CV
1	DIM	17	0.06	0.01	0.04	0.09	0.00	0.01	23.05
2	RAV	16	0.10	0.03	0.06	0.13	0.00	0.03	24.35
2s	INN	3	0.12	0.01	0.12	0.13	0.00	0.01	4.68
3	MTG	12	0.07	0.01	0.05	0.10	0.00	0.01	20.47
4	LYN	5	0.11	0.05	0.06	0.18	0.00	0.05	45.08
5	CHA	6	0.06	0.02	0.03	0.08	0.00	0.02	28.78
6	HUG	4	0.07	0.02	0.05	0.09	0.00	0.02	26.08
7	PRA	4	0.11	0.04	0.05	0.15	0.00	0.04	38.56
8	BAR	22	0.13	0.04	0.04	0.18	0.00	0.04	31.78
9	ALP	11	0.13	0.03	0.08	0.16	0.00	0.03	25.33
10	ANA	9	0.11	0.05	0.05	0.22	0.00	0.05	48.56
10s1	EME	3	0.09	0.00	0.09	0.09	0.00	0.00	0.00
10s2	MOU	3	0.07	0.02	0.06	0.09	0.00	0.02	20.83
11	GLE	9	0.11	0.02	0.09	0.13	0.00	0.02	14.37
12	INJ	6	0.13	0.03	0.09	0.17	0.00	0.03	20.29
12s	RNJ	3	0.08	0.03	0.06	0.11	0.00	0.03	37.65
13	ROM	7	0.13	0.03	0.08	0.16	0.00	0.03	23.91
14	MIL	11	0.12	0.02	0.06	0.15	0.00	0.02	18.97
15	CHI	11	0.13	0.02	0.10	0.15	0.00	0.02	14.71
15s1	RIV	10	0.11	0.03	0.06	0.14	0.00	0.03	26.22
15s2	CAL	13	0.13	0.02	0.11	0.17	0.00	0.02	12.76
15s3	CON	4	0.08	0.01	0.07	0.10	0.00	0.01	17.68
16	KOG	16	0.13	0.01	0.11	0.16	0.00	0.01	10.99
16s	TOO	5	0.13	0.01	0.12	0.14	0.00	0.01	5.44
17	WAR	13	0.14	0.02	0.11	0.17	0.00	0.02	12.29
17s	LAM	12	0.07	0.02	0.04	0.10	0.00	0.02	26.36
18	LEG	14	0.14	0.07	0.04	0.23	0.01	0.07	50.33
18s	MOO	13	0.17	0.02	0.13	0.20	0.00	0.02	12.97
19	SAN	10	0.21	0.03	0.17	0.25	0.00	0.03	14.33
20	BOL	9	0.23	0.05	0.12	0.28	0.00	0.05	21.62
21	DEE	9	0.24	0.08	0.13	0.38	0.01	0.08	35.23
22	LLA	10	0.30	0.04	0.25	0.35	0.00	0.04	12.06
23	BLA	5	0.33	0.02	0.31	0.37	0.00	0.02	7.42
24	ARD	8	0.26	0.10	0.03	0.35	0.01	0.10	40.06
24s	NEW	5	0.34	0.01	0.33	0.36	0.00	0.01	3.60
25	WAL	11	0.24	0.14	0.02	0.35	0.02	0.14	57.82
25s	APS	5	0.36	0.15	0.10	0.46	0.02	0.15	41.57
26	WER	3	0.17	0.07	0.12	0.25	0.01	0.07	43.41
27	MUR	4	0.26	0.06	0.20	0.35	0.00	0.06	25.04
28	DEN	4	0.11	0.01	0.10	0.12	0.00	0.01	8.70

Table 7. Descriptive statistics for the song variable DUR, song duration (sec).

LOC		N	MEAN	SD	MIN	MAX	VAR	SE	CV
1	DIM	17	0.38	0.03	0.33	0.46	0.00	0.01	9.18
2	RAV	16	0.36	0.04	0.30	0.41	0.00	0.01	10.04
2s	INN	3	0.46	0.01	0.46	0.47	0.00	0.00	1.25
3	MTG	12	0.42	0.03	0.34	0.48	0.00	0.01	8.27
4	LYN	5	0.33	0.13	0.13	0.48	0.02	0.06	38.03
5	CHA	6	0.46	0.14	0.20	0.56	0.02	0.06	30.17
6	HUG	4	0.41	0.10	0.27	0.49	0.01	0.05	23.81
7	PRA	4	0.32	0.08	0.27	0.45	0.01	0.04	25.93
8	BAR	22	0.33	0.05	0.26	0.47	0.00	0.01	16.06
9	ALP	11	0.28	0.03	0.24	0.33	0.00	0.01	11.86
10	ANA	9	0.41	0.09	0.22	0.48	0.01	0.03	22.64
10s1	EME	3	0.45	0.01	0.45	0.46	0.00	0.00	1.27
10s2	MOU	3	0.42	0.04	0.39	0.46	0.00	0.02	9.09
11	GLE	9	0.38	0.08	0.27	0.46	0.01	0.03	20.46
12	INJ	6	0.50	0.02	0.46	0.52	0.00	0.01	4.65
12s	RNJ	3	0.41	0.12	0.27	0.49	0.01	0.07	29.67
13	ROM	7	0.34	0.07	0.27	0.45	0.00	0.02	19.67
14	MIL	11	0.30	0.07	0.23	0.50	0.01	0.02	23.47
15	CHI	11	0.29	0.04	0.25	0.35	0.00	0.01	12.11
15s1	RIV	10	0.31	0.05	0.24	0.43	0.00	0.02	17.49
15s2	CAL	13	0.28	0.02	0.24	0.31	0.00	0.01	8.96
15s3	CON	4	0.29	0.09	0.24	0.43	0.01	0.05	31.38
16	KOG	16	0.31	0.03	0.26	0.36	0.00	0.01	9.54
16s	TOO	5	0.49	0.11	0.30	0.57	0.01	0.05	22.14
17	WAR	13	0.30	0.03	0.24	0.34	0.00	0.01	10.29
17s	LAM	12	0.44	0.05	0.37	0.54	0.00	0.01	11.08
18	LEG	14	0.28	0.08	0.20	0.43	0.01	0.02	29.50
18s	MOO	13	0.36	0.04	0.29	0.43	0.00	0.01	11.97
19	SAN	10	0.21	0.03	0.17	0.25	0.00	0.01	14.33
20	BOL	9	0.24	0.03	0.18	0.28	0.00	0.01	12.52
21	DEE	9	0.29	0.05	0.22	0.38	0.00	0.02	16.42
22	LLA	10	0.30	0.04	0.25	0.35	0.00	0.01	12.06
23	BLA	5	0.33	0.02	0.31	0.37	0.00	0.01	7.42
24	ARD	8	0.29	0.05	0.20	0.35	0.00	0.02	16.79
24s	NEW	5	0.34	0.01	0.33	0.36	0.00	0.01	3.60
25	WAL	11	0.31	0.03	0.27	0.35	0.00	0.01	8.68
25s	APS	5	0.39	0.09	0.25	0.46	0.01	0.04	22.06
26	WER	3	0.28	0.03	0.25	0.30	0.00	0.02	9.45
27	MUR	4	0.26	0.06	0.20	0.35	0.00	0.03	25.04
28	DEN	4	0.29	0.04	0.23	0.32	0.00	0.02	14.78

Table 8. Descriptive statistics for song variable INT1, interval between first and second song syllable (sec).

LOC		N	MEAN	SD	MIN	MAX	VAR	SE	CV
1	DIM	17	0.11	0.02	0.08	0.16	0.00	0.01	19.36
2	RAV	16	0.14	0.03	0.10	0.20	0.00	0.01	19.67
2s	INN	3	0.19	0.01	0.18	0.20	0.00	0.01	5.26
3	MTG	12	0.12	0.02	0.09	0.15	0.00	0.01	17.07
4	LYN	4	0.16	0.04	0.10	0.20	0.00	0.02	26.62
5	CHA	6	0.08	0.02	0.06	0.12	0.00	0.01	29.36
6	HUG	4	0.04	0.03	0.02	0.08	0.00	0.01	67.70
7	PRA	4	0.03	0.00	0.02	0.03	0.00	0.00	18.18
8	BAR	22	0.03	0.02	0.02	0.08	0.00	0.00	52.34
9	ALP	11	0.04	0.02	0.01	0.06	0.00	0.01	44.97
10	ANA	8	0.10	0.03	0.04	0.15	0.00	0.01	31.18
10s1	EME	3	0.12	0.01	0.11	0.12	0.00	0.00	4.95
10s2	MOU	3	0.12	0.01	0.11	0.13	0.00	0.01	8.33
11	GLE	9	0.07	0.03	0.03	0.11	0.00	0.01	44.72
12	INJ	6	0.09	0.02	0.06	0.12	0.00	0.01	21.83
12s	RNJ	3	0.12	0.07	0.04	0.17	0.01	0.04	58.66
13	ROM	7	0.04	0.04	0.01	0.11	0.00	0.02	95.67
14	MIL	11	0.04	0.03	0.02	0.12	0.00	0.01	76.26
15	CHI	11	0.04	0.01	0.02	0.05	0.00	0.00	23.13
15s1	RIV	10	0.06	0.04	0.02	0.16	0.00	0.01	74.91
15s2	CAL	13	0.04	0.01	0.03	0.05	0.00	0.00	21.94
15s3	CON	4	0.10	0.02	0.08	0.12	0.00	0.01	18.24
16	KOG	16	0.05	0.02	0.01	0.08	0.00	0.00	39.55
16s	TOO	5	0.11	0.04	0.04	0.14	0.00	0.02	36.93
17	WAR	13	0.03	0.01	0.01	0.05	0.00	0.00	49.24
17s	LAM	12	0.13	0.02	0.10	0.17	0.00	0.01	17.53
18	LEG	8	0.06	0.04	0.02	0.11	0.00	0.01	54.94
18s	MOO	13	0.03	0.02	0.01	0.06	0.00	0.01	63.18
19	SAN	0	.	.	.	.	.	.	.
20	BOL	2	0.03	0.00	0.03	0.03	0.00	0.00	0.00
21	DEE	3	0.02	0.01	0.02	0.03	0.00	0.00	24.74
22	LLA	0	.	.	.	.	.	.	.
23	BLA	0	.	.	.	.	.	.	.
24	ARD	1	0.08	.	0.08	0.08	.	.	.
24s	NEW	0	.	.	.	.	.	.	.
25	WAL	3	0.05	0.01	0.05	0.06	0.00	0.00	10.83
25s	APS	1	0.04	.	0.04	0.04	.	.	.
26	WER	2	0.02	0.01	0.02	0.03	0.00	0.01	28.28
27	MUR	0	.	.	.	.	.	.	.
28	DEN	4	0.04	0.02	0.01	0.06	0.00	0.01	59.13

Table 9. Descriptive statistics for the song variable INT2, interval between second and third song syllables (sec).

LOC		N	MEAN	SD	MIN	MAX	VAR	SE	CV
1	DIM	17	0.07	0.01	0.05	0.09	0.00	0.00	16.15
2	RAV	0	.	.	.	.	.	.	.
2s	INN	0	.	.	.	.	.	.	.
3	MTG	11	0.09	0.02	0.06	0.12	0.00	0.00	17.21
4	LYN	0	.	.	.	.	.	.	.
5	CHA	5	0.11	0.03	0.06	0.14	0.00	0.01	27.46
6	HUG	3	0.10	0.01	0.09	0.10	0.00	0.00	5.97
7	PRA	1	0.09	.	0.09	0.09	.	.	.
8	BAR	4	0.10	0.01	0.08	0.11	0.00	0.01	14.14
9	ALP	0	.	.	.	.	.	.	.
10	ANA	7	0.06	0.02	0.04	0.09	0.00	0.01	32.53
10s1	EME	3	0.05	0.00	0.05	0.05	0.00	0.00	0.00
10s2	MOU	3	0.06	0.01	0.05	0.06	0.00	0.00	10.19
11	GLE	4	0.03	0.01	0.02	0.04	0.00	0.00	27.22
12	INJ	6	0.02	0.01	0.02	0.04	0.00	0.00	33.47
12s	RNJ	2	0.10	0.01	0.10	0.11	0.00	0.00	6.73
13	ROM	2	0.07	0.01	0.07	0.08	0.00	0.01	9.43
14	MIL	1	0.03	.	0.03	0.03	.	.	.
15	CHI	0	.	.	.	.	.	.	.
15s1	RIV	1	0.08	.	0.08	0.08	.	.	.
15s2	CAL	0	.	.	.	.	.	.	.
15s3	CON	1	0.09	.	0.09	0.09	.	.	.
16	KOG	0	.	.	.	.	.	.	.
16s	TOO	4	0.03	0.01	0.02	0.04	0.00	0.00	29.46
17	WAR	0	.	.	.	.	.	.	.
17s	LAM	12	0.07	0.03	0.02	0.11	0.00	0.01	39.48
18	LEG	3	0.07	0.01	0.06	0.07	0.00	0.00	8.66
18s	MOO	0	.	.	.	.	.	.	.
19	SAN	0	.	.	.	.	.	.	.
20	BOL	0	.	.	.	.	.	.	.
21	DEE	0	.	.	.	.	.	.	.
22	LLA	0	.	.	.	.	.	.	.
23	BLA	0	.	.	.	.	.	.	.
24	ARD	1	0.06	.	0.06	0.06	.	.	.
24s	NEW	0	.	.	.	.	.	.	.
25	WAL	3	0.05	0.01	0.04	0.05	0.00	0.00	12.37
25s	APS	0	.	.	.	.	.	.	.
26	WER	0	.	.	.	.	.	.	.
27	MUR	0	.	.	.	.	.	.	.
28	DEN	0	.	.	.	.	.	.	.

Table 10. Descriptive statistics for the song variable SEC, highest frequency of second peak in first song syllable (kHz).

LOC		N	MEAN	SD	MIN	MAX	VAR	SE	CV
1	DIM	4	2.15	0.30	1.70	2.30	0.09	0.15	13.95
2	RAV	4	1.97	0.17	1.80	2.20	0.03	0.09	8.65
2s	INN	3	1.93	0.06	1.90	2.00	0.00	0.03	2.99
3	MTG	2	1.90	0.28	1.70	2.10	0.08	0.20	14.89
4	LYN	2	2.25	0.21	2.10	2.40	0.05	0.15	9.43
5	CHA	4	2.00	0.18	1.80	2.20	0.03	0.09	9.13
6	HUG	0	.	.	.	.	.	.	.
7	PRA	2	2.15	0.21	2.00	2.30	0.04	0.15	9.87
8	BAR	18	2.16	0.12	2.00	2.40	0.01	0.03	5.53
9	ALP	10	1.96	0.17	1.70	2.20	0.03	0.05	8.74
10	ANA	4	1.87	0.10	1.80	2.00	0.01	0.05	5.11
10s1	EME	0	.	.	.	.	.	.	.
10s2	MOU	0	.	.	.	.	.	.	.
11	GLE	9	2.06	0.31	1.70	2.60	0.10	0.10	15.21
12	INJ	4	2.20	0.14	2.00	2.30	0.02	0.07	6.43
12s	RNJ	1	1.90	.	1.90	1.90	.	.	.
13	ROM	2	2.35	0.07	2.30	2.40	0.01	0.05	3.01
14	MIL	10	2.21	0.19	1.90	2.50	0.04	0.06	8.65
15	CHI	11	2.13	0.19	1.80	2.40	0.04	0.06	8.94
15s1	RIV	7	2.13	0.14	1.90	2.30	0.02	0.05	6.48
15s2	CAL	13	2.03	0.24	1.60	2.30	0.06	0.07	11.62
15s3	CON	0	.	.	.	.	.	.	.
16	KOG	13	2.01	0.21	1.70	2.40	0.04	0.06	10.26
16s	TOO	5	2.34	0.19	2.00	2.50	0.04	0.09	8.33
17	WAR	13	2.30	0.27	1.90	2.80	0.07	0.07	11.64
17s	LAM	7	2.16	0.35	1.40	2.50	0.12	0.13	16.25
18	LEG	10	2.20	0.19	1.90	2.50	0.04	0.06	8.57
18s	MOO	13	2.18	0.23	1.90	2.60	0.05	0.06	10.63
19	SAN	10	2.09	0.13	1.90	2.30	0.02	0.04	6.16
20	BOL	8	2.46	0.22	2.10	2.70	0.05	0.08	8.93
21	DEE	8	2.41	0.11	2.20	2.50	0.01	0.04	4.67
22	LLA	10	2.58	0.51	2.00	3.30	0.26	0.16	19.83
23	BLA	5	2.40	0.16	2.20	2.60	0.02	0.07	6.59
24	ARD	7	2.49	0.16	2.30	2.80	0.02	0.06	6.33
24s	NEW	1	2.20	.	2.20	2.20	.	.	.
25	WAL	3	2.93	0.23	2.80	3.20	0.05	0.13	7.87
25s	APS	1	2.00	.	2.00	2.00	.	.	.
26	WER	3	2.27	0.15	2.10	2.40	0.02	0.09	6.74
27	MUR	3	2.60	0.10	2.50	2.70	0.01	0.06	3.85
28	DEN	4	2.17	0.17	2.00	2.40	0.03	0.09	7.85

Table 11. Mean coefficients of variation for frequency and duration measurements of songs of *Pardalotus striatus*.

Variable	Mean C.V.
HF	7.32
LF	7.99
SEC	8.88
DUR1	23.83
DUR	15.83
INT1	35.30
INT2	18.15

HF - Highest frequency in first song syllable
LF - Lowest frequency in first song syllable
SEC - Second highest frequency in first syllable
DUR1 - Duration of first syllable in seconds
DUR - Duration of song in seconds
INT1 - Duration of interval between first two syllables
INT2 - Duration between second and third syllables

any of these characters.

The distribution of song types, based on syllable number, among the 345 males studied is depicted in Fig. 8. 15 birds (4.3%) had 4-syllable songs; 79 (22.9%) had 3-syllable songs; 175 (50.7%) had 2-syllable songs; and 76 (22.0%) had 1-syllable songs. 4-syllable songs were found only in six localities north of 24 degrees S latitude. Except for localities 26 and 28 (which have small sample sizes), 1-syllable songs predominated among birds from localities south of the McPherson Range on the eastern Queensland-New South Wales border.

Tests of a posteriori multiple comparisons of means (with unequal sample sizes) for each song variable were performed (SAS PROC GLM/GT2). This program can be used to derive homogeneous subsets of means which are non-significantly different at the $p<.05$ level. The results appear in Figs. 9-16. The results are presented as maps of geographic variation, which include lists of sample means ranked in order of magnitude. Vertical lines adjacent to the means denote homogeneous subsets. Five different symbols on each map indicate the comparative magnitudes of the sample means. The total range of all the means is divided into five equal intervals, and the symbols correspond to each interval. The following qualitative descriptions match each symbol: unshaded circle, "small"; quarter-shaded circle, "moderately small"; half-shaded

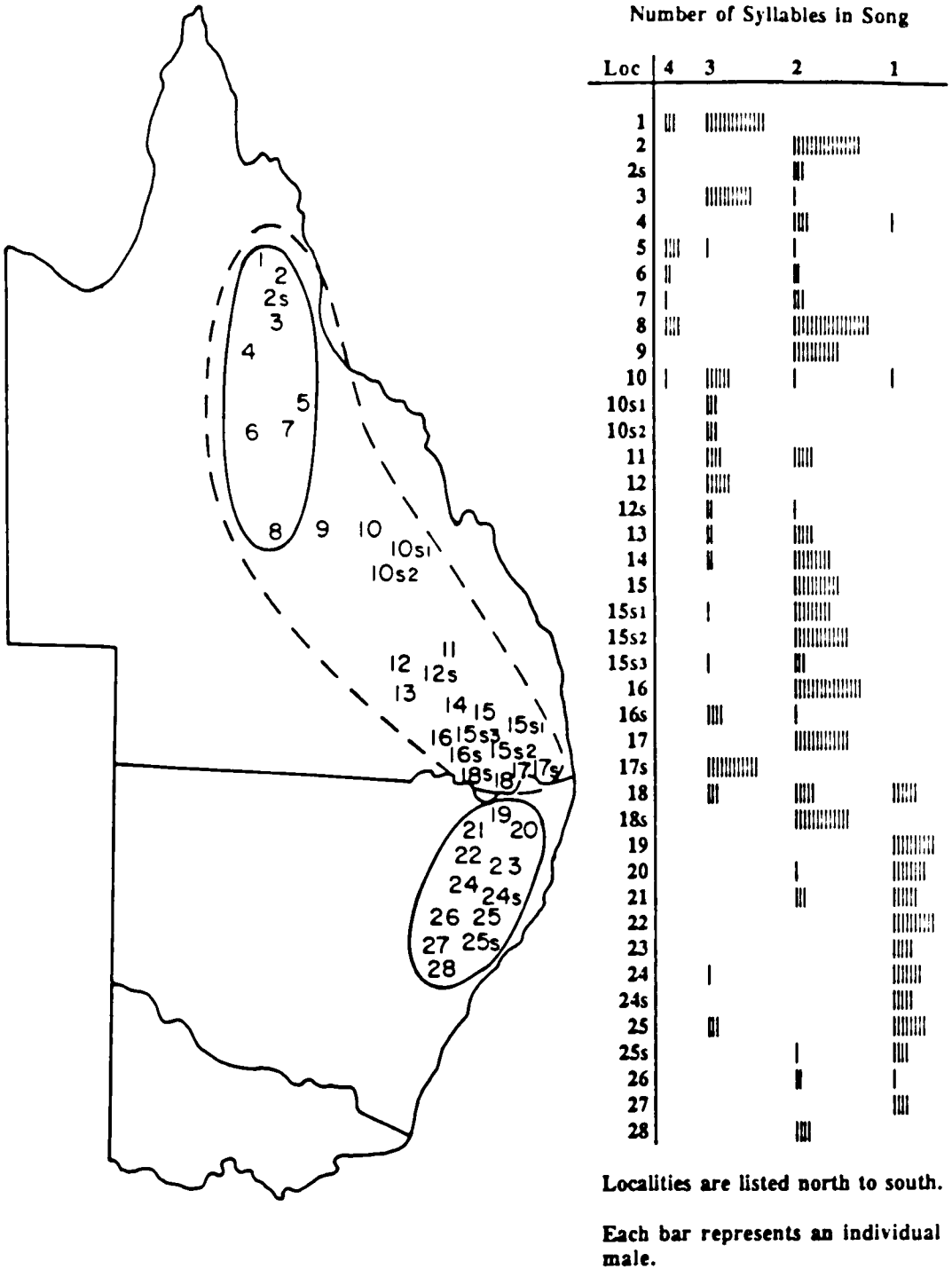


Fig. 8. Geographic distribution of the song variable SYLL, illustrating a decrease in the number of syllables in songs from north to south. Localities enclosed by the dotted line are those where the majority of birds had 2- or 3-syllable songs. Localities 1, 5-8, and 10 are the only sites where birds with 4-syllable songs were found. In localities 19-27 the majority of birds had 1-syllable songs.

circle, "intermediate"; three-quarters-shaded circle, "moderately large"; and solid circle, "large".

It should be noted that homogeneous subsets are formed *independent of* geography, and samples from widely-separated localities may be grouped together if their means are not significantly different. However, inspection of the symbols and of the locality number codes (which indicate relative geographic position, from north to south) readily reveal geographic patterns when they exist. For example, Fig. 9 shows many overlapping subsets of means for song syllable number. Yet the symbols indicate a southern grouping of localities where most individuals have 1-syllable songs; and this group is south of the McPherson Range. Geographic patterns can be seen for several other song variables, as well:

Highest frequency in the first song syllable (HF) was not significantly correlated with latitude. However, inspection of Fig. 10 revealed a north-to-south trend toward higher mean values for this variable (in spite of a few aberrant localities, such as 2s). A similar pattern can be seen for the variable SEC (Fig. 12). A clinal geographic pattern was also shown for DUR1 (Fig. 13), which was the only song variable significantly correlated with latitude. None of the other variables exhibited obvious geographic patterns.

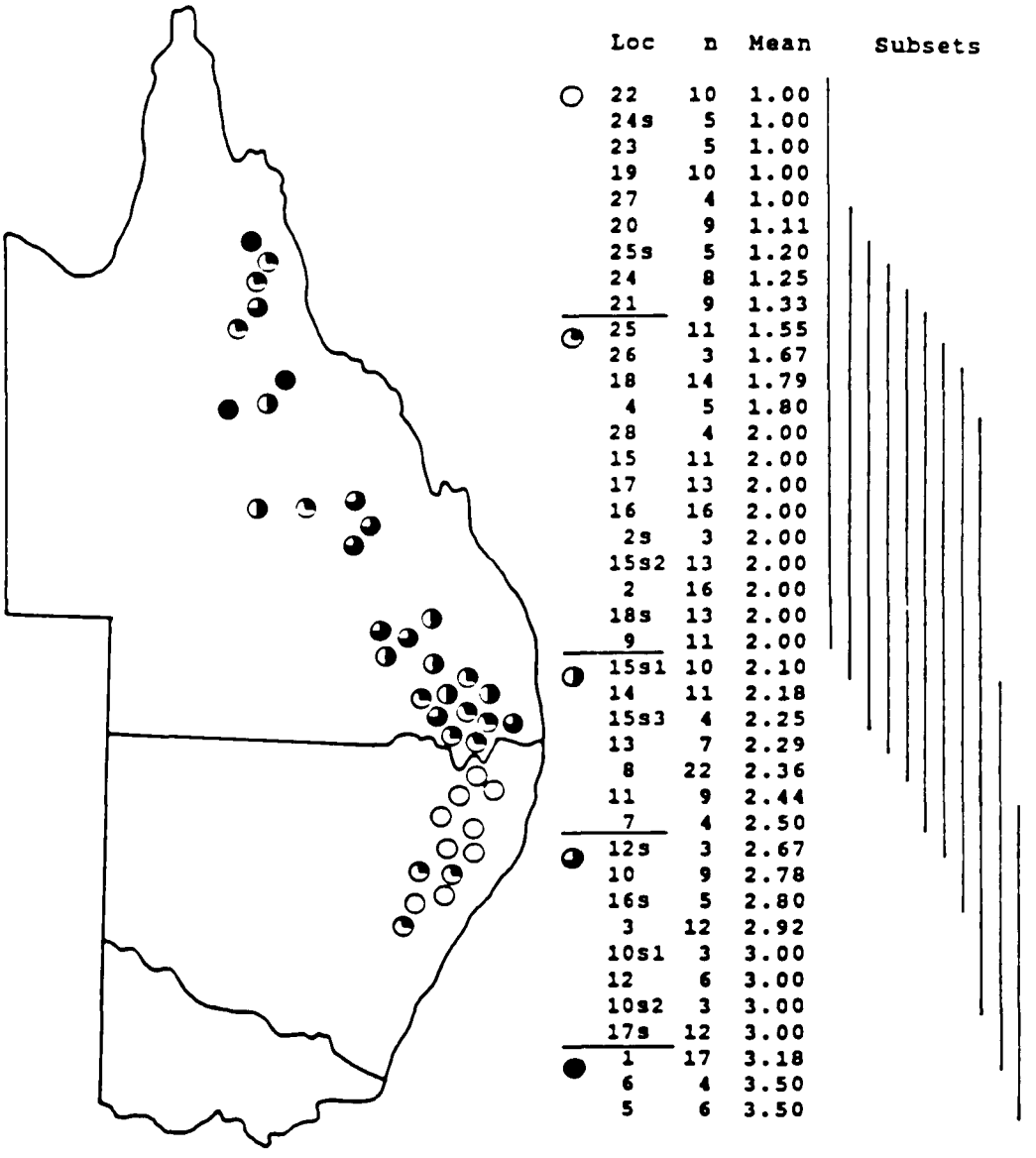


Fig. 9. Geographic variation in mean number of syllables in the song of male Pardalotus striatus in eastern Australia. Means are listed in increasing order of magnitude, adjacent to the number code for each locality. Locality number indicates relative latitude, with 1 being northernmost. Vertical lines represent subsets of means which do not differ significantly from each other. The five symbols correspond to a ranked qualitative description of variation of the measured variable. See text for further explanation.

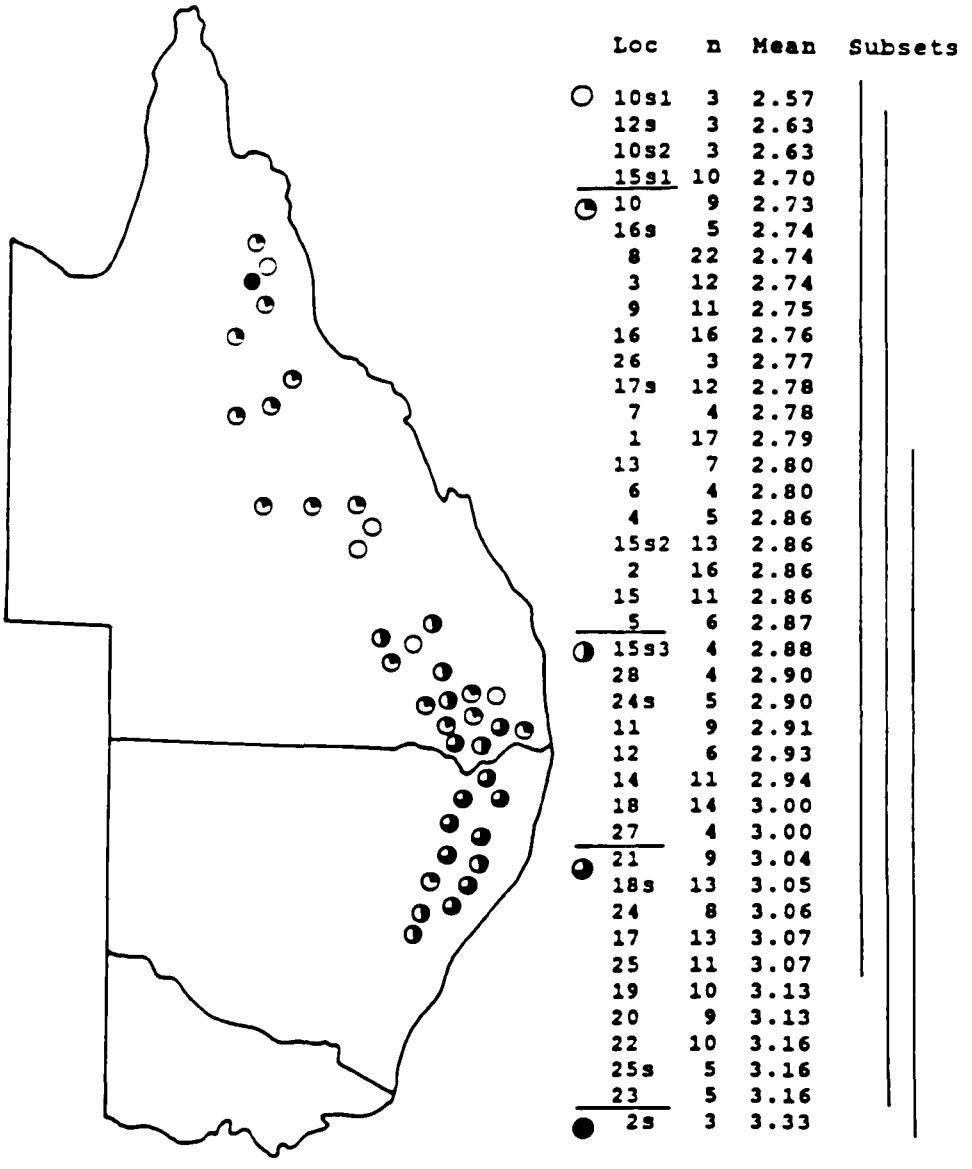


Fig. 10. Geographic variation in mean song variable HF (highest frequency, in kHz, of the first syllable in the song). See Fig. 9 and text for further explanation.

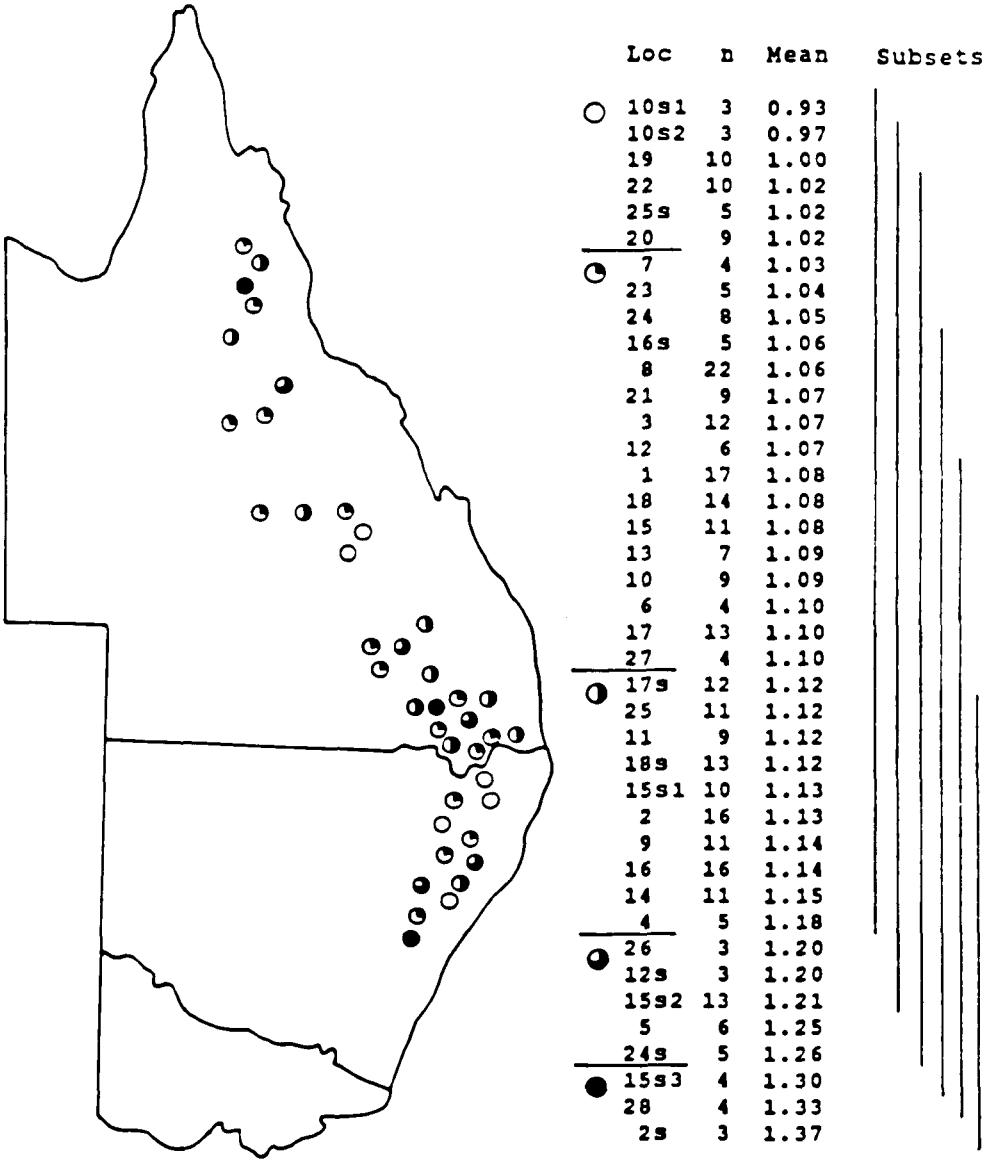


Fig. 11. Geographic variation in mean song variable LF (lowest frequency, in kHz, of the first syllable in the song). See Fig. 9 and text for further explanation.

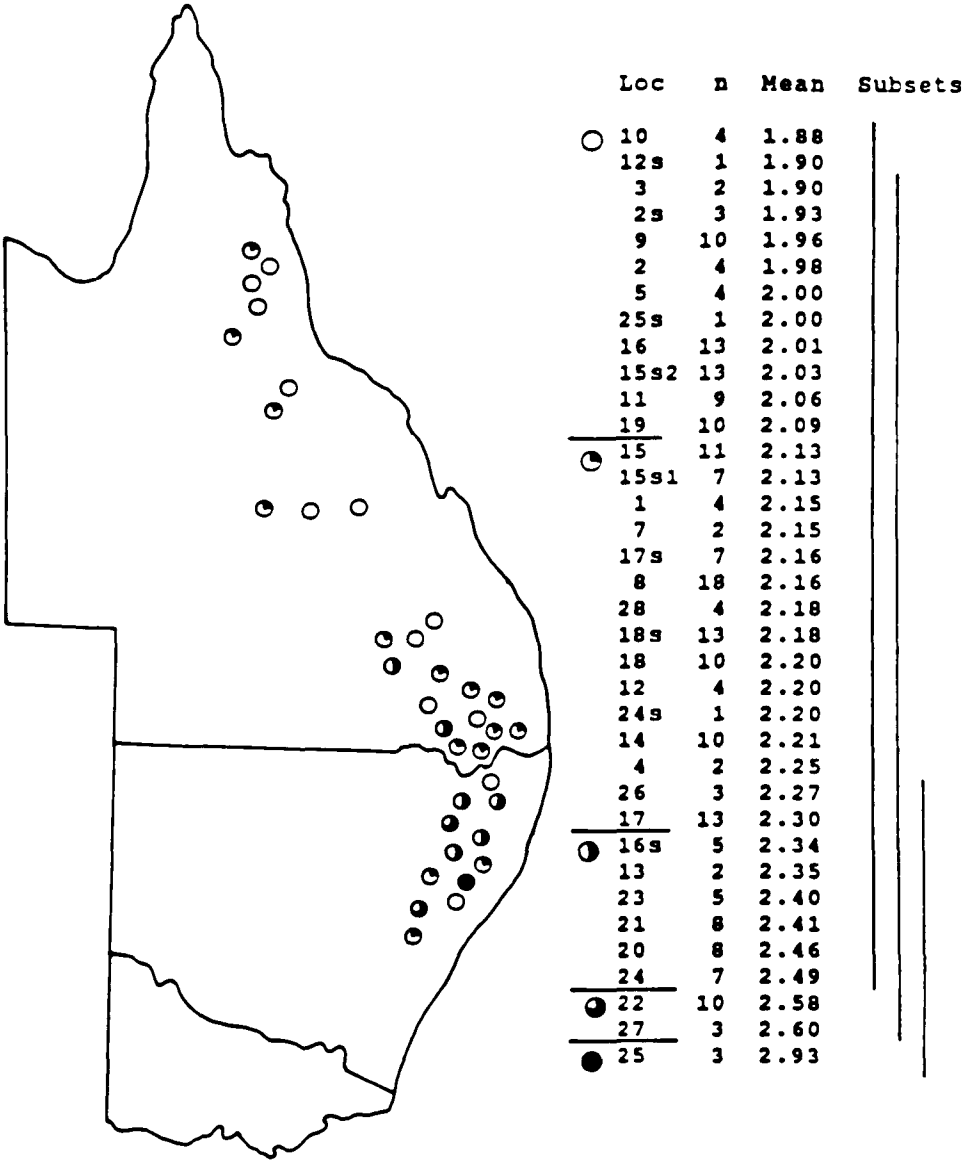


Fig. 12. Geographic variation in mean song variable SEC (highest frequency, in kHz, of the second-highest peak in the first syllable of the song). See Fig. 9 and text for further explanation.

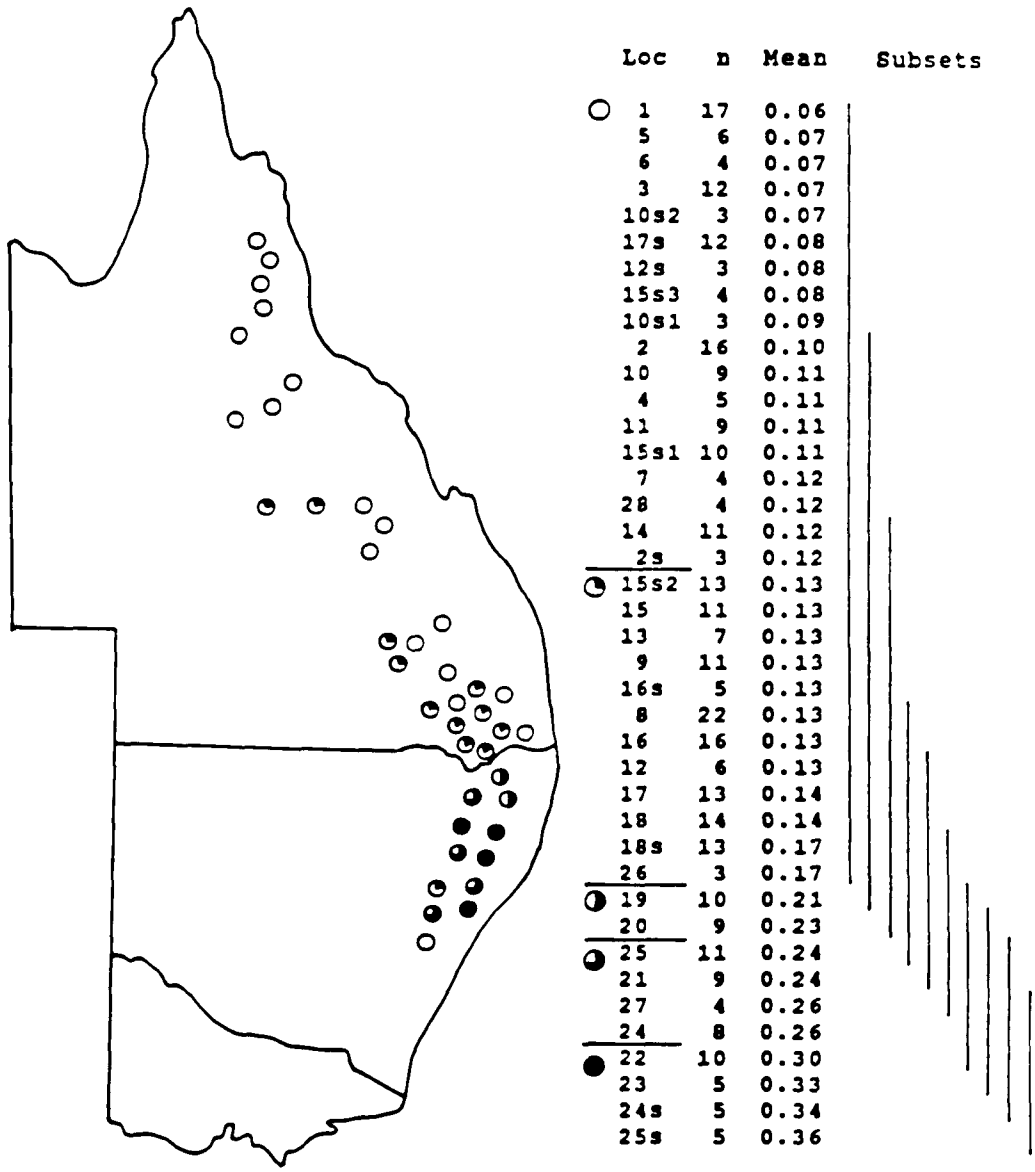


Fig. 13. Geographic variation in mean song variable DUR1 (duration, in seconds, of the first syllable of the song). See Fig. 9 and text for further explanation.

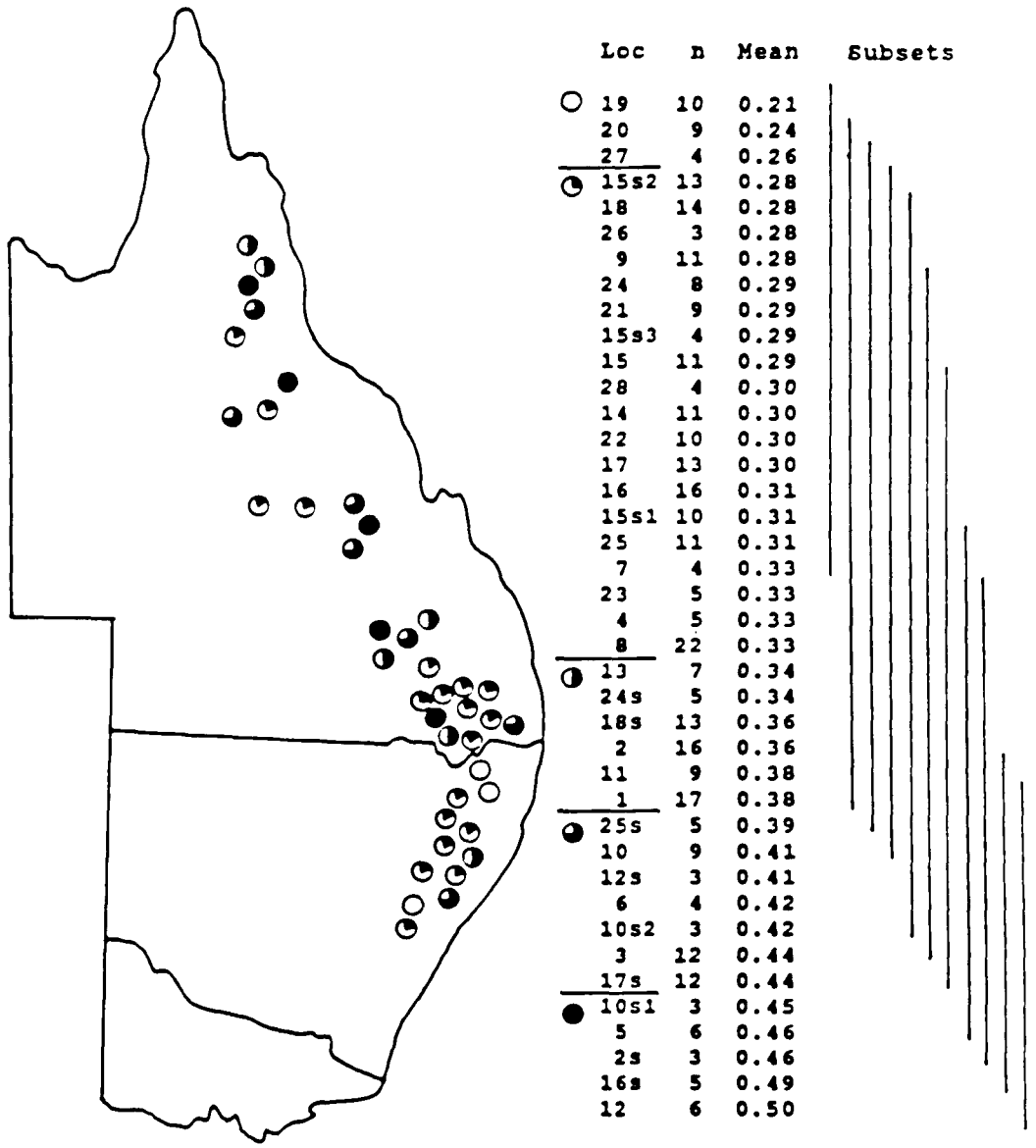


Fig. 14. Geographic variation in mean song variable DUR (duration of the song, in seconds). See Fig. 9 and text for further explanation.

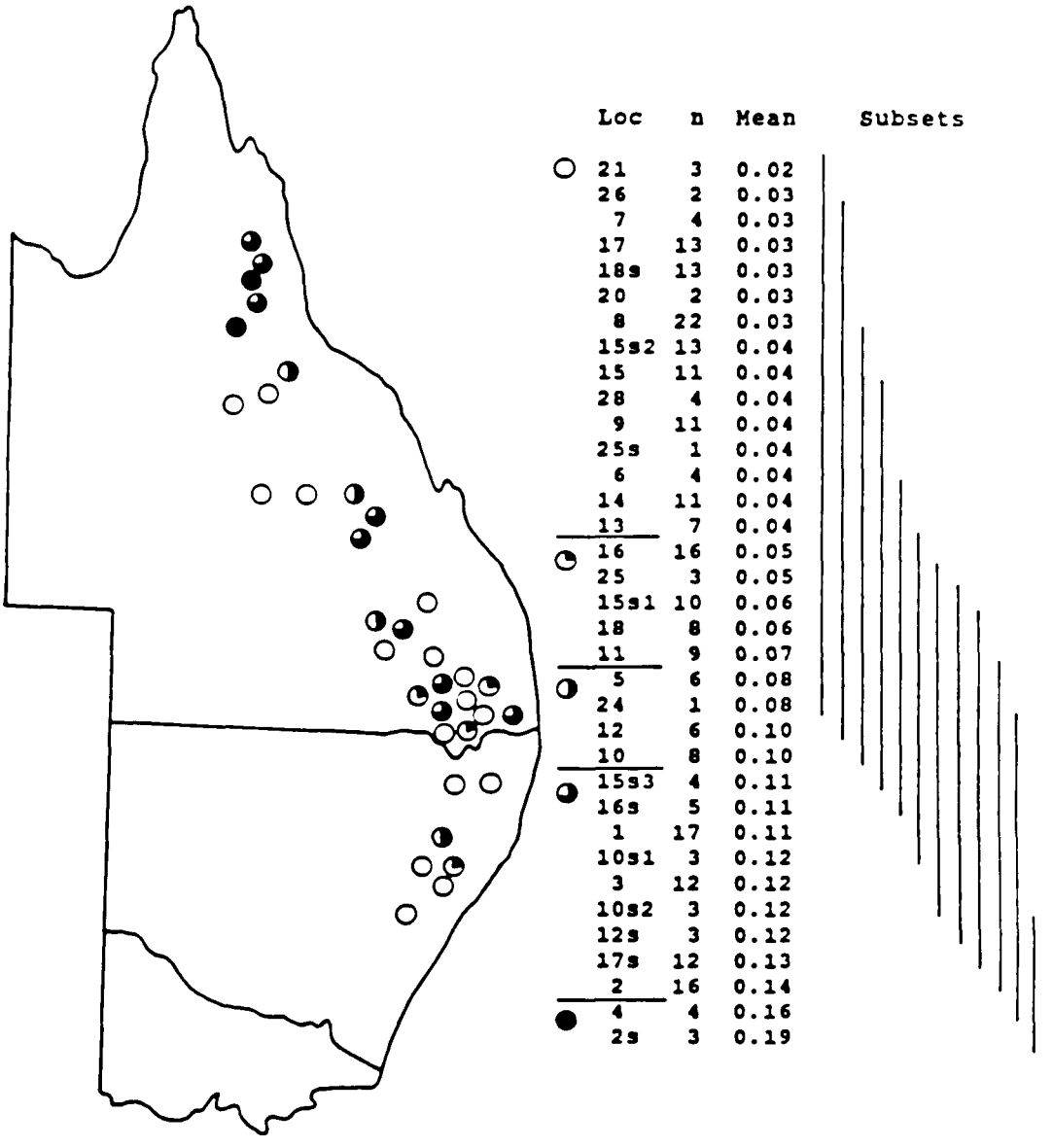


Fig. 15. Geographic variation in mean song variable INT1 (time interval, in seconds, between the first and second syllables of the song). See Fig. 9 and text for further explanation.

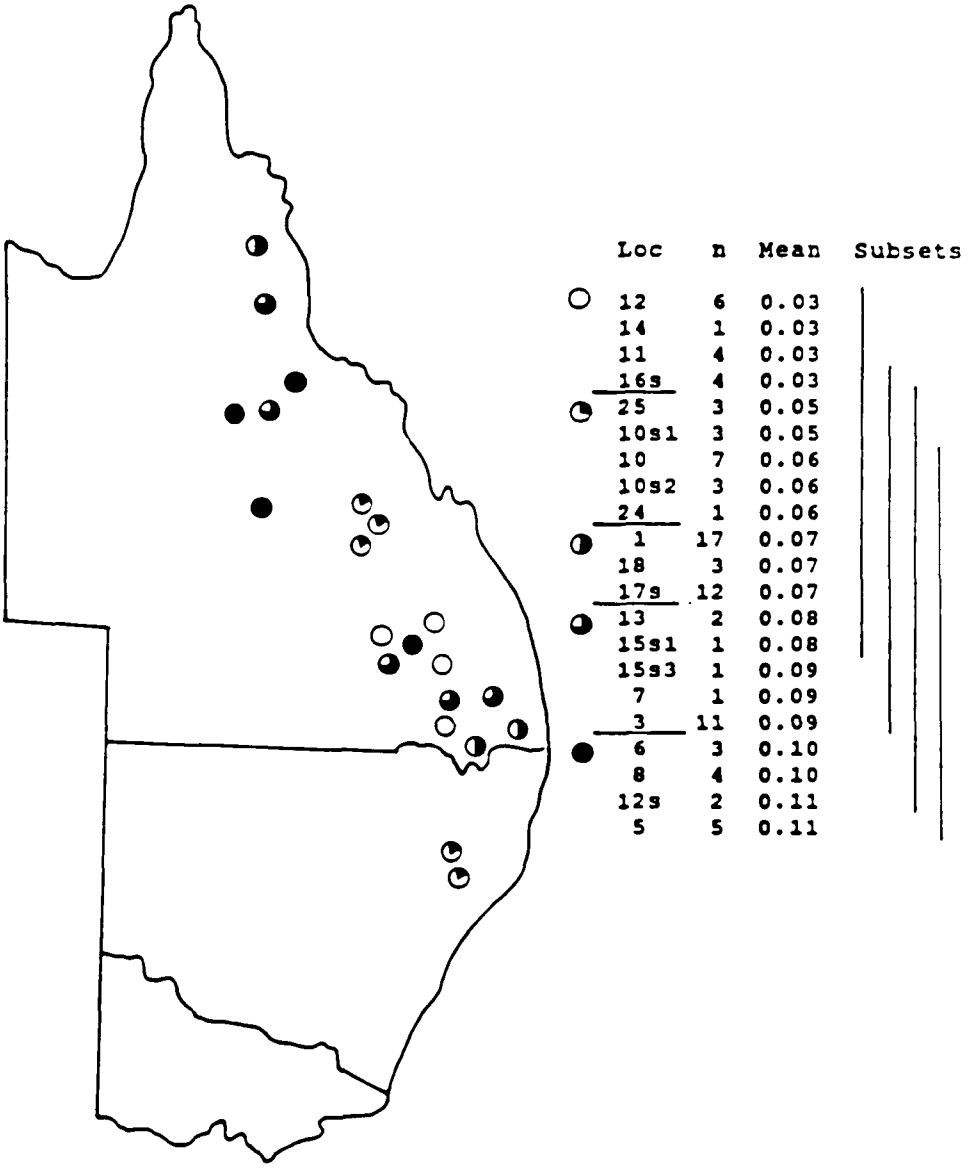


Fig. 16. Geographic variation in mean song variable INT2 (time interval, in seconds, between the second and third syllables of the song). See Fig. 9 and text for further explanation.

Principal components analysis (PCA) was used to examine the relative degree of separation of localities, based on all song variables and on four song variables common to all samples. Loadings on the first four components in the initial analysis are given in Table 12. Loadings on the first three principal components in the second analysis are given in Table 13. In this analysis, the first three PC's accounted for 96% of the variance. HF and DUR1, the two variables which exhibited clinal patterns of variation, had high loadings on PC1 (which accounted for 61% of the variance). In order to examine a possible "better" geographic ordering of localities by PC1 rather than by either HF or DUR1 alone, localities were sorted and listed by standardized PC1 scores (Table 14). Comparisons with the listings of localities in Figs. 10 and 13 shows that PC1 score resulted in a somewhat better ordering of localities by geography than did HF alone, but did not improve the ordering by DUR1 alone.

Nevertheless, the listing by PC1 appeared to show a geographic grouping of southern localities (again ignoring locality 2s), which extends from the Queensland-New South Wales border southward. Therefore, localities were plotted by PC1 score and map distance (distance from the northernmost locality) to examine possible geographic patterns based on the first principal component (Fig. 17). PC1 scores did not group the localities 17s (Lamington), 26

Table 12. Loadings of song variables on the first four principal components. (Data from 40 localities where specimens were recorded were used for this analysis.)

VARIABLE	PC1	PC2	PC3	PC4
SYLL	0.066	-.035	-.039	0.002
HF	-.009	0.015	-.003	-.007
LF	0.002	-.003	0.001	0.003
SEC	-.018	0.032	-.008	0.007
DUR	0.819	0.437	-.287	0.229
INT1	0.294	0.143	0.932	-.155
INT2	0.026	-.389	0.201	0.898
DUR1	-.486	0.796	0.087	0.341
% VARIANCE EXPLAINED:	67.9%	21.3%	5.4%	5.3%

Table 13. Loadings of selected song variables on the first three principal components. (PCA was performed on data from 40 localities where birds were recorded.)

VARIABLE	PC1	PC2	PC3
SYLL	-0.595	-0.042	0.442
HF	0.537	0.231	0.810
LF	-0.060	0.960	-0.225
DUR1	0.595	-0.153	-0.311
% VARIANCE EXPLAINED:	61.3%	26.3%	9.0%

Table 14. Localities listed in order of first principal component score. 40 localities where songs were recorded were used for this analysis. PCA was performed on song variables common to all localities. Standardized PC scores are listed. Means for variables which had high loadings on PC1 (highest frequency in first syllable and duration of first syllable) are given for each locality.

LOCALITY		PC1	DUR1	HF
10s1	EME	-1.3381	0.09	2.57
6	HUG	-1.3014	0.07	2.80
10s2	MOU	-1.2988	0.07	2.63
5	CHA	-1.2545	0.07	2.87
12s	RNJ	-1.2036	0.08	2.87
1	DIM	-1.1821	0.06	2.79
3	MTG	-1.0903	0.07	2.74
17s	LAM	-1.0727	0.08	2.78
10	ANA	-0.8835	0.11	2.73
16s	TOO	-0.7551	0.13	2.74
7	PRA	-0.5859	0.12	2.76
15s1	RIV	-0.5721	0.11	2.70
15s3	CON	-0.5348	0.08	2.88
8	BAR	-0.5247	0.13	2.74
12	INJ	-0.4579	0.14	2.93
13	ROM	-0.3922	0.13	2.80
11	GLE	-0.3518	0.11	2.91
9	ALP	-0.3439	0.13	2.75
16	KOG	-0.3363	0.13	2.76
2	RAV	-0.2485	0.10	2.86
28	DEN	-0.2003	0.12	2.90
15s2	CAL	-0.1759	0.13	2.86
4	LYN	-0.1487	0.11	2.86
15	CHI	-0.1197	0.13	2.86
14	MIL	-0.1180	0.12	2.94
26	WER	0.0053	0.17	2.77
17	WAR	0.3204	0.14	3.07
18	LEG	0.3466	0.14	3.00
18s	MOO	0.4220	0.17	3.05
2s	INN	0.6757	0.12	3.33
25	WAL	1.0458	0.24	3.07
21	DEE	1.1248	0.23	3.05
27	MUR	1.2816	0.26	3.00
24	ARD	1.3120	0.26	3.06
19	SAN	1.3356	0.21	3.13
20	BOL	1.3990	0.23	3.14
24s	NEW	1.4083	0.34	2.90
22	LLA	1.8435	0.30	3.16
23	BLA	1.9626	0.33	3.16
25s	APS	2.0076	0.36	3.16

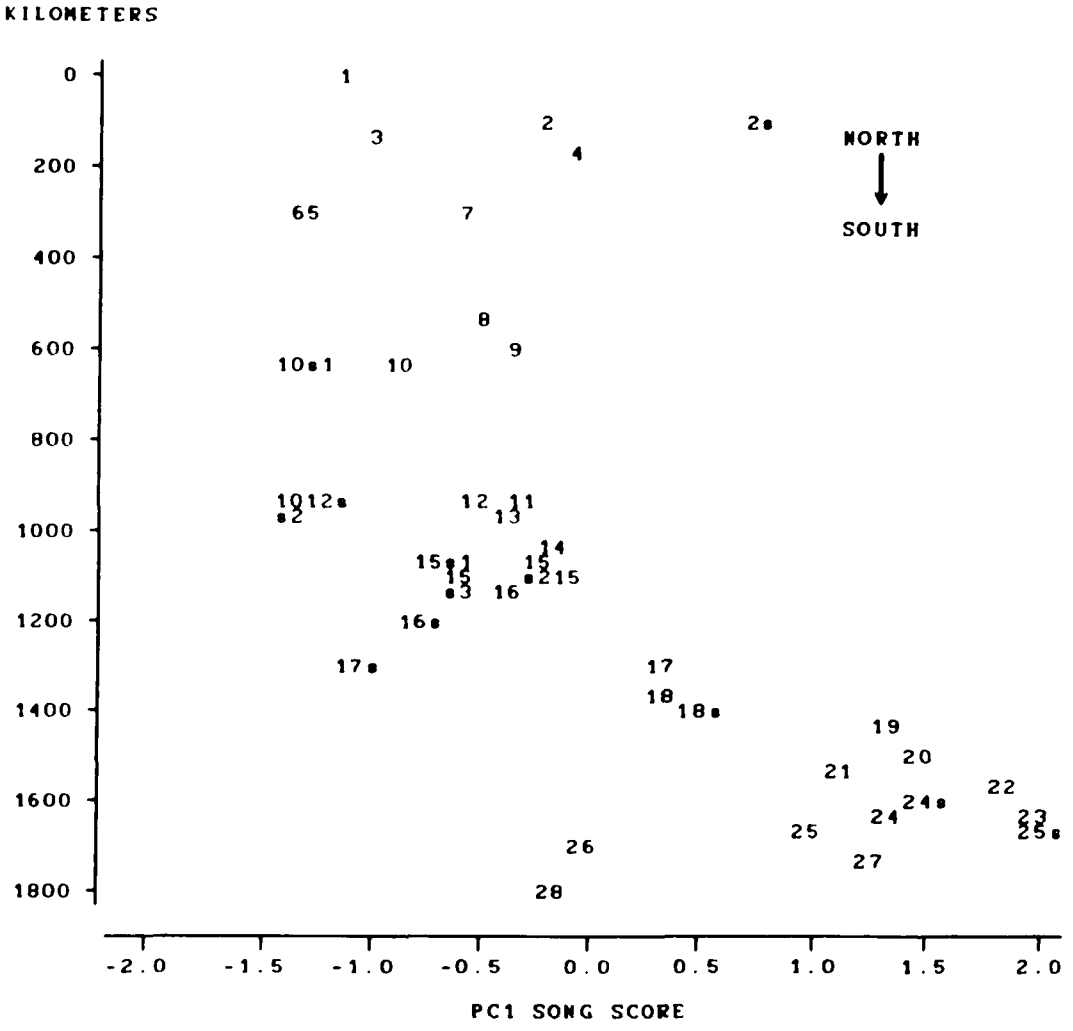


Figure 17. Localities plotted by map distance and PC1 scores derived from a principal components analysis of song frequency and time variables. 40 localities where specimens were recorded were used in this analysis. Variables with high loadings on PC1 were HF (highest frequency in first syllable) and DUR1 (duration of first syllable).

(Werris Creek) or 28 (Denman) with this southern cluster. (Again, the sample sizes for Werris Creek and Denman were small.) Songs of birds from these three localities had relatively shorter first syllables and lower HF values than songs of other birds in the southern group. However, the remaining southern localities, from 17 (Warwick) to 27 (Murrurundi), were segregated by PC1 score from all other localities. Many of the 116 birds recorded in these 13 localities had the type of song that was described in the Introduction as sounding like a "sliding 'wheeo'" (see text and Fig. 7, male 0201). This would account for the relatively long duration of the first syllable in their songs.

Results of the same PCA showed that PC1 and PC2 together accounted for over 87% of the variance (Table 13). The song variable LF, lowest frequency in the first syllable, had a high loading on PC2. Plotting of the first two components (Fig. 18) did not reveal any additional regional trends or clusters of localities.

A distance phenogram of localities, based on a cluster analysis (SAS PROC CLUSTER / UPGMA) of all song variables, is shown in Fig. 19. The results of this method of clustering the song data were in general agreement with results of the PCA. Two major clusters appear in the phenogram, one cluster comprised mostly of localities north of the McPherson Range and one cluster of localities south

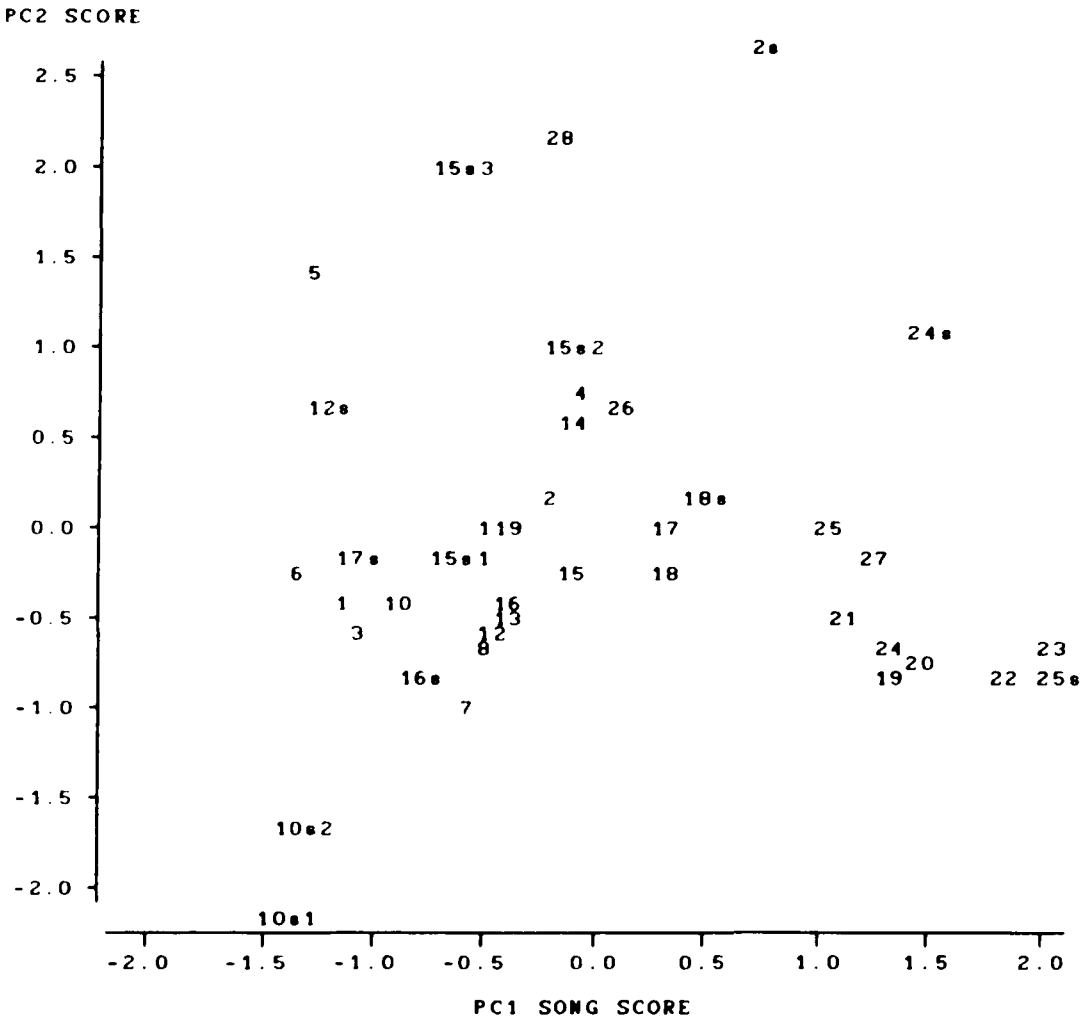
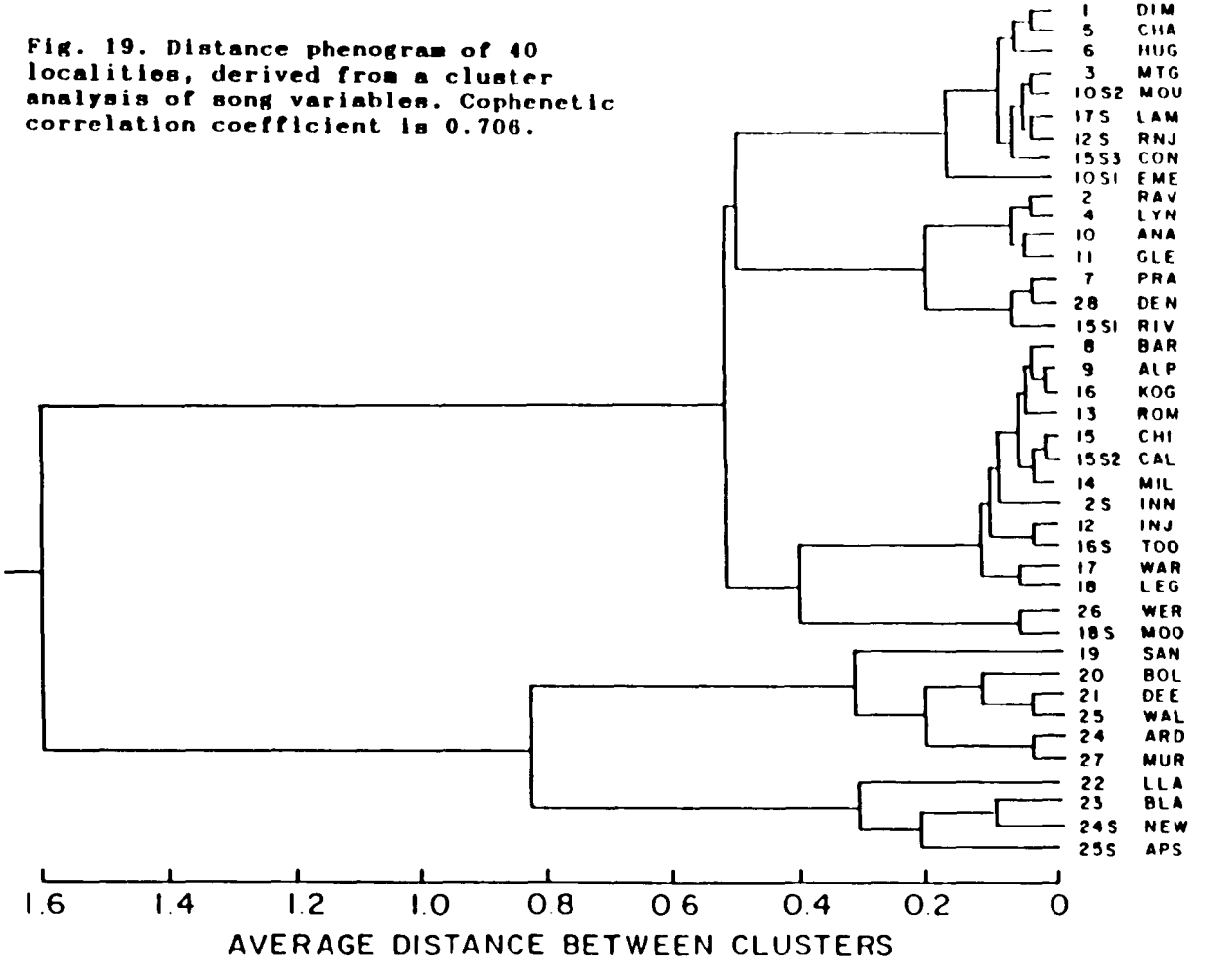


Figure 18. Localities plotted by PC1 and PC2 scores derived from a principal components analysis of song frequency and time variables. 40 localities where specimens were recorded were used in this analysis. Variables with high loadings on PC1 were HF (highest frequency in first syllable) and DUR1 (duration of first syllable). LF (lowest frequency in first syllable) had a high loading on PC2.

Fig. 19. Distance phenogram of 40 localities, derived from a cluster analysis of song variables. Cophenetic correlation coefficient is 0.706.



of them. In this analysis, localities 26 and 28 were again grouped in the northern cluster. In addition, localities 17 (Warwick), 18 (Legume), and 18s (Moorabinda Station) were grouped with more northern localities. A major southern cluster was comprised of localities from 19 (Sandy Flat) to 27 (Murrurundi). The moderate cophenetic correlation coefficient of 0.706 indicated that some distortion had occurred between the matrix constructed from the measurement variables and the corresponding phenogram distances.

Principal components and clustering analyses were also performed separately on song data obtained for collected birds. In this way, comparisons could be made between song data and morphological data for this subset of birds. Results of PCA for this group of data are given in Table 15. The first three components accounted for 97.1% of the variance; but in this analysis, PC1 accounted for 8.4% more of the variance (69.7%, compared to 61.3% for the previous PCA). In this analysis, the variables HF and DUR1 had comparably high loadings on PC1, as LF also had on PC2. However, in this PCA, HF and DUR1 had somewhat higher loadings on PC2 than in the previous analysis. Localities were again ordered by PC1 score (Table 16) and plotted by map distance and PC1 score (Fig. 20). The distance phenogram is shown in Fig. 21. Essentially the same northern and southern clusters, divided by the McPherson Range, were demonstrated for these 28 localities where birds

Table 15. Loadings of selected song variables on the first three principal components. (PCA was performed on data from 28 localities where specimens were collected.)

VARIABLE	PC1	PC2	PC3
SYLL	-0.535	-0.300	0.562
HF	0.530	0.147	0.804
LF	-0.326	0.935	0.116
DUR1	0.571	0.115	-0.177
% VARIANCE EXPLAINED:	69.7%	20.0%	7.4%

Table 16. Localities listed in order of increasing PC1 score. PCA was performed on the correlation matrix derived from measurements of 4 song variables which were common to all songs. 28 localities where specimens were collected were included in the analysis. Standardized PC1 scores are listed. Means for variables which had high loadings on PC1 (duration of first syllable and highest frequency of first syllable) are given for each locality.

LOC	PC1	DUR1	HF
5 CHA	-1.5497	0.07	2.87
6 HUG	-1.2662	0.07	2.80
1 DIM	-1.1257	0.06	2.79
3 MTG	-1.0474	0.07	2.74
10 ANA	-0.9086	0.11	2.73
28 DEN	-0.8056	0.12	2.90
16 KOG	-0.5577	0.13	2.76
9 ALP	-0.5486	0.13	2.75
8 BAR	-0.5302	0.13	2.74
7 PRA	-0.4804	0.12	2.78
4 LYN	-0.4473	0.11	2.86
11 GLE	-0.4436	0.11	2.91
13 ROM	-0.4419	0.13	2.80
2 RAV	-0.4147	0.10	2.86
26 WER	-0.3768	0.17	2.77
12 INJ	-0.3644	0.14	2.93
14 MIL	-0.3041	0.12	2.94
15 CHI	-0.1724	0.13	2.86
17 WAR	0.2741	0.14	3.07
18 LEG	0.3126	0.14	3.00
25 WAL	0.9106	0.24	3.07
21 DEE	1.0724	0.23	3.05
27 MUR	1.1184	0.26	3.00
24 ARD	1.3029	0.26	3.06
19 SAN	1.4365	0.21	3.13
20 BOL	1.4836	0.23	3.14
22 LLA	1.9012	0.30	3.16
23 BLA	1.9729	0.33	3.16

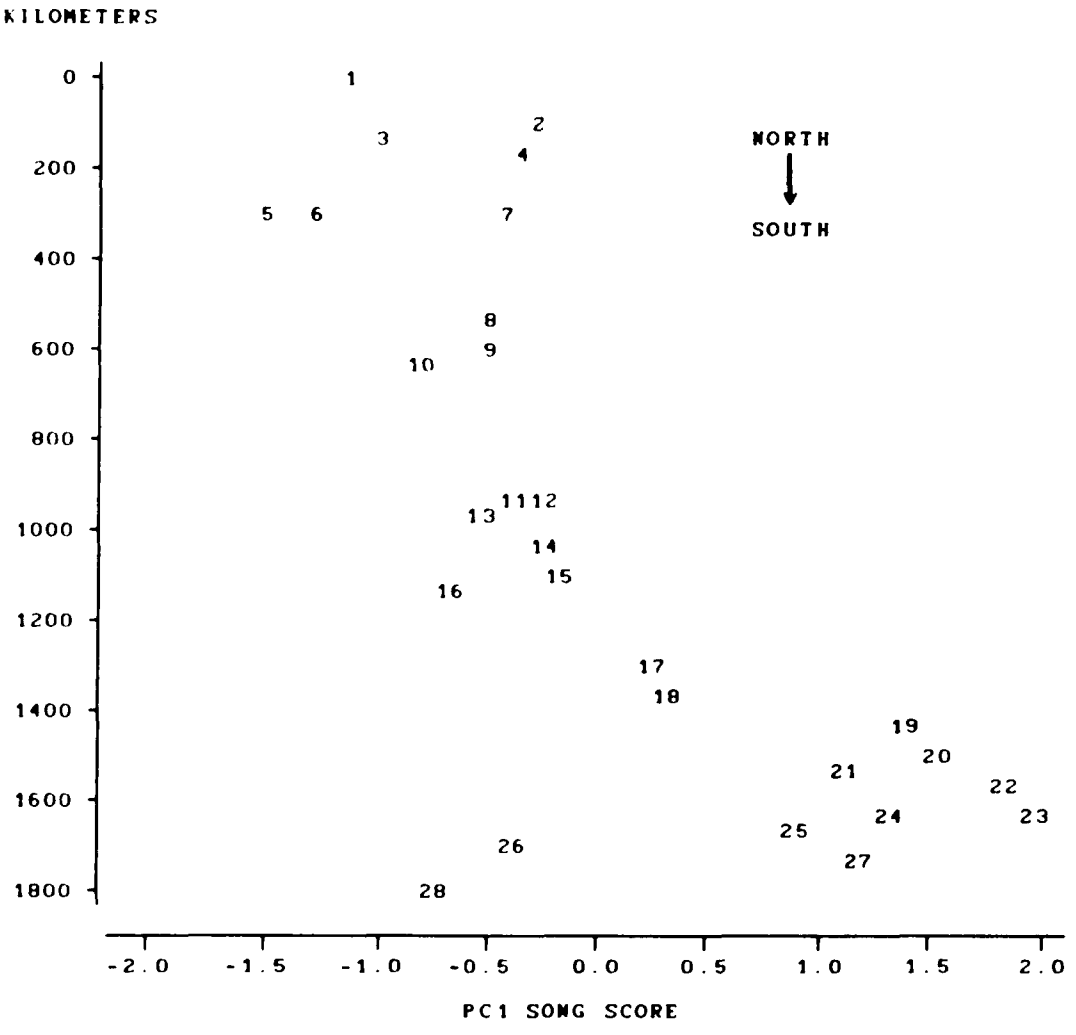
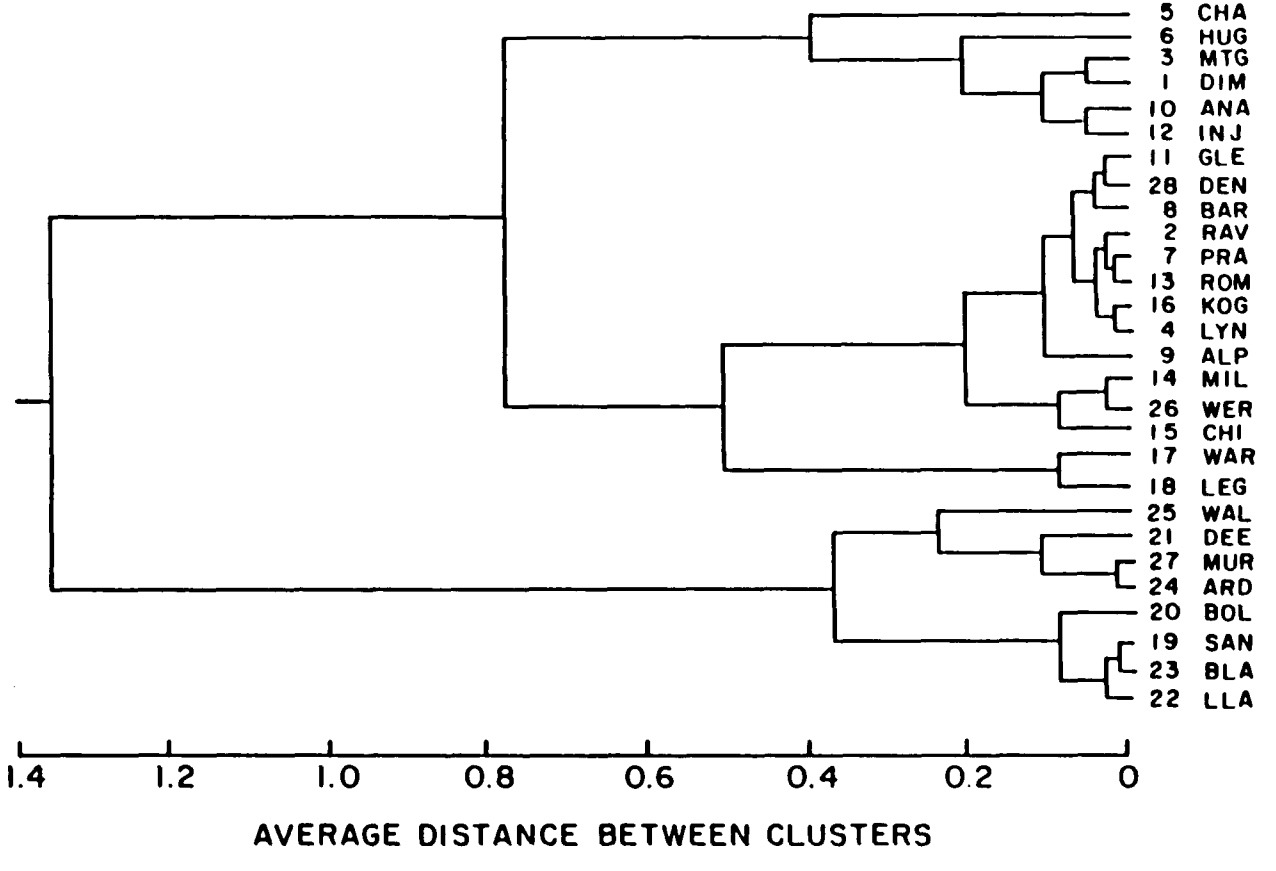


Figure 20. Localities plotted by map distance and PC1 scores derived from a principal components analysis of song frequency and time variables. 28 localities where specimens were collected were used in this analysis. Variables with high loadings on PC1 were HF (highest frequency in first syllable) and DUR1 (duration of first syllable).

Fig. 21. Distance phenogram of 28 localities where specimens were collected, derived from a cluster analysis of song variables. Cophenetic correlation coefficient is 0.754.



were collected, as for the 40 localities above.

I used NTSYS/MXCOMP to test whether song "distance" (the average distance between clusters on the phenogram in Fig. 19) was related to geographic distance between localities. With this program, the matrix of song data used to derive the phenogram was compared with a matrix of geographic distances (km) for all pairs of songs. Results are shown in the scattergram in Fig. 22. If the observed points were statistically independent, there would be a significant linear relationship between song distance and map distance (product-moment correlation coefficient $r=0.485$, $p<.01$). However, because the scattergram represents pairwise comparisons of the matrices and thus each locality is represented more than once, the observed points are not strictly independent. Nevertheless, the pattern of points suggests that distance between clusters on the phenogram is related to geographic distance.

Results of the discriminant function analysis (SAS PROC DISCRIM), which tested the relationship between the classification of a collected individual by the parameters of his song and his subspecies classification based on plumage pattern, were as follows. First, specimens were categorized by subspecies according to the descriptions of plumage patterns discussed in the Introduction and listed in (Table 1). Three specimens which were not easily categorized as a particular subspecies (because of an

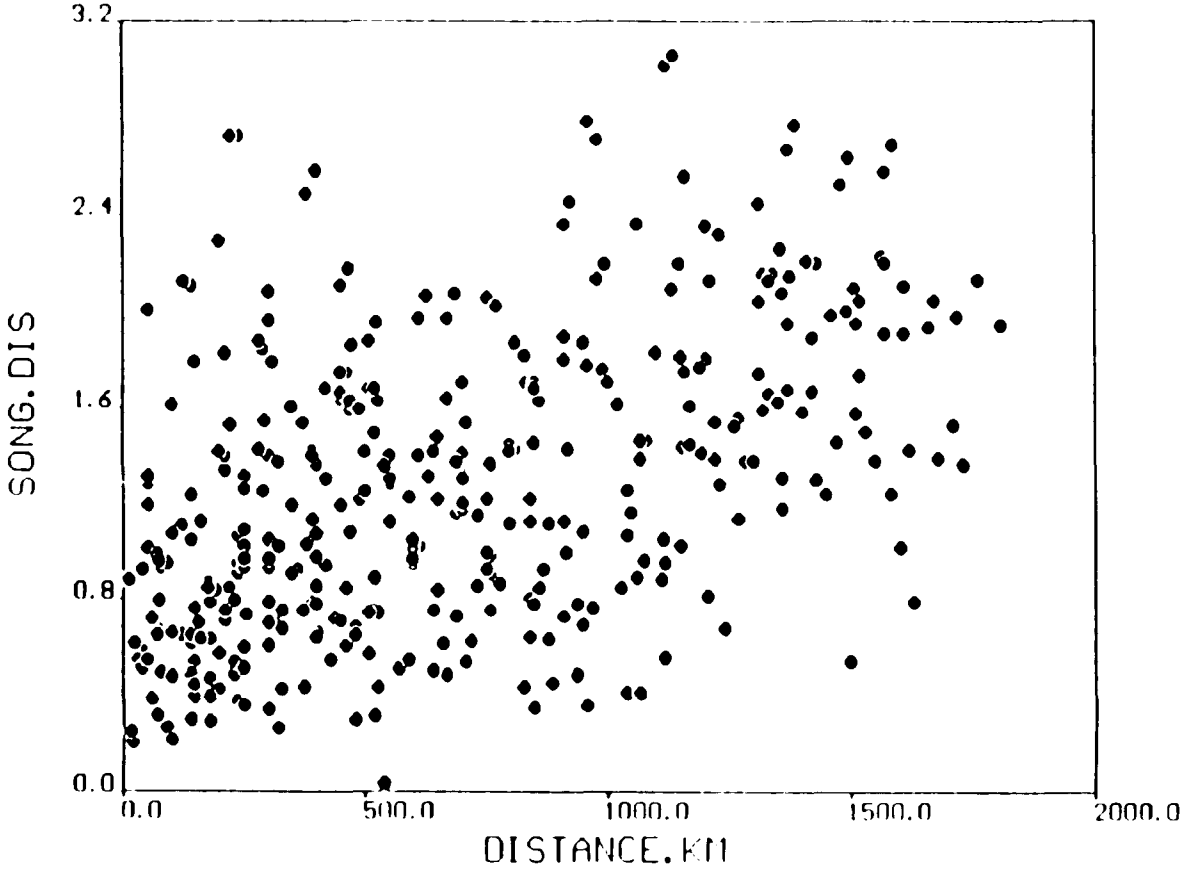


Fig. 22. The relation of song "distance", derived from the phenogram matrix, and geographic distance. r=0.485.

intermediate number of primaries edged in white) were excluded from this analysis. The program was then used to classify individuals based on measurements of song variables, using a quadratic function. I then tested the performance of this criterion against the original classification by subspecies. By this method, 35.6% of all individuals could *not* be classified to subspecies correctly. 46.0% of individuals originally designated substriatus were misclassified by the song function; 35.5% of melanocephalus were misclassified; and 19.6% of ornatus were misclassified.

RESULTS FOR MORPHOLOGY

Data for the 182 museum skins I measured are given in Appendix VI. Samples of 3 or more birds per locality were found for only 8 localities. Descriptive statistics were computed for these samples, and are also presented in the same appendix. I did not include these samples in any further analyses because none was within the geographic range of this study. (In addition, specimens within localities were temporally separated.)

The results of univariate and multivariate analyses of variation in morphological variables for the specimens I collected are presented in this section. First, simple descriptive statistics are presented, by locality, for each variable (weight, body length, wingspan, and wing, tail, tarsus, and culmen lengths). Then the results of analyses of variance for each variable are presented, in the same manner used for song variables. The GT2 method (Hochberg 1974) for multiple *a posteriori* comparisons of pairs of means was used. Variances were considered to be heterogeneous. This method identifies homogeneous subsets of means, which are not significantly different at $p<.05$. These ANOVA results are presented on maps with accompanying lists of means ranked in order of magnitude. Vertical lines next to the means denote homogeneous subsets. Five differently-shaded circles are used to portray the

qualitative degrees of magnitude of the means. The circles stand for the following relative size categories: unshaded circle, "small"; quarter-shaded, "moderately small"; half-shaded, "medium-sized"; three-quarters-shaded, "moderately large"; and solid circle, "large". The total range of means for each variable was divided into five equal intervals and the appropriate symbol assigned to each interval.)

Descriptive statistics are presented in Tables 17-23. Maps containing the ANOVA results are presented in Figs. 23-29.

The following general observations can be made from the tables and maps. Weight in these birds ranged from 7.5 to 13.3 g; wing length, from 57.7 to 69.1 mm; tail length, from 29.8 to 45.8 mm; tarsus length, from 16.0 to 21.6 mm; and culmen length from 6.0 to 8.9mm. Means for the variables weight, body length, wingspan, and wing length appeared to increase in a clinal manner from north to south. These variables were significantly correlated with latitude ($r>0.80$ in all cases). The maps showing homogeneous subsets of means illustrate the clinal patterns in these 4 variables (Figs. 23-26). Subsets of mean wing lengths (Fig. 26) showed the greatest degree of geographic segregation. No geographic patterns were obvious for mean tail, tarsus, and culmen lengths.

Table 17. Descriptive statistics for weight (g).

LOC	N	MEAN	SD	MIN	MAX	VAR	SE	CV
1 DIM	9	9.24	0.99	7.5	10.7	0.98	0.33	10.70
2 RAV	10	9.59	0.39	9.0	10.2	0.15	0.12	4.10
3 MTG	10	9.82	0.62	9.0	10.7	0.38	0.19	6.27
4 LYN	5	9.44	0.13	9.2	9.5	0.02	0.06	1.42
5 CHA	5	9.48	0.45	8.9	10.1	0.20	0.20	4.74
6 HUG	4	9.22	0.33	9.0	9.7	0.11	0.17	3.58
7 PRA	4	9.27	0.32	9.0	9.6	0.10	0.16	3.45
8 BAR	10	9.89	0.43	9.4	10.7	0.18	0.13	4.30
9 ALP	10	9.84	0.55	8.8	10.4	0.30	0.17	5.61
10 ANA	10	9.94	0.42	9.2	10.6	0.18	0.13	4.25
11 GLE	10	10.34	0.81	9.0	11.7	0.66	0.26	7.85
12 INJ	9	10.98	0.51	10.2	11.8	0.26	0.17	4.62
13 ROM	6	10.87	0.62	9.9	11.5	0.38	0.25	5.66
14 MIL	10	11.04	0.50	10.3	12.1	0.25	0.16	4.54
15 CHI	5	10.82	0.56	10.1	11.5	0.32	0.25	5.20
16 KOG	10	11.32	0.72	9.7	12.2	0.52	0.23	6.38
17 WAR	9	11.20	0.54	10.4	12.0	0.29	0.18	4.79
18 LEG	7	11.97	0.39	11.5	12.5	0.15	0.15	3.26
19 SAN	10	12.18	0.38	11.6	13.0	0.15	0.12	3.14
20 BOL	8	11.92	0.48	11.3	12.5	0.23	0.17	4.05
21 DEE	10	12.04	0.56	11.2	12.7	0.31	0.18	4.62
22 LLA	10	12.11	0.59	11.2	13.0	0.35	0.19	4.87
23 BLA	5	12.06	0.66	11.2	13.0	0.44	0.30	5.49
24 ARD	8	12.16	0.54	11.4	12.9	0.30	0.19	4.48
25 WAL	8	11.81	0.40	11.4	12.5	0.16	0.14	3.37
26 WER	5	12.12	0.92	11.2	13.3	0.85	0.41	7.59
27 MUR	3	11.80	0.44	11.5	12.3	0.19	0.25	3.69
28 DEN	1	11.40	.	11.4	11.4	.	.	.

Table 18. Descriptive statistics for body length (mm).

LOC	N	MEAN	SD	MIN	MAX	VAR	SE	CV
1 DIM	9	94.5	2.60	90	98	6.78	0.87	2.75
2 RAV	10	99.0	5.27	94	112	27.78	1.67	5.32
3 MTG	10	97.6	2.59	94	102	6.71	0.82	2.65
4 LYN	5	96.2	3.77	92	102	14.20	1.69	3.92
5 CHA	5	97.4	2.41	94	100	5.80	1.08	2.47
6 HUG	4	98.0	4.69	95	105	22.00	2.35	4.79
7 PRA	4	102.0	4.55	97	108	20.67	2.27	4.46
8 BAR	10	99.7	3.40	95	105	11.57	1.08	3.41
9 ALP	10	99.5	2.84	95	103	8.06	0.90	2.85
10 ANA	10	100.2	2.86	95	105	8.18	0.90	2.85
11 GLE	10	99.7	3.13	95	104	9.79	0.99	3.14
12 INJ	9	102.4	2.30	99	105	5.28	0.77	2.24
13 ROM	6	99.8	2.48	97	103	6.17	1.01	2.49
14 MIL	10	102.1	2.28	100	106	5.21	0.72	2.24
15 CHI	5	99.6	2.88	97	104	8.30	1.29	2.89
16 KOG	9	102.7	2.96	96	106	8.75	0.99	2.88
17 WAR	9	102.1	3.55	96	107	12.61	1.18	3.48
18 LEG	7	106.0	2.83	102	110	8.00	1.07	2.67
19 SAN	10	106.9	4.09	102	114	16.77	1.29	3.83
20 BOL	8	105.4	3.20	100	110	10.27	1.13	3.04
21 DEE	10	106.3	2.75	104	112	7.57	0.87	2.59
22 LLA	9	107.1	2.93	104	113	8.61	0.98	2.74
23 BLA	5	108.0	2.35	105	110	5.50	1.05	2.17
24 ARD	7	106.6	2.07	103	109	4.29	0.78	1.94
25 WAL	8	104.9	3.83	101	112	14.70	1.36	3.66
26 WER	5	107.6	8.11	97	117	65.80	3.63	7.54
27 MUR	3	104.7	3.06	102	108	9.33	1.76	2.92
28 DEN	1	109.0	.	109	109	.	.	.

Table 19. Descriptive statistics for wingspan (mm).

LOC	N	MEAN	SD	MIN	MAX	VAR	SE	CV
1 DIM	9	172.1	9.53	158	183	90.86	3.18	5.54
2 RAV	10	171.5	6.85	161	183	46.94	2.17	4.00
3 MTG	10	174.3	8.77	161	190	76.90	2.77	5.03
4 LYN	5	168.2	2.17	165	170	4.70	0.97	1.29
5 CHA	5	180.8	2.28	177	183	5.20	1.02	1.26
6 HUG	4	169.5	5.32	163	176	28.33	2.66	3.14
7 PRA	4	168.5	4.73	162	172	22.33	2.36	2.80
8 BAR	10	174.8	7.89	155	185	62.18	2.49	4.51
9 ALP	10	178.8	5.20	172	188	27.07	1.65	2.91
10 ANA	10	179.7	5.52	170	186	30.46	1.75	3.07
11 GLE	10	183.5	6.13	174	195	37.61	1.94	3.34
12 INJ	9	184.8	4.74	179	192	22.44	1.58	2.56
13 ROM	6	181.5	2.17	179	185	4.70	0.89	1.19
14 MIL	10	185.3	5.29	178	195	28.01	1.67	2.86
15 CHI	5	182.6	5.46	177	190	29.80	2.44	2.99
16 KOG	10	185.3	5.06	176	191	25.57	1.60	2.73
17 WAR	9	183.9	3.48	178	189	12.11	1.16	1.89
18 LEG	7	185.7	4.92	180	192	24.24	1.86	2.65
19 SAN	10	187.3	5.85	179	199	34.23	1.85	3.12
20 BOL	8	191.4	3.34	189	197	11.13	1.18	1.74
21 DEE	9	189.7	5.29	177	196	28.00	1.76	2.79
22 LLA	10	191.1	4.84	182	198	23.43	1.53	2.53
23 BLA	5	194.0	3.39	191	199	11.50	1.52	1.75
24 ARD	8	190.9	5.89	183	199	34.70	2.08	3.09
25 WAL	8	188.0	5.32	184	198	28.29	1.88	2.83
26 WER	5	192.4	6.47	185	202	41.80	2.89	3.36
27 MUR	3	194.0	2.00	192	196	4.00	1.15	1.03
28 DEN	1	188.0	.	188	188	.	.	.

Table 20. Descriptive statistics for wing length (mm).

LOC	N	MEAN	SD	MIN	MAX	VAR	SE	CV
1 DIM	9	60.0	1.53	58.5	63.2	2.34	0.51	2.55
2 RAV	10	60.1	1.33	57.7	62.1	1.77	0.42	2.21
3 MTG	10	60.5	0.89	58.9	62.0	0.80	0.28	1.47
4 LYN	5	59.9	1.47	58.2	62.2	2.17	0.66	2.46
5 CHA	5	61.8	1.38	60.6	64.2	1.90	0.62	2.23
6 HUG	4	60.2	0.67	59.6	61.1	0.44	0.33	1.11
7 PRA	4	60.5	1.27	59.6	62.3	1.62	0.64	2.10
8 BAR	10	61.8	2.02	56.9	63.7	4.08	0.64	3.27
9 ALP	10	61.5	1.85	58.0	64.0	3.43	0.59	3.01
10 ANA	10	62.0	1.29	59.6	63.7	1.66	0.41	2.08
11 GLE	10	62.4	3.42	58.7	67.1	11.70	1.08	5.48
12 INJ	9	62.9	2.79	59.0	66.4	7.77	0.93	4.43
13 ROM	6	62.6	2.37	60.0	66.1	5.61	0.97	3.79
14 MIL	10	62.4	2.29	57.9	64.8	5.23	0.72	3.67
15 CHI	5	60.5	1.31	59.2	62.3	1.71	0.58	2.16
16 KOG	10	62.8	2.13	60.1	65.8	4.54	0.67	3.39
17 WAR	9	62.8	1.60	61.2	66.0	2.56	0.53	2.54
18 LEG	7	63.3	1.94	61.4	67.1	3.76	0.73	3.05
19 SAN	10	64.7	2.69	61.2	68.9	7.24	0.85	4.14
20 BOL	8	65.0	1.77	62.5	68.2	3.14	0.63	2.71
21 DEE	10	65.7	1.99	61.6	68.5	3.97	0.63	3.03
22 LLA	10	65.5	1.55	62.9	68.5	2.39	0.49	2.35
23 BLA	5	64.8	1.13	63.6	66.3	1.29	0.51	1.74
24 ARD	8	65.6	2.02	63.5	69.3	4.07	0.71	3.06
25 WAL	8	65.6	1.58	63.7	67.5	2.49	0.56	2.40
26 WER	5	67.6	1.74	64.8	69.1	3.02	0.78	2.57
27 MUR	3	67.8	0.80	67.0	68.6	0.64	0.46	1.18
28 DEN	1	66.8	.	66.8	66.8	.	.	.

Table 21. Descriptive statistics for tail length (mm).

LOC	N	MEAN	SD	MIN	MAX	VAR	SE	CV
1 DIM	9	34.2	2.22	30.4	36.3	4.92	0.74	6.49
2 RAV	10	35.9	2.21	31.4	39.8	4.88	0.70	6.15
3 MTG	10	34.5	2.48	31.6	38.5	6.16	0.78	7.18
4 LYN	4	38.1	2.52	35.6	41.3	6.36	1.26	6.62
5 CHA	5	32.2	1.76	29.8	34.5	3.10	0.79	5.46
6 HUG	4	37.6	2.42	35.5	40.8	5.86	1.21	6.43
7 PRA	4	37.7	0.50	37.2	38.3	0.25	0.25	1.32
8 BAR	10	35.5	3.91	31.2	40.6	15.27	1.24	11.01
9 ALP	10	35.5	4.50	30.6	41.1	20.26	1.42	12.69
10 ANA	10	36.4	4.44	31.5	42.1	19.75	1.41	12.20
11 GLE	10	36.8	4.80	31.4	42.7	23.03	1.52	13.03
12 INJ	9	36.9	4.93	28.8	42.5	24.26	1.64	13.35
13 ROM	6	37.5	5.65	31.8	44.4	31.98	2.31	15.07
14 MIL	10	37.9	5.75	31.5	44.6	33.02	1.82	15.17
15 CHI	5	42.3	2.09	40.0	44.3	4.38	0.94	4.95
16 KOG	9	38.7	5.35	32.3	45.8	28.60	1.78	13.80
17 WAR	9	36.1	3.31	31.4	40.1	10.98	1.10	9.12
18 LEG	7	37.9	4.42	31.4	42.6	19.57	1.67	11.55
19 SAN	10	38.1	3.08	34.0	42.3	9.51	0.98	7.93
20 BOL	8	39.6	3.10	34.5	43.0	9.59	1.09	7.78
21 DEE	10	39.0	4.14	33.9	45.0	17.15	1.31	10.57
22 LLA	9	39.0	3.80	34.4	43.5	14.43	1.27	9.67
23 BLA	5	42.2	0.72	41.4	43.2	0.52	0.32	1.70
24 ARD	7	39.5	3.23	35.5	43.2	10.43	1.22	8.12
25 WAL	8	39.4	3.01	36.0	44.0	9.08	1.07	7.63
26 WER	5	37.2	1.07	36.2	38.4	1.15	0.48	2.88
27 MUR	2	36.5	2.97	34.4	38.6	8.82	2.10	8.14
28 DEN	1	36.6	.	36.6	36.6	.	.	.

Table 22. Descriptive statistics for tarsus length (mm).

LOC	N	MEAN	SD	MIN	MAX	VAR	SE	CV
1 DIM	9	18.6	1.07	16.8	20.0	1.15	0.36	5.77
2 RAV	10	18.4	0.69	16.7	19.2	0.48	0.22	3.77
3 MTG	10	18.7	0.94	17.2	20.1	0.89	0.30	5.04
4 LYN	5	17.2	0.53	16.3	17.7	0.28	0.24	3.07
5 CHA	5	19.9	0.50	19.4	20.6	0.25	0.22	2.49
6 HUG	4	18.4	1.69	16.7	19.9	2.85	0.84	9.17
7 PRA	4	17.9	1.06	16.6	18.9	1.11	0.53	5.89
8 BAR	10	18.6	1.17	16.2	20.2	1.37	0.37	6.28
9 ALP	10	18.5	1.50	16.0	20.2	2.25	0.47	8.10
10 ANA	10	18.7	1.23	16.7	20.6	1.52	0.39	6.61
11 GLE	10	18.4	1.38	16.4	19.9	1.89	0.43	7.48
12 INJ	9	19.1	1.23	17.5	20.7	1.52	0.41	6.47
13 ROM	6	18.6	0.75	17.4	19.4	0.56	0.31	4.02
14 MIL	10	18.8	1.52	17.0	21.4	2.32	0.48	8.11
15 CHI	5	17.7	0.72	17.0	18.7	0.52	0.32	4.10
16 KOG	10	19.1	1.36	17.6	21.2	1.85	0.43	7.12
17 WAR	9	18.9	0.92	17.4	19.8	0.84	0.31	4.87
18 LEG	7	18.8	0.66	17.9	19.7	0.44	0.25	3.54
19 SAN	10	19.8	0.73	18.7	21.0	0.53	0.23	3.70
20 BOL	8	20.0	0.95	18.9	21.6	0.91	0.34	4.76
21 DEE	10	19.5	0.86	17.7	20.1	0.75	0.27	4.43
22 LLA	10	19.5	0.76	18.5	21.1	0.58	0.24	3.93
23 BLA	5	19.1	0.92	18.0	20.0	0.85	0.41	4.84
24 ARD	8	19.5	0.91	18.2	21.0	0.84	0.32	4.70
25 WAL	8	19.8	1.18	18.2	21.6	1.40	0.42	5.99
26 WER	5	19.7	1.20	18.2	21.4	1.44	0.54	6.07
27 MUR	3	20.2	0.15	20.0	20.3	0.02	0.09	0.76
28 DEN	1	19.9	.	19.9	19.9	.	.	.

Table 23 . Descriptive statistics for culmen length (mm).

LOC	N	MEAN	SD	MIN	MAX	VAR	SE	CV
1 DIM	9	7.33	0.70	6.0	8.2	0.49	0.23	9.52
2 RAV	10	7.50	0.31	7.1	7.9	0.09	0.10	4.07
3 MTG	10	7.39	0.35	6.7	7.8	0.13	0.11	4.79
4 LYN	5	7.30	0.46	6.6	7.9	0.21	0.21	6.35
5 CHA	5	7.50	0.35	7.1	7.9	0.13	0.16	4.71
6 HUG	4	7.38	0.75	6.3	7.9	0.57	0.38	10.23
7 PRA	4	7.28	0.26	6.9	7.5	0.07	0.13	3.62
8 BAR	10	7.60	0.47	6.7	8.2	0.22	0.15	6.14
9 ALP	10	7.33	0.56	6.5	8.1	0.31	0.18	7.64
10 ANA	10	7.63	0.24	7.4	8.1	0.06	0.08	3.15
11 GLE	10	7.51	0.73	6.7	8.6	0.54	0.23	9.75
12 INJ	9	7.92	0.44	7.2	8.7	0.20	0.15	5.60
13 ROM	6	7.28	0.37	6.9	7.8	0.14	0.15	5.09
14 MIL	10	7.28	0.66	6.0	8.4	0.44	0.21	9.11
15 CHI	5	8.10	0.33	7.8	8.5	0.11	0.15	4.09
16 KOG	10	7.52	0.84	6.1	8.7	0.71	0.27	11.18
17 WAR	9	7.28	0.28	7.0	7.8	0.08	0.09	3.81
18 LEG	7	7.36	0.32	6.7	7.7	0.10	0.12	4.29
19 SAN	10	7.55	0.27	7.2	8.1	0.07	0.09	3.60
20 BOL	8	7.73	0.42	7.1	8.3	0.18	0.15	5.48
21 DEE	10	7.48	0.58	7.0	8.9	0.34	0.18	7.79
22 LLA	10	7.57	0.44	7.0	8.3	0.20	0.14	5.84
23 BLA	5	7.74	0.27	7.3	8.0	0.07	0.12	3.49
24 ARD	8	7.69	0.41	7.1	8.4	0.17	0.14	5.32
25 WAL	8	7.90	0.41	7.3	8.4	0.17	0.15	5.24
26 WER	5	7.28	0.45	6.8	7.9	0.21	0.20	6.25
27 MUR	3	7.60	0.10	7.5	7.7	0.01	0.06	1.32
28 DEN	1	7.10	.	7.1	7.1	.	.	.

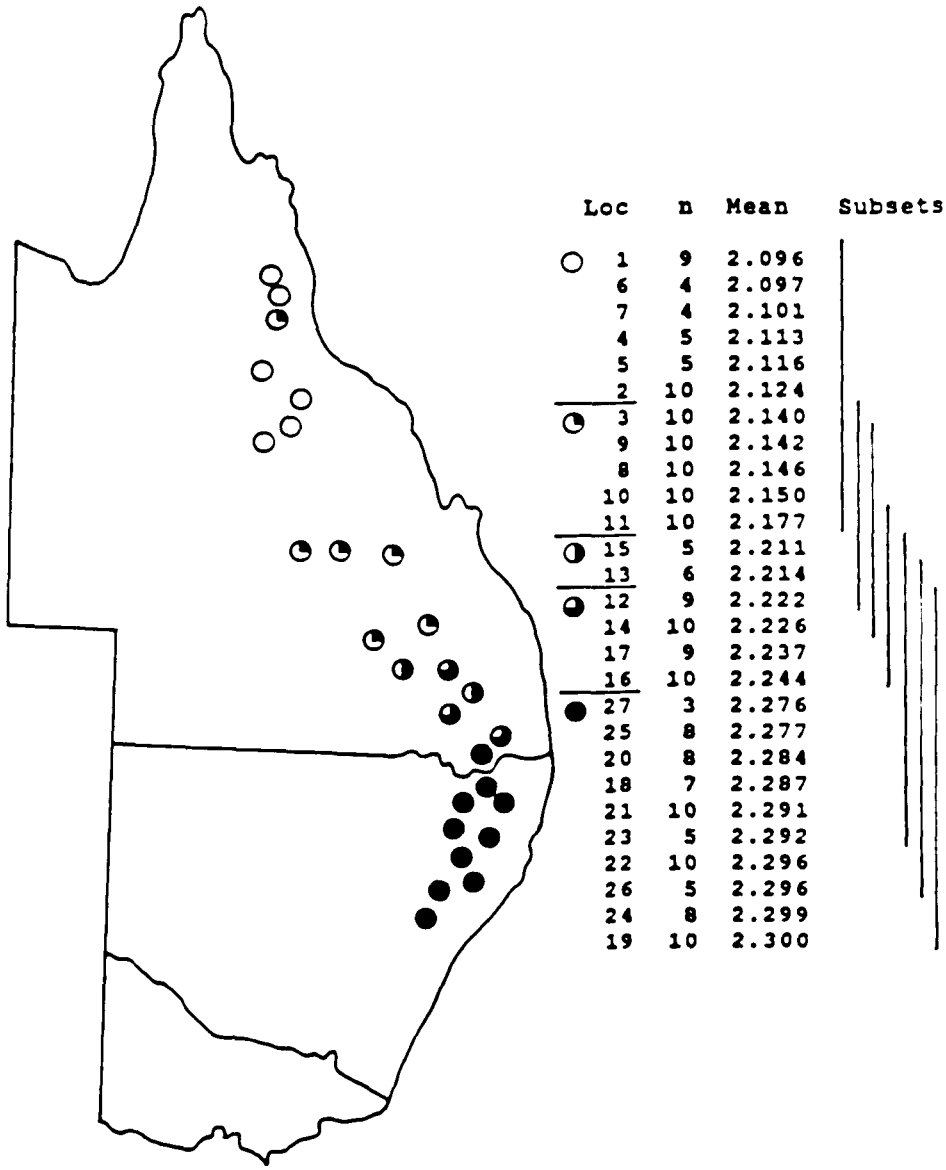


Fig. 23. Geographic variation in mean cube root of weight of male Pardalotus striatus in eastern Australia. Means are listed in increasing order of magnitude, adjacent to the number code for each locality. Locality numbers indicate relative latitude, with 1 being northernmost. Vertical lines represent subsets of means which do not differ significantly from each other. The five symbols correspond to a ranked qualitative description of variation of the measured variable. See text for further explanation.

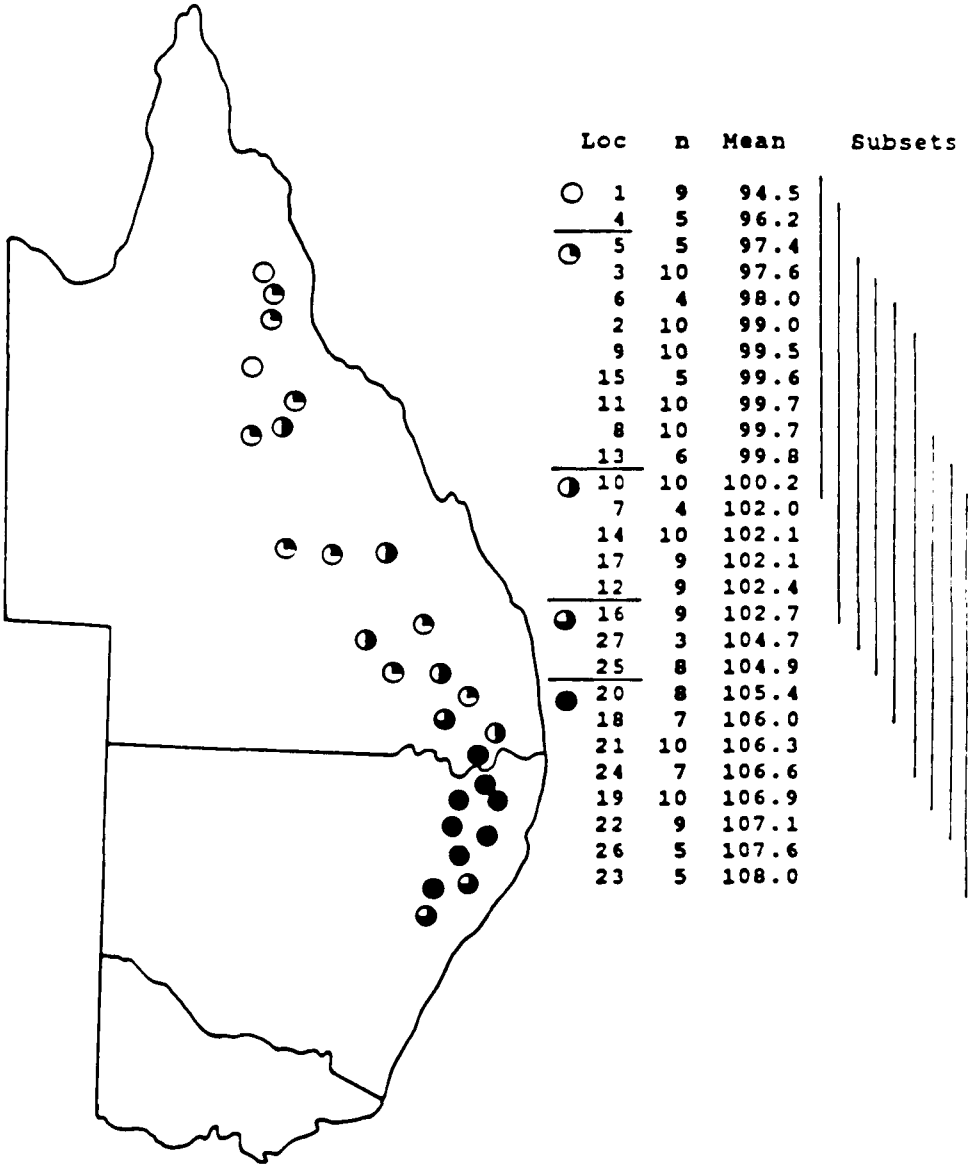


Fig. 24. Geographic variation in mean body length of male Pardalotus striatus in eastern Australia. See Fig. 23 and text for further explanation.

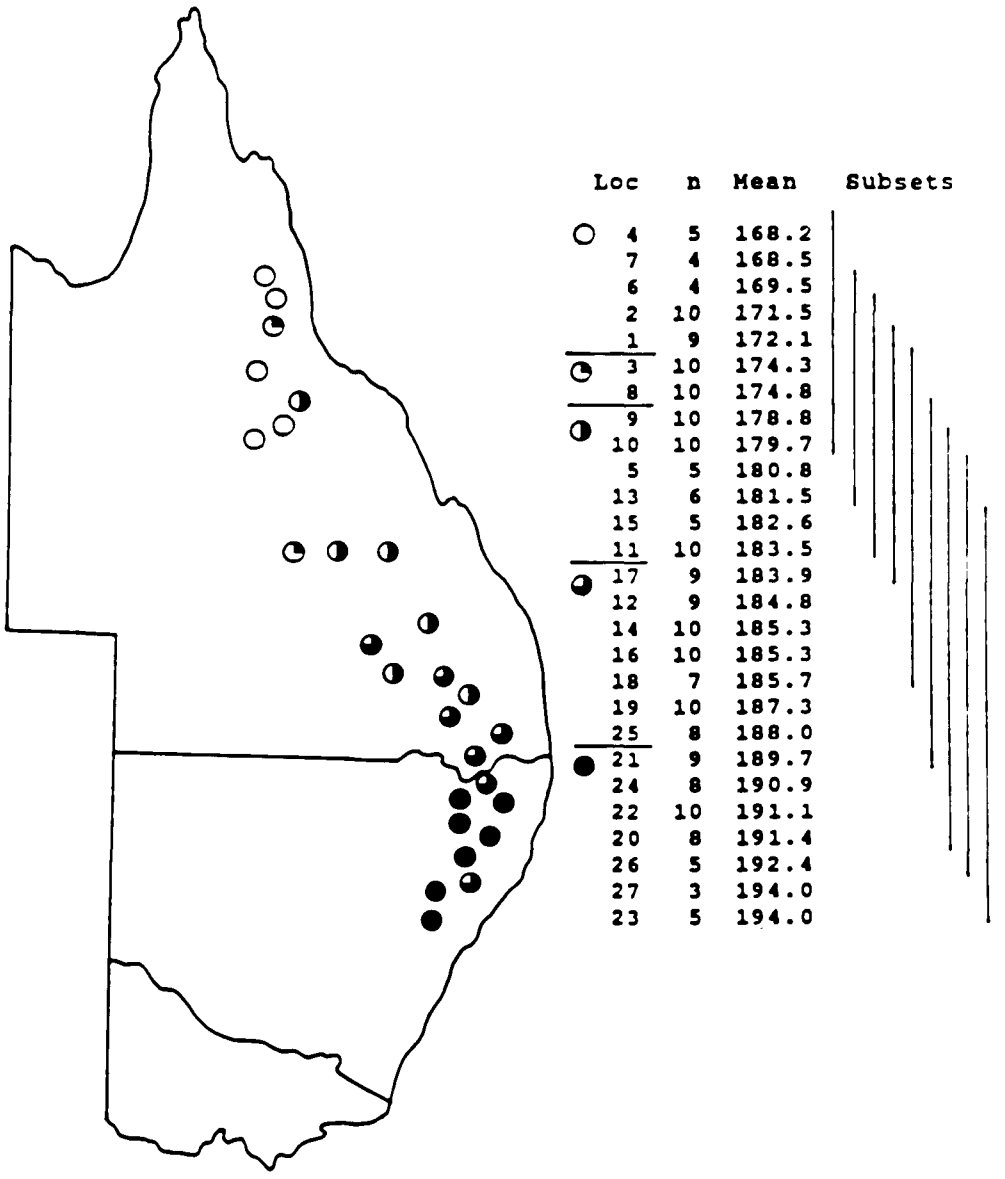


Fig. 25. Geographic variation in mean wingspan male Pardalotus striatus in eastern Australia. See Fig. 23 and text for further explanation.

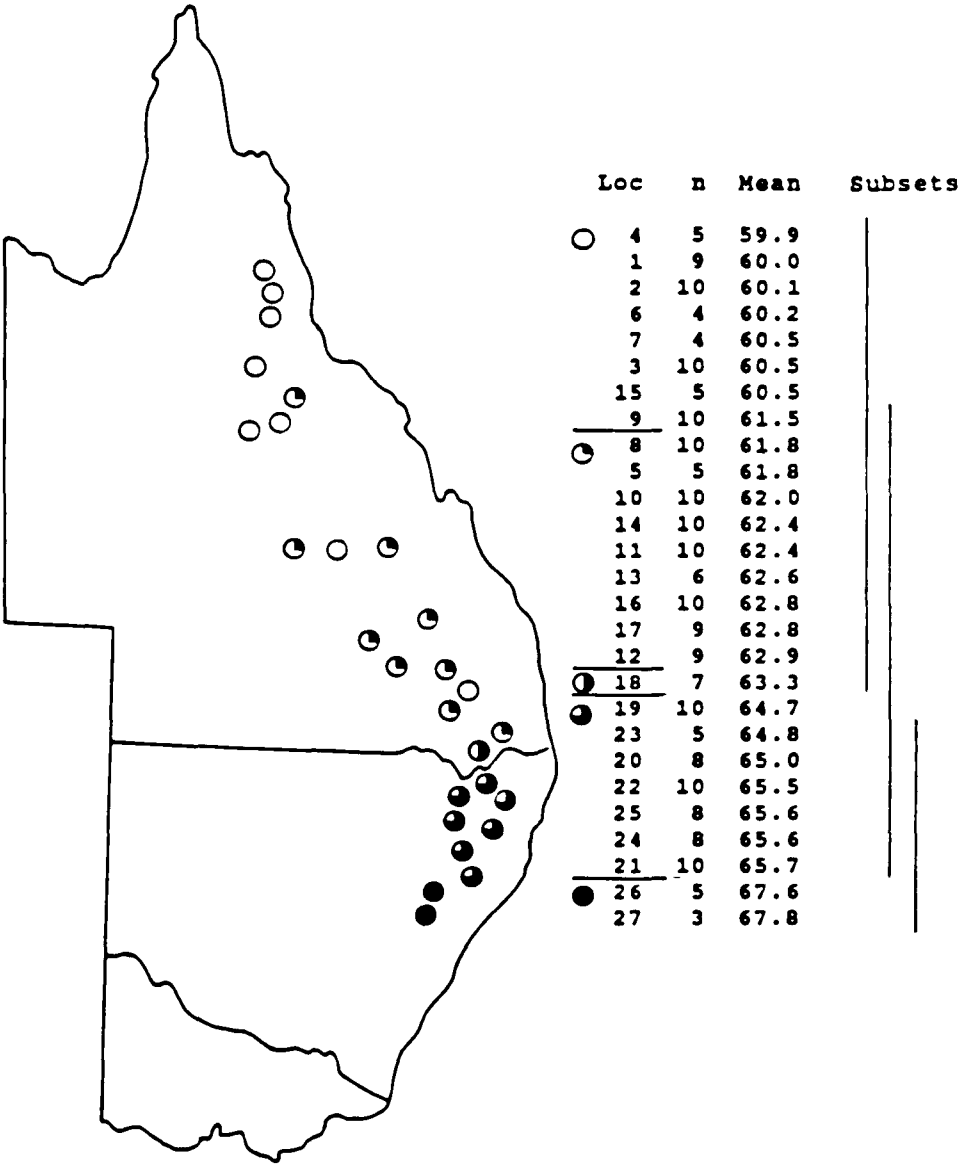


Fig. 26. Geographic variation in mean wing length of male Pardalotus striatus in eastern Australia. See Fig. 23 and text for further explanation.

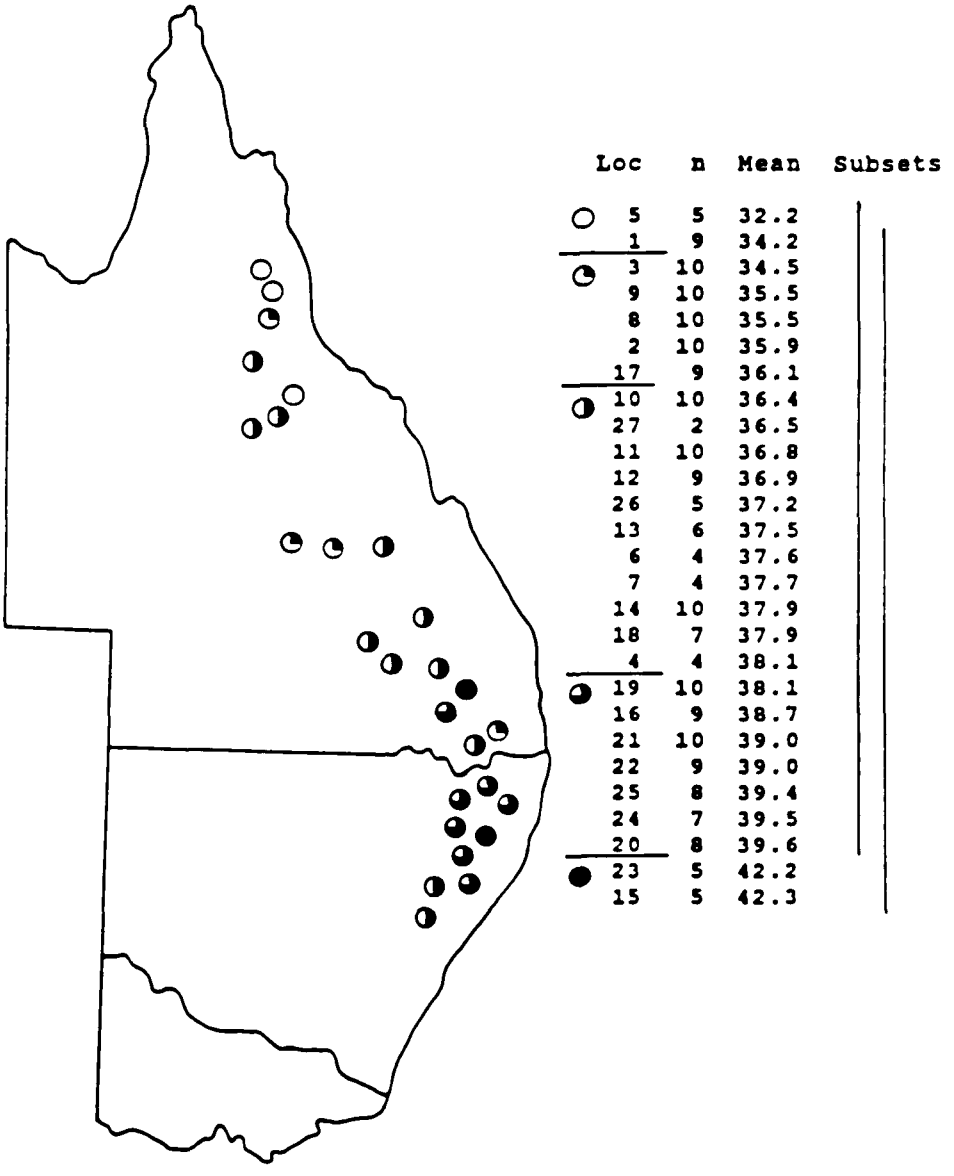


Fig. 27. Geographic variation in mean tail length of male Pardalotus striatus in eastern Australia. See Fig. 23 and text for further explanation.

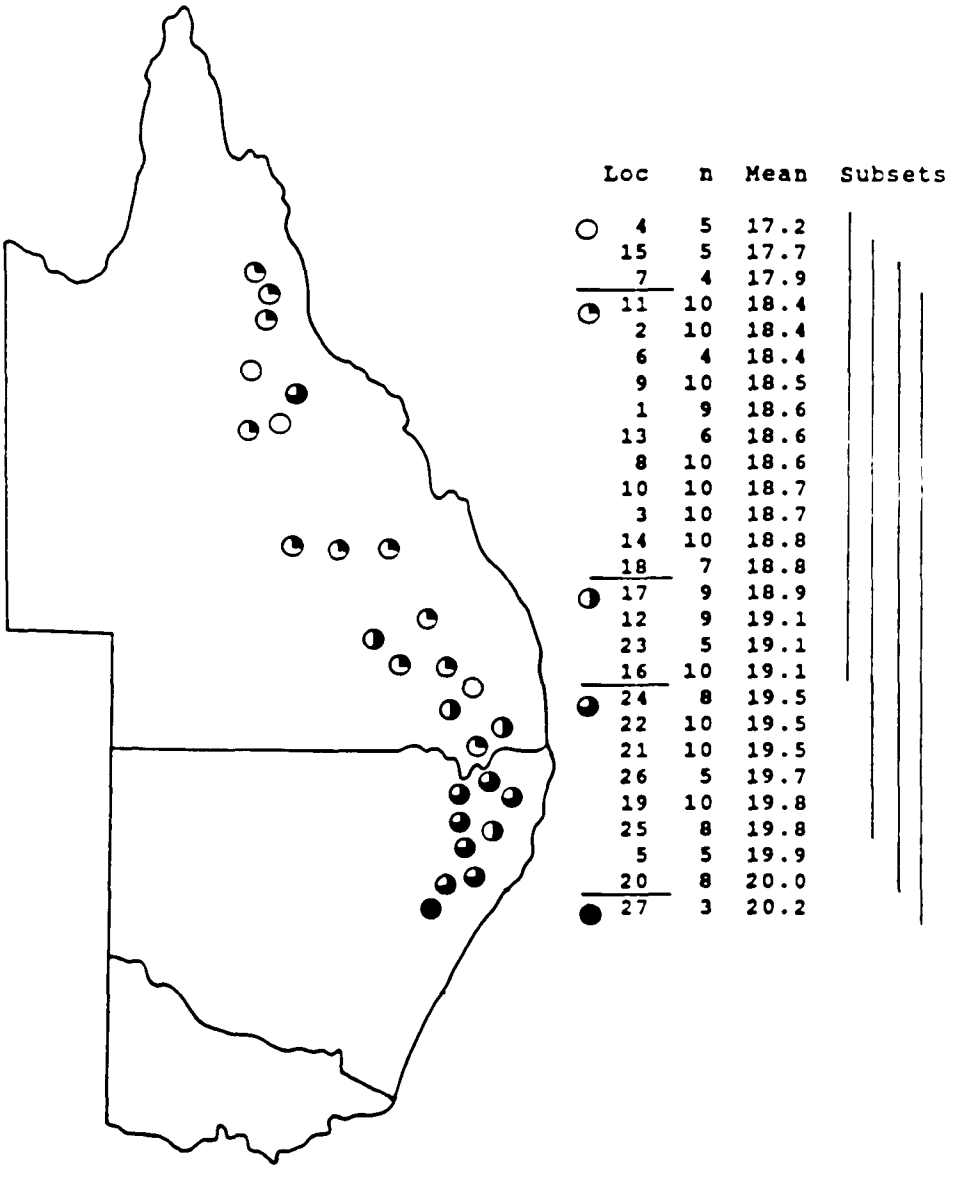


Fig. 28. Geographic variation in mean of tarsus length of male Pardalotus striatus in eastern Australia. See Fig. 23 and text for further explanation.

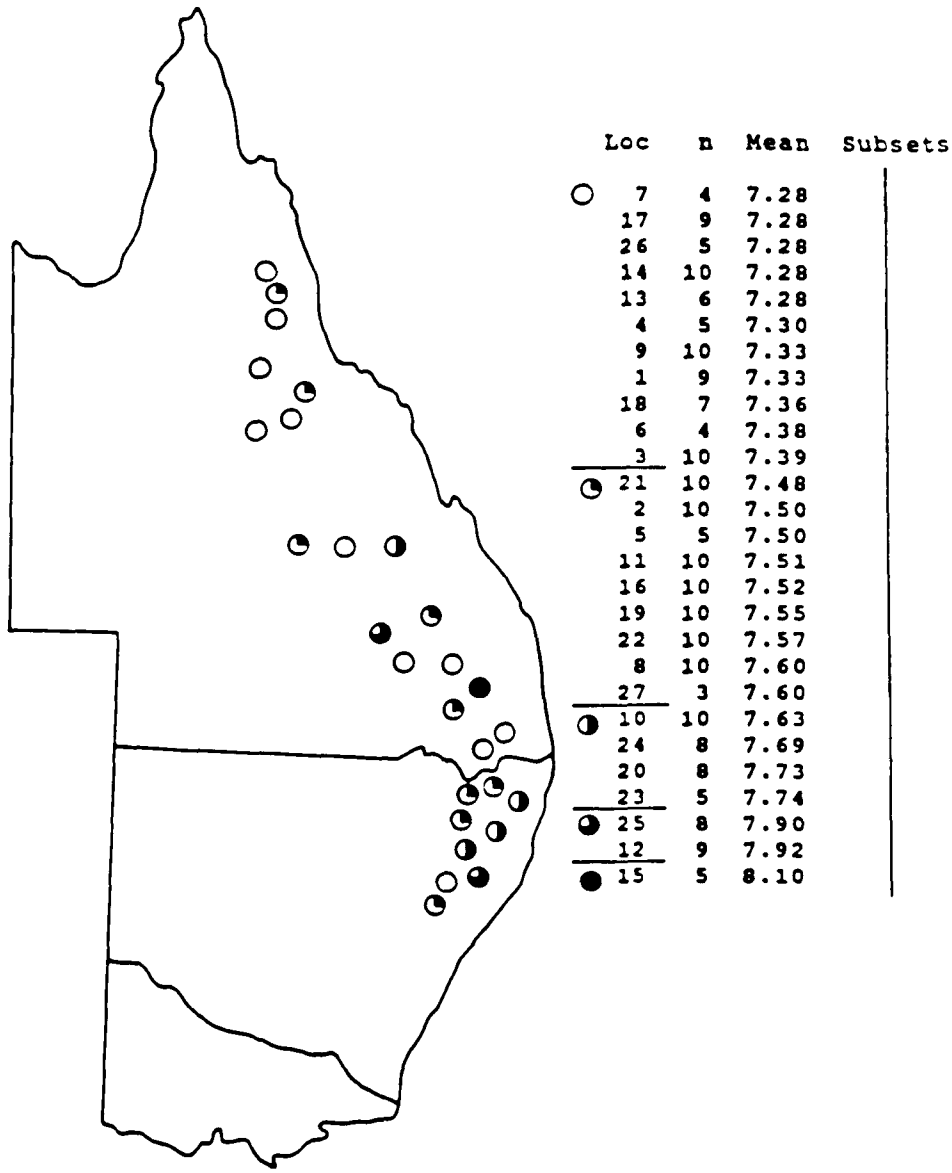


Fig. 29. Geographic variation in mean culmen length of male Pardalotus striatus in eastern Australia. See Fig. 23 and text for further explanation.

Mean coefficients of variation (CV) for each variable, computed over all localities, are given in Table 24. CV's for weight, wing length, and culmen length were comparable to those compiled by Johnson (1980) for six species of small North American passerines. CV's for weight and winglength reported by Woinarski et al. (1983) for P. striatus in southeastern Australia were also comparable to those presented here. However, the mean CV's for tail and tarsus lengths were significantly different from the ones reported by Woinarski for this species.

Three different nested analyses of variance (ANOVA, SAS PROC NESTED) were performed on each of the morphological variables in order to evaluate possible different sources of geographic variation. The purpose was to determine how much of the variation for each character could be attributed to particular different levels of classification. The levels investigated were subspecies, regional cluster (identified by a multivariate cluster analysis, described below, which grouped localities into 3 distinct geographic regions), locality, and individual/error. First, ANOVA was performed using locality as a single hierarchical level. Second, a two-level ANOVA was performed using subspecies and locality as levels. Finally, another two-level ANOVA was performed using region and locality as levels. Results are shown in Table 25. For all variables but tail and culmen length, "region" accounted for somewhat more of the variation than

Table 24. Mean coefficients of variation for morphological measurements in *Pardalotus striatus*.

Variable	Mean C.V.
Body weight	4.89
Wing length	2.75
Tail length	9.15
Tarsus length	5.22
Culmen length	5.83
Body length	3.26
Wingspan	2.81

	WS	BL	WL	TL	WT	TRS	CLM
Subspecies	55	51	47	16	72	18	1
Locality	12	8	11	1	9	3	6
Error	33	41	42	83	19	79	93
Region	64	55	59	16	79	21	1
Locality	4	6	1	2	3	3	4
Error	32	39	40	82	17	76	95
Locality	60	52	54	16	77	19	5
Error	40	48	46	84	23	80	95

Table 25. Summary of three Nested ANOVA performed on each of 7 morphological variables (wingspan, body length, wing length, tail length, cube root of weight, tarsus length, and culmen length). The numbers are the percent of the variance ascribed to each level. Levels are described in the text.

subspecies. For example, for wing length, the single-level analysis showed that 54% of the variance was among localities and 46% was within (plus error term). In the second analysis, 47% of the variance for wing length was among subspecies, 11% among localities, and 42% within localities. In the third analysis, 59% of the variance was among regions, 1% among localities, and 40% within localities. For five of the seven characters measured, the three geographic regions explained more of the variation than did the three subspecies.

Principal Components Analysis (PCA) was performed to examine the possibility that all the variables could be reduced to a single component which could be used to explain most of the variance. Loadings of the seven morphological variables on the first three principal components are given in Table 26. PC1 accounted for almost 90% of the variance; and wingspan, body length, and wing length had high loadings on this component. In order to look for geographic pattern based on this component, localities were sorted and listed by standardized PC1 scores (Table 27). Because PC1 did appear to order localities geographically, localities were then plotted by map distance and PC1 score to look for possible regions of steep change in scores (Fig.30). No region of steep change was detected.

Table 26. Loadings of morphological variables on the first three principal components.

VARIABLE	PC1	PC2	PC3
cube root weight	0.008	0.005	-.002
body length	0.395	0.664	0.525
wingspan	0.872	-.389	-.258
wing length	0.253	0.016	0.376
tail length	0.125	0.631	-.695
tarsus length	0.063	-.096	0.165
culmen length	0.007	0.001	-.073
% VARIANCE EXPLAINED:	89.9%	5.7%	3.7%

Table 27. Localities listed in order of increasing mean size of birds, as determined by the first principal component. PCA was performed on the covariance matrix derived from measurements of 7 morphological variables. Standardized PC1 scores are listed. Means for variables which had high loadings on PC1 (body length, wingspan, wing length, and tail length) are given for each locality.

LOC	PC1	MBL	MWSP	MWL	MTL
4 LYN	-1.7712	96.2	168.2	59.9	38.1
6 HUG	-1.5576	98.0	169.5	60.2	37.6
1 DIM	-1.5065	94.5	172.1	60.0	34.2
7 PRA	-1.4727	102.0	168.5	60.5	37.7
2 RAV	-1.3454	99.0	171.5	60.1	35.9
3 MTG	-1.1429	97.6	174.3	60.5	34.5
8 BAR	-0.9537	99.7	174.8	61.8	32.2
9 ALP	-0.5869	99.5	178.8	61.5	35.5
5 CHA	-0.5108	97.4	180.8	61.8	32.2
10 ANA	-0.4388	100.2	179.7	62.0	36.4
13 ROM	-0.2520	99.8	181.5	62.6	37.5
15 CHI	-0.1531	99.6	182.6	60.5	42.3
11 GLE	-0.0796	99.7	183.5	62.4	36.8
17 WAR	0.0775	102.1	183.9	63.1	36.3
12 INJ	0.1838	102.4	184.8	62.9	36.9
14 MIL	0.2148	102.1	185.3	62.4	37.9
16 KOG	0.2652	102.7	185.3	62.8	38.8
18 LEG	0.4653	106.0	185.7	63.6	38.3
19 SAN	0.7122	106.9	187.3	65.0	38.9
25 WAL	0.7236	104.9	188.0	65.8	39.5
28 DEN	0.8908	109.0	188.0	66.8	36.6
21 DEE	0.9380	106.3	189.7	66.8	39.2
20 BOL	1.0639	105.4	191.4	65.4	39.8
24 ARD	1.0774	106.6	190.9	65.9	39.8
22 LLA	1.1135	107.1	191.1	65.8	39.3
26 WER	1.2826	107.6	192.4	67.6	37.2
27 MUR	1.3087	104.7	194.0	67.8	36.5
23 BLA	1.4539	108.0	194.0	65.1	42.4

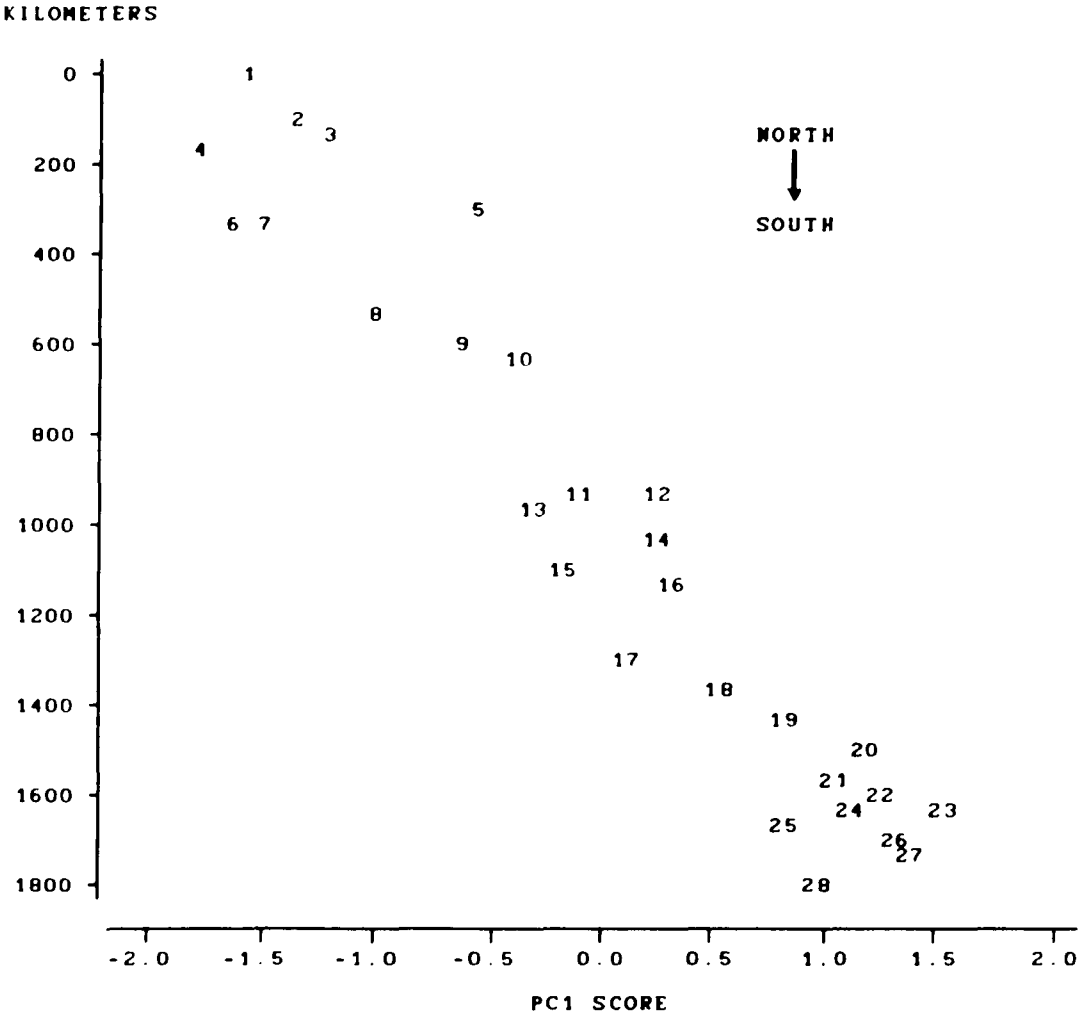


Figure 30. Localities plotted by map distance and PC1 scores derived from a principal components analysis of morphological variables. Variables with high loadings on PC1 were body length, wingspan, wing length, and tail length.

In order to look for clusters or outliers along the first two principal components, localities were plotted by PC1 and PC2 scores (Fig. 31). Among the far northern localities, locality 5 (Charters Towers) and locality 7 (Prairie) were outliers on the second component. The birds from Charters Towers had greater mean wingspan than birds from nearby localities; while birds from Prairie had greater mean body lengths. When PC2 and PC3 were plotted (not shown), locality 15 (Chinchilla) was an outlier on PC3. Birds from this locality had greater mean tail lengths than birds from nearby localities. Although a few outliers were found, neither of these plots delineates a geographic region of increased variability.

A distance phenogram of localities, based on a cluster analysis (SAS PROC CLUSTER/UPGMA) of all morphological variables, is shown in Fig. 32. Three major geographic clusters appear in the phenogram: a northern cluster, which excludes locality 5, Charters Towers, but extends south to include locality 8, Barcaldine; a central cluster, which includes Charters Towers and extends south to the McPherson Range; and a southern cluster of localities which lies essentially south of the range. A cophenetic correlation coefficient of 0.816 indicates a good association between the matrix derived from the measurement variables and the corresponding phenogram distances.

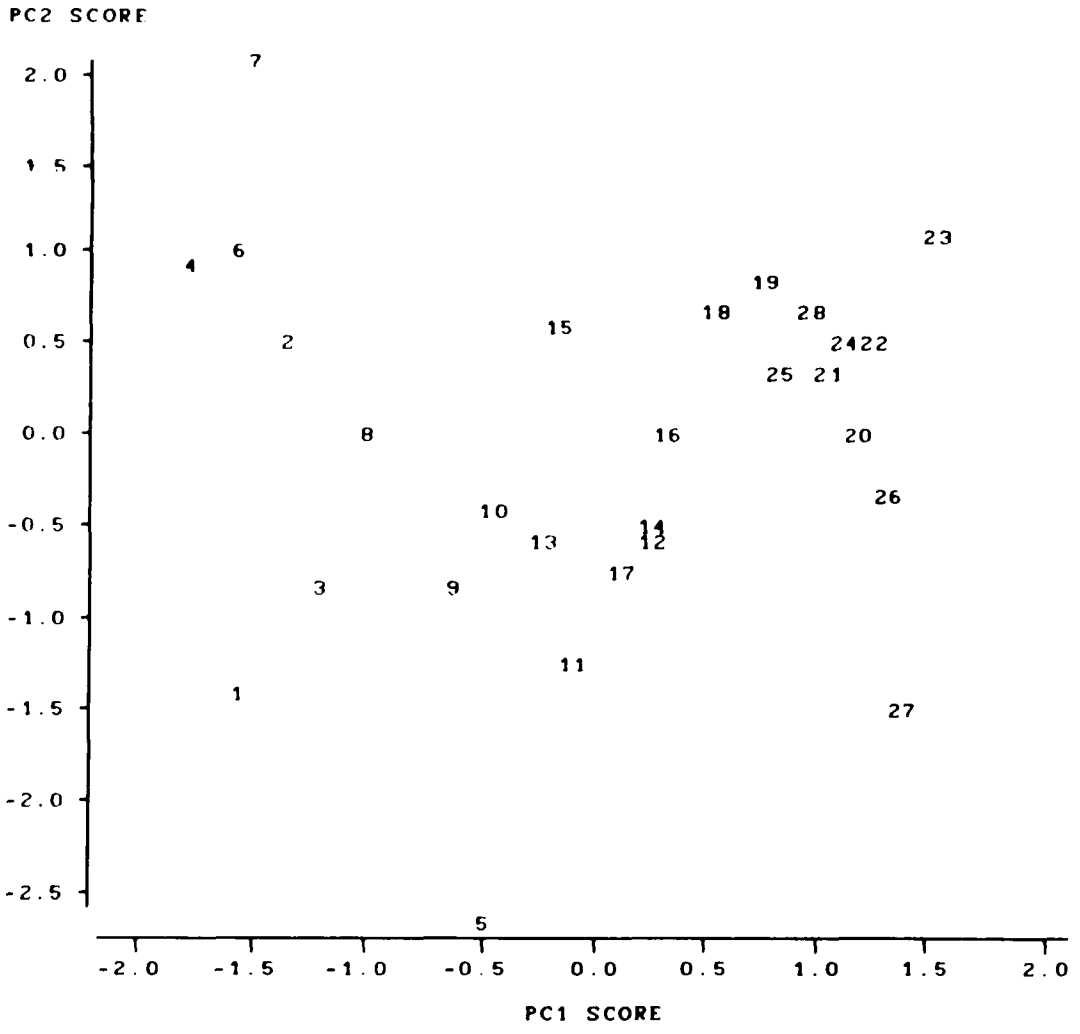
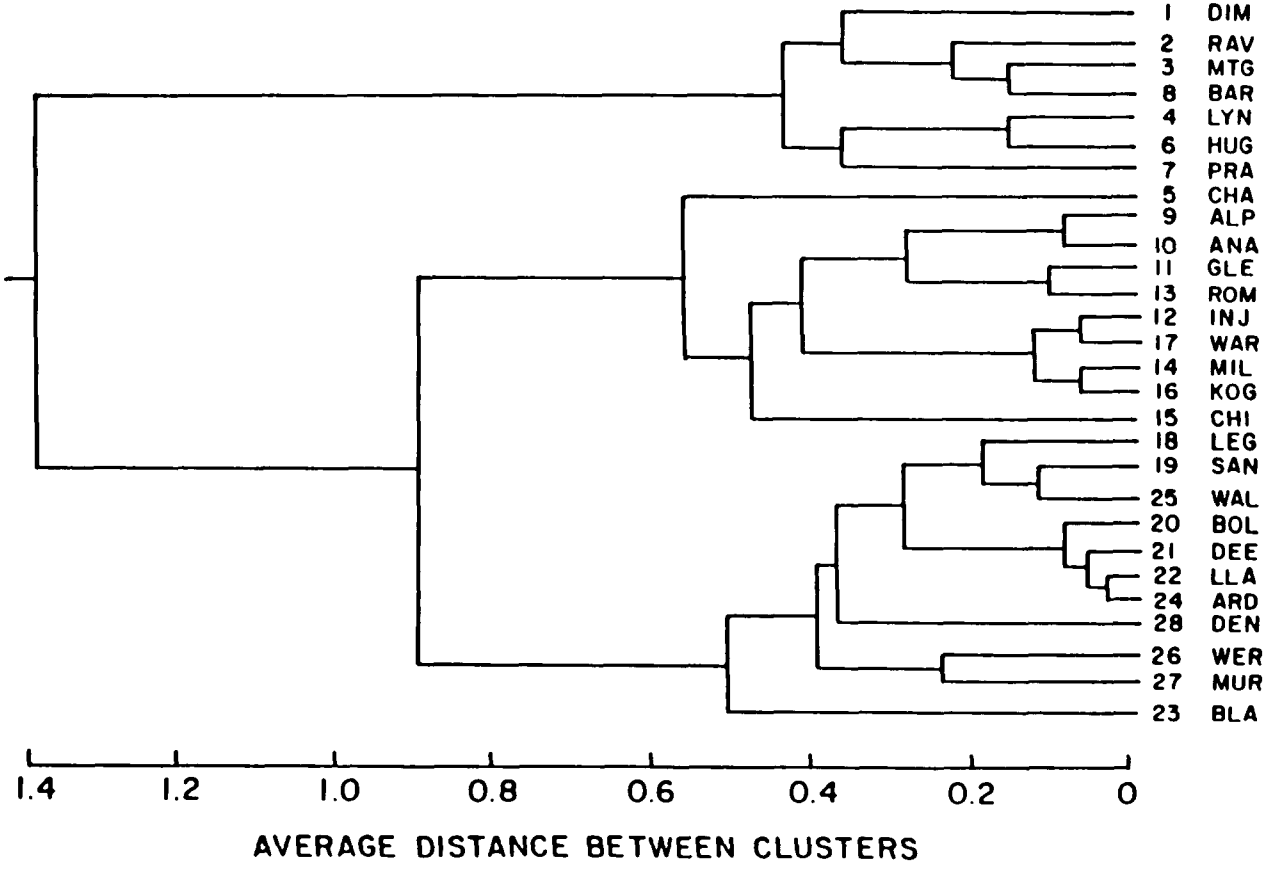


Figure 31. Localities plotted by PC1 and PC2 scores derived from a principal components analysis of morphological variables. Variables with high loadings on PC1 were body length, wingspan, wing length, and tail length.

Fig. 32. Distance phenogram of 28 localities in eastern Australia, derived from cluster analysis of morphological variables. Cophenetic correlation coefficient is 0.816.



As in the analysis of song variables, NTSYS/MXCOMP was used to test whether morphological "distance" (the average distance between clusters on the phenogram in Fig. 32) was related to geographic distance. This program makes pairwise comparisons from the matrix of morphological variables used to derive the phenogram and the matrix of map distances between localities. Results are shown in a scattergram in Fig. 33. If the observed points were statistically independent, the linear relationship between morphological distance and map distance would be significant (product-moment correlation coefficient $r=0.79$, $p<0.001$). However, because the scattergram represents pairwise comparisons of the matrices and thus each locality is represented more than once, the observed points are not strictly independent. Nevertheless, the pattern of points on the scattergram suggests that distance between clusters on the phenogram is related to map distance. The three major geographic clusters identified by the phenogram are shown on the map in Fig. 34.

As in the analysis of song data, I used a discriminant function analysis (SAS PROC DISCRIM) to classify individuals by morphological variables, and then tested the goodness of this criterion to discriminate individuals already classified by subspecies. 28.7% of all birds were misclassified using the DF. 16.4% of melanocephalus, 30.8% of ornatus, and 38.0% of substriatus were misclassified

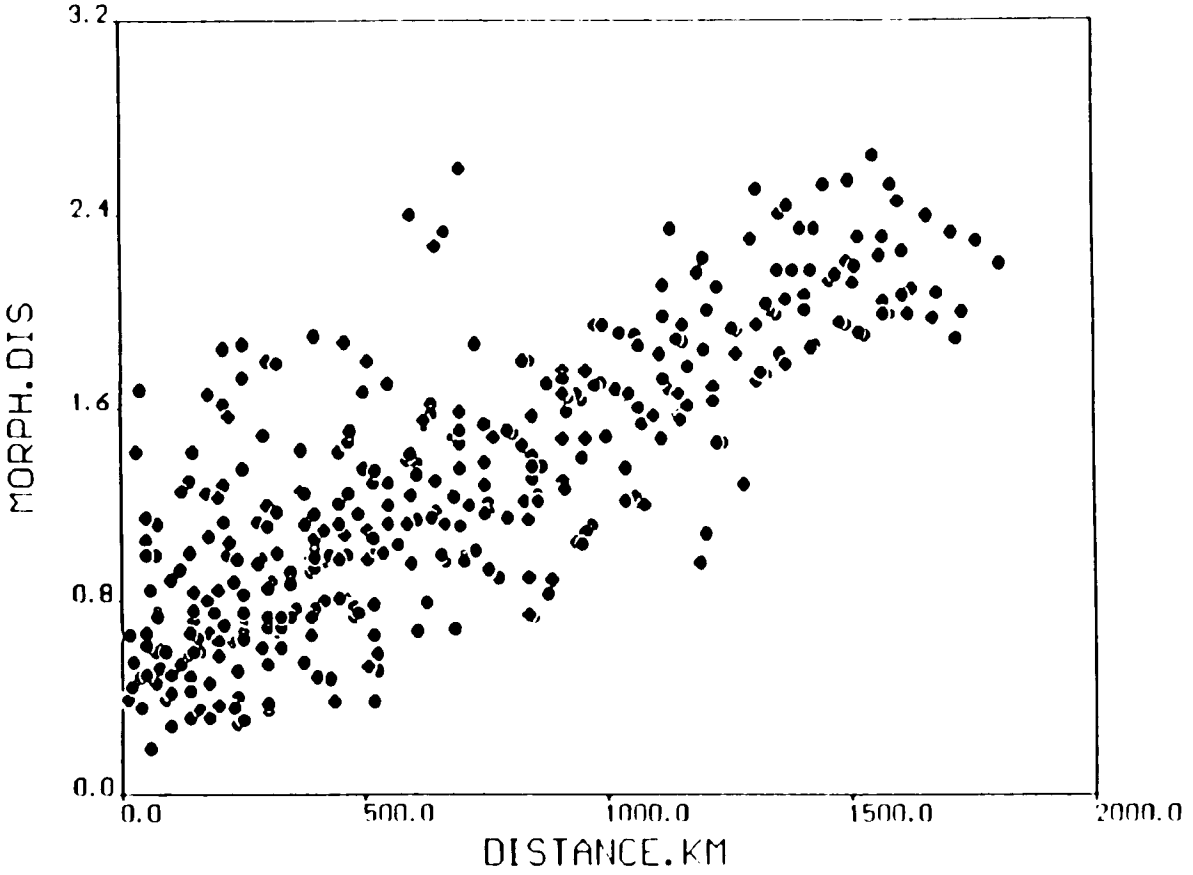
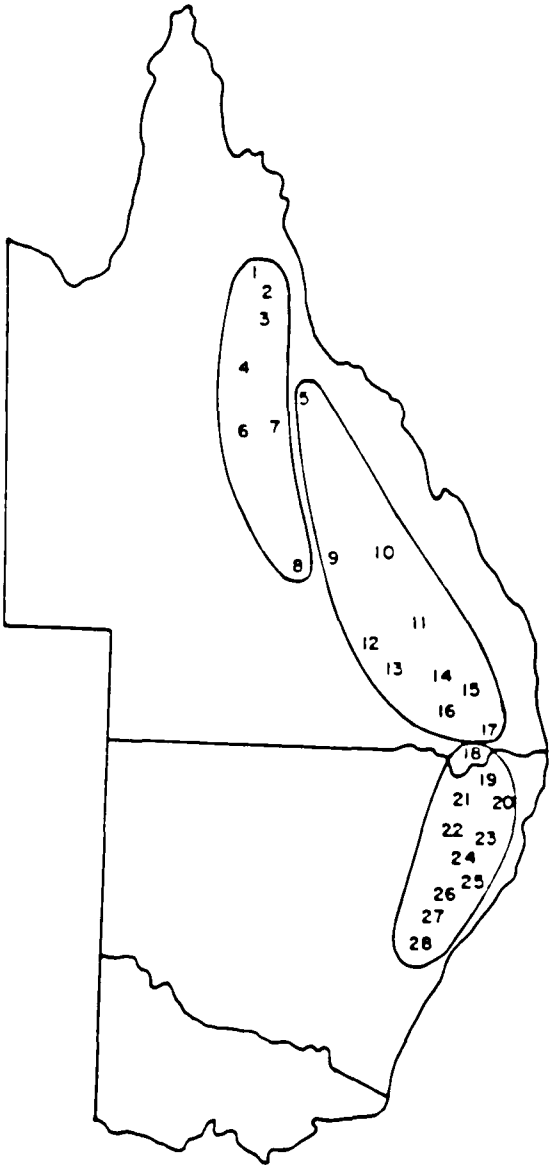


Fig. 33. The relation of morphological "distance", derived from the phenogram matrix, and geographic distance. r=0.79.



Locality		n
1	DIM	9
2	RAV	10
3	MTG	10
4	LYN	5
5	CHA	5
6	HUG	4
7	PRA	4
8	BAR	10
9	ALP	10
10	ANA	10
11	GLE	10
12	INJ	9
13	ROM	6
14	MIL	10
15	CHI	5
16	KOG	10
17	WAR	9
18	LEG	7
19	SAN	10
20	BOL	8
21	DEE	10
22	LLA	10
23	BLA	5
24	ARD	8
25	WAL	8
26	WER	6
27	MUR	3
28	DEN	1

Fig. 34. Geographic clusters identified by UPGMA cluster analysis of morphological variables.

using a discriminant function derived from the morphological variables.

Next, individuals were assessed by the plumage scoring method described in the Introduction. A discriminant function was derived from the set of plumage scores for all birds, and then used to classify individuals. The performance of this DF against the classification of individuals by subspecies was tested. All but 3 specimens of 136 ornatus and melanocephalus were classified correctly to subspecies by the DF. 32% of substriatus were not classified correctly; most were reclassified as ornatus by the DF. This was probably due to the variability of wingspot plumages, since there is no clearcut difference between these two subspecies for this character; and there were some individuals which were difficult to score.

Mean plumage scores were computed for each locality and then plotted by map distance (Fig. 35). A UPGMA analysis was used to cluster localities by plumage score (Fig. 36). Three geographic clusters were evident: localities 1-10, 11-18, and 19-27. Only locality 28 (Denman, n=1) was geographically "misplaced" in this phenogram. Samples within these three clusters, from north to south respectively, were 83% melanocephalus, 82% substriatus, and 80% ornatus. The distribution among all samples of the single plumage character, wide white primary patch (which discriminates melanocephalus and substriatus from ornatus),

is shown on the map in Fig. 37. There were four localities (19, 21, 22, and 23) where all the individuals collected happened to be ornatus.

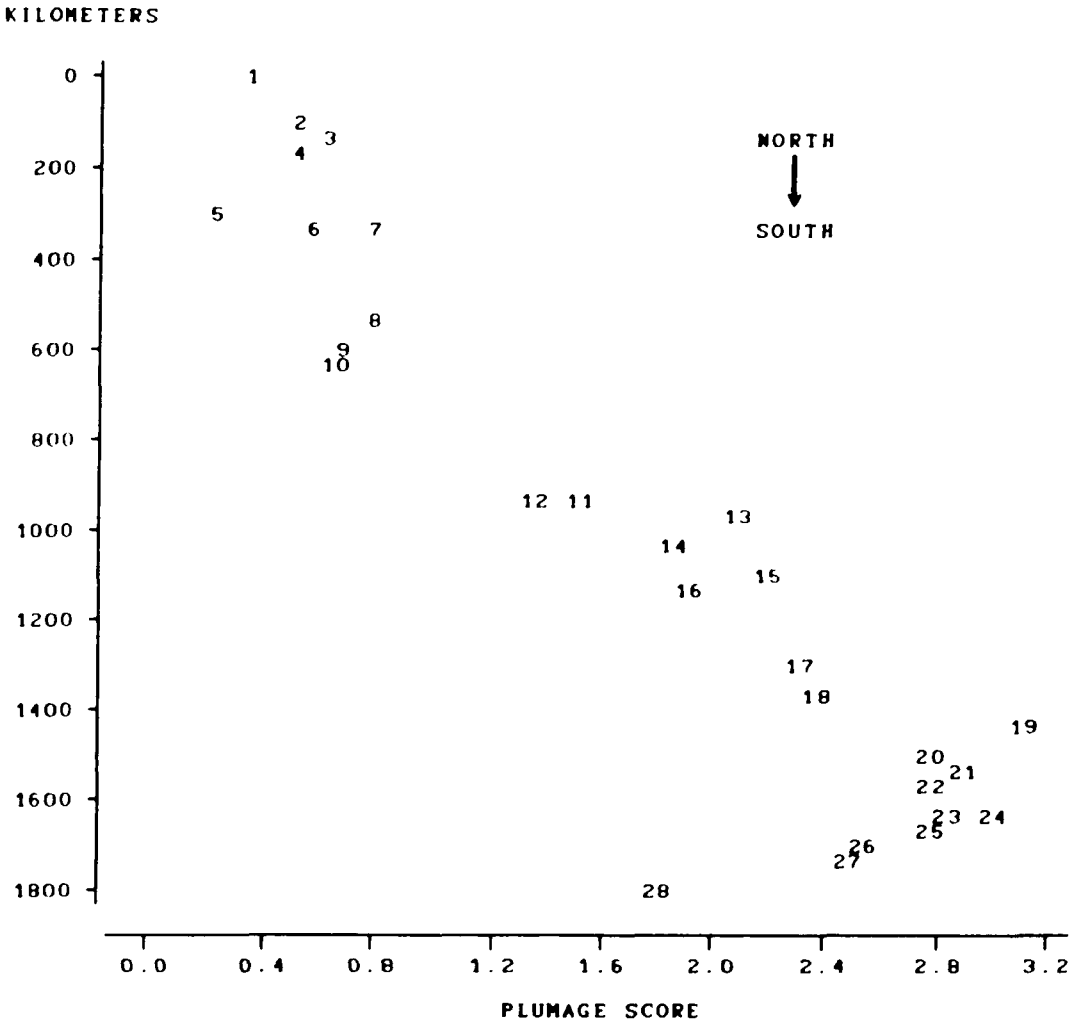


Figure 35. Localities plotted by map distance and mean plumage scores.

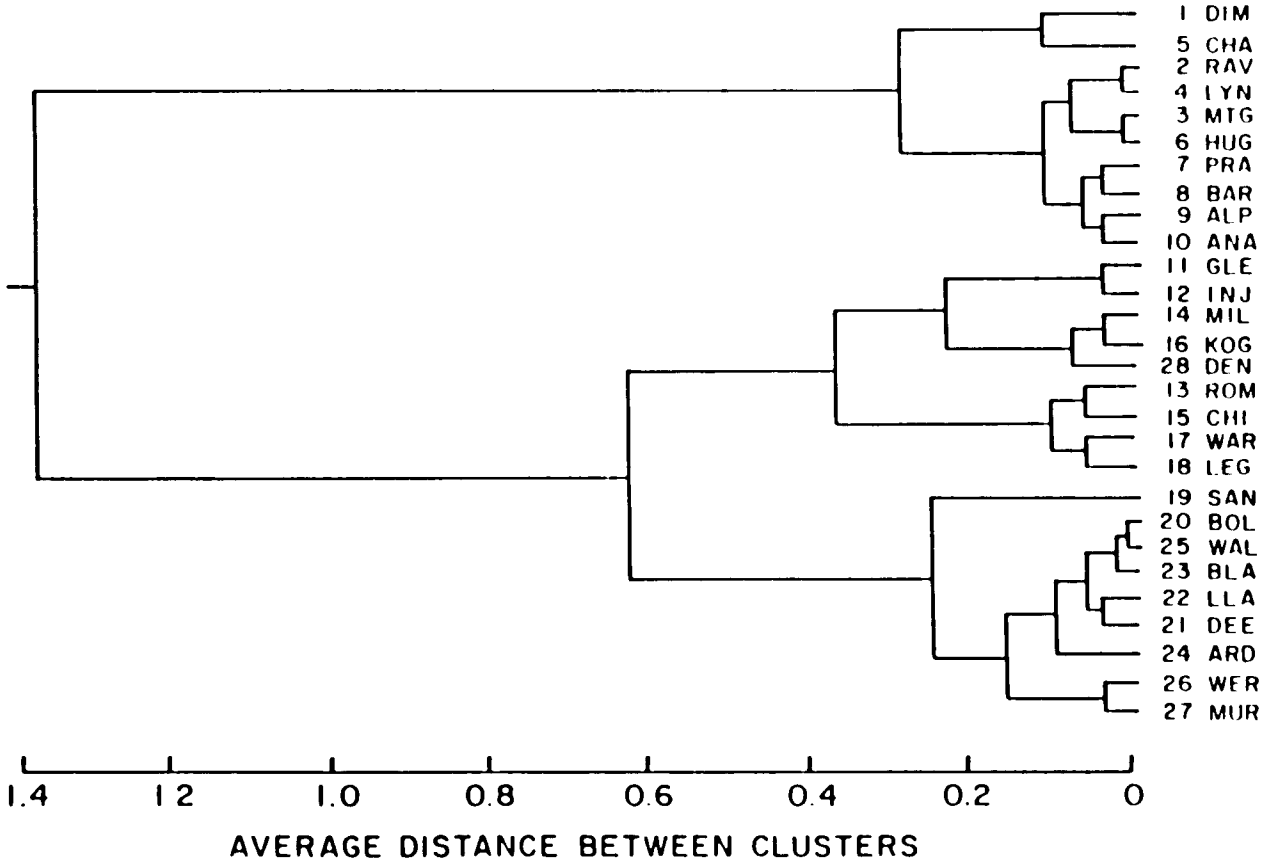
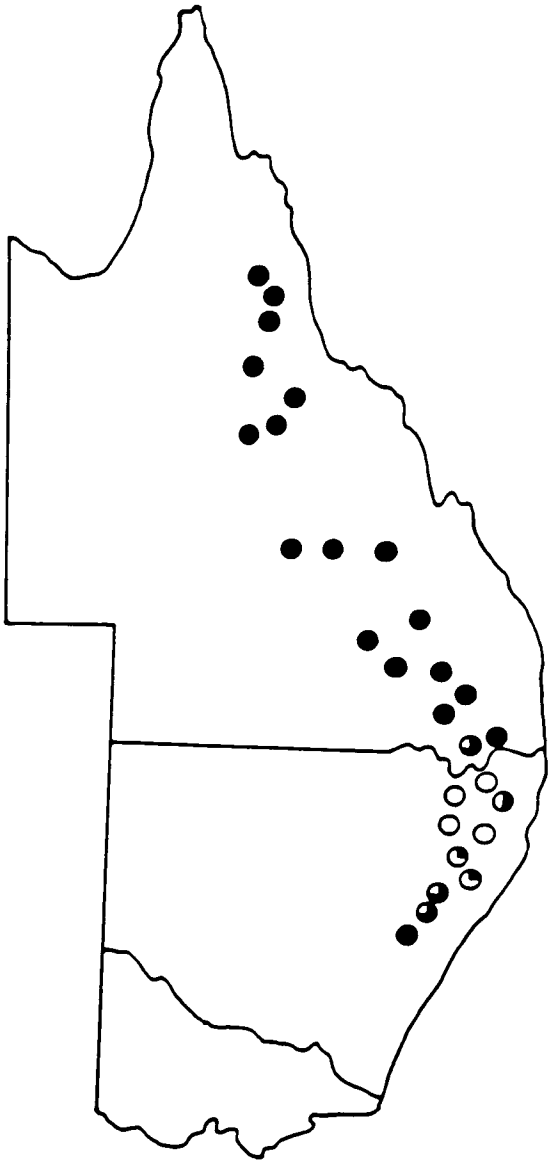


Fig. 36. Distance phenogram of 28 localities, derived from a cluster analysis of plumage scores.



Loc	n
1	10
2	10
3	10
4	5
5	5
6	5
7	5
8	10
9	10
10	10
11	10
12	9
13	6
14	10
15	5
16	10
17	9
18	7
19	10
20	8
21	10
22	10
23	5
24	8
25	8
26	5
27	3
28	1

Fig. 37. Distribution of the plumage character, white patch on primaries. Filled circles indicate that all individuals collected from those localities have wide wing patches. Open circles indicate that all individuals have narrow wing patches. Partially-filled circles indicate the percentage of individuals for that locality having wide or narrow patches.

RESULTS FOR MITOCHONDRIAL DNA

The tissues of 97 males from 23 localities were collected for mtDNA analysis. For the results presented here, n = 92. (The frozen tissues of birds 0124, 0212, and 0214 were misplaced in a storage freezer and were never recovered. The purified sample of 0163 was spilled during lab work. No mtDNA could be extracted from the tissues of 0138.)

Once purified in the lab, the mtDNA samples were treated in the following way. Initially, 13 different endonucleases were applied to six samples, in order to determine which enzymes would cut the mtDNA molecule in this species. All of these were type II restriction endonucleases which recognize and cleave at 6-base pair nucleotide sequences. *Bgl* II, *Sal* I, *Xba* I, and *Xho* II did not cut, and their use was discontinued. The remaining nine endonucleases were applied in the following manner. Samples from all 92 individuals were cut by the two endonucleases *Ava* I and *Hae* II. Samples from 36 of these individuals (representing 12 localities from the northern, central, and southern regions of the sampling area) were cut by the additional endonucleases *BamH* I, *Pst* I, and *Pvu* II. And finally, samples from 12 of the previous 36 individuals (representing two northern and two southern localities) were cut by the additional endonucleases *EcoR* V, *Hinc* II, *Hind* III, and *Nde* I.

For the nine informative endonucleases, a total of 61 fragments was observed, representing 366 base pairs, or 2.2% of the mtDNA molecule. The number of different fragments observed across individuals for each endonuclease was *Ava* I, 5; *BamH* I, 7; *EcoR* V, 4; *Hae* II, 7; *Hinc* II, 11; *Hind* III, 13; *Nde* I, 4; *Pst* I, 2; and *Pvu* II, 8. No heteroplasmy was observed in any of the individuals assayed. The size of the mtDNA molecule in P. striatus was found to be approximately 16,400 base pairs. This falls within the range reported for other avian species (Quinn and White 1987).

In order to compare banding patterns among individuals, I used a notation method which has become conventional for this type of biochemical work (Shields and Wilson 1987b; Ball et al. 1988; Zink 1991). Bands on an agarose gel, visualized by autoradiography, represent fragments of different sizes of an mtDNA molecule, as it has been cut by a particular endonuclease. Each endonuclease may produce one, or several different fragment patterns among all the sample mtDNA's tested. Different fragment patterns produced by a particular endonuclease are assigned different upper-case letters. Letter codes can then be compiled *across* endonucleases for each individual sampled, thus indicating the individual's composite fragment "haplotype." Haplotypes, as designated by these strings of letters, can be compared

among individuals and can also be examined for geographic patterns.

In addition to identifying haplotypes by letter coding, I calculated haplotypic diversity (G), which is analogous to single- locus heterozygosity (Zink 1991). Following the "fragment" method of Nei and Li (1979), I constructed matrices based on the number of fragments common to pairs of haplotypes. From these matrices, the proportion of shared bands between pairs of haplotypes (*F*), the average number of nucleotide substitutions per site (δ), estimates of nucleotide diversity within and among samples (Π), and net nucleotide difference between major haplotype groups (δ_{net}) were calculated. The formula for δ of Upholt (1977) was substituted for the formula of Nei and Li, as suggested by Quinn and White (1987). Mathematical details for these calculations are given in Appendix VII. Quinn and White (1987) cautioned against violating some of the assumptions underlying the Nei-Li model. However, they concluded that the consequences of such violations were small when closely related mtDNA's were being compared.

The haplotypes of the 12 birds whose mtDNA's were cut by 9 enzymes are shown in Table 28. 8 distinct haplotypes occurred. (However, note that haplotype BBBBBBBB* may or may not actually be distinct from haplotype BBBBBBBBA.) The geographic distribution of these 8 haplotypes is shown in Table 29. From this subset

Table 28. MtDNA haplotypes of 12 birds from 4 localities. DIM and RAV are northern localities; LLA and ARD are southern localities. 9 endonucleases were used. For each endonuclease, letters indicate distinct fragment patterns. Fragment profiles distinguish northern birds from southern birds, and there is greater haplotype variation among southern birds.

Locality/ Specimen	AvaI	BamHI	EcoRV	HaeII	HincII	HindIII	NdeI	PstI	PvuII
1 DIM									
0120	A	A	A	A	A	A	A	A	A
0121	A	A	A	A	A	A	A	A	A
0122	A	A	A	A	A	A	A	A	A
2 RAV									
0125	A	A	A	A	A	A	A	A	B
0126	A	A	A	A	A	A	A	A	A
0127	A	A	A	A	A	A	A	A	A
22 LLA									
0200	B	B	B	B	B	B	B	B	*
0201	B	C	B	B	C	B	B	B	A
0202	B	B	B	B	B	A	B	B	A
24 ARD									
0203	B	B	B	B	D	B	B	B	C
0204	B	B	B	B	C	B	B	B	D
0205	B	B	B	B	B	B	B	B	A

*No mtDNA left to run PvuII.

Table 29. Geographic distribution of mtDNA haplotypes for the 12 birds in Table 27. Letters indicate restriction fragment profiles corresponding to the endonucleases AvaI, BamHI, EcoRV, HaeII, HincII, HindIII, NdeI, PstI, and PvuII. The number of individuals having a particular haplotype is indicated. DIM and RAV are northern localities; LLA and ARD are southern localities. Greater haplotype variation among southern birds is illustrated.

mtDNA Haplotype	Locality DIM	RAV	LLA	ARD
1. AAAAAAAAA	3	2		
2. AAAAAAAAB		1		
3. BBBBBBBBA				1
4. BBBBBBBB*			1	
5. BBBBBABBA			1	
6. BCBBCBBBA			1	
7. BBBBDBBBC				1
8. BBBBCBBBD				1

*No mtDNA left to run PvuII.

MtDNA from the following specimens was used: 0120-0122, 0125-0127, and 0200-0205.

of mtDNA samples, haplotypic diversity (G) was calculated to be 0.61.

The haplotypes of the 36 birds whose mtDNA was cut by 5 enzymes are shown in Table 30. (This set includes the 12 previous birds and 24 additional individuals from 8 additional localities.) 9 distinct haplotypes occur. (However, again note that the two haplotypes AAAA* and BBBB* may or may not actually be distinct from some of the other haplotypes that were identified.) The geographic distribution of these haplotypes is shown in Table 31. For this subset of individuals, haplotypic diversity (G) was calculated to be 0.74.

Inspection of the data in Table 28 revealed two main haplotype groups which exhibit a marked north-south distribution. Of the nine enzymes listed, seven (*Ava* I, *BamH* I, *EcoR* V, *Hae* II, *Hinc* II, *Nde* I, and *Pst* I) resulted in distinctly different northern and southern fragment profiles. For *Hind* III, one individual from Llangothlin in the south exhibited a northern fragment profile. For *Pvu* II, fragment profile A was common to all localities; but the fragment profiles B, C, and D supported the north-south groupings. The fragment profiles for these nine enzymes can be interpreted in terms of one or two restriction site changes.

The fragment profiles for five of these enzymes, applied to the additional 24 individuals included in Table 30, supported the same northern and southern

Table 30. MtDNA haplotypes of 36 birds from 12 localities. Localities are listed by their geographic location, from north to south. 5 endonucleases were used. For each endonuclease, letters indicate distinct fragment patterns. Dotted lines indicate geographic divisions in distribution of haplotypes: INJ and ROM are the only localities where northern and southern haplotypes were found together.

Loc/Specimen		AvaI	BamHI	HaeII	PstI	PvuII
1 DIM	0120	A	A	A	A	A
	0121	A	A	A	A	A
	0122	A	A	A	A	A
2 RAV	0125	A	A	A	A	B
	0126	A	A	A	A	A
	0127	A	A	A	A	A
3 MTG	0132	A	A	A	A	A
	0133	A	A	A	A	B
	0134	A	A	A	A	*
5 CHA	0135	A	A	A	A	A
	0136	A	A	A	A	A
	0137	A	A	A	A	A
9 ALP	0145	A	A	A	A	A
	0146	A	A	A	A	A
	0147	A	A	A	A	A
12 INJ	0159	B	B	B	B	A
	0160	A	A	A	C	A
	0161	B	B	B	B	A
13 ROM	0156	A	A	A	A	A
	0157	B	B	B	B	A
	0158	B	C	B	B	A
19 SAN	0187	B	B	B	B	A
	0188	B	B	B	B	A
	0189	B	B	B	B	A
20 BOL	0190	B	B	B	B	A
	0191	B	C	B	B	A
	0192	B	B	B	B	A
22 LLA	0200	B	B	B	B	*
	0201	B	C	B	B	A
	0202	B	B	B	B	A
24 ARD	0203	B	B	B	B	C
	0204	B	B	B	B	D
	0205	B	B	B	B	A
25 WAL	0206	B	B	B	B	C
	0207	B	B	B	B	A
	0208	B	B	B	B	A

*No mtDNA left to run PvuII.

Table 31. Geographic distribution of mtDNA haplotypes for the 36 birds in Table 29. Letters indicate restriction fragment profiles corresponding to the endonucleases AvaI, BamHI, HaeII, PstI, and PvuII. The number of individuals having a particular haplotype is indicated. Greater haplotype variation among southern birds is illustrated.

	North ⟵ Locality ⟶ South											
MtDNA Haplotype	DIM	RAV	MTG	CHA	ALP	INJ	ROM	SAN	BOL	LLA	ARD	WAL
1. AAAAA	3	2	1	3	3		1					
2. AAAAB		1	1									
3. AAAA*			1									
4. AAACA						1						
5. BBBBA						2	1	3	2	1	1	2
6. BBBBC											1	1
7. BBBBD											1	
8. BBBB*										1		
9. BCBBA							1		1	1		

*No mtDNA left to run PvuII.

haplotype groupings, for all individuals from the five northern and five southern localities. Individuals from the two central localities, Injune and Roma, possessed either the northern or the southern haplotype.

The distributions of haplotypes shown in Tables 29 and 31 appeared to indicate greater variation among individuals in the southern group. In order to estimate possible differences in nucleotide variation between northern and southern groups, *F* and δ matrices were constructed for both data sets (9-enzyme and 5-enzyme sets). These values are presented in Tables 32 and 33.

Estimates of nucleotide diversity, $\hat{\pi}$, derived from the δ matrix in Table 32 were 0.000576 for the northern haplotype group and 0.00288 for the southern group. Thus, nucleotide diversity appeared to be greater among southern birds. The average number of nucleotide substitutions per site over all samples, $\hat{\pi}_{AB}$, was 0.0373. The net nucleotide difference between northern and southern haplotype groups, $\hat{\delta}_{net}$, was 0.0356.

Estimates of $\hat{\pi}$, derived from the δ matrix in Table 33, were 0.00127 and 0.00173 for the northern and southern haplotype groups, respectively. However, a minimum of 40 fragments per profile is preferable for this calculation (Quinn and White 1987). Because the maximum number of fragments per profile for this data is 20, these estimates of $\hat{\pi}$ must be considered cautiously. However, these values support the notion that nucleotide diversity is greater for

Table 32. F and δ values calculated from the distribution of 8 mtDNA fragment profiles in 12 birds representing northern and southern populations. F is the proportion of shared bands between pairs of fragment profiles. δ is an estimate of the average number of nucleotide substitutions per site for each pair. F values are given in the upper right; δ values, in the lower left.

1	——	0.94	0.54	0.58	0.62	0.54	0.50	0.62
2	.0034	——	0.49	0.58	0.61	0.48	0.52	0.57
3	.0357	.0416	——	0.83	0.92	0.86	0.94	0.96
4	.0315	.0315	.0105	——	0.95	0.84	0.94	0.90
5	.0275	.0285	.0047	.0029	——	0.84	0.95	0.96
6	.0357	.0429	.0085	.0098	.0098	——	0.86	0.91
7	.0404	.0380	.0034	.0034	.0029	.0085	——	0.96
8	.0275	.0325	.0023	.0059	.0023	.0053	.0023	——
	1	2	3	4	5	6	7	8

Table 33. F and δ values calculated from the distribution of 7 mtDNA fragment profiles in 36 birds representing northern, central, and southern populations. F is the proportion of shared bands between pairs of fragment profiles. δ is an estimate of the average number of nucleotide substitutions per site for each pair. F values are given in the upper right; δ values, in the lower left.

1	——	0.84	0.85	0.51	0.61	0.49	0.46
2	.0098	——	0.73	0.38	0.40	0.35	0.38
3	.0091	.0179	——	0.59	0.69	0.50	0.47
4	.0392	.0572	.0305	——	0.94	0.89	0.94
5	.0285	.0540	.0212	.0034	——	0.72	0.82
6	.0416	.0623	.0404	.0065	.0187	——	0.84
7	.0455	.0572	.0442	.0034	.0112	.0098	——
	1	2	3	4	5	6	7

the southern haplotype group. The net nucleotide difference (δ_{net}) calculated from this matrix was 0.0357.

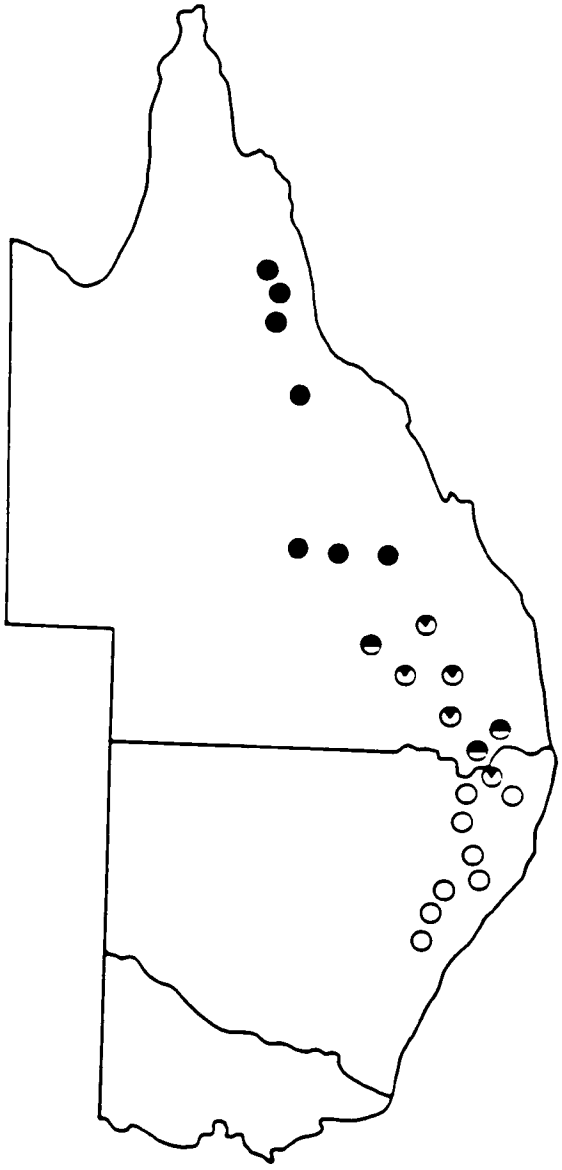
Fragment patterns for the additional 56 birds whose mtDNA's were cut only by the endonucleases *Ava* I and *Hae* II supported the same north-south distinction in haplotypes. Among all 92 mtDNA's cut by *Ava* and *Hae*, only two different fragment profiles occurred for each enzyme. In addition, only two distinct haplotypes were found: individuals were either AA or BB. The geographic distribution of these haplotypes is given in Table 34 and shown on the map in Fig. 38. There is an obvious pattern to this distribution. All 33 birds sampled from the 7 northernmost localities possessed haplotype AA; all 26 birds sampled from the 8 southernmost localities possessed haplotype BB. The birds from 8 central localities possessed either AA or BB haplotype.

There appeared to be no relation between subspecies and one or the other haplotype lineage. For example, male INJ-0159 was a pure melanocephalus phenotype and BB haplotype. Male ROM-0158 was substriatus and BB haplotype, while male MIL-0168 was substriatus and AA haplotype. Males SAN-0185 and LEG-0183 were ornatus and AA haplotypes, while other ornatus birds were BB haplotypes.

These results strongly suggested that Striated Pardalotes in eastern Australia were members of either a northern or a southern mtDNA lineage. Differentiation of the two groups was supported by 1) the geographic

Table 34. Geographic distribution of mtDNA haplotypes for 92 birds from 23 localities. Letters indicate restriction fragment patterns corresponding to the enzymes AvaI and HaeII. Only two haplotypes were found. (Haplotypes AB and BA were never observed.) The number of individuals of each haplotype is shown. Localities are listed from north to south. This distribution of haplotypes appears to corroborate the geographic patterns found for the samples in which larger numbers of endonucleases were used.

Locality	Haplotype AA	BB
1 DIM	4	0
2 RAV	5	0
3 MTG	5	0
5 CHA	4	0
8 BAR	5	0
9 ALP	5	0
10 ANA	5	0
11 GLE	1	4
12 INJ	2	2
13 ROM	1	2
14 MIL	2	3
16 KOG	2	3
17 WAR	2	2
18 LEG	1	1
19 SAN	2	3
20 BOL	0	3
21 DEE	0	5
22 LLA	0	5
24 ARD	0	3
25 WAL	0	3
26 WER	0	4
27 MUR	0	2
28 DEN	0	1



Locality		n
1	DIM	4
2	RAV	5
3	MTG	5
5	CHA	4
8	BAR	5
9	ALP	5
10	ANA	5
11	GLE	5
12	INJ	4
13	ROM	3
14	MIL	5
16	KOG	5
17	WAR	4
18	LEG	2
19	SAN	5
20	BOL	3
21	DEE	5
22	LLA	5
24	ARD	3
25	WAL	3
26	WER	4
27	MUR	2
28	DEN	1

Fig. 38. Distribution of mtDNA haplotypes, for endonucleases Ava I and Hae II. Filled circles indicate <u>all</u> individuals from those localities were haplotype AA; open circles indicate that <u>all</u> individuals were haplotype BB; partially-filled circles indicate the proportion of individuals of each type.

distribution of haplotypes, by 2) differences in nucleotide diversity ($\hat{\pi}$) between the groups, and by 3) genetic distance between the groups, in terms of base substitutions per nucleotide site (δ_{net}).

RESULTS FOR COMBINED DATA AND CONGRUENCE OF GEOGRAPHIC PATTERNS

PCA was performed on morphological and song variables together using the data for collected birds, in order to explore the possibility that some combination of those variables might account for a large portion of the variance. Measurements were standardized, and a correlation matrix was used for the PCA. Loadings of combined variables on the first three principal components are given in Table 35. PC1 accounted for 84% of the variance. Four variables related to overall body size (wingspan, body length, wing length, and tail length) and one song variable (DUR1) had high positive loadings on this component. No other variables had high positive or negative loadings on any of the components.

Localities are listed in order of increasing mean PC1 score in Table 36. Comparisons with the ordering of localities by PC1 scores derived from analysis of song variables alone (PC1-SONG) (Table 16) or by PC1 scores derived from analysis of morphological variables alone (PC1-MORPH) (Table 27) revealed that ordering by PC1 scores derived from the combined variables (PC1-COMBINED) resulted in a somewhat better geographic ordering of the localities.

Localities are plotted by map distance and these PC1-COMBINED scores in Fig. 39. Comparisons of this plot with the same types of plots for the PC1-SONG scores (Fig. 20) and for PC1-MORPH scores (Fig. 30) also showed that PC1-

Table 35. Loadings of combined morphological and song variables on the first three principal components.

VARIABLE	PC1	PC2	PC3
weight	0.093	-.039	0.066
body length	0.324	-.079	0.877
wingspan	0.692	-.586	-.348
wing length	0.202	-.155	0.207
tail length	0.124	0.269	0.148
tarsus length	0.047	-.082	0.006
culmen length	0.007	0.016	-.045
syllable number	-.055	-.058	-.034
high frequency	0.010	0.009	0.001
low frequency	-.001	-.011	0.006
duration syll 1	0.588	0.736	-.191
% VARIANCE EXPLAINED:	84.4%	10.3%	3.0%

Table 36. Localities listed in order of increasing mean body size and increasing duration of first song syllable, as determined by the first principal component. PCA was performed on 7 morphological and 4 song variables. Standardized PC1 scores are listed. Means for variables which had high loadings on PC1 (body length, wingspan, wing length, tail length, and duration of first song syllable) are given for each locality.

LOC	PC1	MBL	MWSP	MWL	MTL	MDUR1
1 DIM	-1.5023	94.5	172.1	60.0	34.2	0.06
6 HUG	-1.4895	98.0	169.5	60.2	37.6	0.07
4 LYN	-1.4152	96.2	168.2	59.9	38.1	0.11
3 MTG	-1.2123	97.6	174.3	60.5	34.5	0.07
2 RAV	-1.1925	99.0	171.5	60.1	35.9	0.10
7 PRA	-1.1836	102.0	168.5	60.5	37.7	0.11
5 CHA	-0.8044	97.4	180.8	61.8	32.2	0.07
8 BAR	-0.7750	99.7	174.8	61.8	35.5	0.13
10 ANA	-0.5194	100.2	179.7	62.0	36.4	0.11
9 ALP	-0.5123	99.5	178.8	61.5	35.5	0.13
13 ROM	-0.3197	99.8	181.5	62.6	37.5	0.13
11 GLE	-0.2930	99.7	183.5	62.4	36.8	0.11
15 CHI	-0.1210	99.6	182.6	60.5	42.3	0.15
17 WAR	-0.0729	102.1	183.9	63.1	36.3	0.13
14 MIL	-0.0358	102.1	185.3	62.4	37.9	0.12
12 INJ	0.0190	102.4	184.8	62.9	36.9	0.13
16 KOG	0.0630	102.7	185.3	62.8	38.8	0.13
18 LEG	0.1654	106.0	185.7	63.6	38.3	0.12
28 DEN	0.4166	109.0	188.0	66.8	36.6	0.12
19 SAN	0.7753	106.9	187.3	65.0	38.9	0.21
25 WAL	0.7978	104.9	188.0	65.8	39.5	0.21
26 WER	0.9301	107.6	192.4	67.6	37.2	0.17
21 DEE	1.0718	106.3	189.7	65.8	39.2	0.23
20 BOL	1.1397	105.4	191.4	65.4	39.8	0.23
27 MUR	1.2666	104.7	194.0	67.8	36.5	0.23
24 ARD	1.3112	106.6	190.9	65.9	39.8	0.26
22 LLA	1.5592	107.1	191.1	65.8	39.3	0.30
23 BLA	1.9345	108.0	194.0	65.1	42.4	0.33

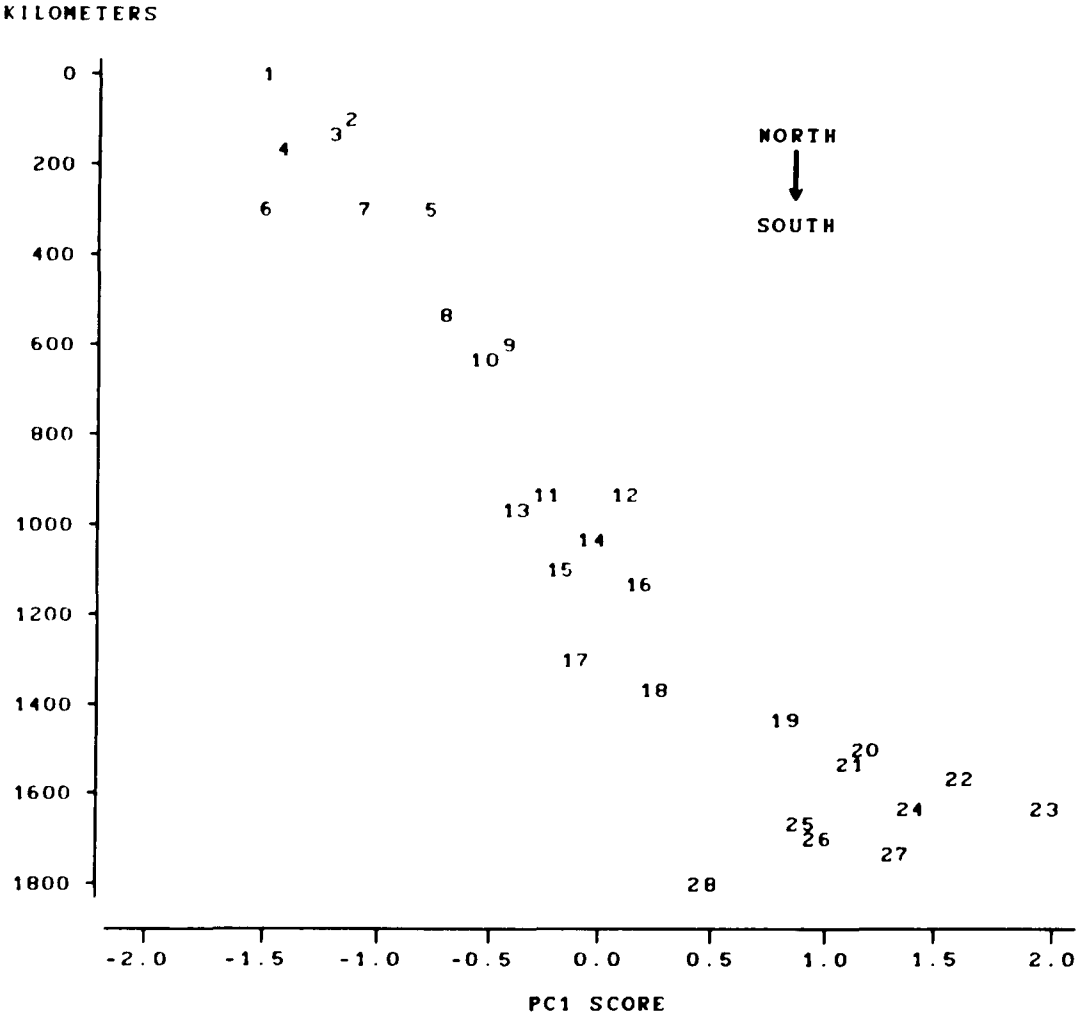


Figure 39. Localities plotted by map distance and PC1 scores derived from a principal components analysis of 7 morphological and 4 song variables. Variables with high loadings on PC1 were 4 variables related to body size and the song variable DUR1 (duration of first song syllable).

MORPH and PC1-COMBINED scores corresponded to the geographical position of localities better than PC1-SONG scores. Correlations of map distance with PC1-SONG, with PC1-MORPH, and with PC1-COMBINED scores were all highly significant (Pearson rank correlations $r=0.713$, 0.957, and 0.926, respectively; $p<0.0001$ in each case).

A test for multiple comparisons of means was performed on PC1-COMBINED scores. The results, showing non-significantly different overlapping subsets of means in the same manner as for other data sets, are depicted on the map in Fig. 40.

A UPGMA phenogram of localities derived from a cluster analysis of the PC1-COMBINED scores is shown in Fig. 41. Three major geographic clusters resulted. This phenogram was similar to the two phenograms derived from morphological and plumage variables (Figs. 32 and 36). However, the orientation of the major clusters with respect to one another was different for the PC1-COMBINED scores. That is, in this case the greatest average distance between clusters separated the southern cluster from other major clusters north of the McPherson Range. (Locality 28, Denman, for which $n=1$, has been excluded from the southern cluster.)

Results of Mantel's tests (using NTSYS/MXCOMP) for pairwise comparisons of the distance matrices used to construct phenograms from song and morphometric variables

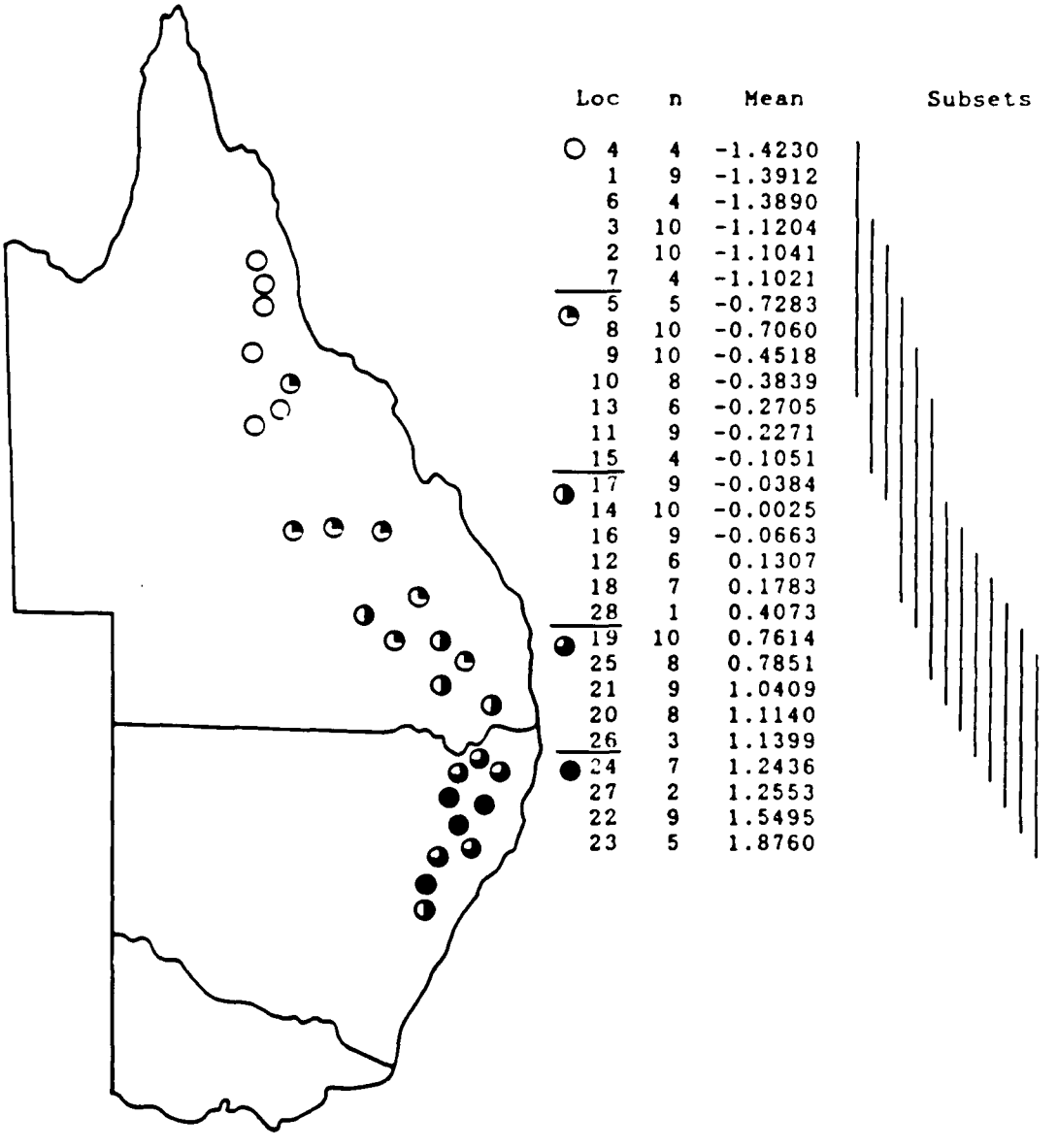


Fig. 40. Geographic distribution of mean PC1 scores, derived from an analysis of combined morphological and song variables.

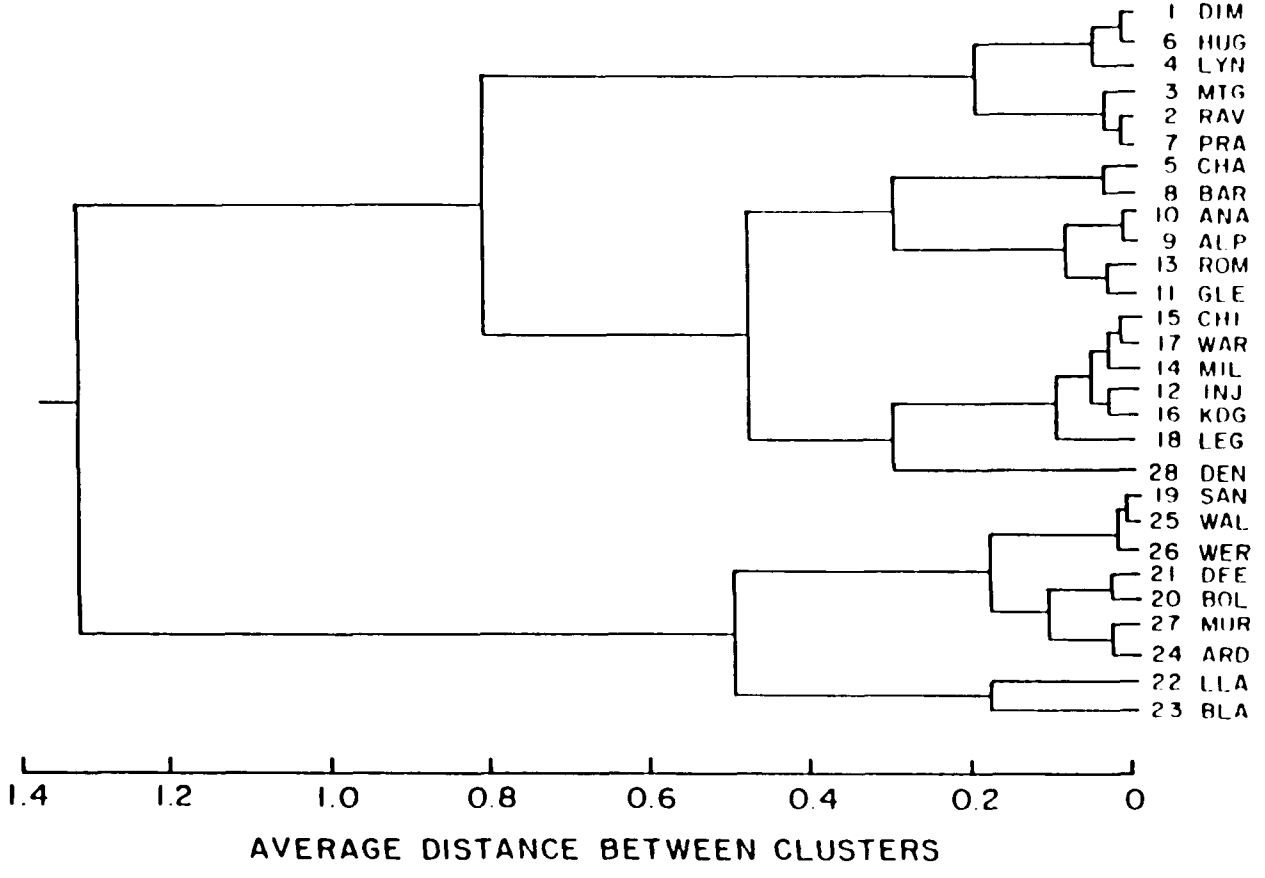


Fig. 41. Distance phenogram of 28 localities, based on PC1 scores, derived from an analysis of combined morphological and song variables.

indicated that the two matrices had some structure in common ($r=0.56$, $t=7.638$, $p=1.00$).

Major geographic clusters derived from the phenograms were plotted on maps. Because many overlapping plots on a single map would have been difficult to decipher, the results have been presented here on two different maps. The map in Fig. 42 depicts the major clusters for morphology, song, and mtDNA. The map in Fig. 43 depicts clusters for PC1-COMBINED scores, plumage, and again mtDNA. The three mtDNA clusters were not derived from phenograms, but were based on haplotype distributions as presented in Fig. 38. It should be kept in mind that the two maps are redundant in several ways: the mtDNA clusters are the same on each, and PC1 score represents elements from both the morphology and the song data sets.

Several concordant patterns can be seen. With some exceptions (locality 28 for song, plumage, and PC1; and locality 26 for song), a major division between clusters for all character sets occurs on or near the border between Queensland and New South Wales. In this region, a fairly well-defined southern cluster (localities 18-19 to 27-28) appears to be separated from localities to the north. A northern cluster (localities 1-10) and a central cluster (localities 11-18 or 11-19) occur, which are based on analysis of plumage and mtDNA data. Based on morphological data alone or on PC1 score (which includes the loading of

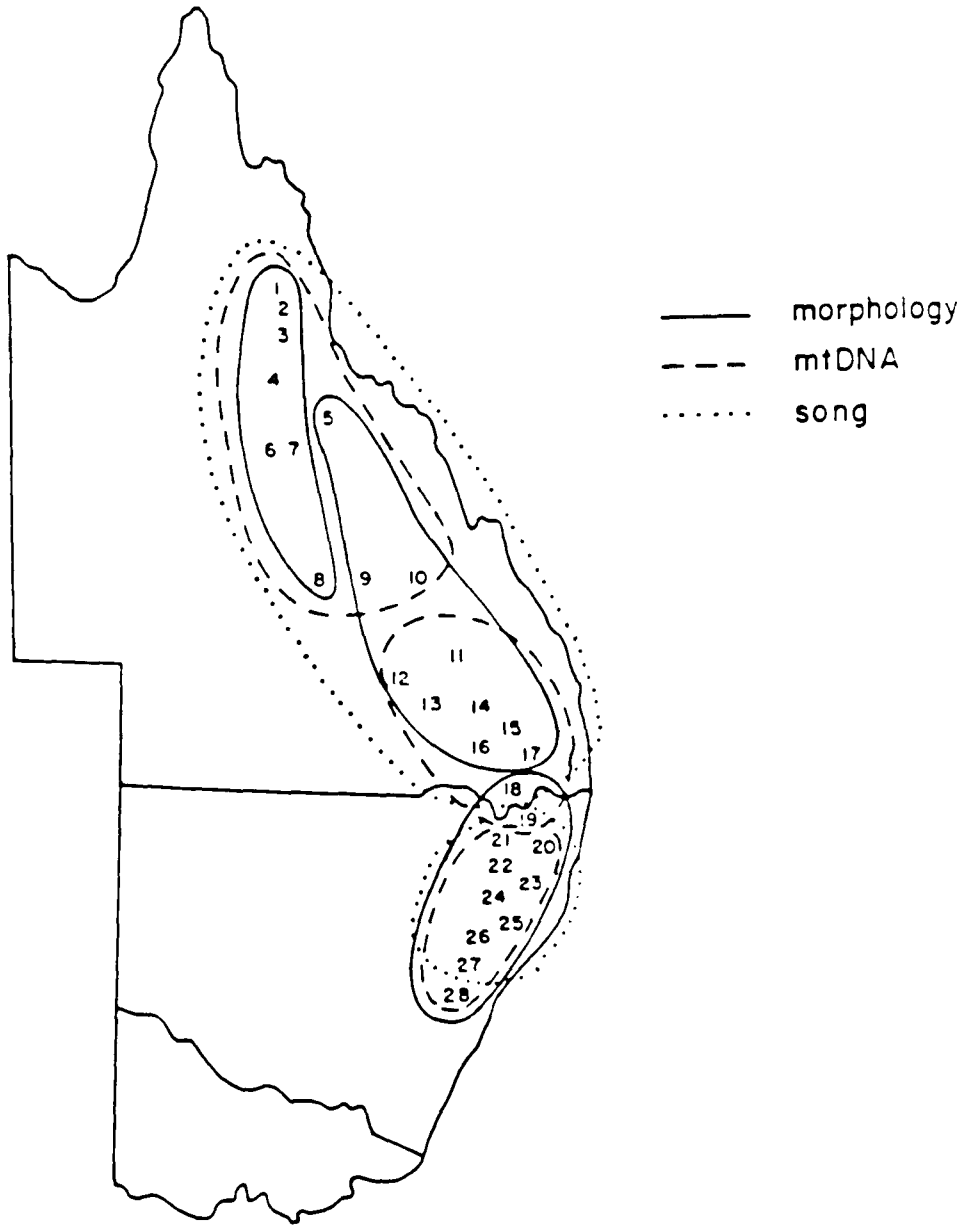


Fig. 42. Major geographic clusters identified for three sets of data: morphology, song, and mtDNA. (Localities 26 and 28 belong in the northern "song cluster.")

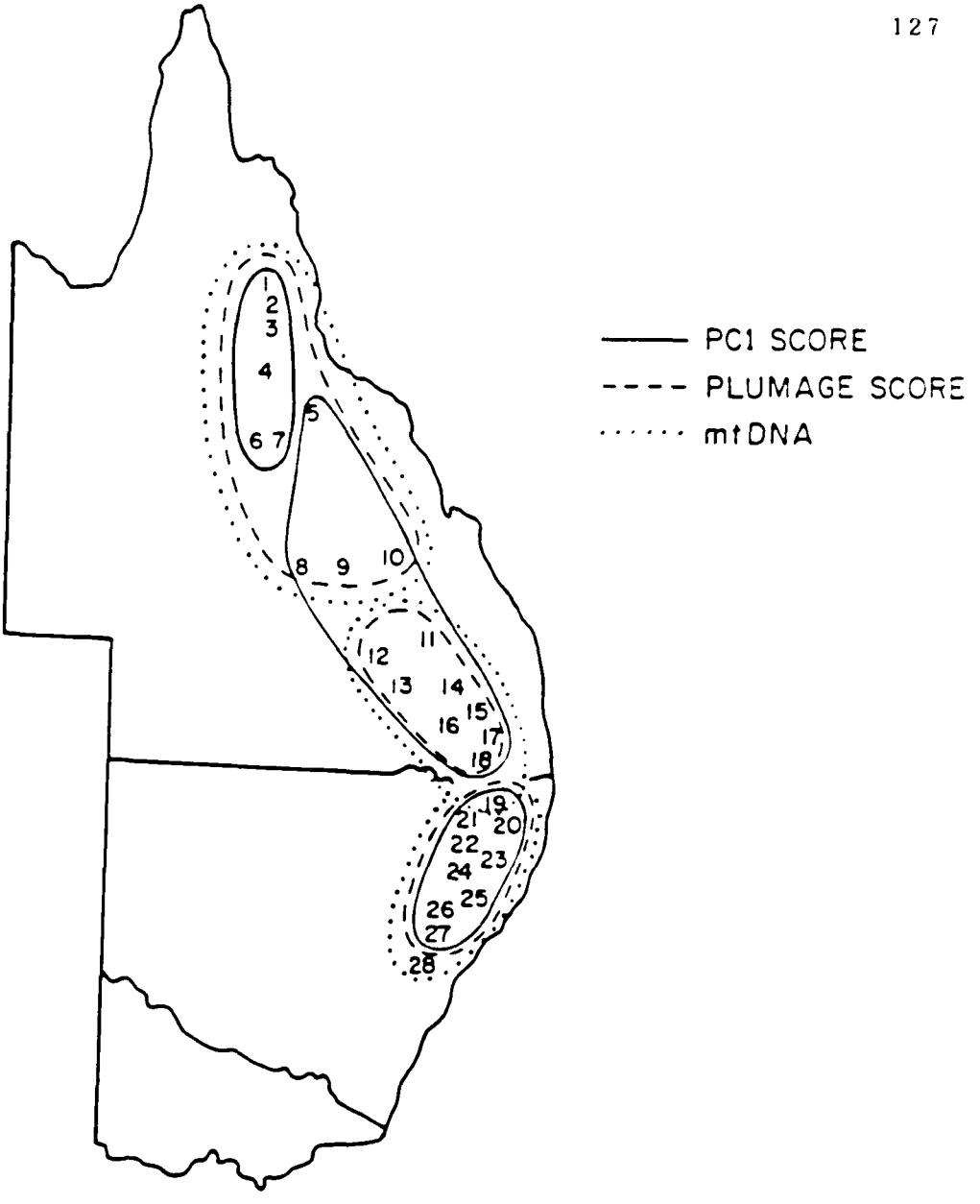


Fig. 43. Major geographic clusters identified for three sets of data: PC1 score, plumage score, and mtDNA. (Locality 28 belongs in the central clusters for PC1 and plumage scores.)

one song variable, in addition to morphological variables), locality 5 (Charters Towers) is clustered with central localities and not with northern localities which are closer. However, if the distribution of mtDNA haplotypes is considered as the most direct indicator of historical population structure, then three simple clusters can be discerned: a northern cluster of localities 1-10, where all individuals possessed the "northern" haplotype; a southern cluster of localities 20-28, where all individuals possessed the "southern" haplotype; and a central cluster of localities 11-19, where northern and southern haplotypes were found.

DISCUSSION

Several general patterns of geographic variation in P. striatus have been found. Univariate analyses revealed clinal patterns for some song and morphological variables, while multivariate analyses generally clustered localities into three large regional groups.

The major regional clusters found for P. striatus in this study (Figs. 42 and 43) can be examined in terms of hypotheses concerning the general patterns for bird distributions in eastern Australia. Older hypotheses (Serventy 1953; Salomonsen 1961) incorporated the classic biogeographic regions of Spencer (1896) and postulated that differences among the species P. striatus, P. substriatus, and P. melanocephalus were due to their different ancient origins in separate biogeographic regions. They also proposed that P. ornatus was a species of "hybrid origin," which had resulted from contact between P. striatus and P. substriatus. More recently (Mees 1965; Macdonald 1969), these ideas have been replaced by the hypothesis that these taxa originated from some ancient common stock which became geographically fragmented due to climatic and habitat changes. It was thought that the forms differentiated in isolation from each other, but were subsequently able to hybridize when range expansion brought them into secondary contact.

Many hybrid zones have been described for Australian

birds (Keast 1961; Ford 1974). Ford (1987) presented a summary of hybrid zones for 87 taxa. A number of major hybrid zones occurred in eastern Australia. Ford argued that because the positions of these zones overlapped for so many different taxon pairs, the hybridizing taxa probably had a similar history of vicariance and secondary contact. (Although several hybrid zones appeared to coincide with ecotones, most hybrid zones extended well beyond ecotonal belts.) In addition, Ford thought that many of these taxa would have been affected by the same geographic barriers to dispersal. The major hybrid zones appeared to coincide with prominent geographic features in eastern Australia which were thought to be partial barriers to dispersal and gene flow for many species of birds. These barriers are illustrated in Fig. 44.

Three of the barriers shown-- the Burdekin-Lynd Divide, the Burdekin Barrier, and the McPherson Range-- lie across my transect for this study. The Hunter Barrier marks the southern edge of my study area. The Burdekin-Lynd Divide is a somewhat broad area of the Great Dividing Range which partially separates the lowland of Cape York to the north from central coastal Queensland to the south. Localities 1-4 lie north of the Burdekin-Lynd Divide. Localities 5-7 lie between the Burdekin-Lynd Divide and the Burdekin Barrier to the south. The Burdekin Barrier is a narrow sweep of lower-elevation, dry country. The McPherson Range, which runs

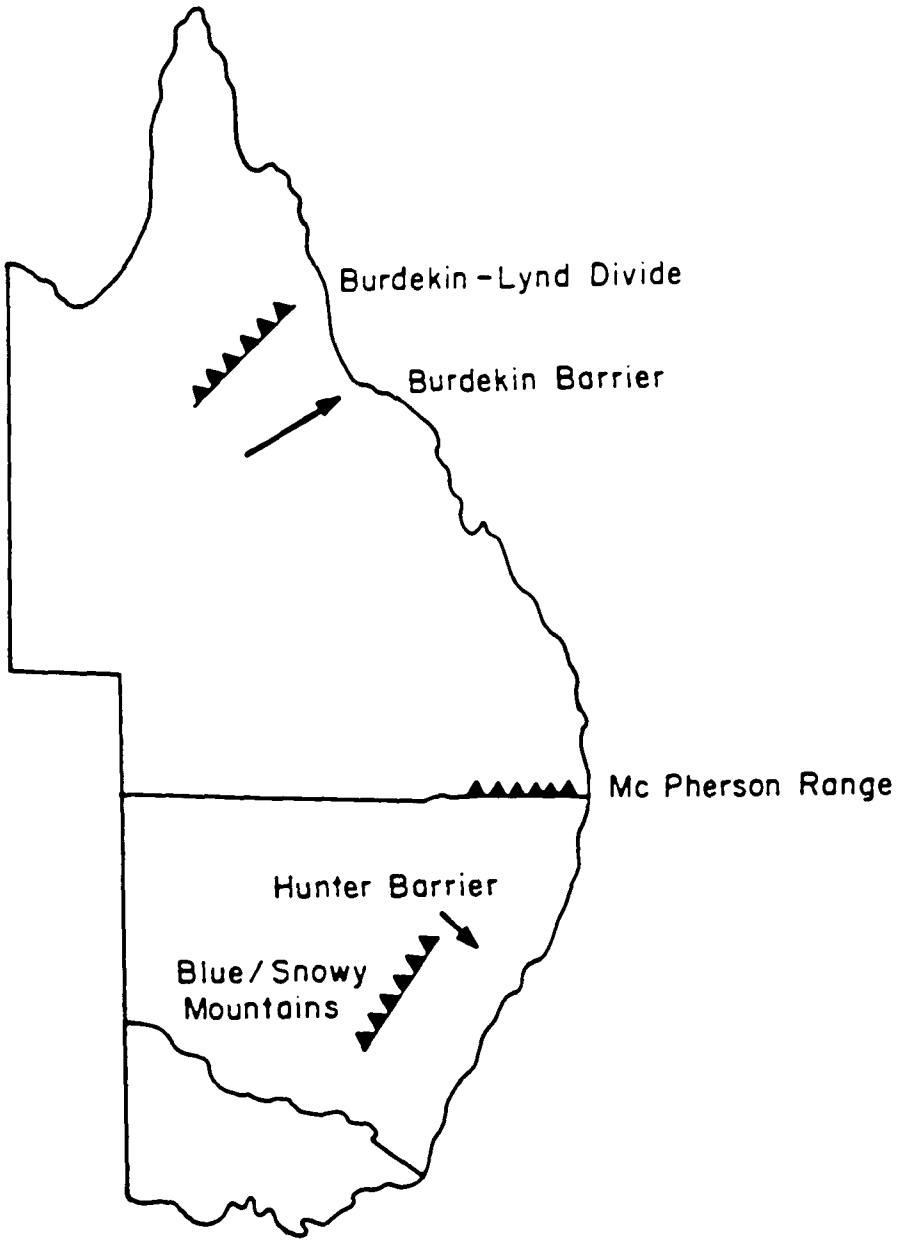


Fig. 44. Some geographic barriers to dispersal in eastern Australia. Modified from Ford (1986), after Keast (1961).

east-west along the border separating Queensland and New South Wales, is a range of mountains rising to about 4000-5000 feet. The higher elevations are rainforest, while the lower elevations are eucalypt forest. Localities 19-28 lie south of these mountains.

In addition to physiographic barriers to dispersal, historical climatic changes were thought to have influenced the geographic patterns of the major hybrid zones. The concept of refugia has been used to explain these patterns (Serventy 1951; Keast 1961). The majority of species for which hybrid zones have been demonstrated are woodland or forest species (Ford 1987). Climatic changes produced alternating contraction and expansion of the woodlands, causing expansion and contraction of the associated avian populations. Pleistocene climates in Australia alternated between arid, cooler phases and wet, warmer phases (Bowler et al. 1976). Periods of extreme aridity generally corresponded to periods of glaciation in the Northern hemisphere (Bowler 1982). During those arid periods, the forests-- arranged in more or less concentric circles with rainforests closest to the coast and mesic forests inland-- contracted toward the coast, as the arid interior expanded. Generally, concentric circles of rainforest were (and still are) surrounded by closed eucalypt forest, then open eucalypt woodland, then savanna. Keast (1961) proposed that refuges during the dry interpluvials probably retained this

essentially concentric configuration. Therefore, as the rainforest contracted, eucalypt forests and woodlands would also have contracted, constricting populations of woodland birds (including Striated Pardalotes) as well as rainforest populations. Keast hypothesized that the major coastal refuges (including those in eastern Australia) which existed during long-term phases of aridity coincided with present-day regions of high rainfall and remnant rainforest around the continental periphery. The map in Fig. 45 shows the locations of hypothetical refuges in eastern Australia.

The "barriers" and "refugia" hypotheses have been based primarily on the use of *plumage* characters to identify taxa and their geographic distributions. The results of my analyses-- based on song, morphology, and mtDNA, as well as plumage characters-- provide additional evidence of a division between populations of P. striatus north of the McPherson Range and populations south of it (Figs. 42 and 43). Striated Pardalotes do not inhabit rainforests and today are not found in the upper forests of these mountains, above about 2000 feet. Presumably, they would also have been excluded from Pleistocene rainforest refuges. If severe contraction of eucalypt forests during dry interpluvials had been coupled with extinction of local pardalote populations on or near the latitude of the McPherson Range (even though rainforest contraction would also have occurred), effective separation of northern and

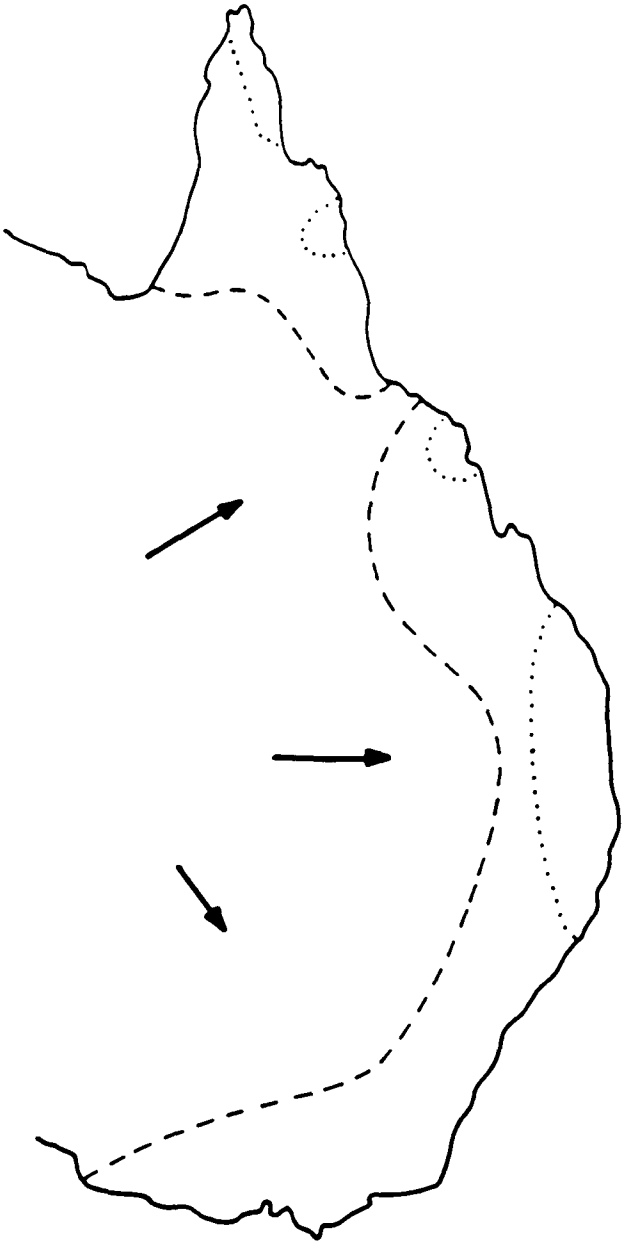


Fig. 45. Postulated coastal refuges in eastern Australia at the peak of the last Pleistocene arid period, about 18,000 years ago (dashed lines). Dotted lines denote rainforest refuges. Arrows indicate the direction of expansion of aridity. Because of lower sea levels, the coastline was probably somewhat different. Modified from Ford (1986), after Keast (1961).

southern populations could have resulted. That is, both the presence of unsuitable rainforest and the lack of suitable eucalypt woodland could have eliminated P. striatus from this region (essentially fitting the pattern encompassed by the lower dotted line in Fig. 45.)

[The two other physiographic features shown in Fig. 44, the Burdekin-Lynd Divide and the Burdekin Barrier, have not been demonstrated by my results to be barriers to dispersal for Striated Pardalotes. Although the cluster analysis of morphological variables resulted in a separation of localities 5, 9, and 10 from the other northern localities (Fig. 42, p. 126), this split does not coincide geographically with either barrier. Nor does it coincide with orientation of these localities to east or west of the Great Dividing Range. The sample sizes for localities 4 to 7 were smaller than for the other 6 northern localities, but it is unknown how means and variances (and therefore clustering) might have changed with larger sample sizes.]

The distributions of a number of other taxon pairs, noted by Keast (1961) and Ford (1987), support a hypothesis of historical separation of populations, followed by secondary contact in the same region around the McPherson Range. The geographic distributions of these taxa overlap in the same manner as forms of the Striated Pardalote. Forms of the Leaden Flycatcher (Myiagra rubecula), the White-browed Scrubwren (Sericornis frontalis), and Eastern

Rosella (Platycercus eximius and P. adscitus) provide striking examples. (See Ford, 1987, for hybrid zones in these taxa.) Recent evidence from allozymes for the Scrubwrens (Christidis et al. (1988) and from mtDNA for the Rosellas (Ovenden et al. 1987) also point to a shared history of vicariance and recontact in the same area of eastern Australia as for P. striatus.

The results of my mtDNA fragment analyses do not refute the refugium hypothesis, and are perhaps best explained by that hypothesis. The results strongly suggest that Striated Pardalotes in eastern Australia are members of either a northern or a southern mtDNA lineage. These two lineages would have differentiated in isolation in the past and come into contact again more recently. A hypothesis of differentiation of two lineages is supported by the geographic distribution of mtDNA haplotypes (Fig. 38, p. 116); by differences in estimated nucleotide diversity (π) between the northern and southern mtDNA's; and by the estimate of genetic distance between the northern and southern samples, in terms of base substitutions per nucleotide site (δnet).

Ovenden et al. (ibid.), in their study of Rosella phylogeny, also used restriction endonucleases to examine mtDNA evolution. They computed nucleotide diversities (π) for Platycercus eximius and P. adscitus, two closely-related taxa of the "eximius" superspecies, which have traditionally

been identified by plumage patterns. As mentioned, these two forms of the Eastern Rosella have distributions and a hybrid zone in eastern Australia which are very similar to those of P. striatus. Ovenden et al. stated that the current populations of Rosellas were "plausibly believed to result from the expansion of refugial populations." Interestingly, π estimates for the northern adscitus and the southern eximius differed by the same order of magnitude as the estimates for the northern and southern haplotype groups in P. striatus. (Values were 0.0027 for adscitus and 0.0142 for eximius, and 0.0006 for the northern P. striatus haplotype group and 0.0029 for the southern group.) Thus there is evidence, based on geographic patterns in plumage and mtDNA, that Eastern Rosellas and Striated Pardalotes have shared a similar history of population fragmentation. For both, nucleotide diversities for northern mtDNA's were an order of magnitude lower than southern mtDNA's.

Lower mtDNA nucleotide diversities in the north may be the result of greatly reduced populations and a greater rate of extinction of local populations during past harsh interpluvials. Modern census data (Blakers et al. 1984) indicates much smaller population sizes for P. striatus for the northern half of my study area than for the southern half. If this has been the historical pattern as well, smaller P. striatus populations in the north could have been more negatively affected than in the south during periods of

severe aridity. In their study, Ovenden et al. (1987) concluded that effective long-term population sizes for Rosellas were several orders of magnitude smaller than the modern estimates. They thought that the hypothesis of Barrowclough and Shields (1984) of bottlenecks as affecting an entire population best explained this.

The mtDNA δnet value of 0.0356 estimated for Striated Pardalotes was high compared to genetic distance estimates for mtDNA's in North American passerines: 0.008 for Red-winged Blackbirds (Ball et al. 1988), 0.004 for Black-crested Titmice (Avise and Zink 1988), 0.0086 for Fox Sparrows and 0.0027 for Song Sparrows (Zink 1991). The value for pardalotes was of the same order of magnitude as distances found for large versus small subspecies of Canada Geese in western North America (Shields and Wilson 1987b). If this estimate for pardalotes is correct, it implies that there was a fairly long period of separation of the northern and southern P. striatus populations. If the mean rate of mtDNA divergence is 2% per 1 million years-- which was originally calculated by Brown et al. (1979) using primate mtDNA's and has since been used for mtDNA's in Canada Geese (Shields and Wilson 1987a, 1987b), Pacific Black Brant (Shields 1990), Fox Sparrows (Zink 1991b), and the Eastern Rosellas mentioned above-- then the divergence times of the mtDNA nucleotide sequences, representing the northern and southern lineages of P. striatus, would have diverged from

each other over a period of 1,780,000 years.

If, in fact, northern and southern populations of P. striatus have been separated, and if this is reflected in the geographic distribution of mtDNA haplotypes, then the central mtDNA cluster (Fig. 42, p. 126) might represent the area of recontact and overlap of the previously-separated populations. This cluster of localities extends over about 450 km, between 25°S and 29°S latitude. Macdonald (1969), using traditional plumage characters to identify hybrid individuals, stated that one hybrid zone for P. striatus extended from south central Queensland to southeastern Queensland and northeastern New South Wales. Other workers (Hindwood and Mayr 1946; Lord 1956; Cooper 1961; Salomonsen 1961; Short and Horne, Schodde, pers. comm.) also identified hybrids from museum collections and reported sitings of ornatus x substriatus mated pairs in the field in the same region. Does the central cluster of localities identified in this study delineate the hybrid zone? Although mtDNA is representative of maternal lineage only and cannot be used to identify hybrid individuals, patterns for morphological (and perhaps song?) variables within the clusters delineated by the mtDNA might be used to identify the hybrid zone.

Hybrid zones have been defined as regions of steep phenotypic or genotypic intergradation occurring between populations which are relatively uniform (Mayr 1963; Short 1969). These regions should contain hybrid populations

which exhibit increased variability (Schueler and Rising 1976). Therefore, I next examined the results for evidence of increased variability in samples from the central cluster of localities.

I calculated an estimate of π (mtDNA nucleotide diversity) for samples from the central cluster. Individual mtDNA's from Injune and Roma (localities 12 and 13) were used; and the estimate was made from the F and δ matrix shown in Table 33 (p. 113). The value obtained was 0.0095, which *was* higher than the values obtained for northern and southern mtDNA's (0.0006 and 0.0029, respectively). This value for π should be interpreted cautiously, however, because the matrix was based on fragment patterns generated by only 5 endonucleases, resulting in a relatively small number of fragments in each profile. Quinn and White (1987) warned that a minimum of 40 fragments per profile was preferable if Upholt's (1977) formula was used in calculations of δ (from which π is calculated).

The results of univariate analyses appeared to show relatively smooth clinal variation for a number of song and morphological characters. The results of GLM/GT2 comparisons suggested that sample means of four song variables varied in this fashion. Both highest frequency of the first syllable (Fig. 10, p. 48) and frequency of the second highest peak in the first syllable (Fig. 12, p. 50) tended to increase from north to south. Syllable number

(Fig. 9, p. 47) decreased and duration of the first syllable (Fig. 13, p. 51) increased from north to south; both variables were significantly correlated with latitude. Means for the morphological variables weight, body length, wingspan, and wing length (Figs. 23-26, pp. 80-83) increased from north to south and were significantly correlated with latitude. There was no evidence for any discrete subset of means for any of these variables.

Some comparisons of mean coefficients of variation showed increased variability for samples from the central cluster, when compared with CV's from the northern and southern clusters, while other comparisons did not. When mean CV's were computed over all individuals in each cluster, CV's for wing, tail, and culmen lengths were found to be significantly *higher* in the contact zone; but mean CV's for body length and wingspan were *lower* than in the north or south. Mean CV's for the song frequency variables HF and LF were higher in the contact zone, but lower for the time variables DUR1 and DUR.

I next examined the ranges of principal components scores (PC1-SONG, PC1-MORPH, and PC1-COMBINED) for localities in each of the three geographic clusters. If there was increased variability in the contact zone, the range of PC1 scores for the central cluster would be greater than for the ranges of scores in the north or south. The easiest way to visualize this was to look at the spread of

localities 11-19 along the x-axes (PC1 scores) in Figs. 20, 30, and 39 (pp. 66, 93, and 121, respectively), in which PC1-SONG, PC1-MORPH, and PC1-COMBINED scores were plotted against map distances. The ranges of PC1 scores for the central cluster of localities were *not* greater.

Interestingly, the range of PC1-COMBINED scores (Fig. 39) for samples from the *southern* cluster was greater than the ranges of scores for the central and northern clusters. If in fact a greater "spread" of PC1 scores is an indication of increased variability, then birds from the southern localities exhibit greater variability than birds from north of the McPherson Range, in terms of the composite of morphometric and song variables represented by the first principal component. Thus, there is evidence for both increased variability and higher mtDNA diversity in the southern samples. One possible explanation for this is that effective population sizes in Striated Pardalotes north of the McPherson Range have been (and are) small compared to populations south of the range.

I compared some of my results with observations made by other workers regarding geographic distributions and characters associated with the three races of P. striatus:

Lord (1956) found breeding substriatus commonly and melanocephalus sparingly in southern Queensland (Toowoomba and Murphy's Creek). I found no pure melanocephalus from that far south. He also found ornatus and substriatus

mating in southern Queensland. He found substriatus common and ornatus "fewer in number." In both years of collecting, I found ornatus in greater numbers than substriatus in localities 19, 21, 22 and 23 (Fig. 27, p. 103). Hindwood and Mayr (1946) thought substriatus was "extremely rare" in coastal New South Wales. They thought ornatus was common near Sydney, while substriatus was rare there. Ornatus "occurs commonly in coastal areas between the seaboard and the Great Dividing Range in New South Wales," but they thought this form was rare in the highlands. However, all the ornatus I found were in highlands inland from the coast. It is perhaps possible that changes in the distributions of these forms have occurred since the 1950's.

For one of the diagnostic characters separating substriatus and ornatus, wide versus narrow white wing patch on the primaries (Fig. 3, p. 8), I found very few intermediate individuals. This was in agreement with previous authors. Woinarski et al. (1983) studied variation in P. striatus in southeastern Australia, across a contact zone for substriatus and ornatus in Victoria. They found that 19 individuals, or 6.6% of the birds they sampled, were intermediate for the amount of white in the primaries. Hindwood and Mayr (1946) examined 520 museum specimens and found only 6 birds (1.2%) to be intermediate for this plumage character. I found only 3 individuals (1.4%) which were intermediate (Fig. 36, p. 102). Intergrading occurs

extensively in the other plumage characters. At present, it is unclear why so few intergrades have been found for the primary-white character. Moore (1987) argued that the dynamics of mate choice among individuals in hybrid zones might drive the evolution of differing bright and contrasting plumages. However, no evidence as yet exists for patterns of mate choice in ornatus and substriatus; although as mentioned on p. 138, mixed breeding pairs are known from museum collections and field observations. In addition, the discriminant functions I computed from the morphological variables related to body size and from the song variables did not provide reasonable separation of ornatus and substriatus specimens (identified by plumage).

Hindwood and Mayr (1961) reported that Hindwood agreed with Morse (1922) about differences in the calls of substriatus and ornatus. Morse stated that ornatus "utters a double note, rendered a 'chip-chip', whilst substriatus gives a three-syllable note which has been recorded as 'wit-e-chu'." They used this fact in support of species status for these taxa. Mees (1965), however, thought there was no difference in voice between ornatus and substriatus. He cited Serventy (1946), Cooper (1961), Sedgwick (1962), and Nielsen (1962) as evidence that both forms "can produce the double call note as well as the three-tone." The cluster analyses of song variables in this study demonstrated a separation between localities 19-25 and all other localities

(Fig. 19, p. 62; Fig.21, p. 67). Specimens collected in localities 19-25 *were* predominantly ornatus. However, the discriminant function analysis (pp. 69-70) demonstrated that song (at least as it was characterized by the variables used in this study, *including* syllable number) was *not* a good discriminator of ornatus, substriatus, and melanocephalus.

Subspecies designations based on plumage patterns remain useful for identifying individuals in the field. However, results of this study showed that classification functions in discriminant function analysis, based on song variables or morphological variables, did not fit subspecies designations. 36% (song DFA) and 28% (morphology DFA) of individuals were misclassified as to subspecies when morphological or song variables were used. Nor did mtDNA clonal type match with subspecies (p. 114).

More study is required of P. striatus in eastern Australia-- and in other parts of the range of this taxon-- to examine additional patterns of variation and to begin to identify other factors which may have shaped those patterns. Field work should be continued in the region of overlap in southeastern Queensland of the northern and southern mtDNA lineages defined by this study. Investigation is needed of the frequency of mixed breeding pairs; the reproductive success of individuals; post-breeding dispersal and philopatry; temporal shifts in the zone of overlap; and the relative fitness of subspecies, intermediates, or mtDNA

haplotypes. Field studies of banded birds, followed over several generations, would be possible for this species. Existing museum collections proved to be unhelpful for this study; more large series, collected within short time periods, would be useful. My series contains no specimens from between 21.5° and 23.5° latitude, an area where probably all melanocephalus could be expected. There is also a gap in my series between Barcaldine and Alpha south to about Injune. This might prove to be a very interesting area to investigate, because of the numbers of intergrades of melanocephalus and substriatus which might be found there, and because habitat changes are dramatic. (The Carnarvon Ranges and Carnarvon Gorge are found here.)

In this study, I have not tried to identify ecological variables contributing to the observed patterns of variation. Woinarski et al. (1983) tried to identify environmental correlates of variation in their study of P. s. ornatus and P. s. substriatus in Victoria. They used a canonical correlation analysis to examine whether morphological characters were related to several environmental parameters. They found that variables related to body size (weight, wing length, and some bill and tarsus measurements) were positively correlated with altitude and rainfall. However, they found no correlations of characters with nest site location or with vegetation density.

The relatively recent effects of human populations on

the distribution patterns in this species have not been studied. It appears that Striated Pardalotes may benefit from the activities of humans, in terms of clearing of the types of forests which exclude this species and in terms of an increase in nest site availability (Appendix II, p. 159; Appendix III, p. 160). Thus, the ecological effects on geographic variation in P. striatus, including those effects which can be attributed to humans, require further study.

APPENDIX I

TAXONOMY. The pardalotes are a group of small, colorful songbirds endemic to Australia. The status of the family Pardalotidae and of species within the genus Pardalotus has been controversial. Until recently, they were classified as an uncharacteristic genus in the family Dicaeidae (Flowerpeckers). However, pardalotes do not share the features of the true flowerpeckers -- tongues adapted for nectar-eating, a muscular stomach reduced to a blind sac, and a purselike, hanging nest.

The current R.A.O.U. classification (Schodde 1975, 1981) places the pardalotes in their own family, Pardalotidae. The family includes only the genus Pardalotus, which is comprised of four species: P. quadragintus (Forty-spotted Pardalote), P. rubricatus (Red-browed Pardalote), P. punctatus (Spotted Pardalote), and P. striatus (Striated Pardalote). The monophyly of this group is not in question.

Sibley and Ahlquist (1990), in their classification based on DNA-DNA hybridization, have expanded the family Pardalotidae to include Acanthiza, Sericornis, Gerygone, Smicrornis, and other genera of the Acanthizinae; the Dasyornithinae; and the Pardalotinae. These authors consider Pardalotidae, as they have defined it, to be one of the old endemic groups of Australia and New Guinea, with its

closest relatives being the meliphagids, malurids, and corvoids. They also consider the genus Pardalotus to be more closely related to the other corvoid genera (Sericornis to Malurus) than to the passeroid genera such as Dicaeum, Prionochilus, and Zosterops, with which it had been previously allied.

STATUS OF P. STRIATUS. Schodde (1975) considers P. striatus to be a single polytypic species made up of a number of forms which were previously considered separate species. These forms, which include the races P. s. striatus, ornatus, substriatus, melanocephalus, and uropygialis, each occupies a broad geographic area, with some degree of overlap among adjacent forms. This treatment remains under discussion, however (McGill 1976; Noske 1978; Schodde 1981).

A number of previous studies, based primarily on museum collections and on some field observations, remain important. These are summarized briefly here, particularly as they relate to my own study.

Hindwood and Mayr (1946) analyzed 520 museum specimens and redefined the Striated Pardalote complex to include three sibling species, P. striatus, P. substriatus, and P. ornatus. (They did not consider the form melanocephalus.) Changes in their classification were proposed by Salomonsen (1961), Mayr (1961), and Mees (1965). Reports of interbreeding between the taxa substriatus and ornatus (e.g.

Cooper 1961; Lord 1956) and between other forms prompted Schodde (1975) to reclassify the group as a single species.

Woinarski et al. (1983) proposed that previous studies had relied too heavily on museum collections, and had included non-breeding birds and birds taken at unknown distances from breeding sites. They also felt that previous workers had concentrated on too narrow a range of plumage characters and had "pigeonholed" specimens by subspecies a priori. They attempted to describe variation across a contact zone for ornatus and substriatus. They captured live birds at breeding sites and measured 9 morphometric variables and 18 plumage variables for a principal components analysis. They found that the first five components accounted for only 38% of the variance, and morphometric variables of size had high loadings on PC3 and PC5 and accounted for only 12% of the variance. Citing their analysis, they questioned the use of the character, wide versus narrow white primary stripe, as a descriptor of the two subspecies. As a result of their analysis, they also questioned the existence of a well-defined contact zone for ornatus and substriatus across Victoria, in spite of the evidence for it which they themselves present in a map (Woinarski et al. 1983, p.88).

APPENDIX II

BEHAVIOR AND ECOLOGY. Striated Pardalotes are common birds of forest and woodland throughout Australia. Because of their small size (90-115 mm) and habit of foraging high in the canopy, and because they have a loud and often persistent call, they are sometimes described in field guides as being easier to hear than to see. They have stubby bodies and short tails, and a rapid, undulating flight. Pizzey (1980) has described them as looking like "flying beetles."

The feeding behavior of Striated Pardalotes has been described in a number of different studies. They are insectivorous and use their thick, partly-notched bills to remove insects from the leaves and twigs of Eucalyptus trees. In a comparative study of foraging behavior in several species of pardalotes in eucalypt woodlands in Victoria, Woinarski (1988) found that Striated Pardalotes spent most of their time gleaning invertebrates from the sturdier outer twigs and leaves. He also observed that three different forms of P. striatus (ornatus, striatus, and substriatus) forage in an almost identical manner. In a year-round study of small insectivorous birds in eucalypt woodland in New South Wales, Ford et al. (1986) found that P. striatus gleaned insects about 79% and snatched insects about 20% of the time; that almost 99% of their feeding time was spent on leaves and twigs; that the tree species most

frequently used were Eucalyptus caliginosa, E. viminalis, E. melliodora, and E. blakelyi; and that the tree heights at which most foraging took place were above 6 meters. Recher et al. (1985) obtained similar results in a study which was conducted only in summertime.

In their study, Ford et al. (1986) classified six species as foliage gleaners. In addition to P. striatus, these were P. punctatus (Spotted Pardalote), Gerygone olivacea (White-throated Gerygone), Melithreptus brevirostris (Brown-headed Honeyeater), M. lunatus (White-naped Honeyeater), and Lichenostomus fuscus (Fuscous Honeyeater). These species-- as well as others with similar feeding habits in the genera Melithreptus, Lichenostomus, and Manorina (Keast 1968a; Ford and Paton 1976; Paton 1980)-- are probably the major competitors of Striated Pardalotes for food resources.

Pardalotes eat a variety of invertebrates and exudates of insects and plants. Psyllids, coccids, and aphids, which are widespread in Australia and found on most species of Eucalyptus (Paton 1980), are probably the insects most commonly eaten by pardalotes. Spiders and insects from the orders Orthoptera, Coleoptera, Thysanoptera, Diptera, Lepidoptera, and Hymenoptera have also been identified from stomach contents (Hindwood and Mayr 1946; Ford et al. 1986). Lerp (the protective covering over many psyllid species), manna (an exudate of damaged plant material), and honeydew

(the secretions of aphid nymphs) -- all of which are high in carbohydrates -- constitute some portion of the diet in pardalotes (Paton 1980; Woinarski 1985b).

The breeding season may extend for as long as six months (Bell 1959; Woinarski 1985) and begins in early winter in the northern parts of the species' range and late winter or spring farther south. Nest sites are used year after year (Lord 1942; Green 1971; Woinarski et al. 1983). Individuals are "strongly philopatric" and "usually faithful in mate choice" (ibid.). Several broods may be raised in a season. There is evidence that even third clutches may be laid, and that mates are sometimes monogamous during the season and sometimes not (Woinarski, pers. comm.).

Relatively little has been published on courtship and mating. Courting males display on bare branches, while spreading and quivering their wings and tails (Pizzey 1980) and singing. This display appears to both attract females and to agitate other males (pers. obs.). I have observed one or more females responding to a displaying male by landing near him, by spreading and quivering the wings, and by sometimes appearing to examine a prospective nest hole. Females may sing a characteristic trill in apparent response to male song; but they do not seem to sing a true song, at least during courtship activity.

Whether or not females sing full songs has not been studied, however. There is no sexual dimorphism, except

perhaps in P. s. melanocephalus (Hindwood and Mayr 1946; Salomonsen 1961; Short, Schodde, pers. comm.). Therefore, in the field it is not possible to tell the sex of a singing bird. But, of 211 birds which I observed singing at nest sites, and which I subsequently collected, *all* proved to be males with developed testes. This would seem to provide some evidence that only males sing during the breeding period.

Male songs are simple and distinctive, and consist of one to four simple syllables (sensu Jellis 1977) repeated over and over. Local variations of the song have been described by Slater et al. (1986) as sounding like "wit-wit," "witta witta," and "pick-it-up;" and by Pizzey (1980) as "chip-chip," "pick-pick," "wittachew," "cheeoo," and "pee-ew peeow."

Both sexes share in nest building. Nests are placed in holes in dirt banks or trees. Holes in manmade structures such as brickwork (Hindwood and Mayr 1946), birdhouses, drainage pipes, eaves, hanging flower baskets, and farm equipment (pers. obs.). In addition to natural banks in creeks or hillsides, places where the earth has been disturbed by human activities-- such as roadcuts, railroad cuts, construction sites, stock dam banks, quarries, etc.-- attract pardalotes looking for nest sites.

When a bank is used, an excavation is dug horizontally about 0.5 to 1.5 meters into the earth (Bell 1959; Beruldsen

1980). The birds use their bills and feet to break up and remove dirt from the tunnel. The nest, which is dome-shaped with a side opening, is constructed within an enlarged chamber at the end of the tunnel, and is usually made of bark strips, grass rootlets, and fine twigs and leaves (Bell 1959; Slater et al. 1986). Old tunnels are often repaired and used from year to year.

Two to five white eggs, approximately 16-19 x 13-15 mm in size, are laid. The most common clutch size is 4, and somewhat less often 3 (Beruldsen 1980). Incubation lasts three weeks. Whether both male and female incubate the eggs has not been studied. The young are insectivorous and are fed by both parents, and sometimes by auxilliary birds (Rogers 1966; Dow 1980; Woinarski et al. 1983). These helpers are probably non-breeders, and they are most likely fledged birds from an earlier brood of the season (Woinarski pers. comm.). The mean fledging period is 23 days (Woinarski 1985a).

Comparing data on small insectivorous birds from Europe and North America with birds from Australia, Woinarski (ibid.) found that Australian species have smaller clutches, longer incubation and fledging periods, and longer breeding seasons. Of the 81 Australian species represented in the study, P. striatus had the longest incubation and fledging periods. He hypothesized that these differences are due to the relatively minor seasonal fluctuations in food resources

in Australia.

Small insectivorous Australian birds were found to be more sedentary, possibly for the same reason. Insectivory appears to be directly related to degree of sedentariness and nomadism (Keast 1968a; Schodde 1982). Year-round production of foliage by eucalypts, and therefore year-round availability of foliage insects, probably enables many leaf-gleaning birds to overwinter within their breeding ranges (ibid.). Pardalotes may form flocks which move more or less nomadically in the non-breeding months (Woinarski 1988). However, although there may be some post-breeding dispersal, the distances are probably not extensive; and breeding and post-breeding ranges overlap substantially (Woinarski 1985a).

Schodde (1982) proposed that there is a close correlation between sedentariness and independence from water. Although his discussion was of Eyrean species (including Pardalotus rubricatus, the Red-browed Pardalote of the arid inland region), he considered the family Pardalotidae to be one of the "non-drinking" families. Members of this group, which also includes the families Acanthizidae, Maluridae, and Climacteridae, rarely or never drink. Because of this, pardalotes may be less likely than many other species to disperse widely during moderate droughts.

Densities of P. striatus vary with habitat and time of

year. Ford et al. (1986) reported the density in eucalypt woodland, averaged over the whole year, to be 0.69 birds/ha. Blakers et al. (1984) reported densities during the breeding season to average about 1.41/ha in eucalypt woodland, 0.98/ha in eucalypt forest, and 0.85/ha in mallee and woodland.

Little is known about molt, fat deposition, or gonadal development in this species. In comparing molt in birds from the arid zone, Keast (1968b) found that species which were seasonal wanderers molted more consistently and quickly than their sedentary allies. If being relatively sedentary and having a long breeding season results in a prolonged molt, then perhaps this is the case for P. striatus. Although the data are not analyzed in this paper, a summary of my observations on the state of molt, fat, and testes size of the specimens I collected appears in Appendix IV.

The effects of humans and their activities on the behavior, ecology, and distribution of Striated Pardalotes has not been studied. However, it appears that in some ways this species has adapted well to changes humans have made. Because this is predominantly a species of open forest and woodland, and not of dense eucalypt forest, expansion of its range may have become possible as humans cleared the land (Bell 1959; Ford 1987b). In addition, pardalotes will readily use manmade structures and earthworks as nest sites; so perhaps nest site availability has increased for this species as a result of human activity.

APPENDIX III

The following observations were made on nest sites chosen by the birds collected for this study.

Total nest sites: 211
Treeholes: 56
Dirt banks: 150 (56 in natural river, creek, or lake banks; and 94 in manmade banks created by road cuts, railroad cuts, quarries, excavation sites, or stock dams.
Other: 5 manmade sheds, buildings

Pardalotes were also observed nesting or nestbuilding in drain pipes, manmade birdhouses, a kayak hanging in a shed, a packed bunch of burlap bags hanging from rafters in a barn, and in the stanchions on a tennis court.

Collected birds identified as melanocephalus (n=80) were found only using banks. Those identified as substriatus (n=72) were usually found in banks, but 10 used treeholes and 5 used "other". Those identified as ornatus (n=56) were usually found using treeholes, but 11 used banks. Of the 3 birds identified as intermediates, 2 used banks and 1 used a treehole.
In six localities where substriatus and ornatus were found together, nest sites were distributed as follows:

	substriatus		ornatus		intermediate	
	tree	bank	tree	bank	tree	bank
LEG (7)	1	4	1	1		
BOL (8)		3		4		1
ARD (8)	1		7			
WAL (8)	1		6		1	
WER (5)	2	2		1		
MUR (3)	2		1			

This data, with admittedly small samples, appears to show that pardalotes regardless of subspecies use whatever sites are available for nesting. For example, birds at the locality Bolivia were attracted to a steep railroad cut. There were many nest holes from previous breeding seasons at this site. Birds from Arding were collected at treeholes in a stand of eucalypts that was situated between two cleared sheep paddocks. There appeared to be no suitable dirt banks in the vicinity. At Werris Creek, birds were collected in a paddock that had both a stream bank and Eucalyptus trees that provided suitable sites; and birds were found using those sites.

APPENDIX IV

The following observations were made on the state of molt, fat deposition, and gonadal development in specimens collected for this study.

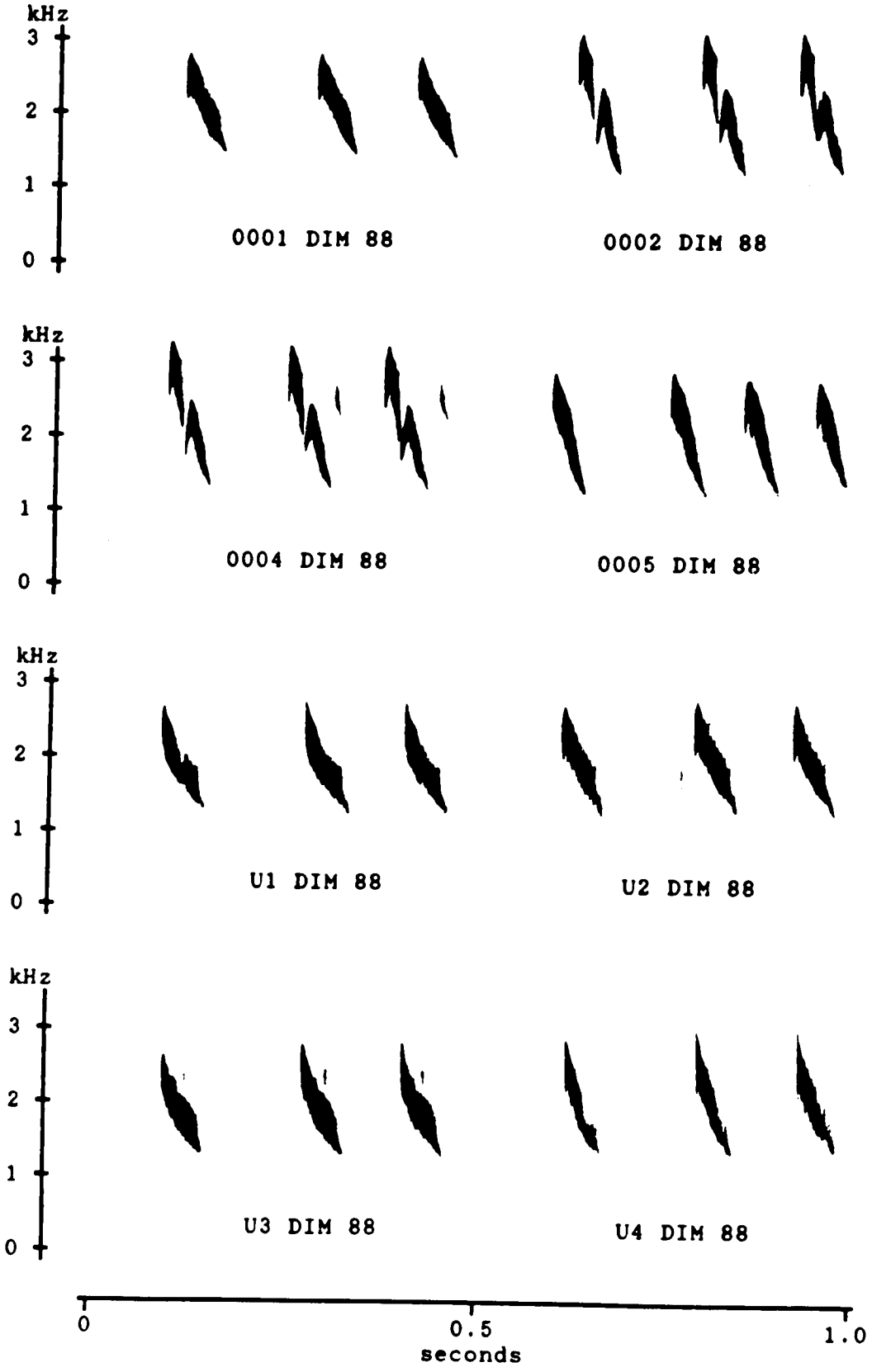
Molt: 25% of the collected specimens (55 out of 217, which includes females) had some degree of molt. There appears to be no pattern related to geography or month collected. For example, no greater number of molting birds is found in southern samples which may have been collected somewhat later into their breeding season than samples collected farther north. The degree of molt found ranged from one or a few crown feathers to one bird that appears to have molted all of its tail feathers at once (perhaps due to loss to a predator?). Most of the 55 molting birds had pin feathers on the crown and/or throat exclusively.

Fat: Assessed by amount of breast fat found lying in and around the depression formed by the furcula, noted when the specimen was prepared. Assessments were subjective, but followed the scale used for mistnetted birds: 0=no fat, 1=slight fat, 2=moderate fat (fat fills depression), 3=greatest fat (fat extends out of depression). Birds tended to get fatter from north to south. Birds in 1989 were generally fatter that birds in 1988. (1989 was a much wetter year.) The fact that birds from the southern localities had more fat may be related to 1) greater food abundance in those localities, 2) generally more fat deposition in larger birds that live in what may be somewhat colder environments, 3) assessment of the southern birds relatively later in their breeding season (doubtful), or 4) differences among years in the way I assessed amount of fat.

Testes: 209 males (out of 211) had visible left testes. In most, the right testis was also visible. Left testes ranged in diameter from 1-5 mm.

APPENDIX V

Sonagram catalog. Sound spectrograms of the songs of Pardalotus striatus recorded for this study are shown here. Each song, representing an individual male, is identified by a field number, a 3-letter locality code, and the year in which the recording was made. (Field numbers beginning with "u" indicate that the bird was not collected after its song was recorded.) For an explanation of locality codes, see Table 2 in the text. The recordings have been deposited in the archive of The Library of Natural Sounds of The Cornell Laboratory of Ornithology in Ithaca, New York. The LNS catalog numbers (46621-46823, 48377-48399, 48427-48540) are cross-referenced with the field numbers which appear here.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kHz
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0005 DIM 88
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2
1
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kHz
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U4 DIM 88
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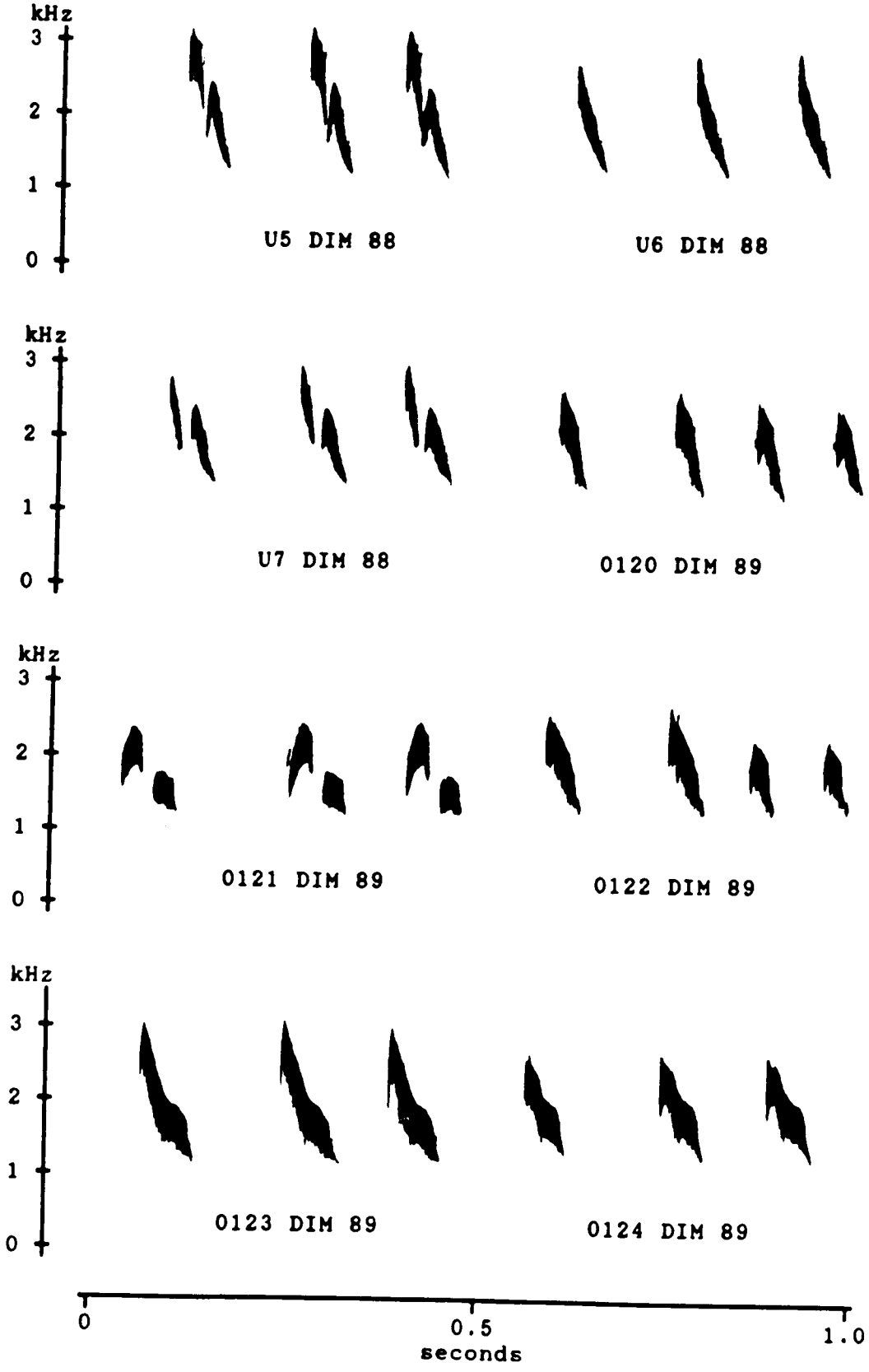
0.5
1.0
seconds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kHz
3
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kHz
3
2
1
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kHz
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seconds
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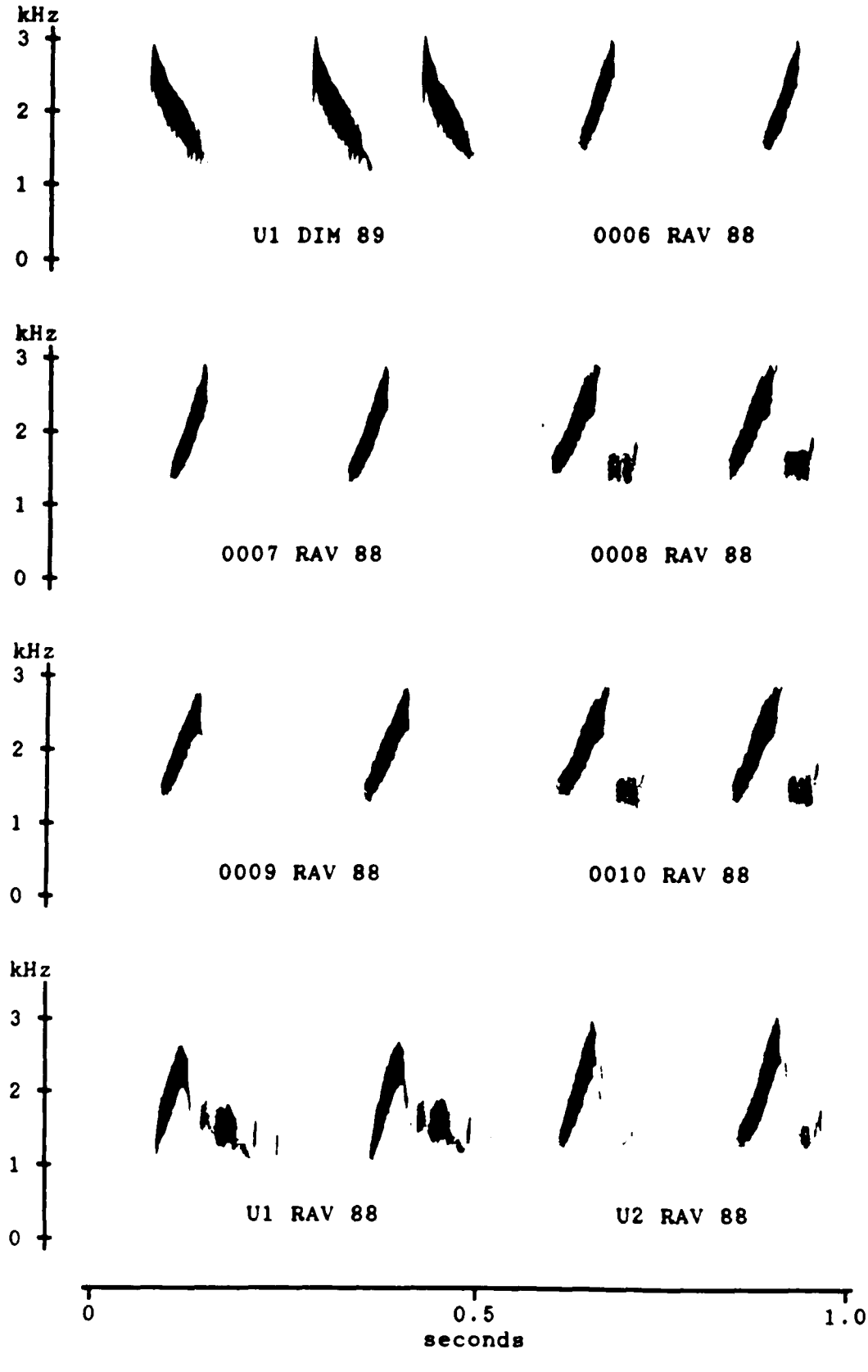
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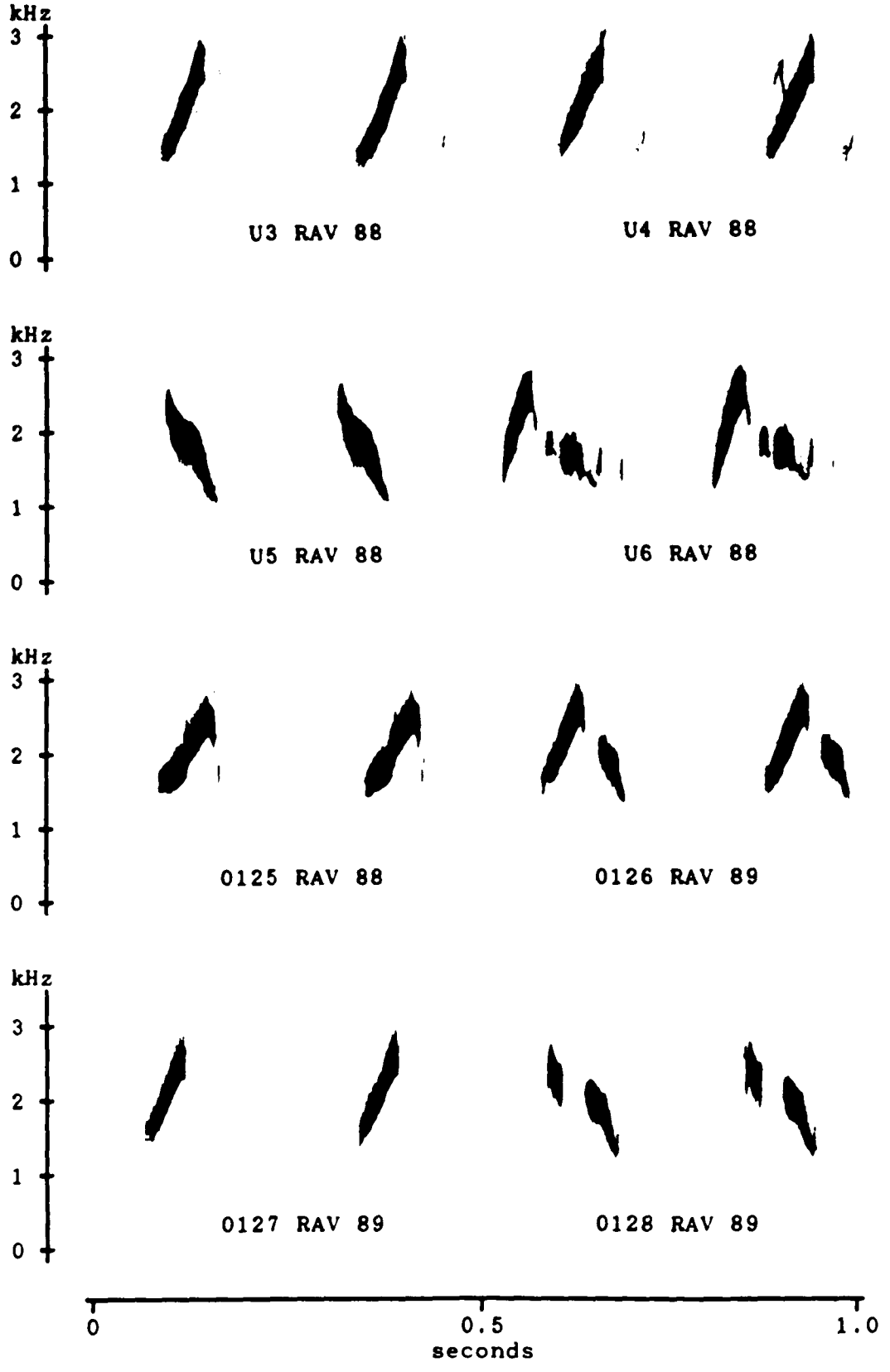
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kHz
3
2
1
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kHz
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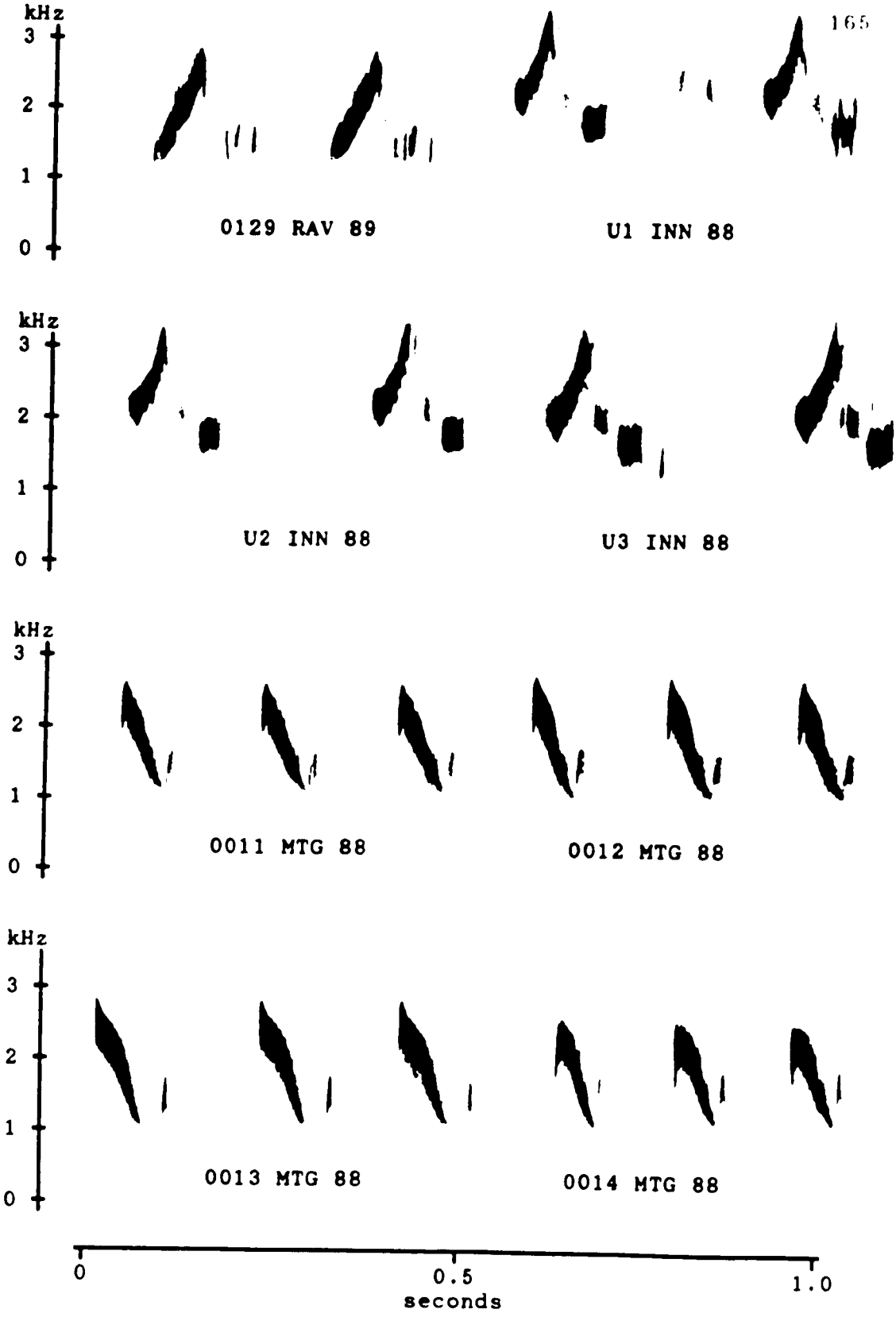
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0012 MTG 88
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seconds
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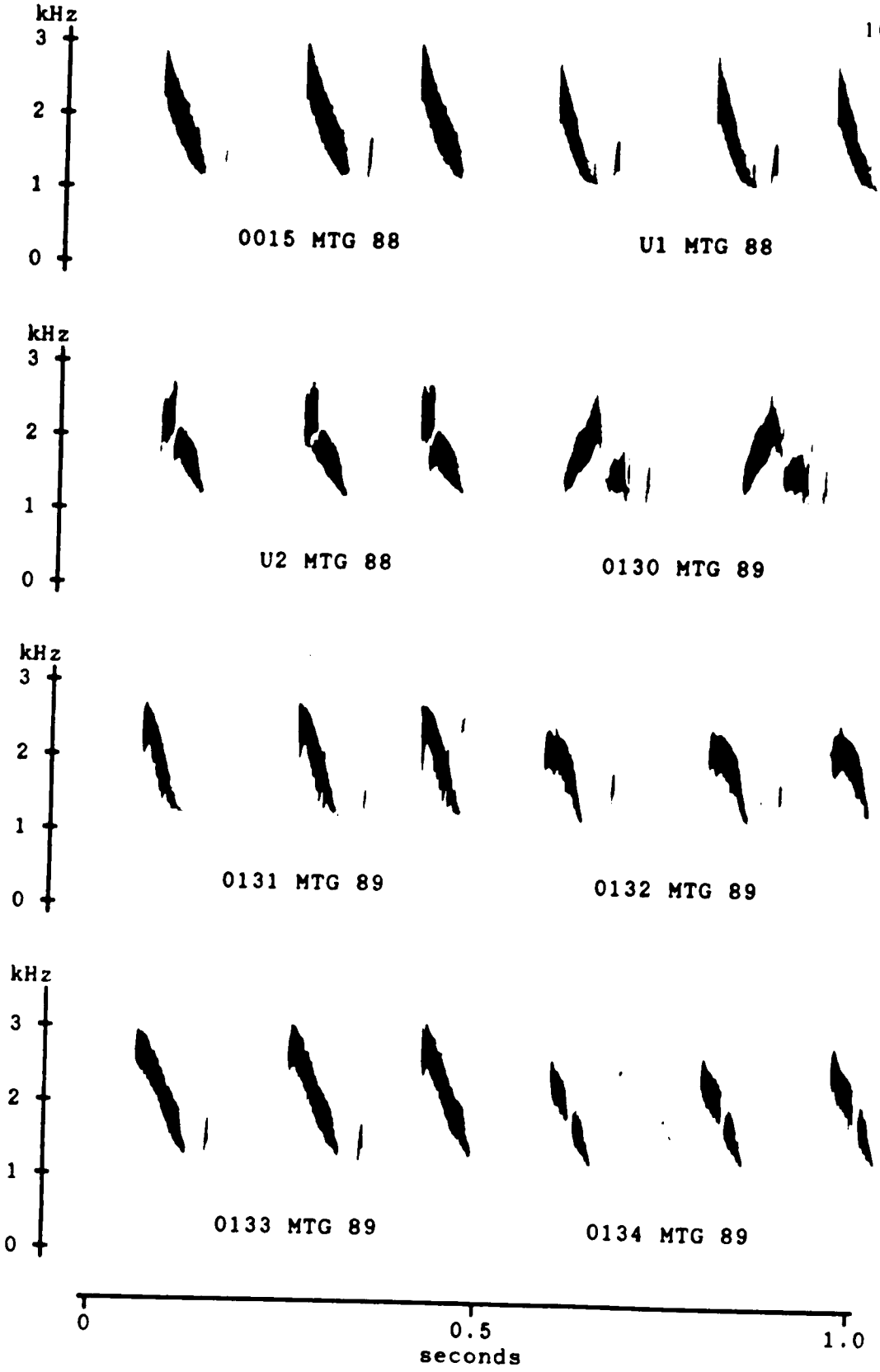
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2
1
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kHz
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seconds
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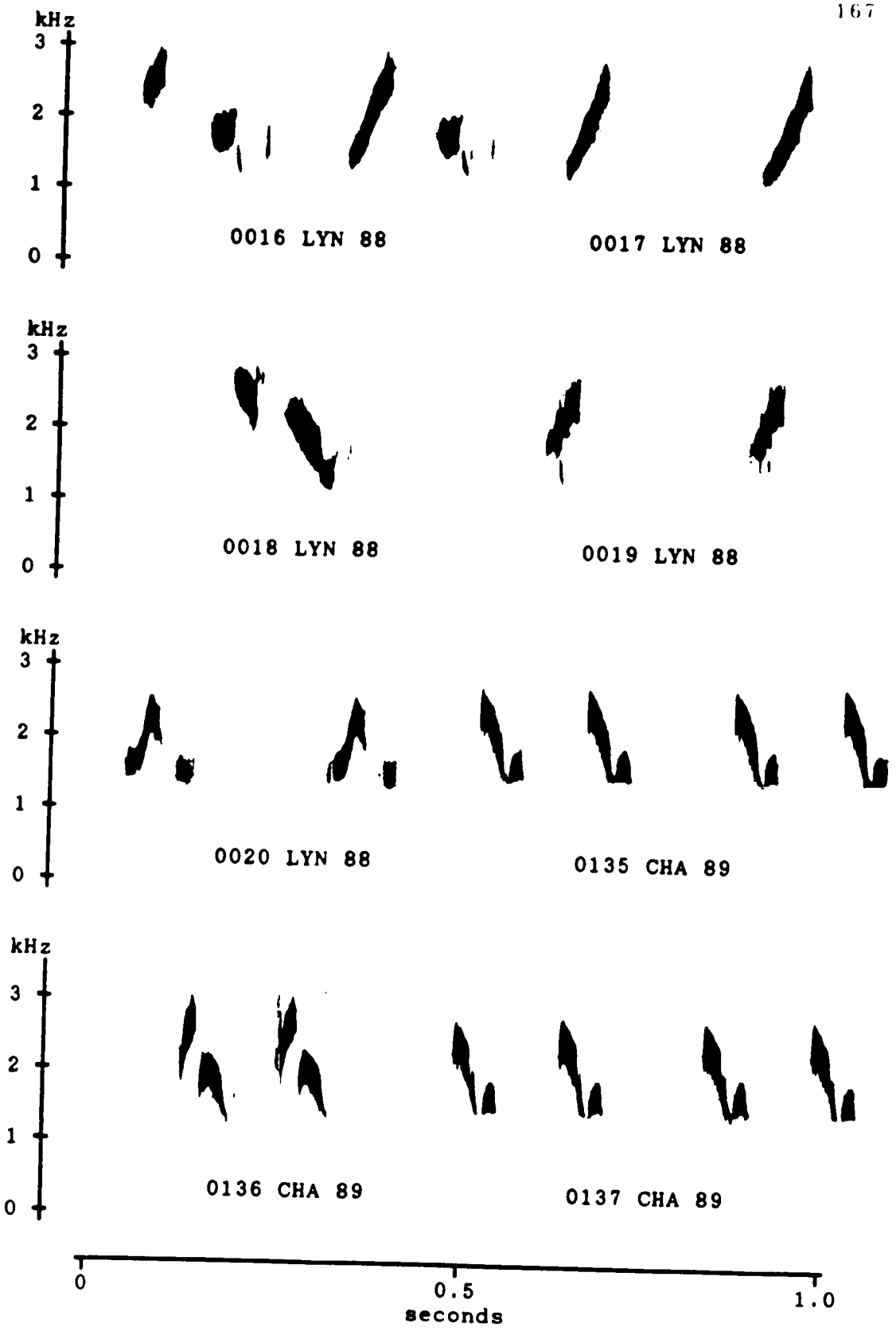
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2
1
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kHz
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seconds
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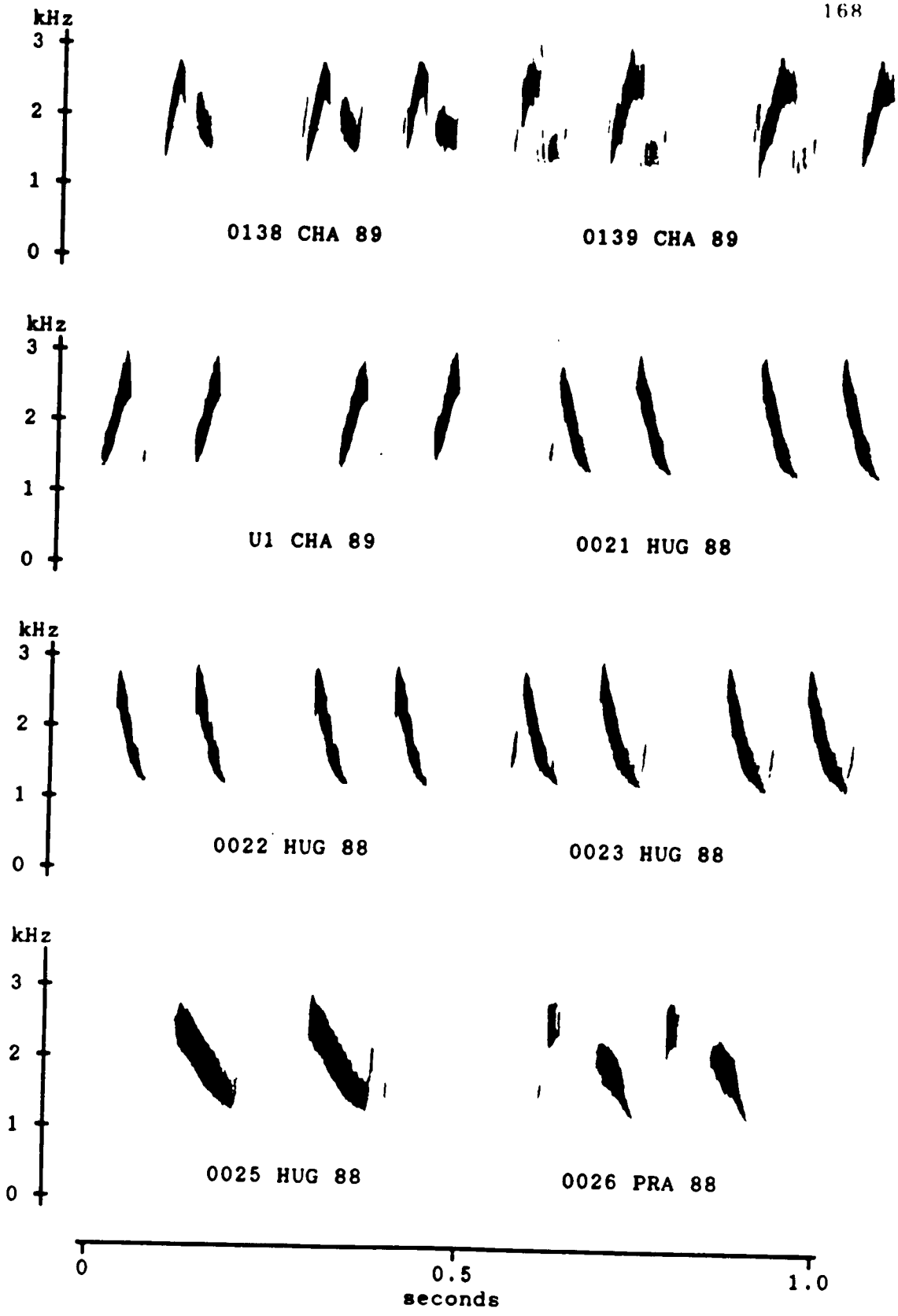
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3
2
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1.0
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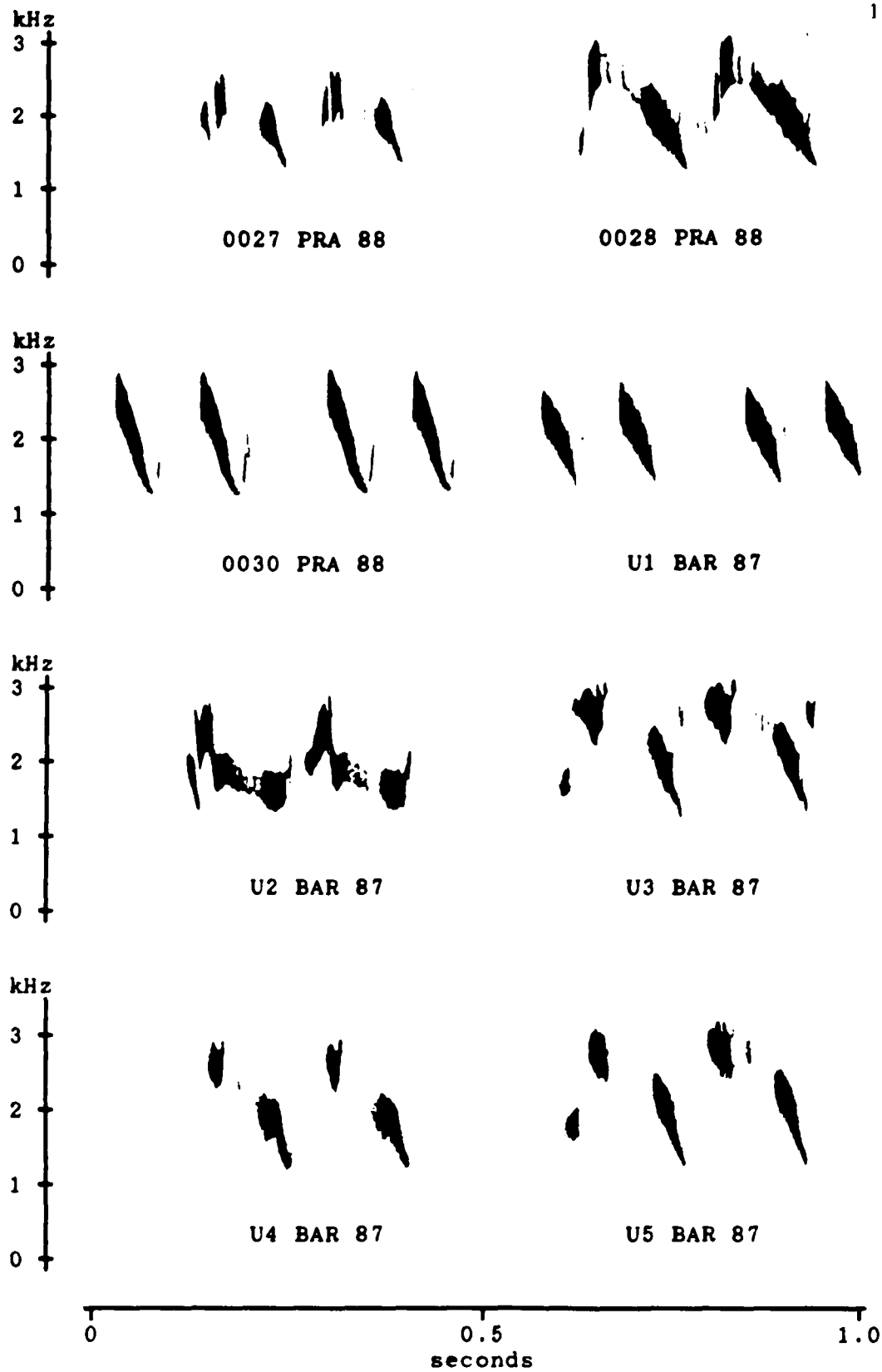
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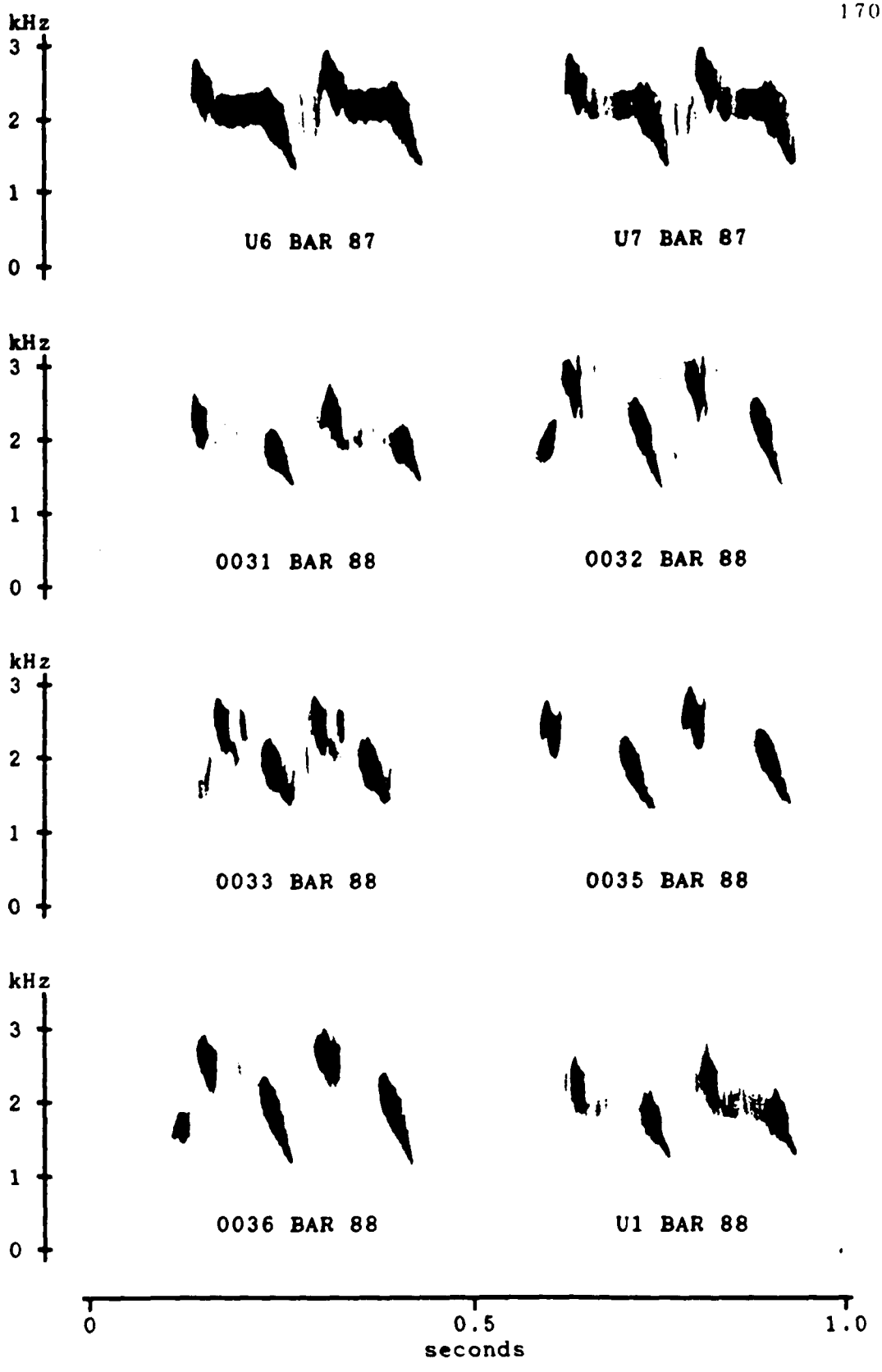
seconds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0035 BAR 88
kHz
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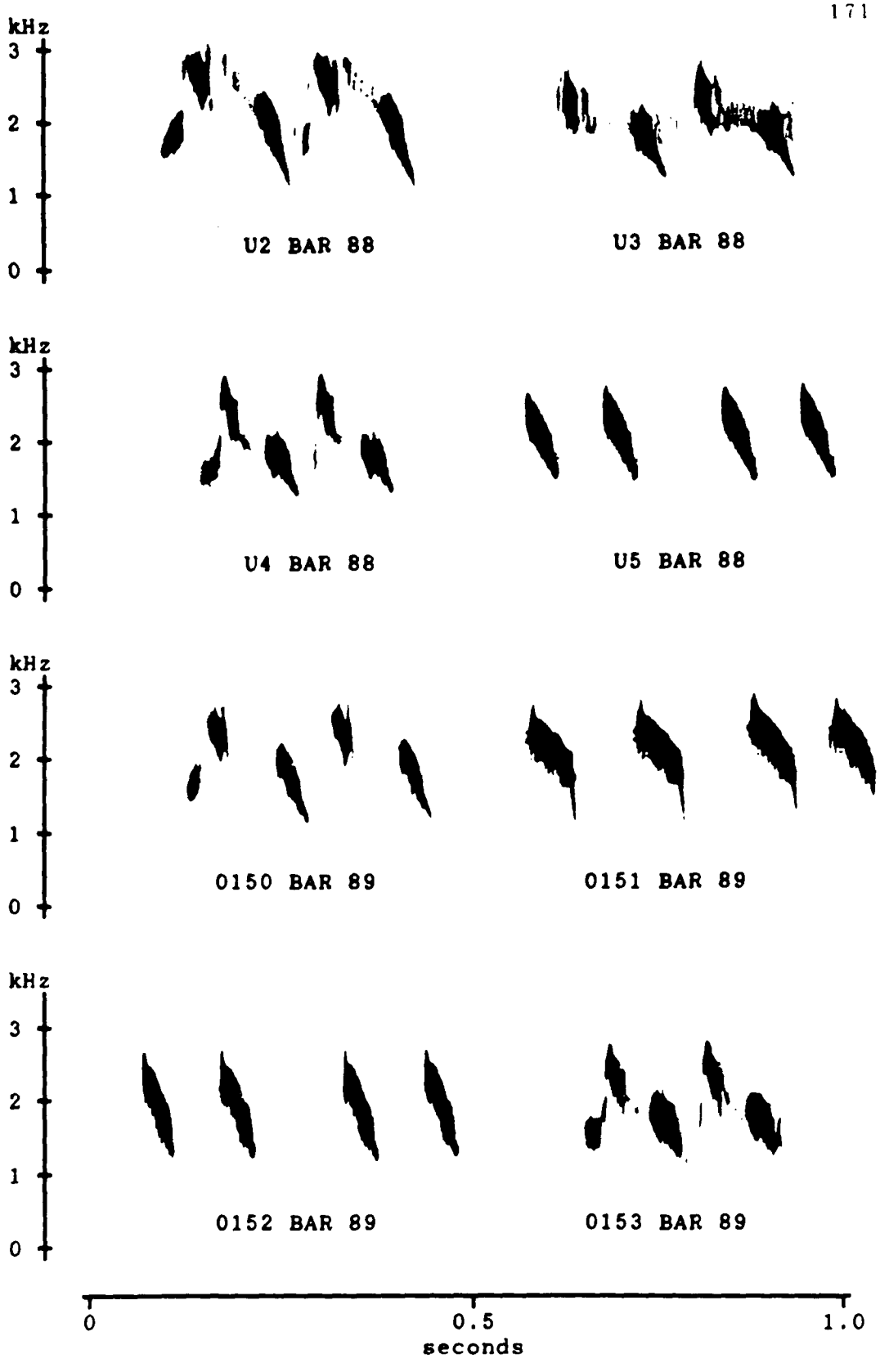
0.5
1.0
seconds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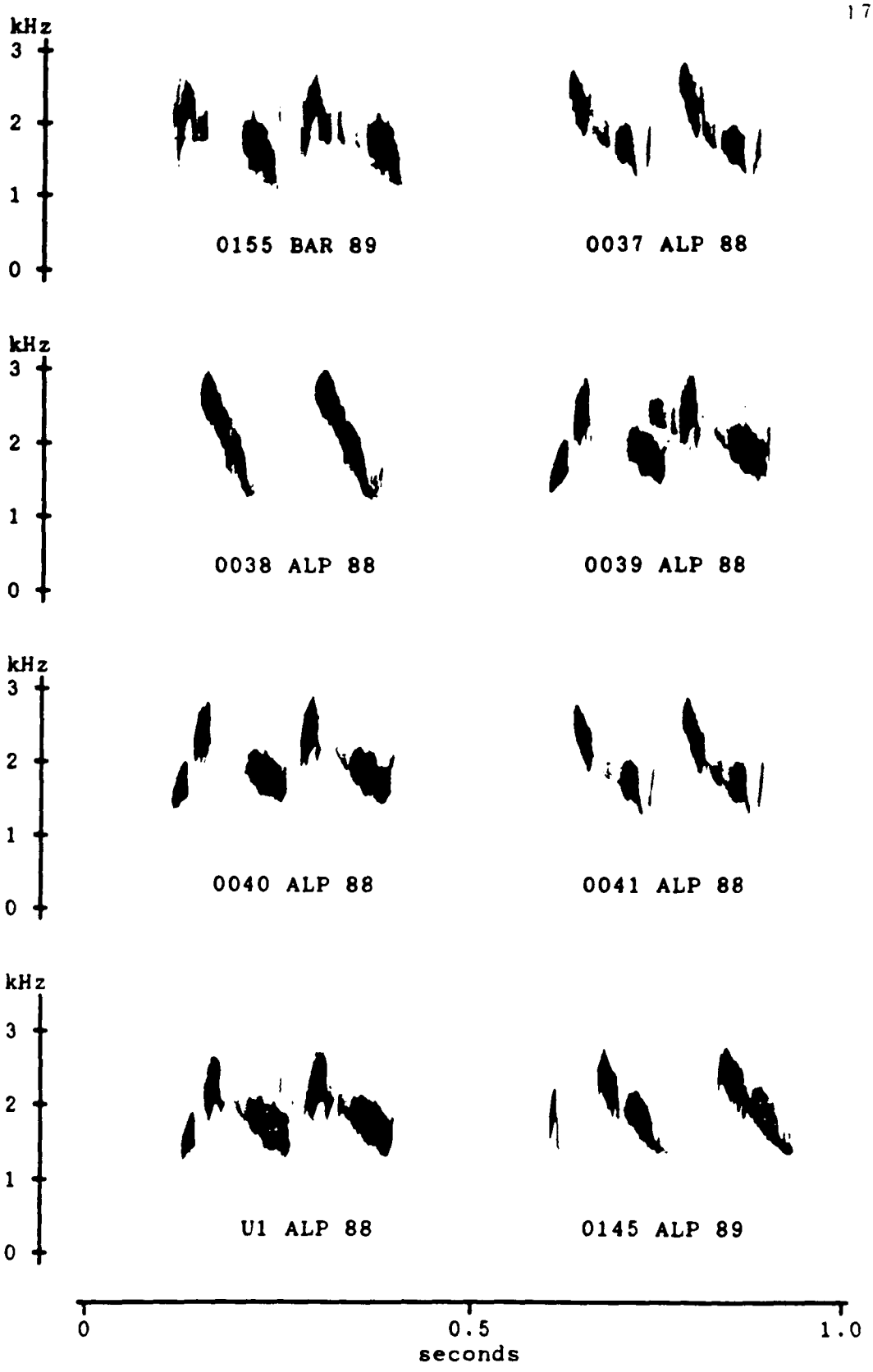
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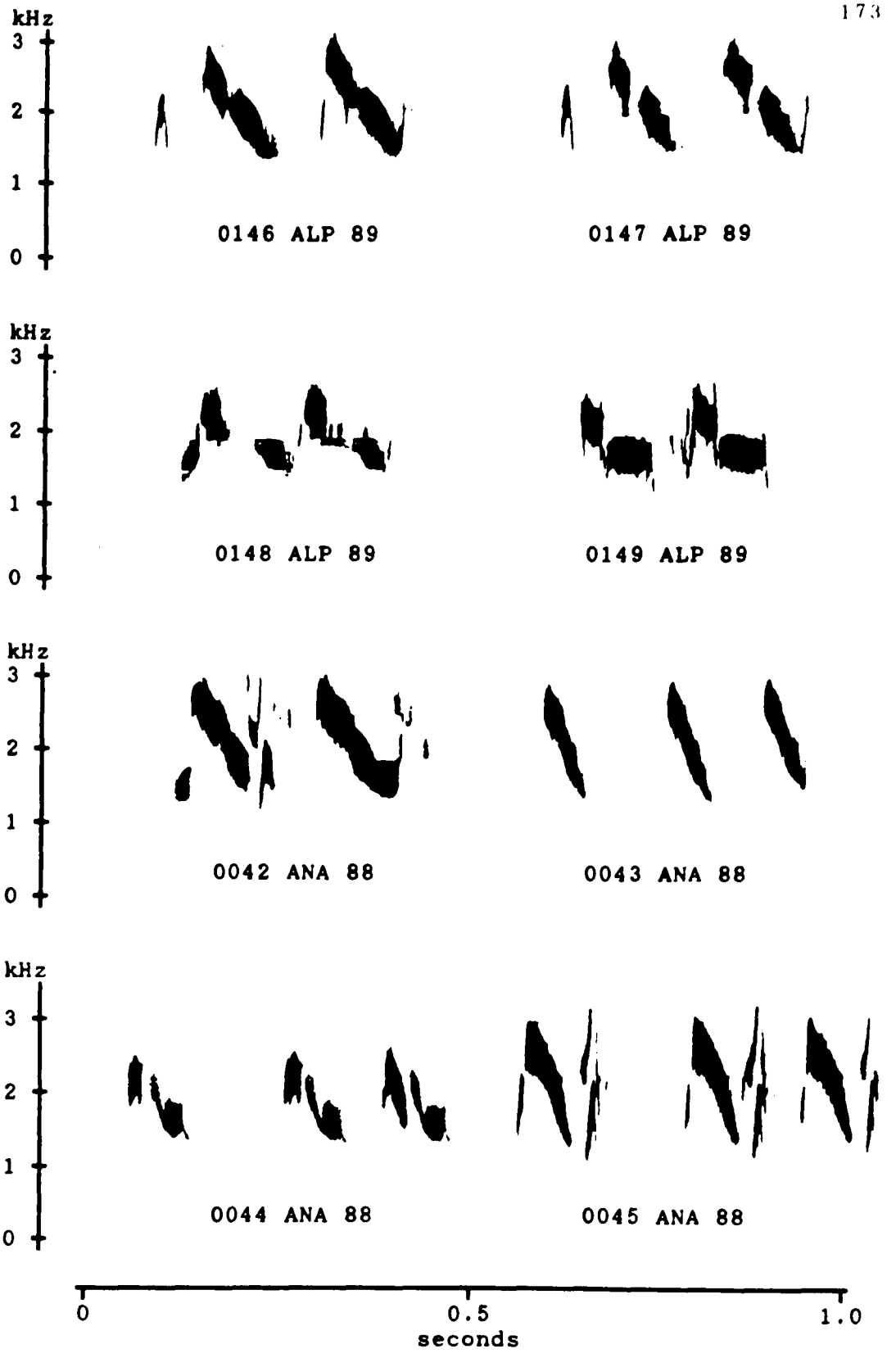
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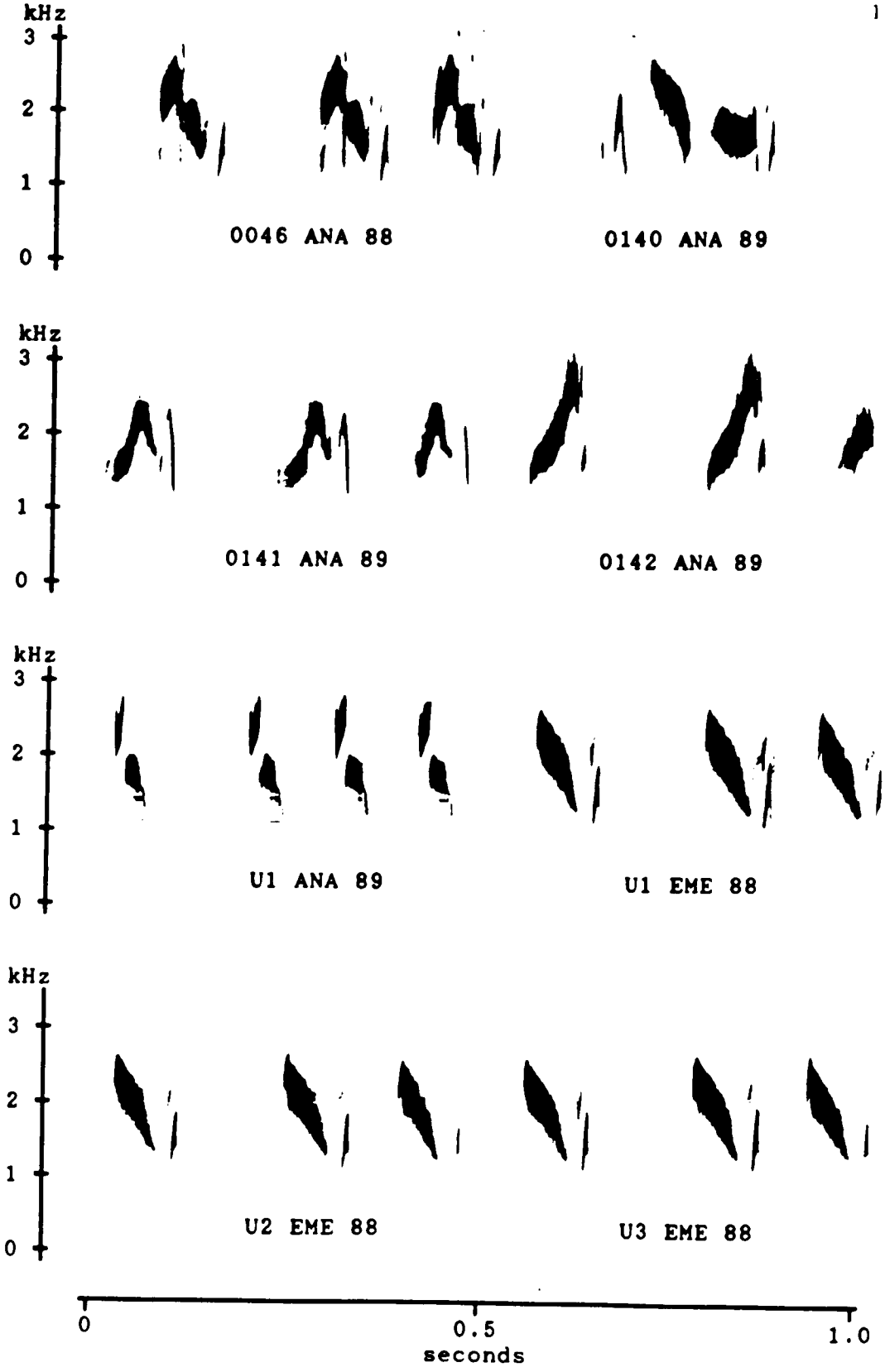
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1
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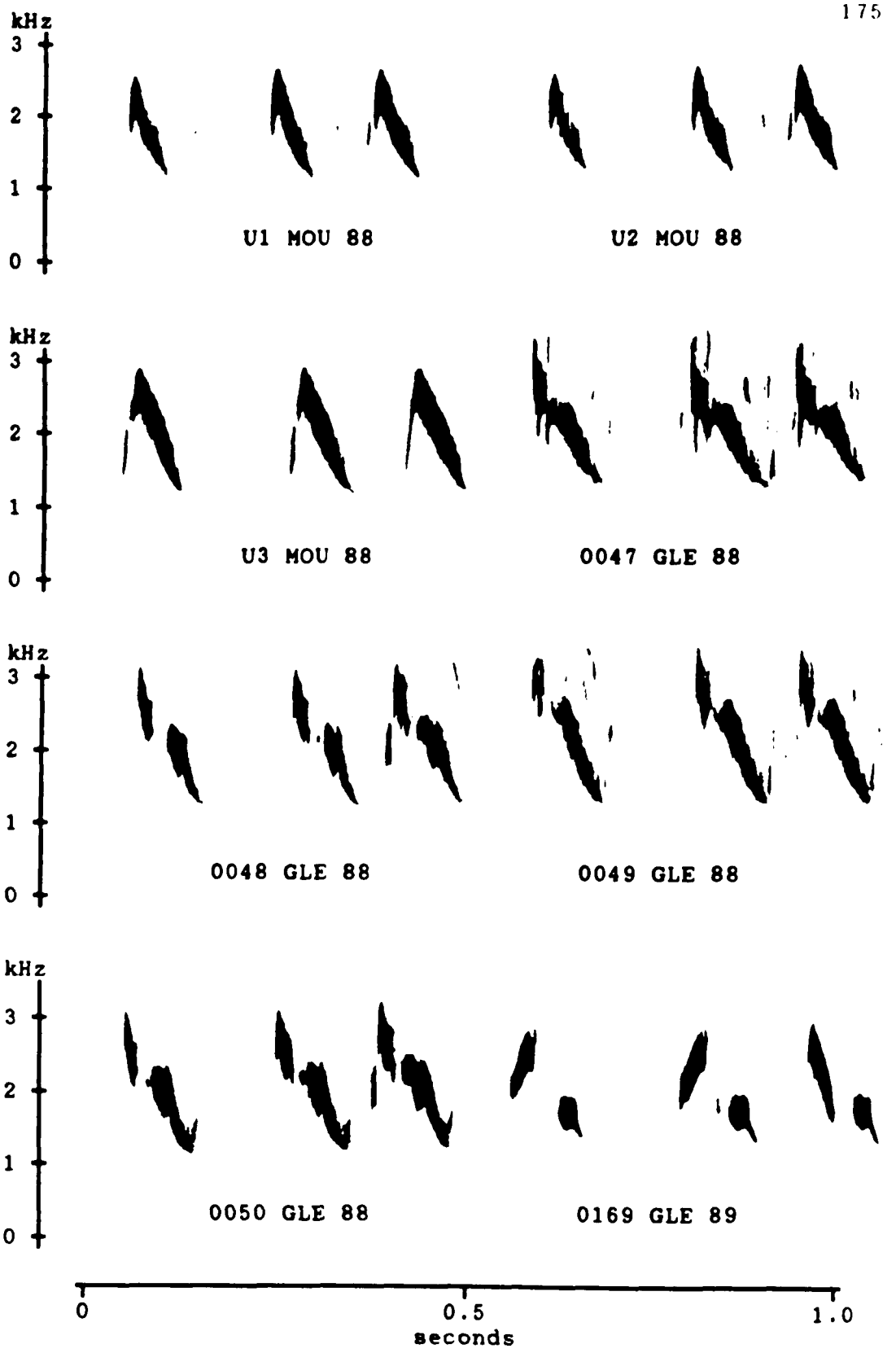
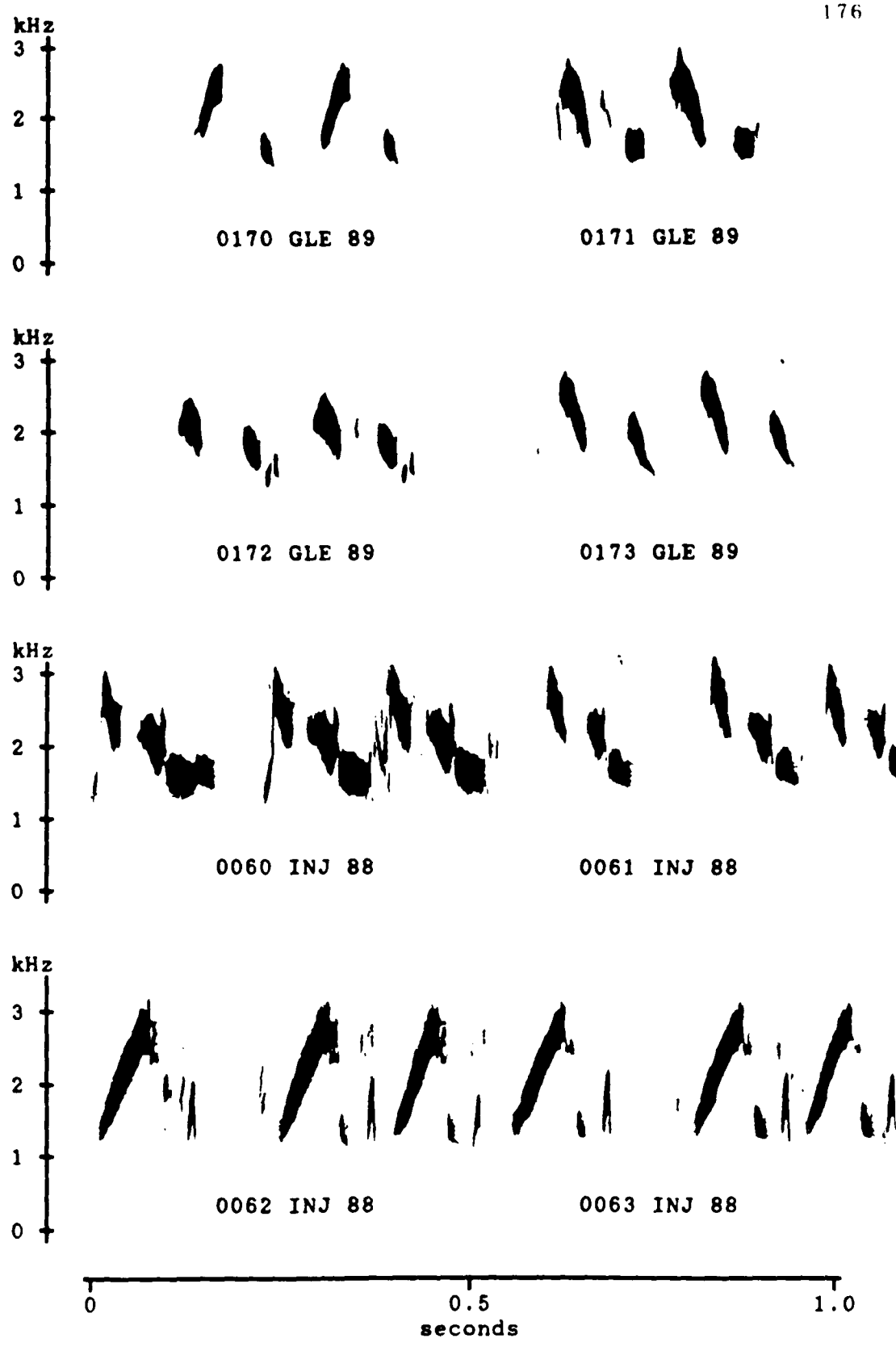
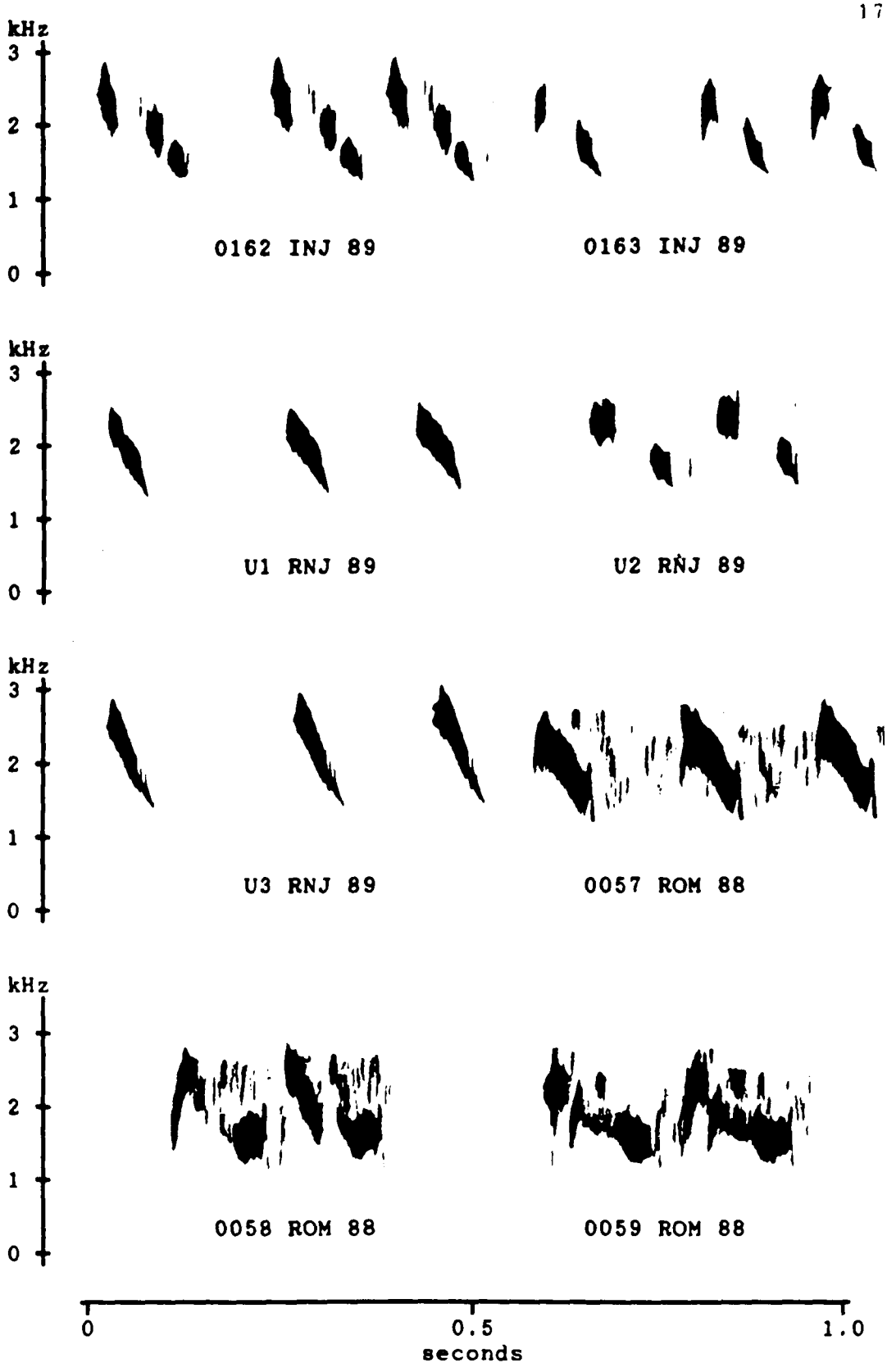
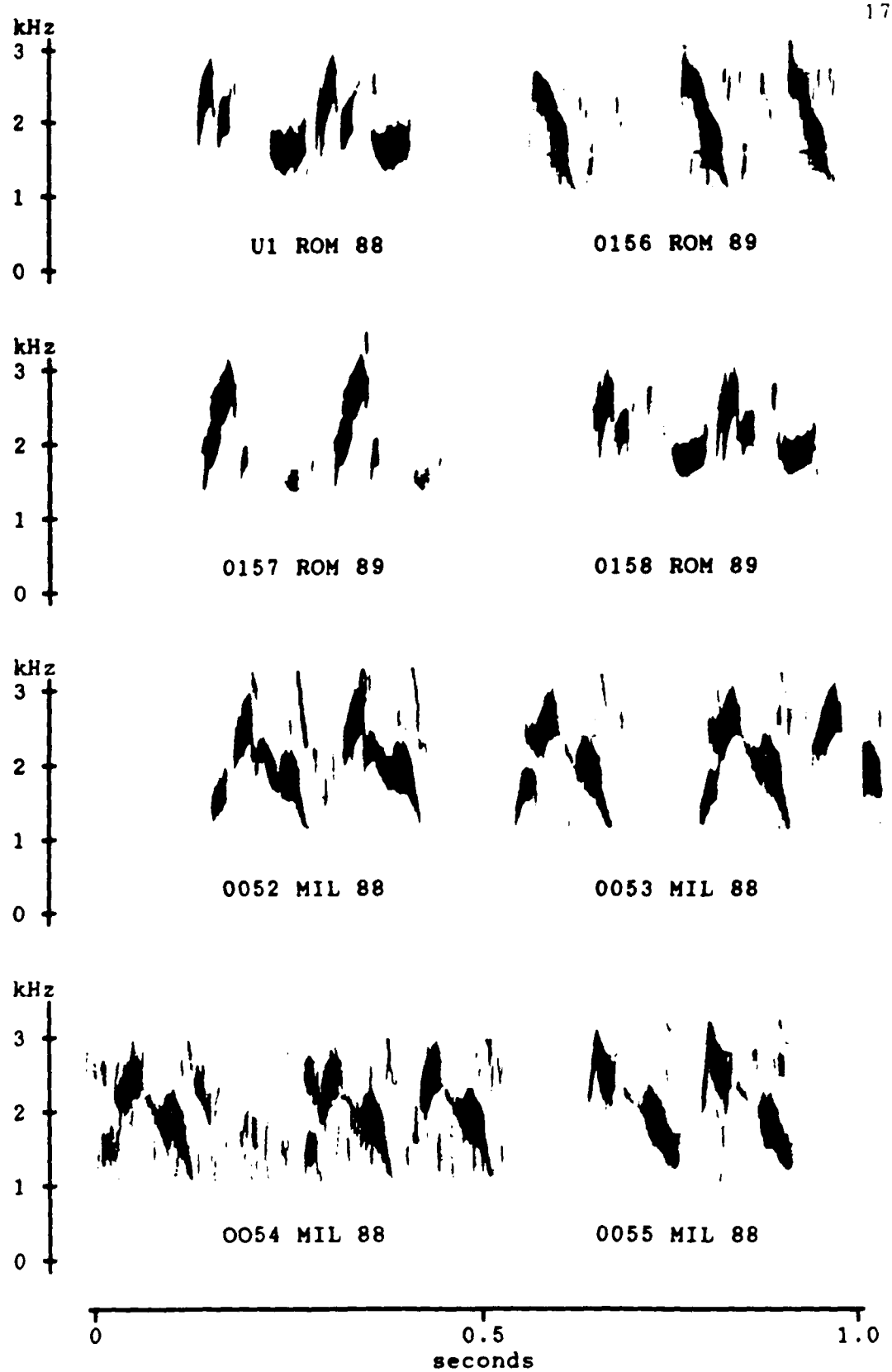
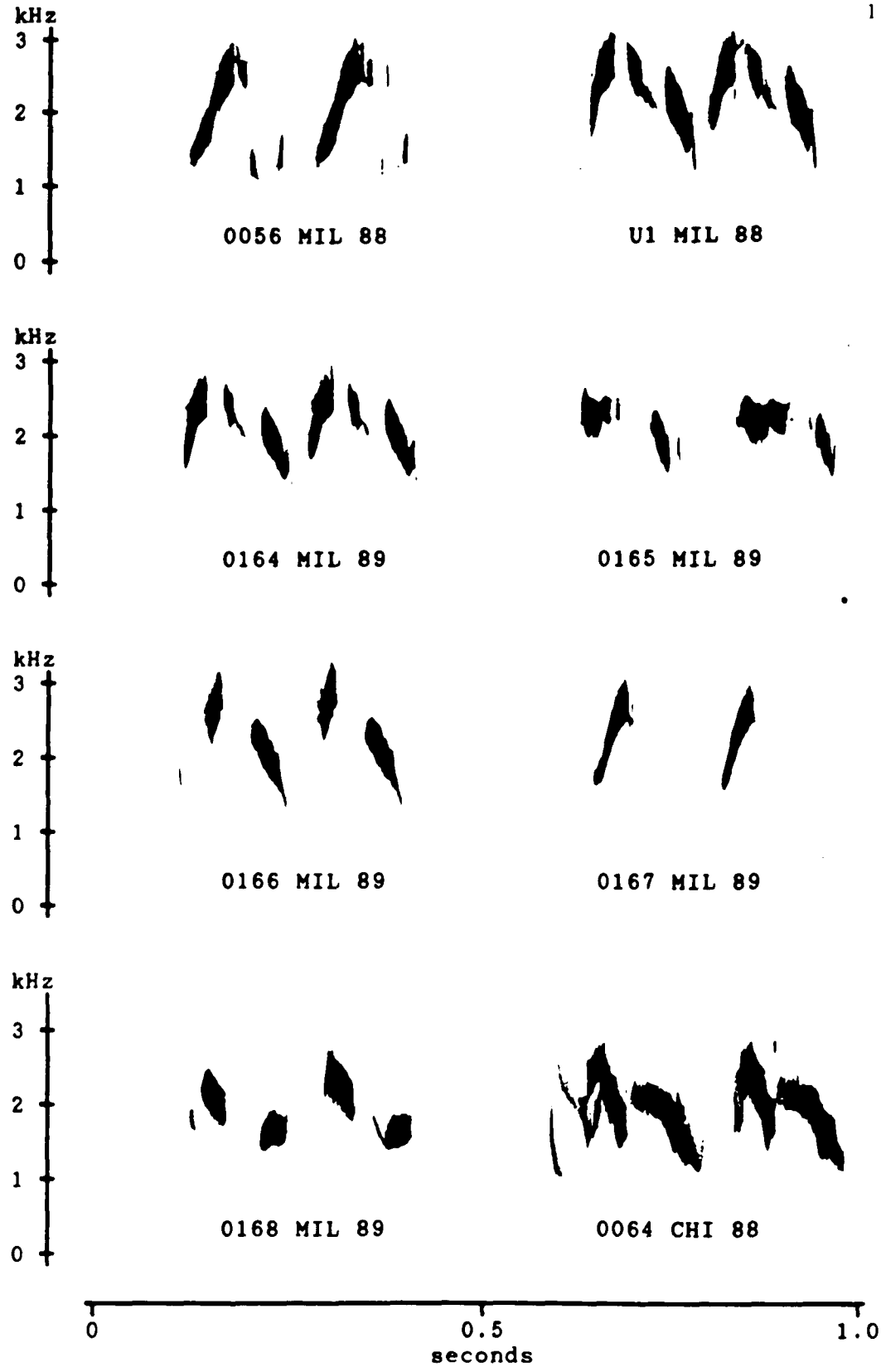
U1 EME 88
kHz
3
2
1
0
U2 EME 88
U3 EME 88
0
0.5
seconds
1.0

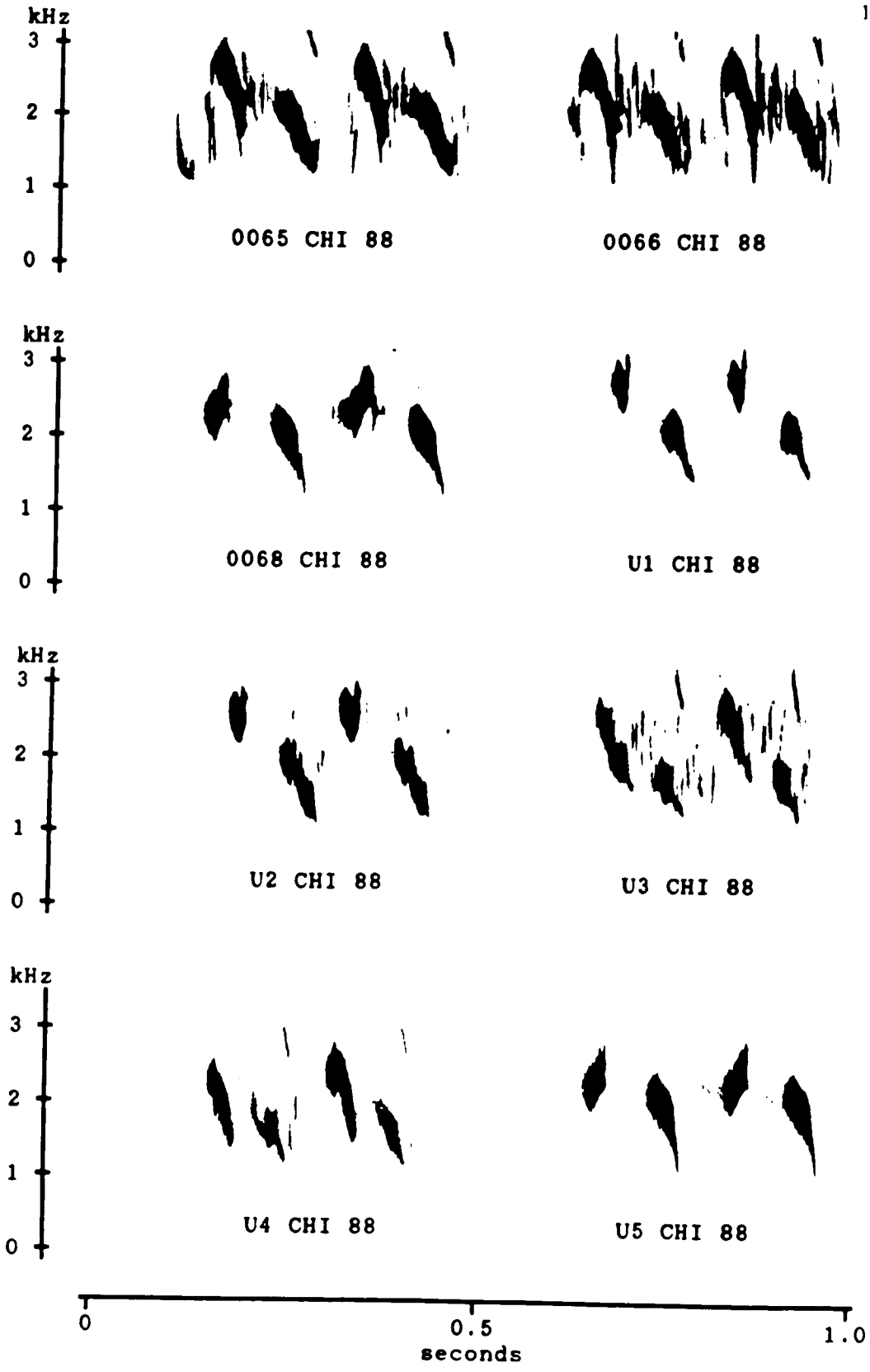

kHz
3
2
1
0
U1 MOU 88
U2 MOU 88
U3 MOU 88
0047 GLE 88
0048 GLE 88
0049 GLE 88
0050 GLE 88
0169 GLE 89
0
0.5
1.0
seconds

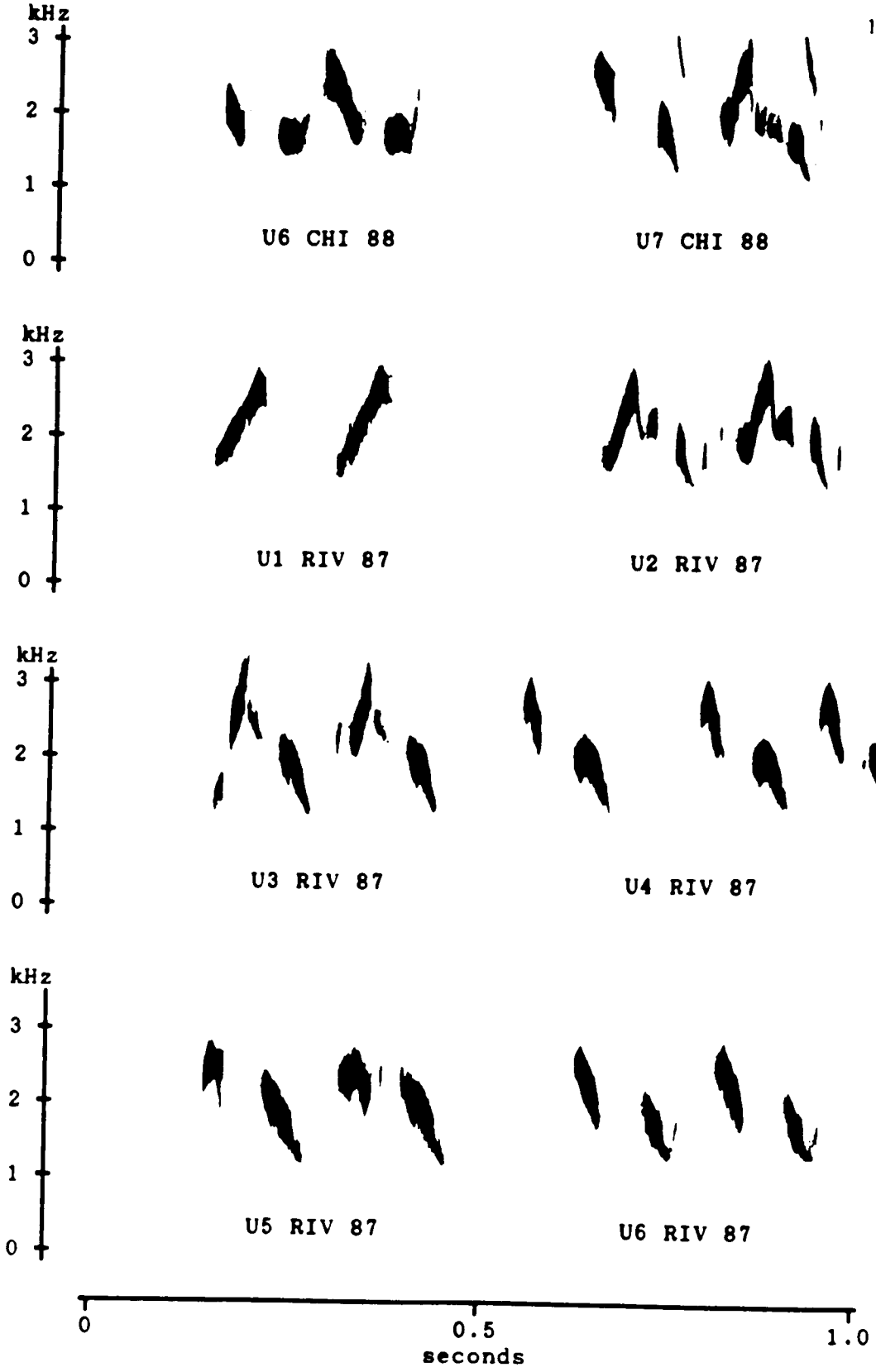

kHz
3
2
1
0
0170 GLE 89
0171 GLE 89
kHz
3
2
1
0
0172 GLE 89
0173 GLE 89
kHz
3
2
1
0
0060 INJ 88
0061 INJ 88
kHz
3
2
1
0
0062 INJ 88
0063 INJ 88
0
0.5
1.0
seconds

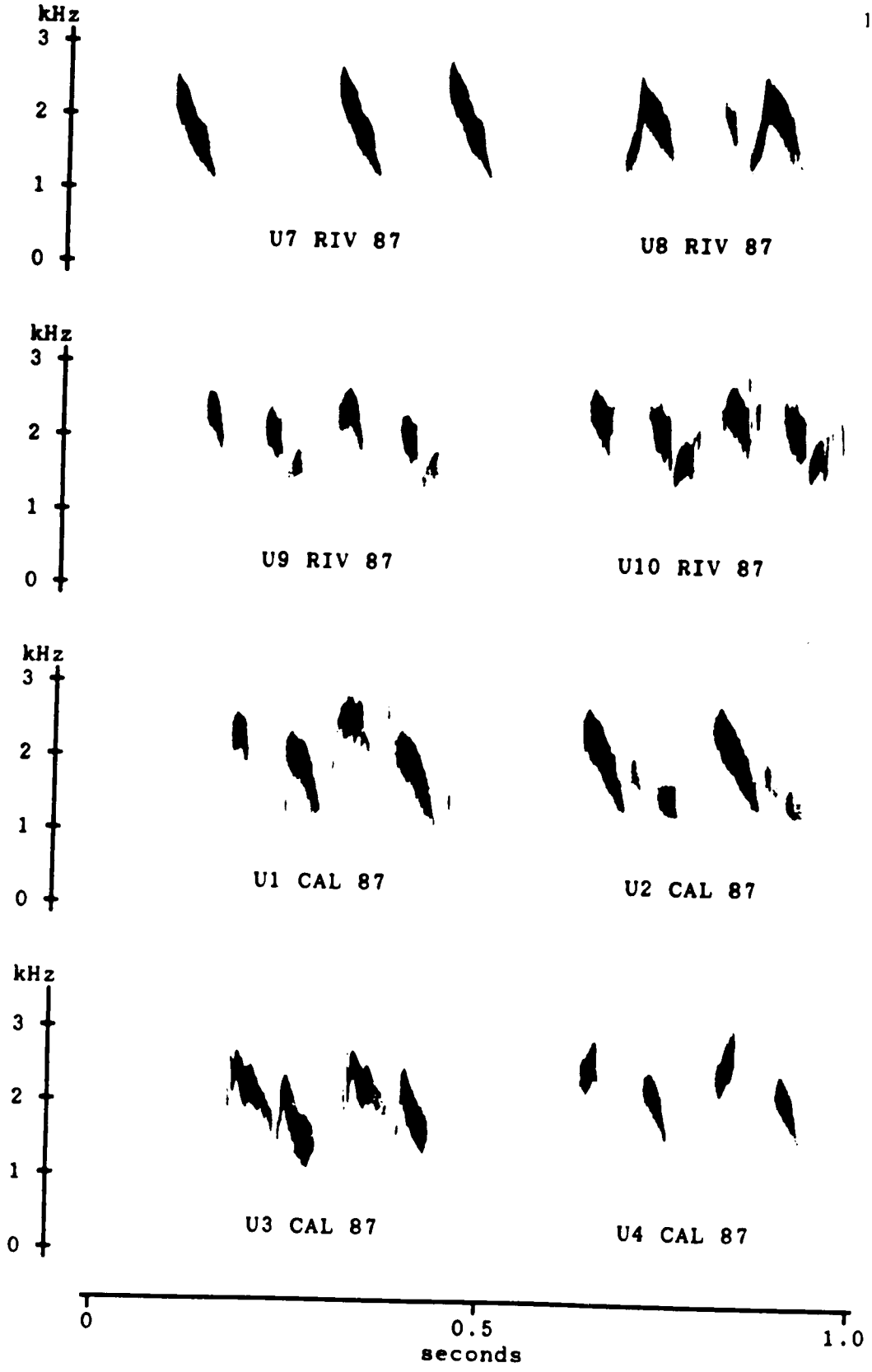

kHz
3
2
1
0
0162 INJ 89
0163 INJ 89
kHz
3
2
1
0
U1 RNJ 89
U2 RNJ 89
kHz
3
2
1
0
U3 RNJ 89
0057 ROM 88
kHz
3
2
1
0
0058 ROM 88
0059 ROM 88
0
0.5
1.0
seconds

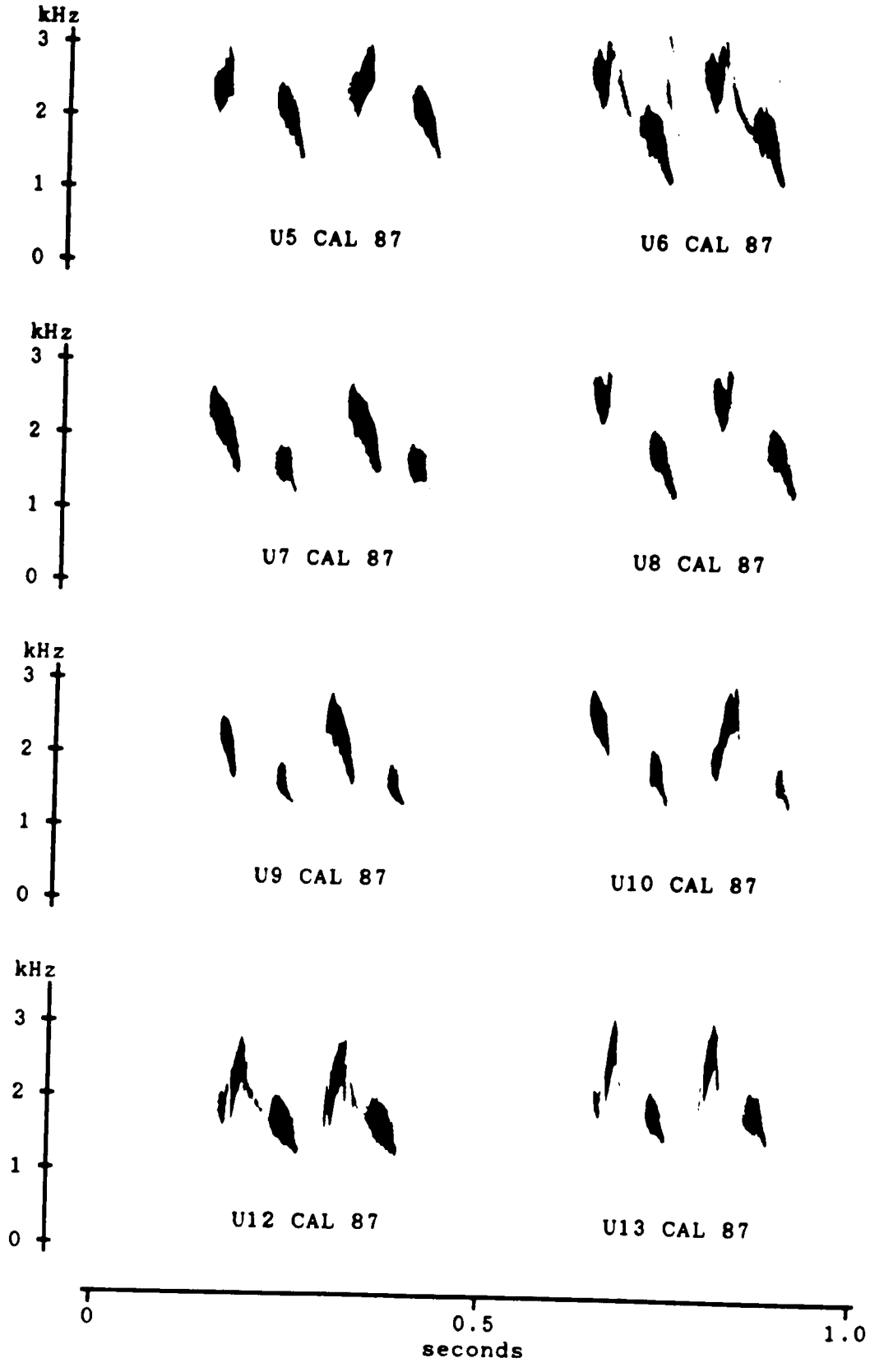

kHz
3
2
1
0
U1 ROM 88
0156 ROM 89
kHz
3
2
1
0
0157 ROM 89
0158 ROM 89
kHz
3
2
1
0
0052 MIL 88
0053 MIL 88
kHz
3
2
1
0
0054 MIL 88
0055 MIL 88
0
0.5
1.0
seconds

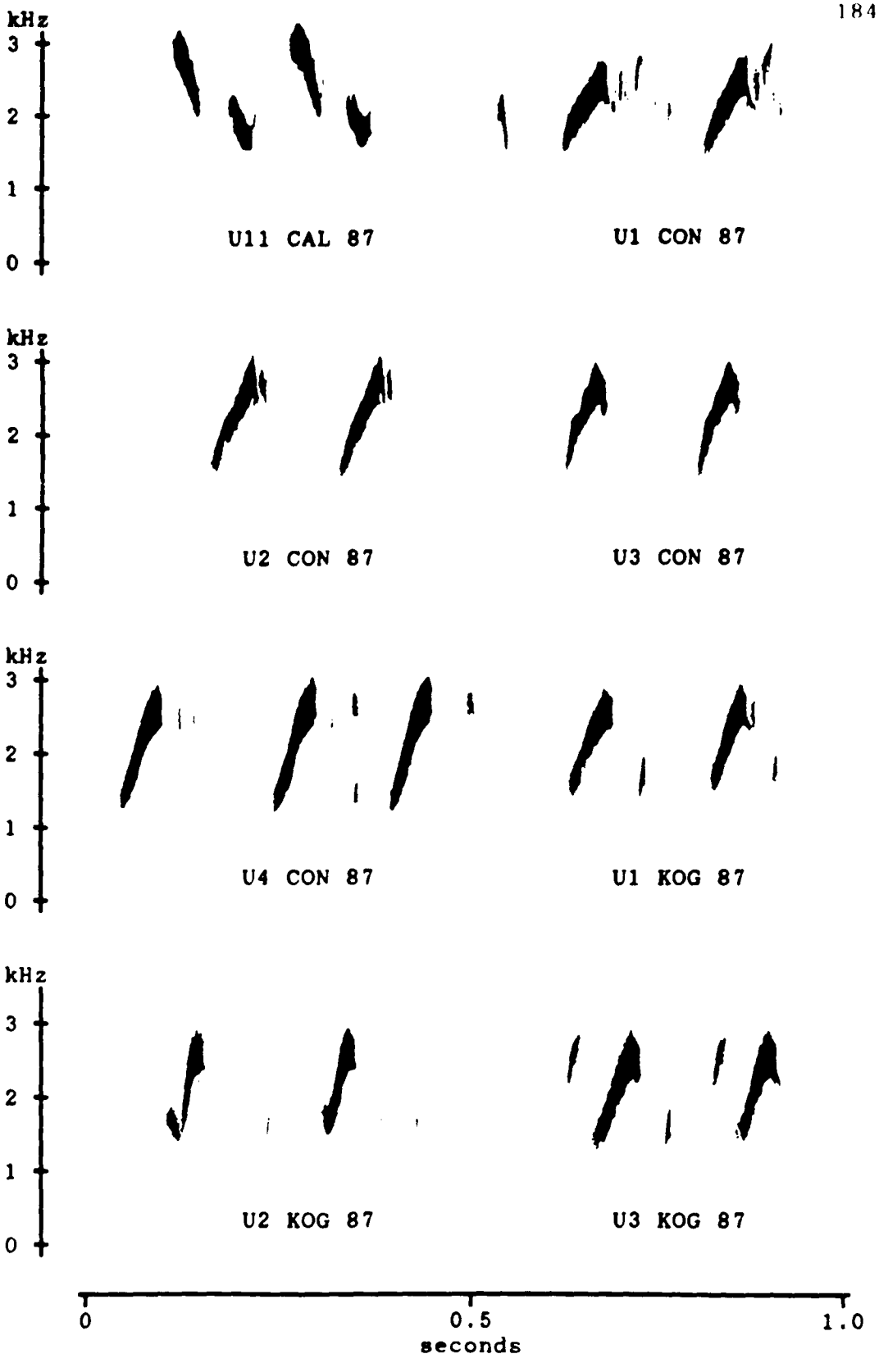

kHz
3
2
1
0
0056 MIL 88
U1 MIL 88
kHz
3
2
1
0
0164 MIL 89
0165 MIL 89
kHz
3
2
1
0
0166 MIL 89
0167 MIL 89
kHz
3
2
1
0
0168 MIL 89
0064 CHI 88
0
0.5
1.0
seconds

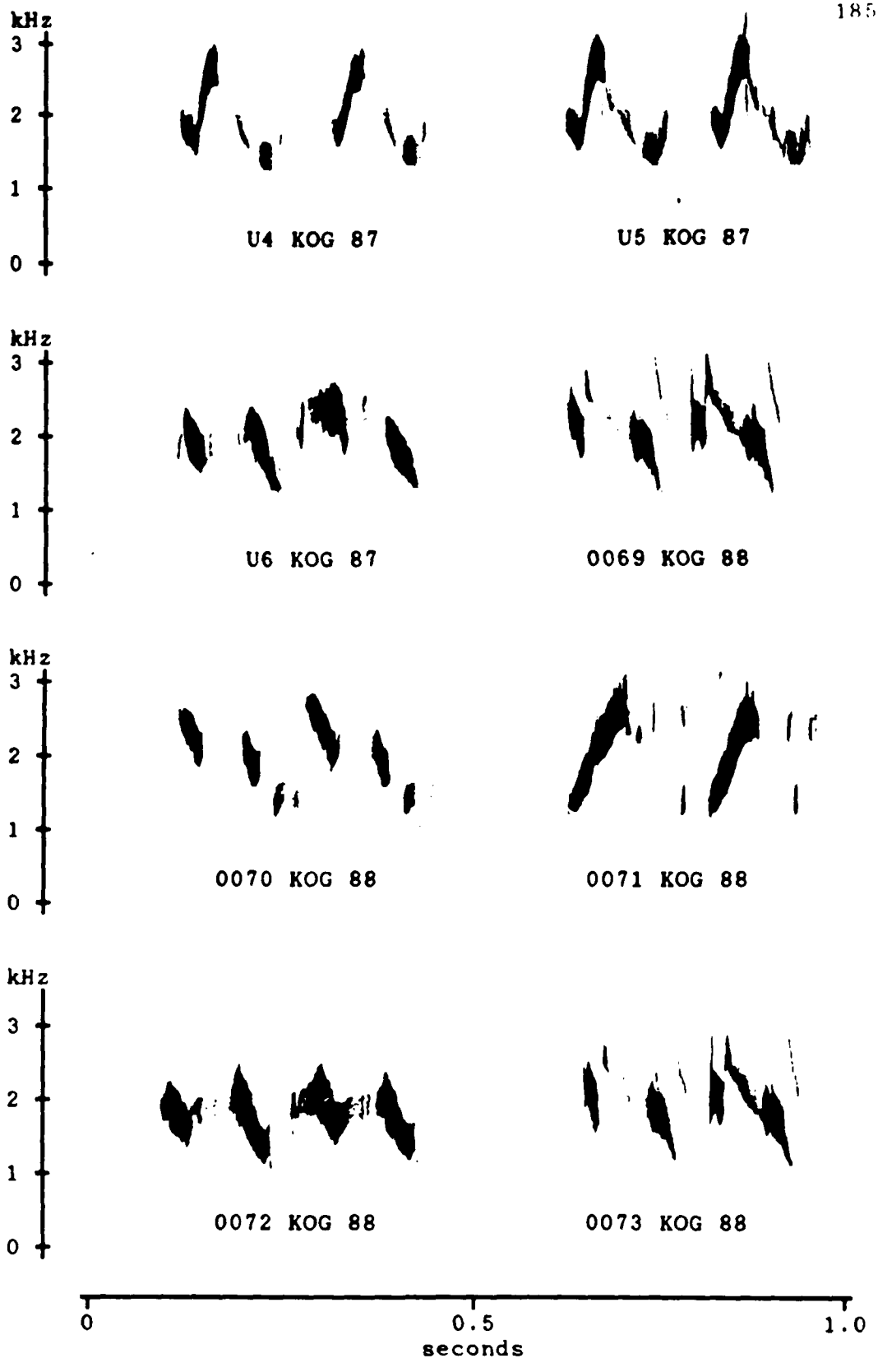

kHz
3
2
1
0
0065 CHI 88
0066 CHI 88
kHz
3
2
1
0
0068 CHI 88
U1 CHI 88
kHz
3
2
1
0
U2 CHI 88
U3 CHI 88
kHz
3
2
1
0
U4 CHI 88
U5 CHI 88
0
0.5
1.0
seconds

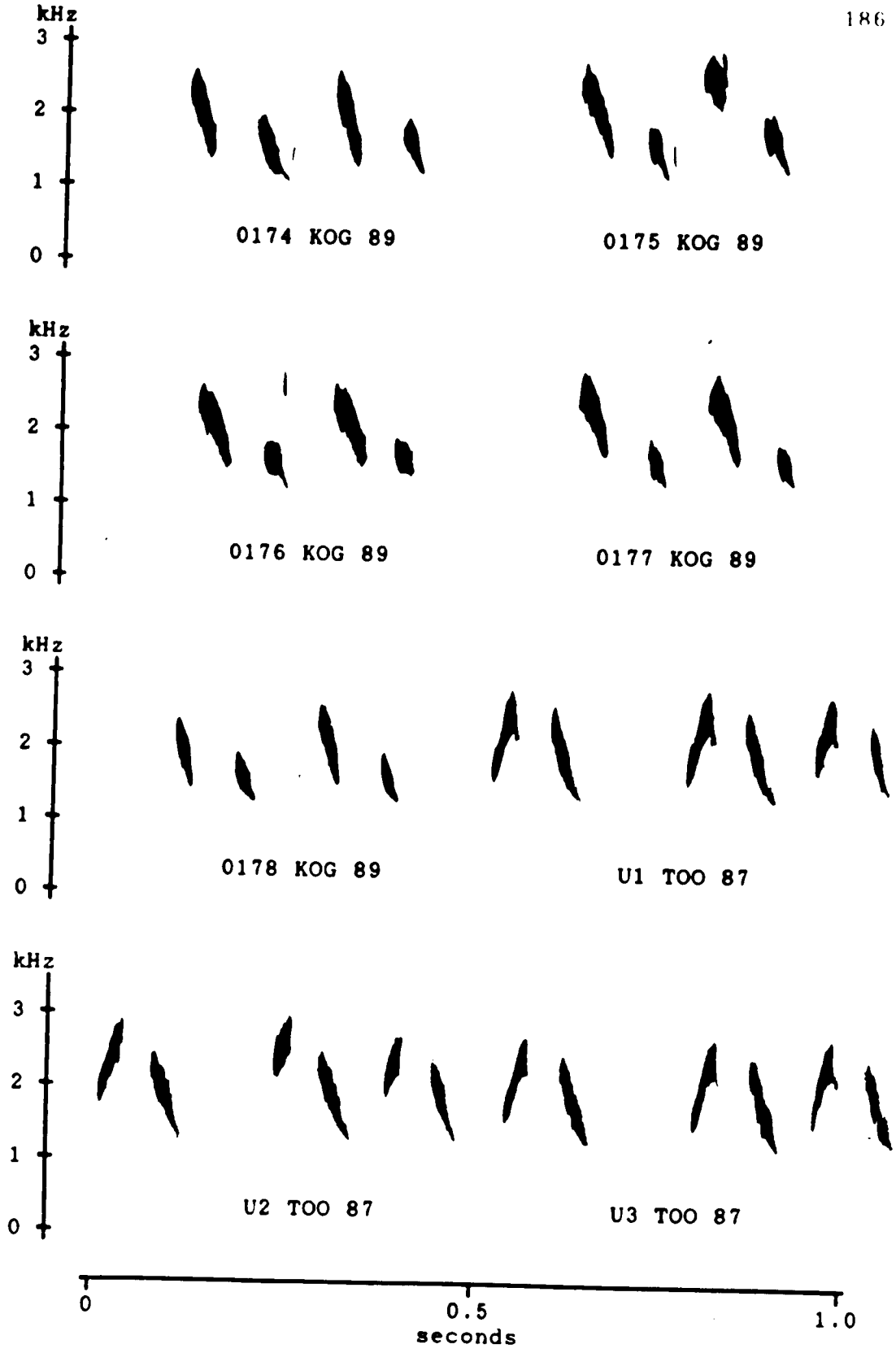

kHz
3
2
1
0
U6 CHI 88
U7 CHI 88
kHz
3
2
1
0
U1 RIV 87
U2 RIV 87
kHz
3
2
1
0
U3 RIV 87
U4 RIV 87
kHz
3
2
1
0
U5 RIV 87
U6 RIV 87
0
0.5
seconds
1.0

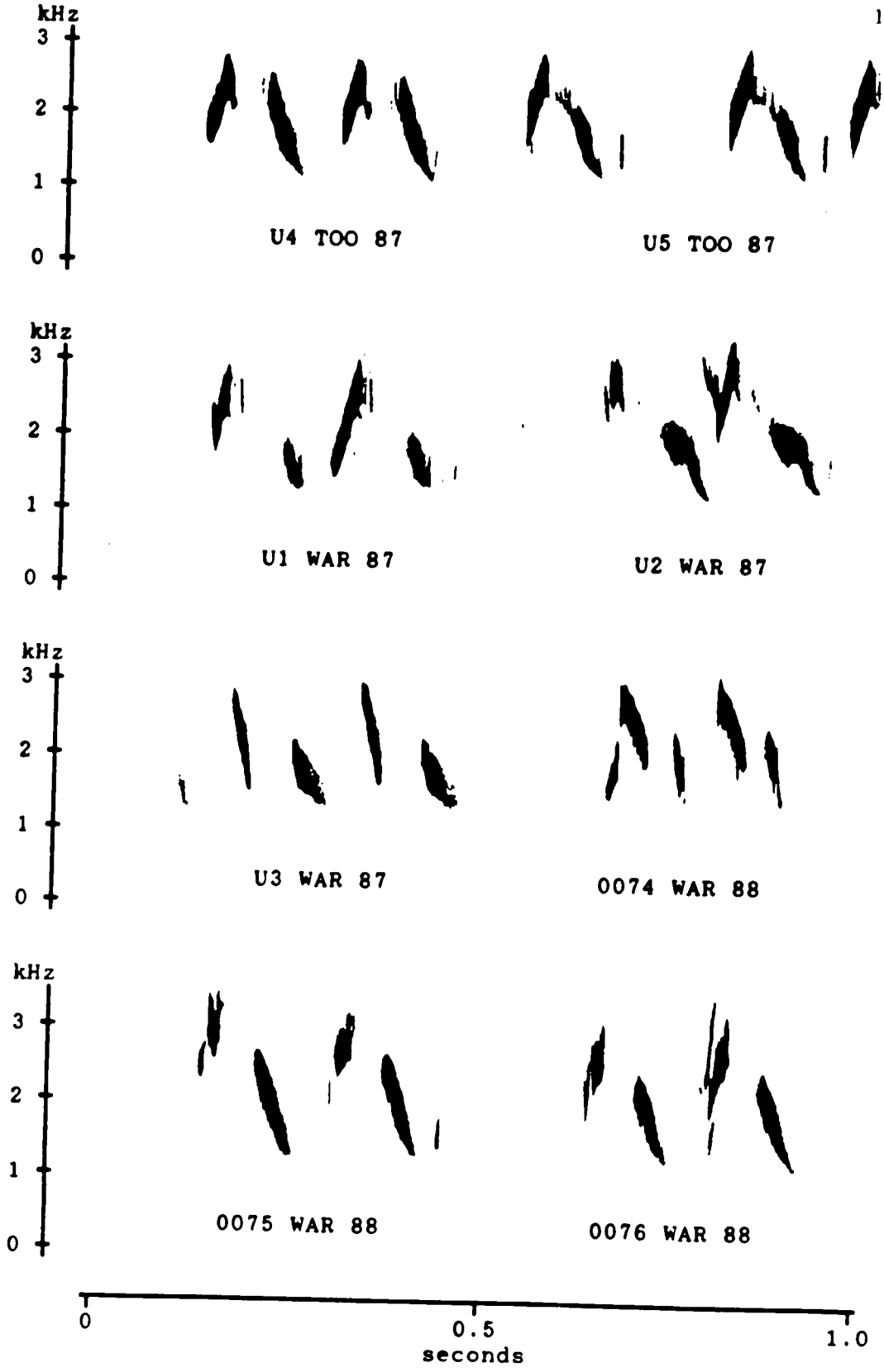

kHz
3
2
1
0
U7 RIV 87
U8 RIV 87
kHz
3
2
1
0
U9 RIV 87
U10 RIV 87
kHz
3
2
1
0
U1 CAL 87
U2 CAL 87
kHz
3
2
1
0
U3 CAL 87
U4 CAL 87
0
0.5
seconds
1.0

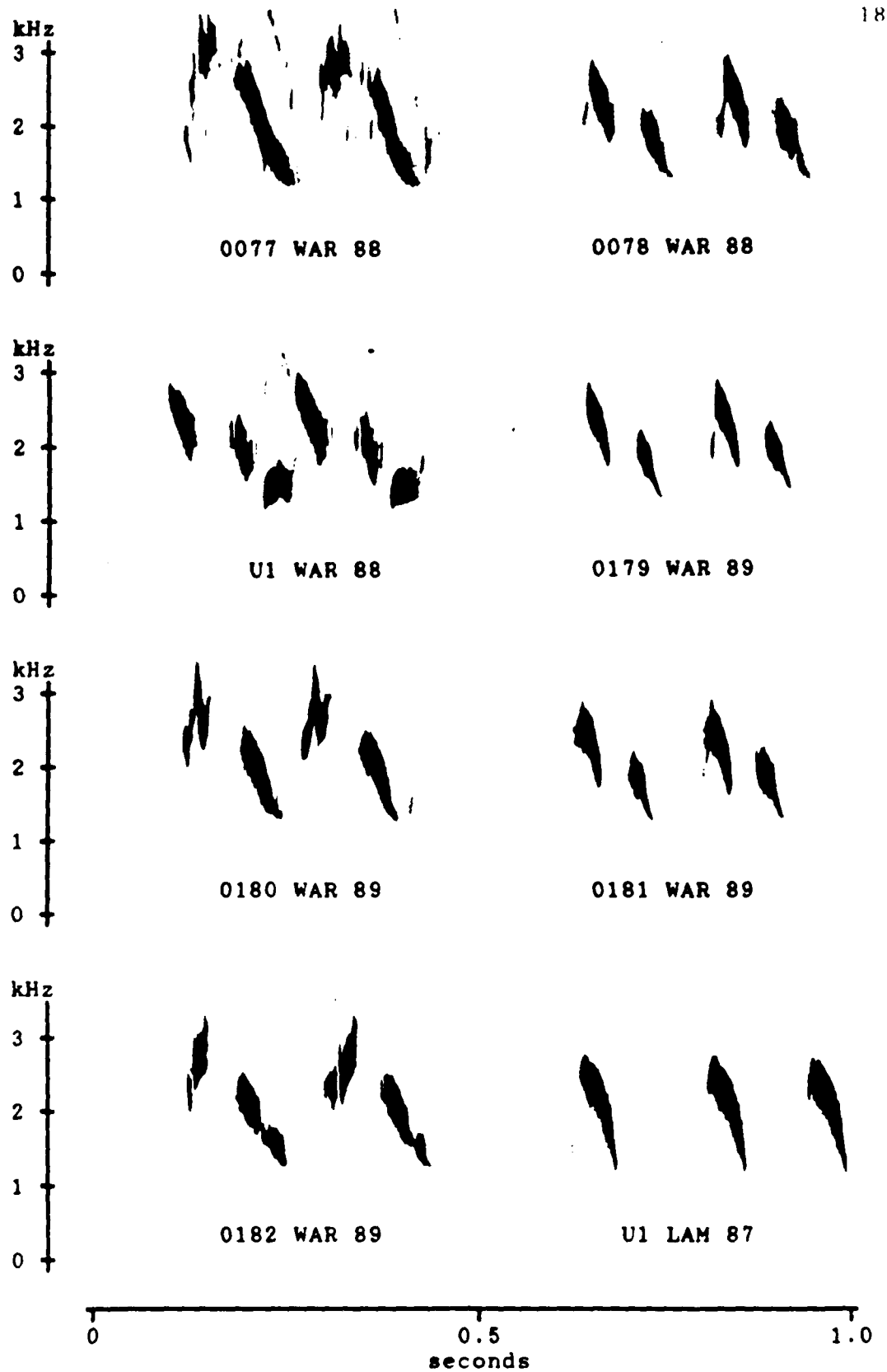

kHz
3
2
1
0
U5 CAL 87
U6 CAL 87
U7 CAL 87
U8 CAL 87
U9 CAL 87
U10 CAL 87
U12 CAL 87
U13 CAL 87
0
0.5
1.0
seconds

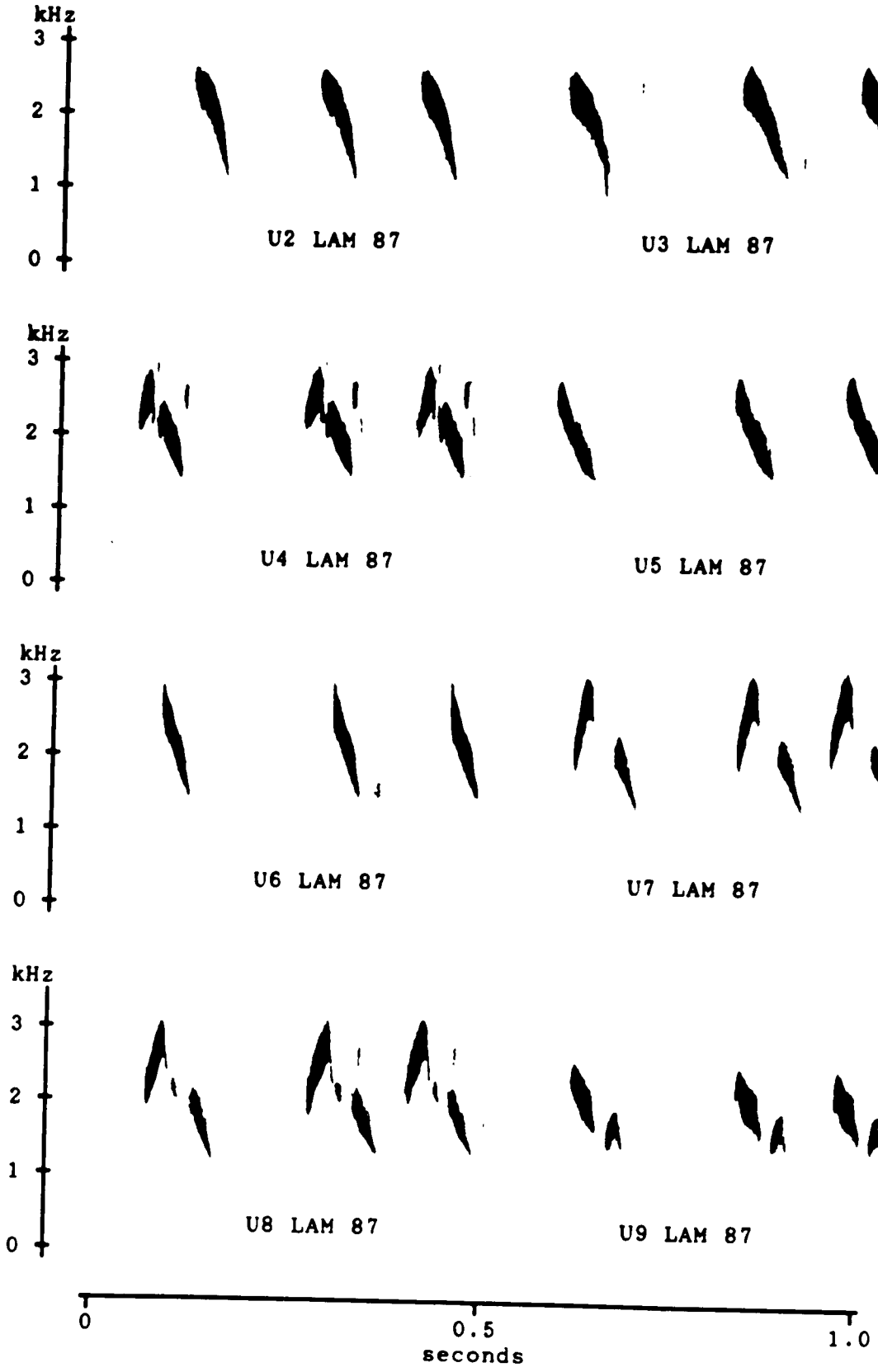

kHz
3
2
1
0
U11 CAL 87
U1 CON 87
kHz
3
2
1
0
U2 CON 87
U3 CON 87
kHz
3
2
1
0
U4 CON 87
U1 KOG 87
kHz
3
2
1
0
U2 KOG 87
U3 KOG 87
0
0.5
1.0
seconds

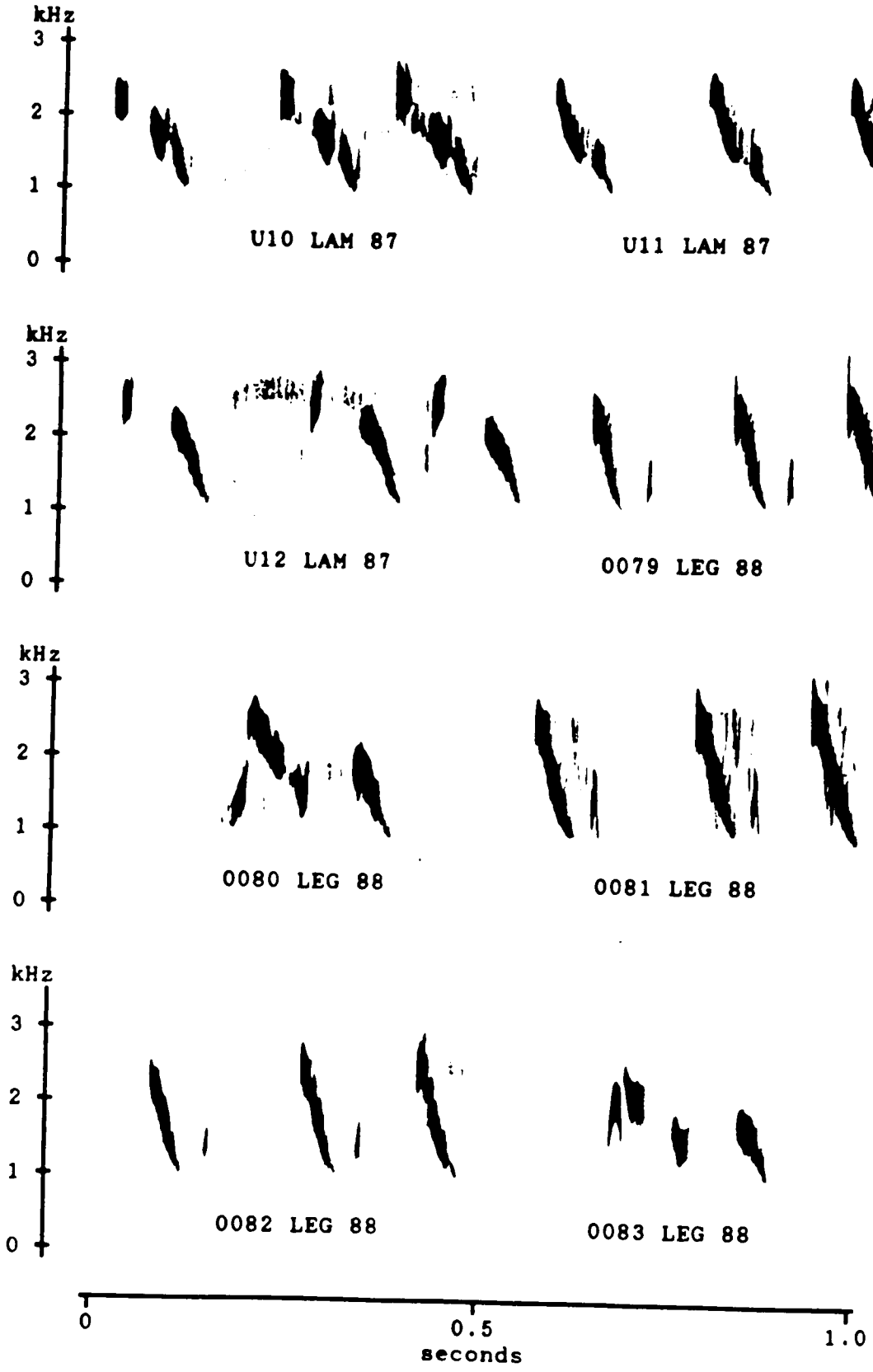

kHz
3
2
1
0
U4 KOG 87
U5 KOG 87
U6 KOG 87
0069 KOG 88
0070 KOG 88
0071 KOG 88
0072 KOG 88
0073 KOG 88
0
0.5
1.0
seconds

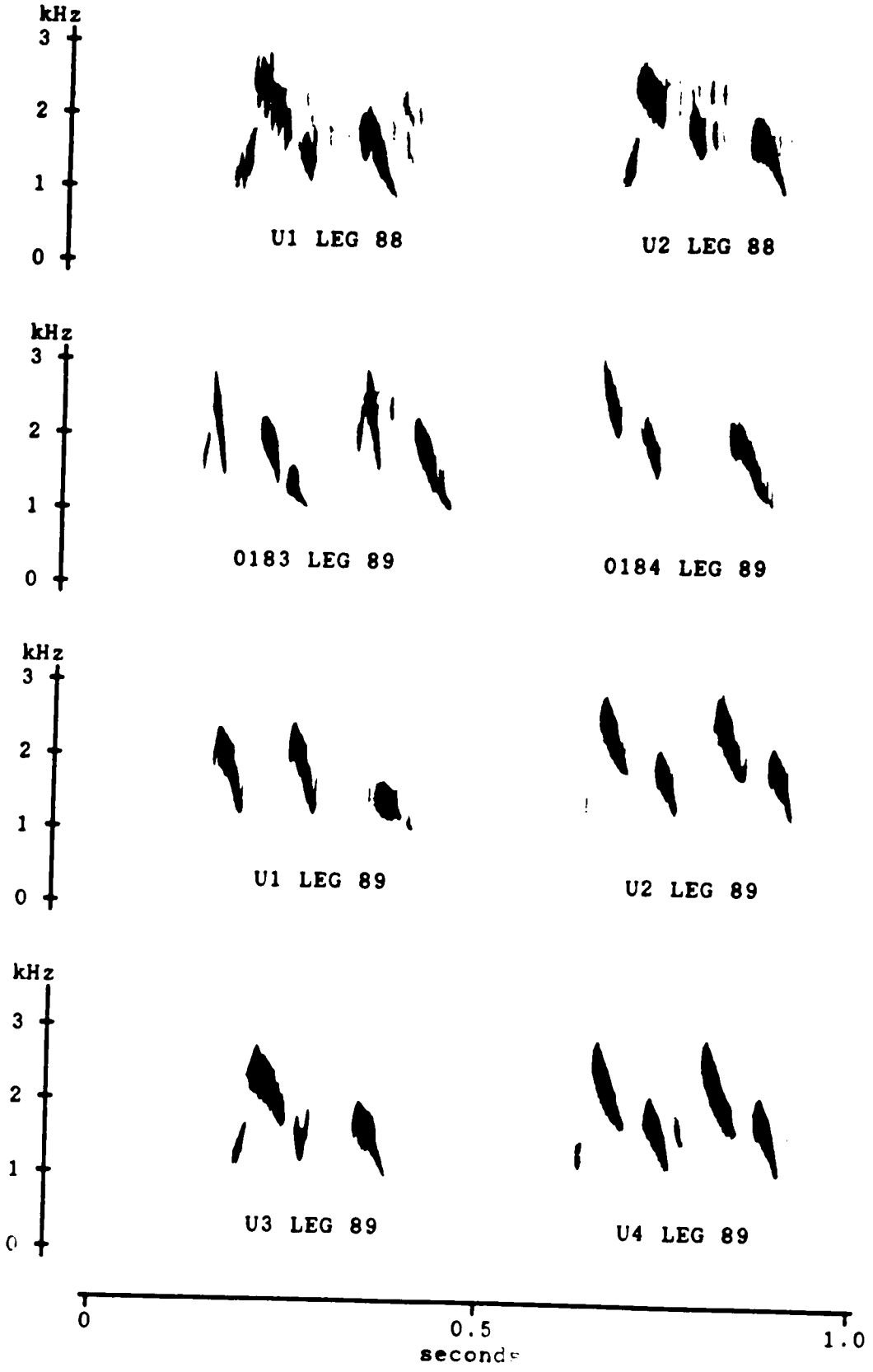

kHz
3
2
1
0
0174 KOG 89
0175 KOG 89
kHz
3
2
1
0
0176 KOG 89
0177 KOG 89
kHz
3
2
1
0
0178 KOG 89
U1 TOO 87
kHz
3
2
1
0
U2 TOO 87
U3 TOO 87
0
0.5
seconds
1.0

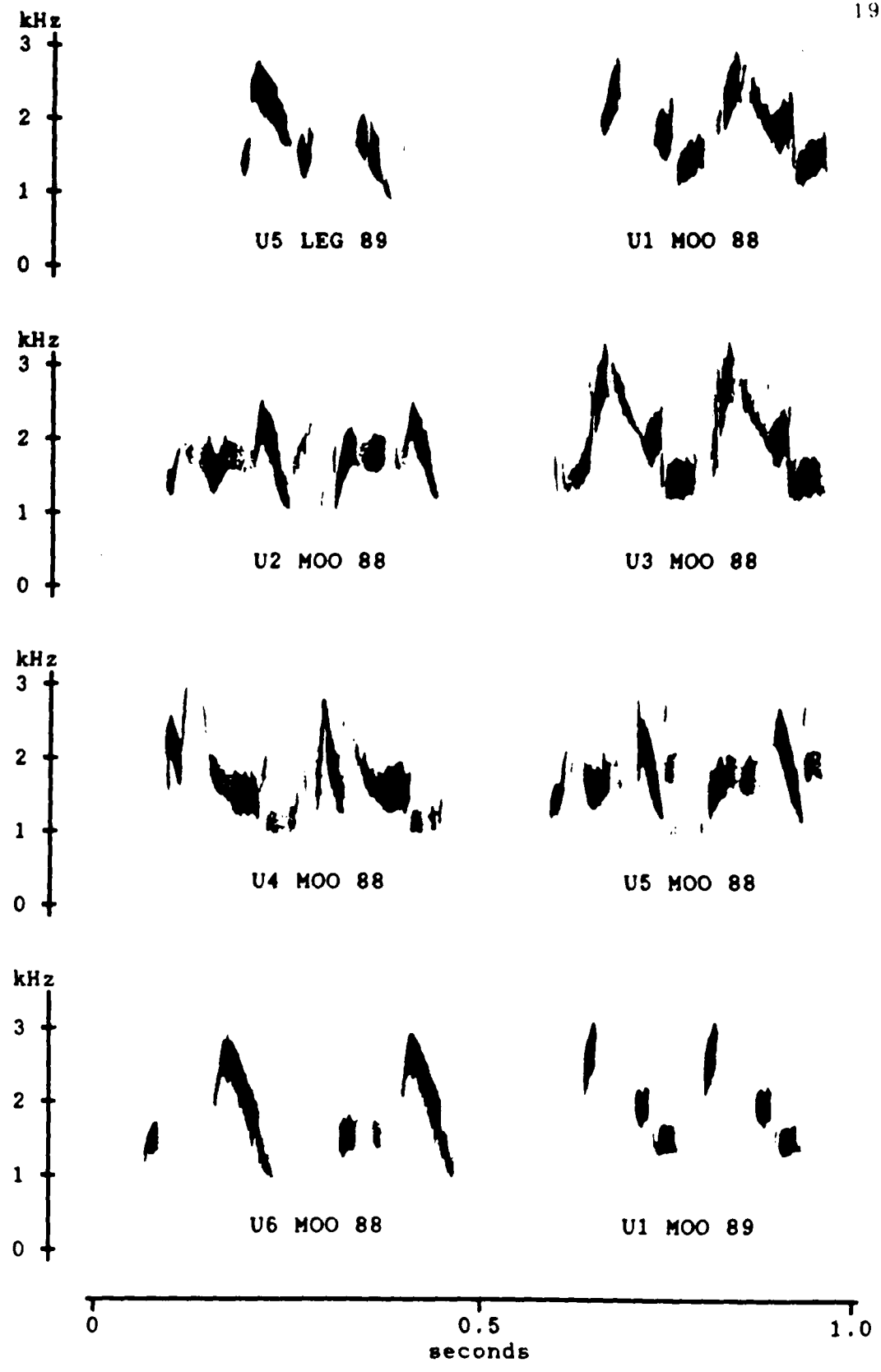

kHz
3
2
1
0
U4 TOO 87
U5 TOO 87
kHz
3
2
1
0
U1 WAR 87
U2 WAR 87
kHz
3
2
1
0
U3 WAR 87
0074 WAR 88
kHz
3
2
1
0
0075 WAR 88
0076 WAR 88
0
0.5
seconds
1.0

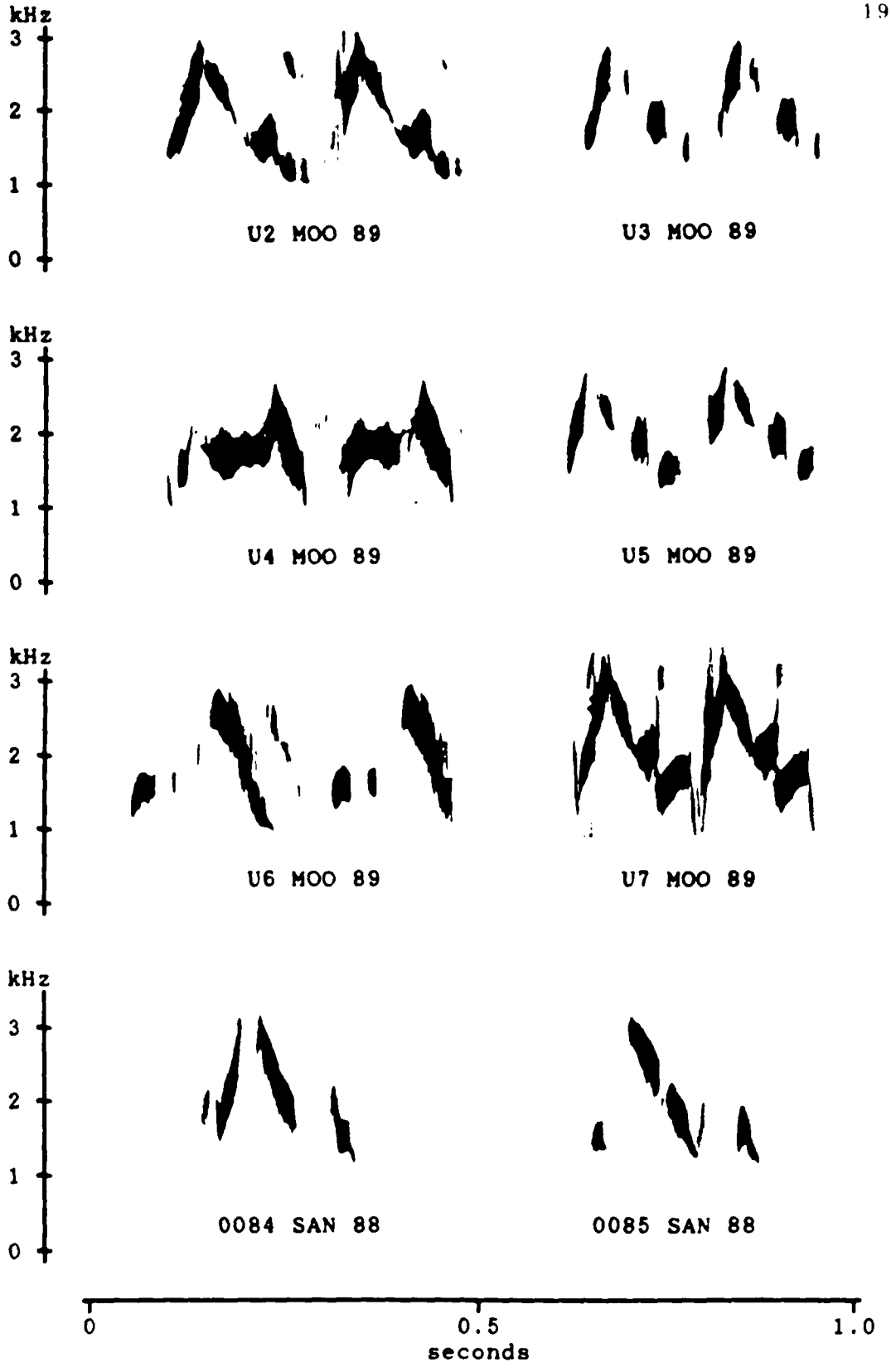

kHz
3
2
1
0
0077 WAR 88
0078 WAR 88
kHz
3
2
1
0
U1 WAR 88
0179 WAR 89
kHz
3
2
1
0
0180 WAR 89
0181 WAR 89
kHz
3
2
1
0
0182 WAR 89
U1 LAM 87
0
0.5
1.0
seconds

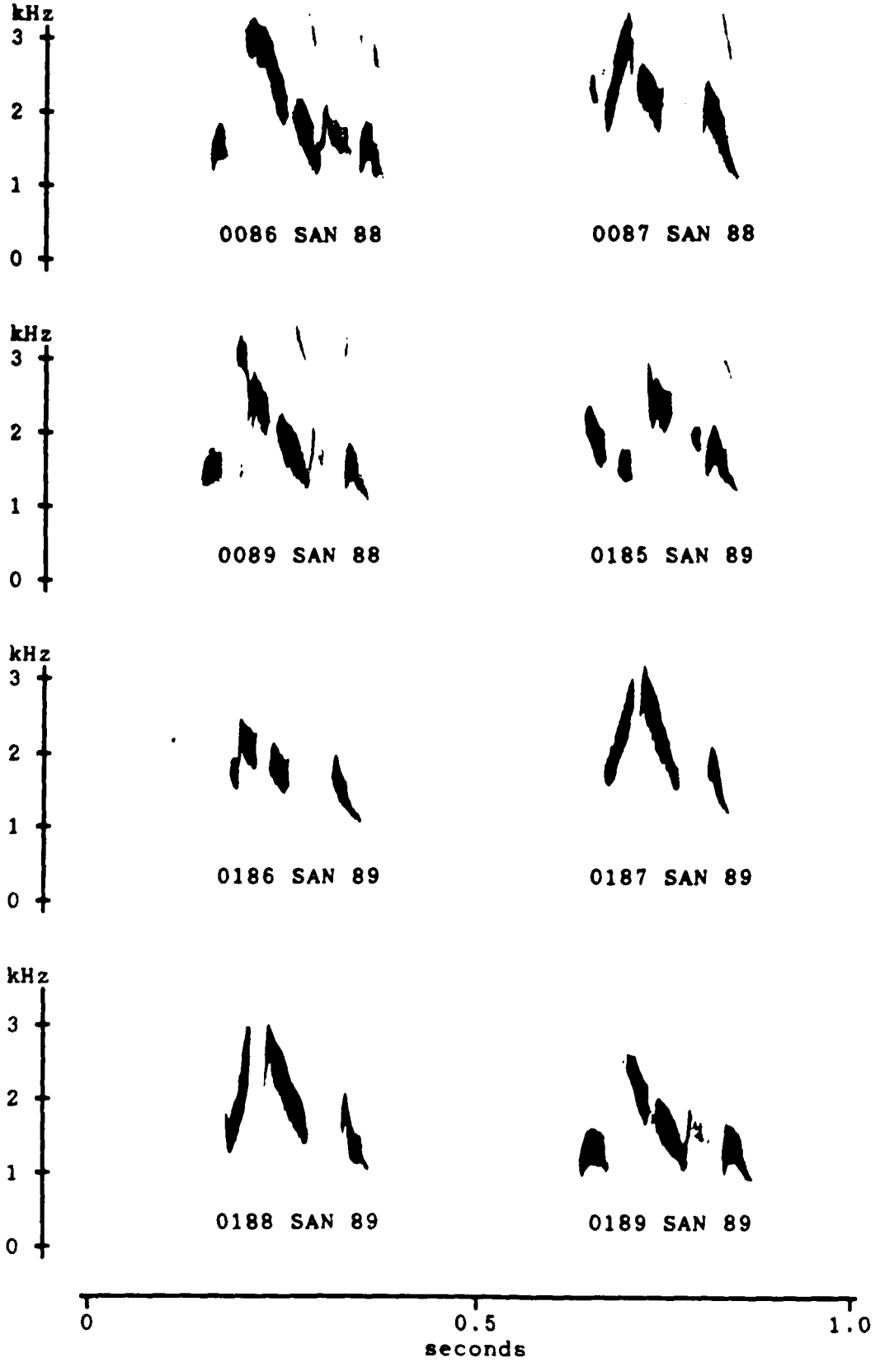

kHz
3
2
1
0
U2 LAM 87
U3 LAM 87
kHz
3
2
1
0
U4 LAM 87
U5 LAM 87
kHz
3
2
1
0
U6 LAM 87
U7 LAM 87
kHz
3
2
1
0
U8 LAM 87
U9 LAM 87
0
0.5
seconds
1.0

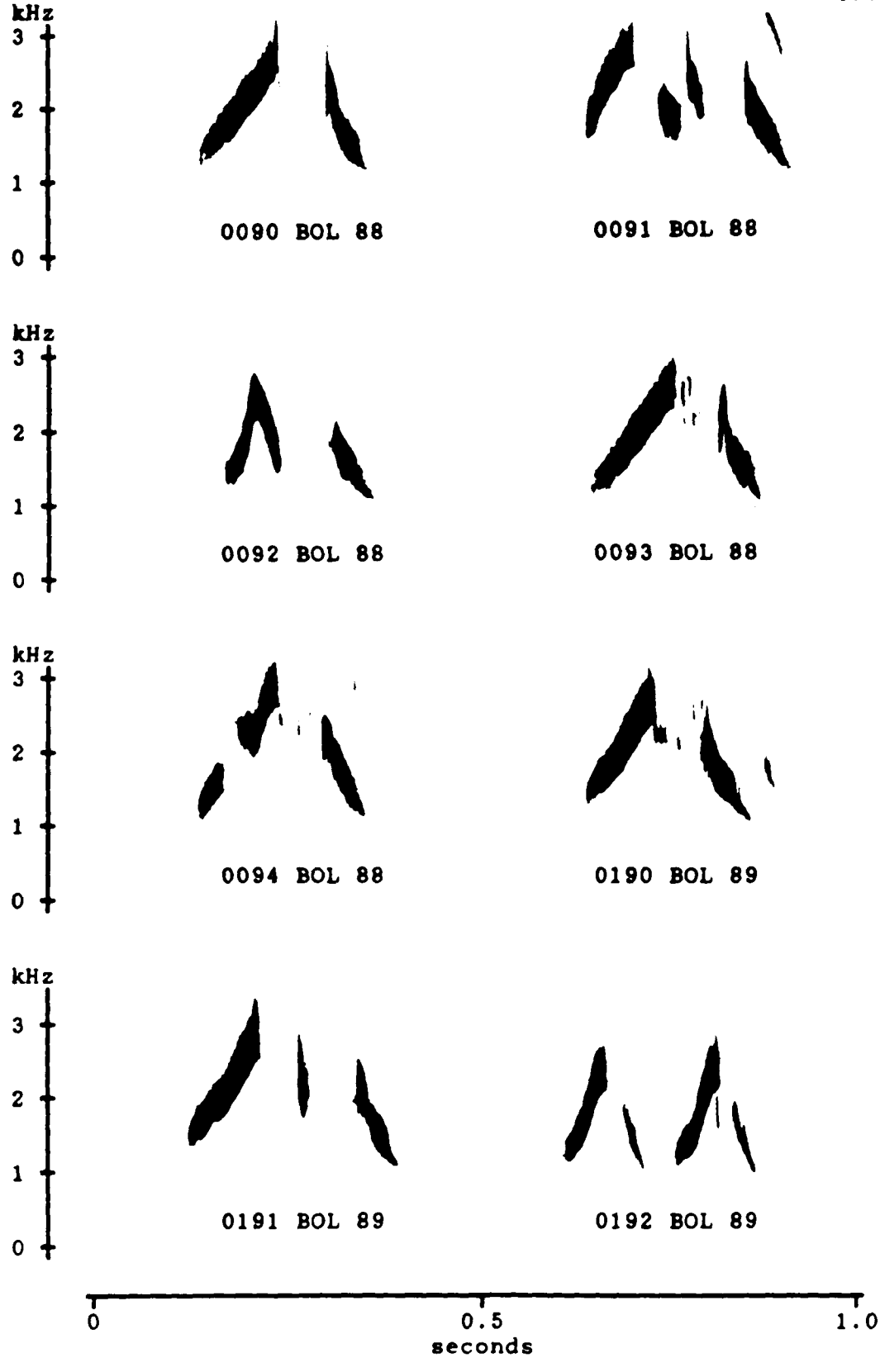

kHz
3
2
1
0
U10 LAM 87
U11 LAM 87
kHz
3
2
1
0
U12 LAM 87
0079 LEG 88
kHz
3
2
1
0
0080 LEG 88
0081 LEG 88
kHz
3
2
1
0
0082 LEG 88
0083 LEG 88
0
0.5
1.0
seconds

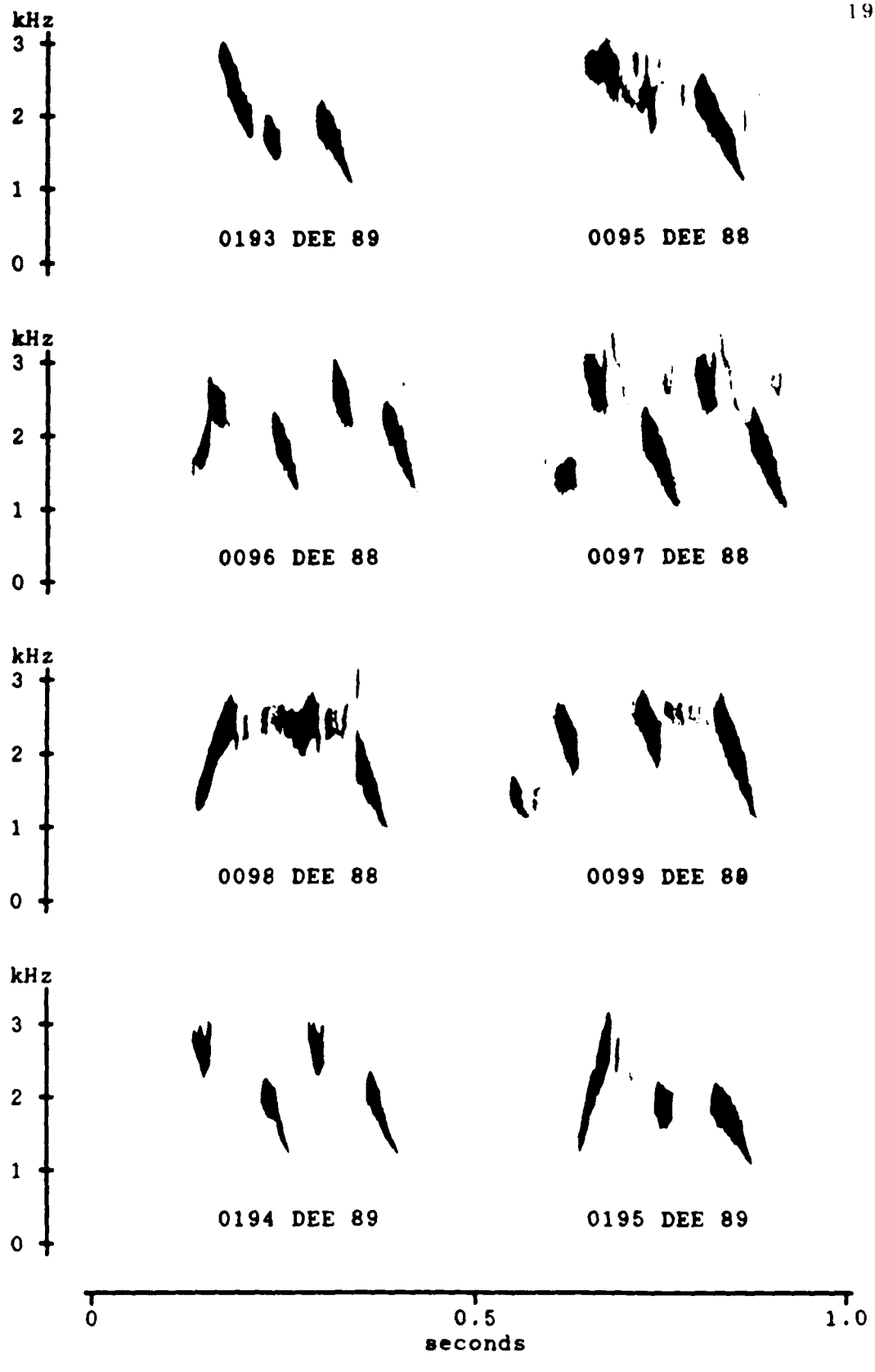

kHz
3
2
1
0
U1 LEG 88
U2 LEG 88
kHz
3
2
1
0
0183 LEG 89
0184 LEG 89
kHz
3
2
1
0
U1 LEG 89
U2 LEG 89
kHz
3
2
1
0
U3 LEG 89
U4 LEG 89
0
0.5
seconds
1.0

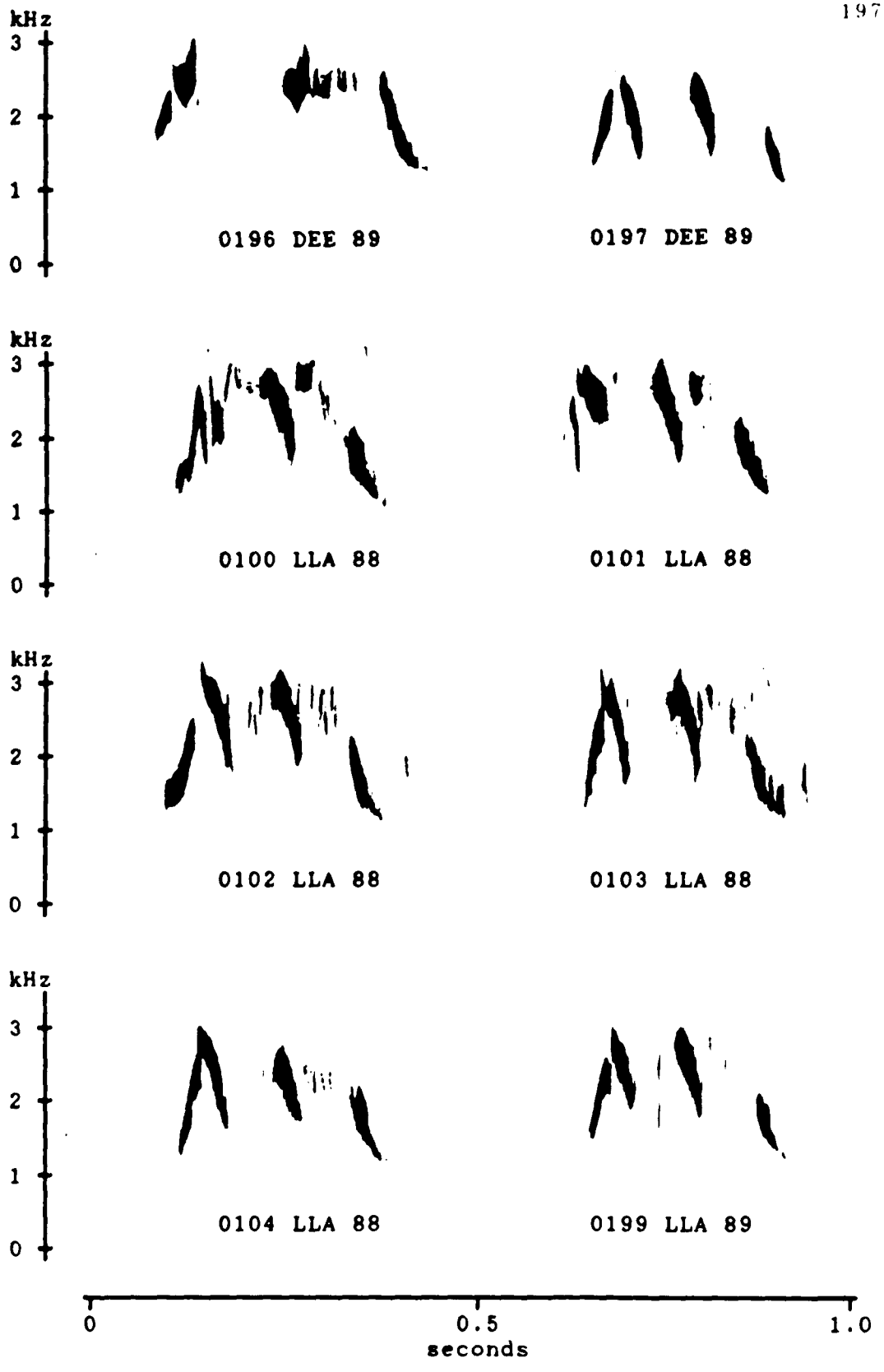

kHz
3
2
1
0
U5 LEG 89
U1 MOO 88
kHz
3
2
1
0
U2 MOO 88
U3 MOO 88
kHz
3
2
1
0
U4 MOO 88
U5 MOO 88
kHz
3
2
1
0
U6 MOO 88
U1 MOO 89
0
0.5
1.0
seconds

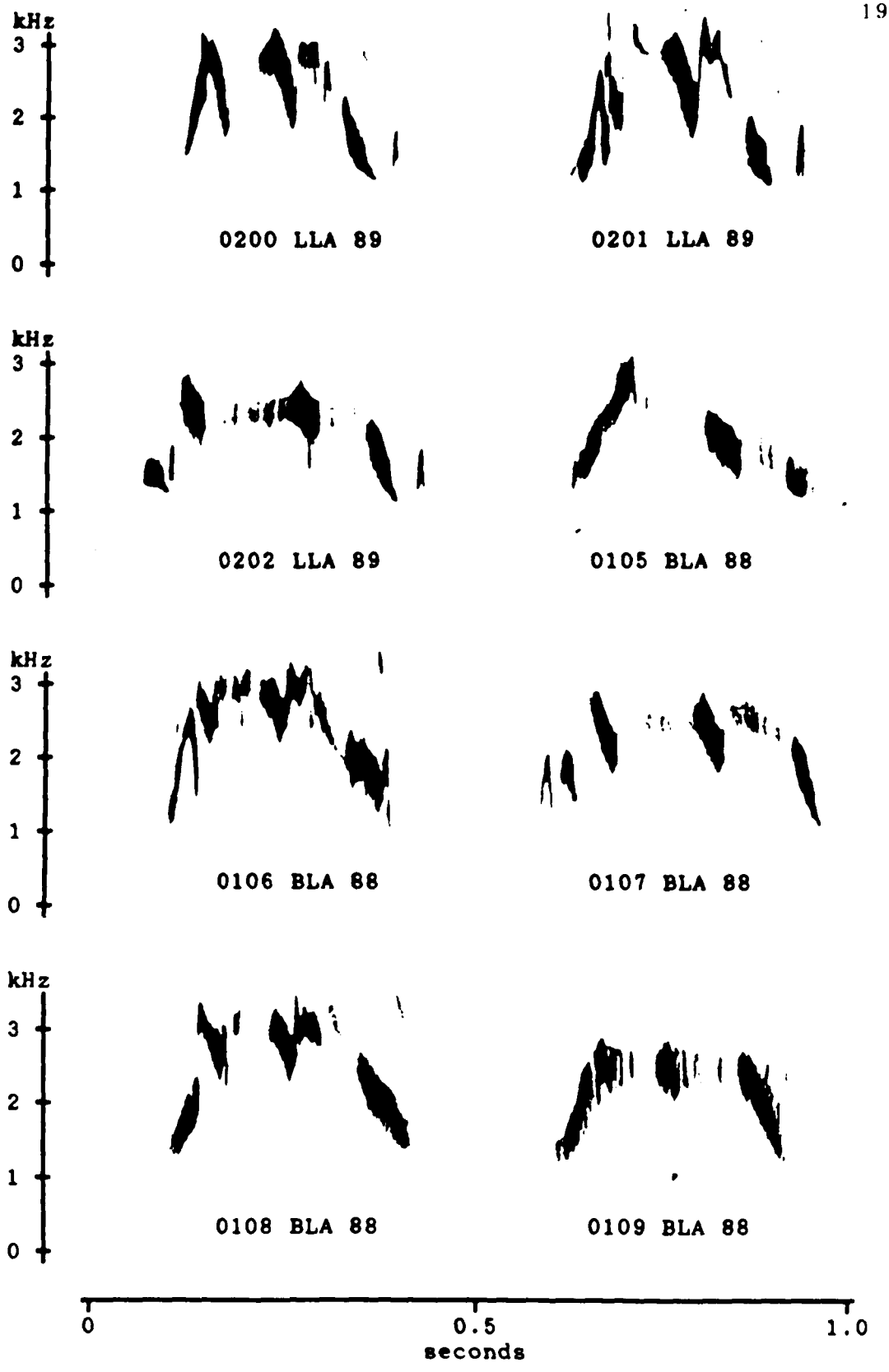

kHz
3
2
1
0
U2 MOO 89
U3 MOO 89
U4 MOO 89
U5 MOO 89
U6 MOO 89
U7 MOO 89
0084 SAN 88
0085 SAN 88
0
0.5
1.0
seconds

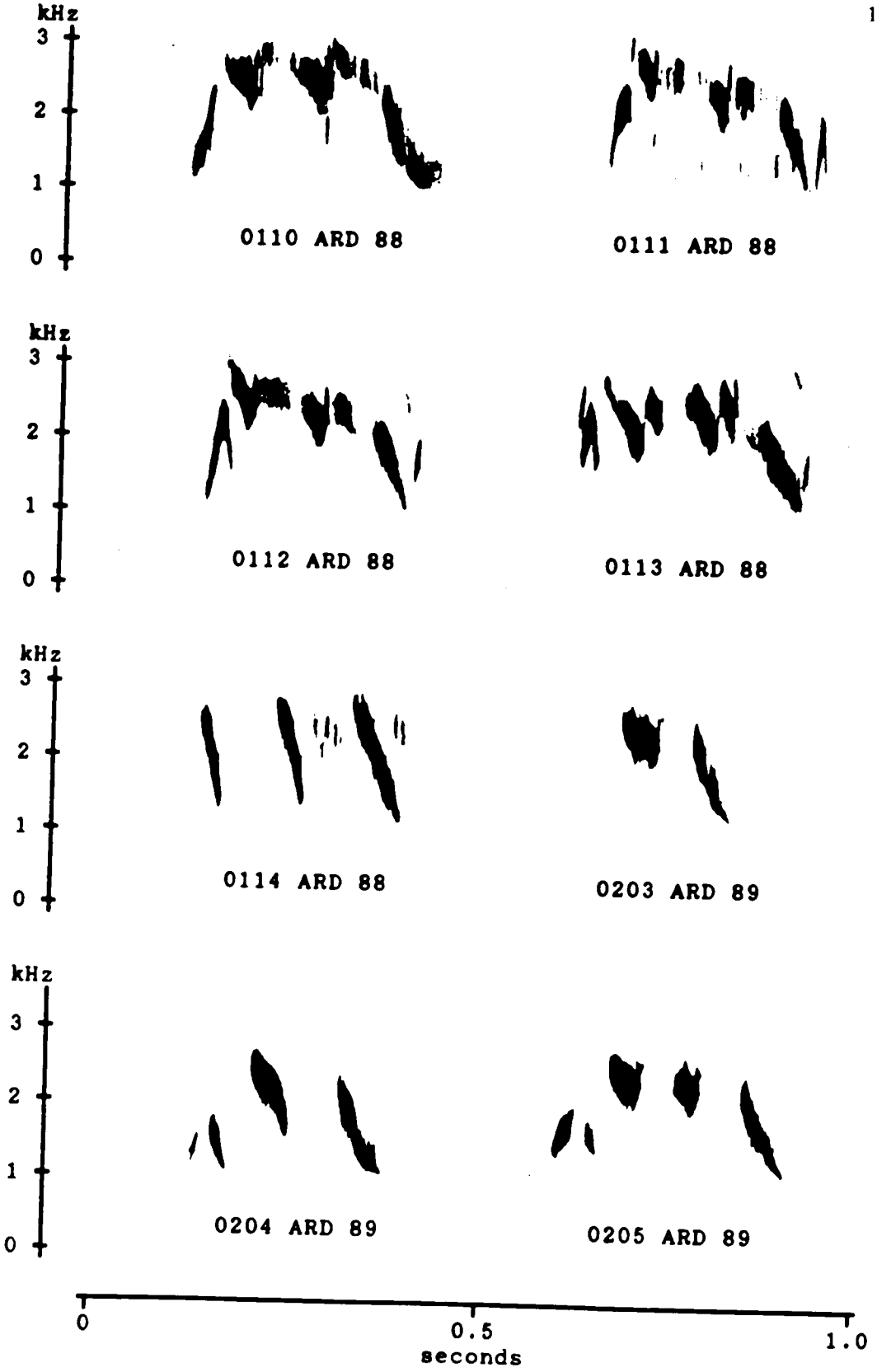

kHz
3
2
1
0
0086 SAN 88
0087 SAN 88
kHz
3
2
1
0
0089 SAN 88
0185 SAN 89
kHz
3
2
1
0
0186 SAN 89
0187 SAN 89
kHz
3
2
1
0
0188 SAN 89
0189 SAN 89
0
0.5
1.0
seconds

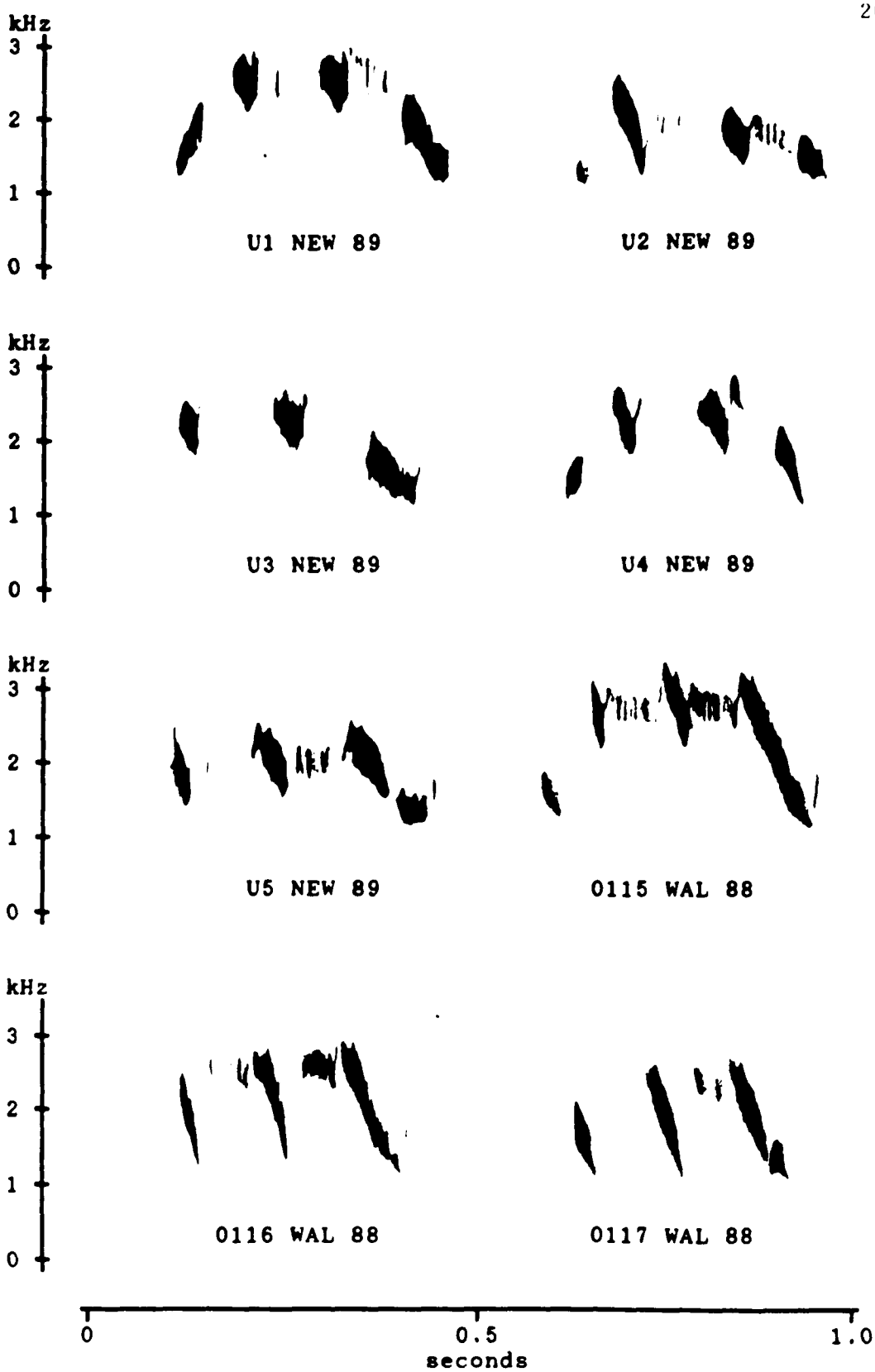

kHz
3
2
1
0
0090 BOL 88
0091 BOL 88
kHz
3
2
1
0
0092 BOL 88
0093 BOL 88
kHz
3
2
1
0
0094 BOL 88
0190 BOL 89
kHz
3
2
1
0
0191 BOL 89
0192 BOL 89
0
0.5
1.0
seconds

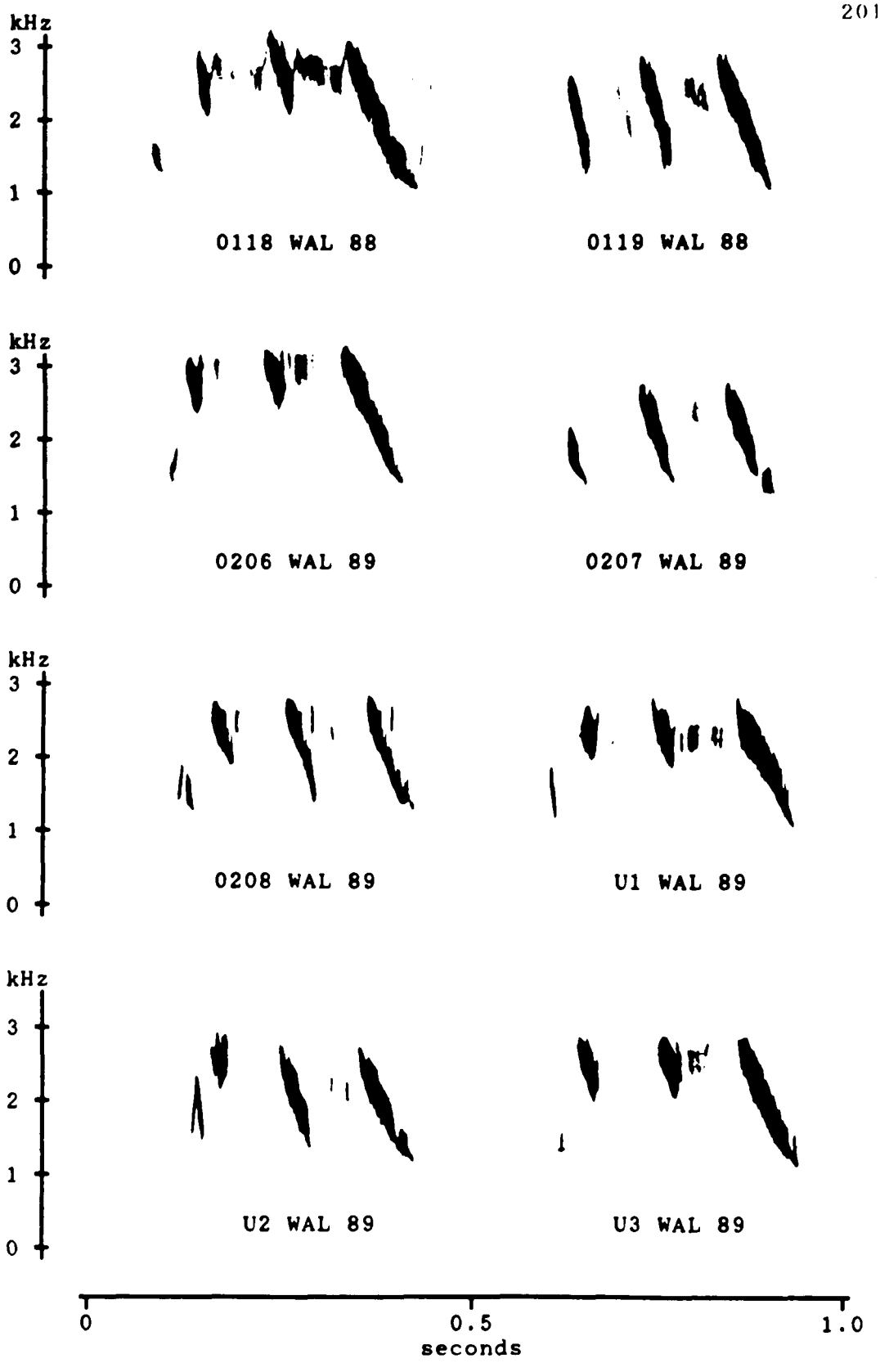

kHz
3
2
1
0
0193 DEE 89
0095 DEE 88
kHz
3
2
1
0
0096 DEE 88
0097 DEE 88
kHz
3
2
1
0
0098 DEE 88
0099 DEE 88
kHz
3
2
1
0
0194 DEE 89
0195 DEE 89
0
0.5
1.0
seconds

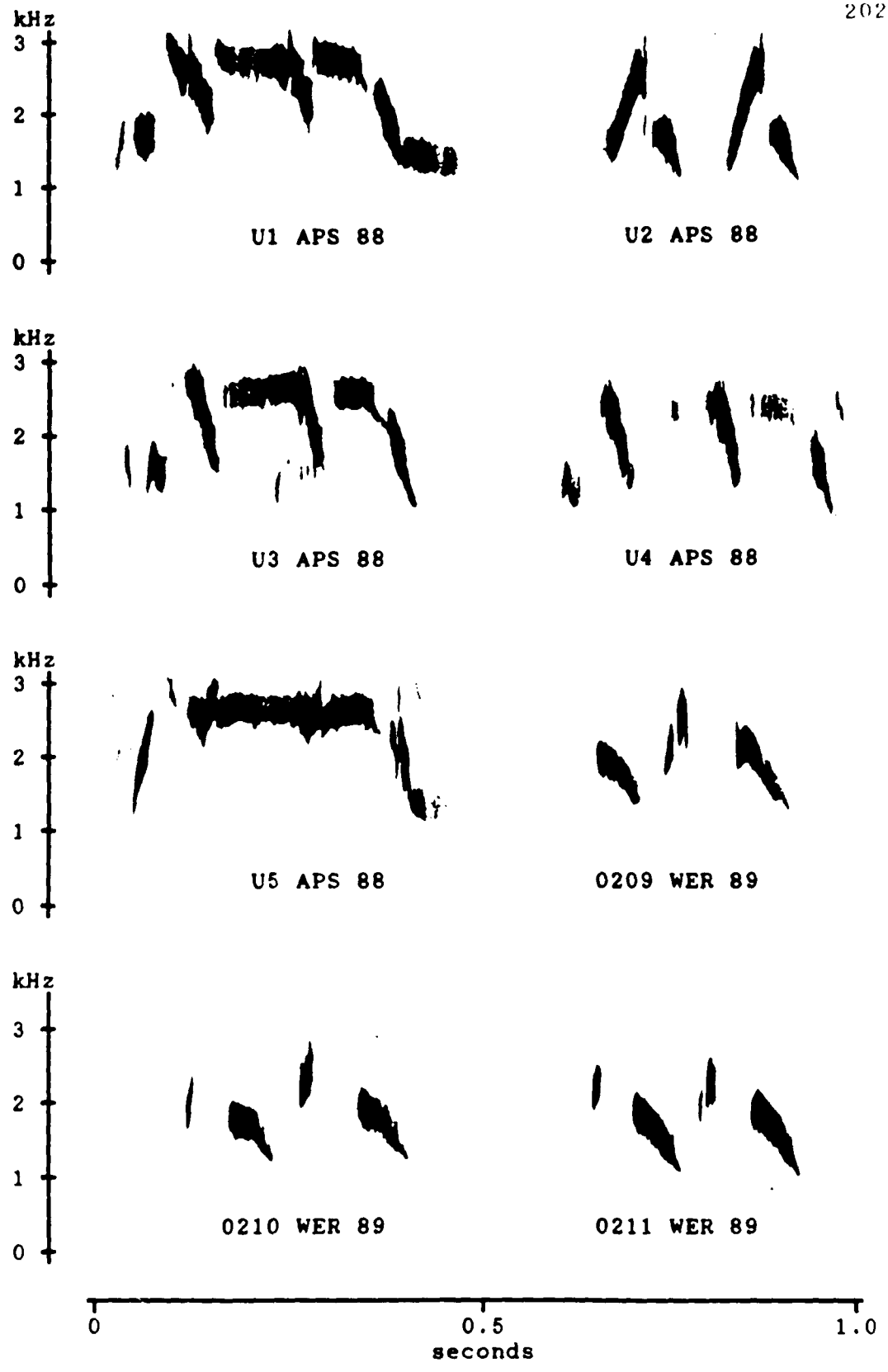

kHz
3
2
1
0
0196 DEE 89
0197 DEE 89
kHz
3
2
1
0
0100 LLA 88
0101 LLA 88
kHz
3
2
1
0
0102 LLA 88
0103 LLA 88
kHz
3
2
1
0
0104 LLA 88
0199 LLA 89
0
0.5
1.0
seconds

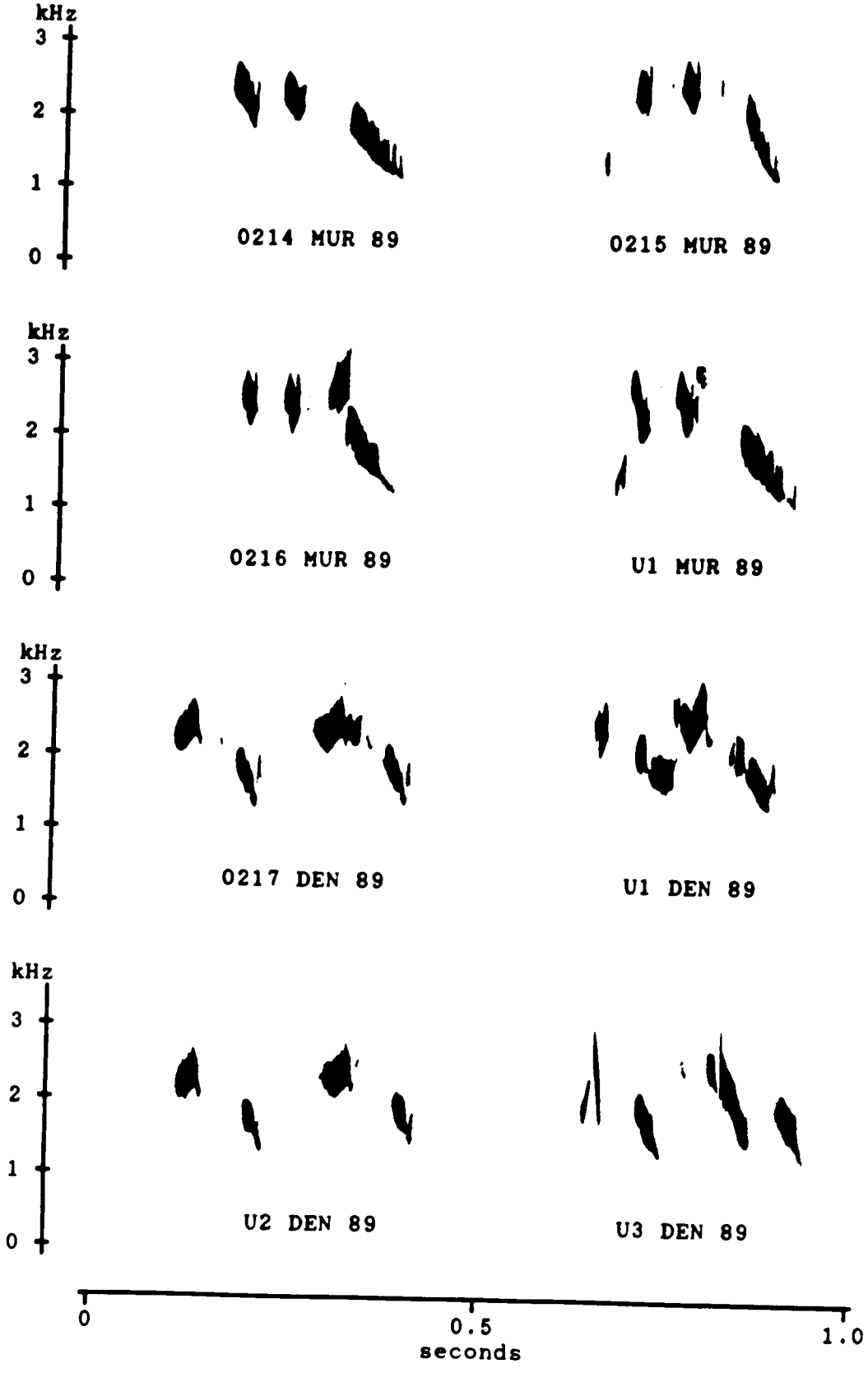

kHz
3
2
1
0
0200 LLA 89
0201 LLA 89
0202 LLA 89
0105 BLA 88
0106 BLA 88
0107 BLA 88
0108 BLA 88
0109 BLA 88
0
0.5
1.0
seconds


kHz
3
2
1
0
0110 ARD 88
0111 ARD 88
kHz
3
2
1
0
0112 ARD 88
0113 ARD 88
kHz
3
2
1
0
0114 ARD 88
0203 ARD 89
kHz
3
2
1
0
0204 ARD 89
0205 ARD 89
0
0.5
seconds
1.0


kHz
3
2
1
0
U1 NEW 89
U2 NEW 89
U3 NEW 89
U4 NEW 89
U5 NEW 89
0115 WAL 88
0116 WAL 88
0117 WAL 88
0
0.5
1.0
seconds


kHz
3
2
1
0
0118 WAL 88
0119 WAL 88
0206 WAL 89
0207 WAL 89
0208 WAL 89
U1 WAL 89
U2 WAL 89
U3 WAL 89
0
0.5
1.0
seconds


kHz
3
2
1
0
U1 APS 88
U2 APS 88
kHz
3
2
1
0
U3 APS 88
U4 APS 88
kHz
3
2
1
0
U5 APS 88
0209 WER 89
kHz
3
2
1
0
0210 WER 89
0211 WER 89
0
0.5
1.0
seconds


kHz
3
2
1
0
0214 MUR 89
0215 MUR 89
0216 MUR 89
U1 MUR 89
0217 DEN 89
U1 DEN 89
U2 DEN 89
U3 DEN 89
0
0.5
1.0
seconds

APPENDIX VI

Of about 500 specimens of Pardalotus striatus which I examined from museum collections, 183 specimens fit the criteria of this study. These were adult males of the races ornatus, substriatus, and melanocephalus, collected during the breeding season (as determined by plumages and dates on the specimen tags). Data gathered from those specimens are presented in this appendix on pages 205-208. Columns correspond to museum abbreviation, specimen number, collection date, locality, weight (g), wing length, tail length, tarsus length, culmen length, midcrown streaking, hindcrown streaking, color of wingspot, and number of primaries (excluding outer primary) edged in white, body length, and wingspan. All measurements are in mm. The museums listed are the Australian National Wildlife Collection (ANWC), Australian Museum (AM), South Australia Museum (SAM), National Museum of Victoria (NMV), Western Australia Museum (WAM), Queensland Museum (QM), and American Museum of Natural History (AMNH). In addition, descriptive statistics for morphological measurements were calculated for samples from the following 8 localities, where n>2: Bendigo, Heywood, Mildura, and Ouyen, VICT; Big Heath Conservation Park and Mt. Crawford, SA; Murrumbidgee, NSW; and the Southern Tablelands, ACT. Those statistics are given on pages 209-210.

ANWC	38576	311084	TABL	NSW	12.0	66	35	18.2	8.0	1	1	O	1			
ANWC	39900	200785	CHAR	QLD	11.3	61	30	17.5	7.2	0	0	SC	6			
ANWC	39620	080785	MARE	QLD	10.0	60	31	17.6	7.5	0	0	SC	7			
ANWC	39637	080785	MARE	QLD	9.6	60	32	16.3	6.5	0	0	SC	7			
ANWC	38589	301084	TABL	ACT	11.5	62	34	18.7	7.6	1	1	S	7			
ANWC	37079	081176	TABL	ACT		64	35	19.3	8.0	1	1	C	1			
ANWC	37068	290882	MURR	NSW	12.5	65	33	18.3	7.8	1	1	O	6			
ANWC	37362	190882	MURR	NSW	12.5	66	34	18.9	7.4	1	1	S	6			
ANWC	38012	130983	TABL	ACT	14.0	67	35	17.9	7.5	1	1	O	1			
ANWC	37363	190882	MURR	NSW	12.5	63	34	18.8	8.5	1	1	O	6			
ANWC	38412	220984	DARL	NSW	10.5	64	34	16.5	7.6	1	1	O	7			
ANWC	37361	190882	MURR	NSW	12.0	60	32	19.3	7.9	1	1	O	6			
ANWC	19654	111077	WILU	WA	10.5	63	34	18.0	7.8	-1	1	O	7			
ANWC	140	301258	GELA	VIC	10.0	60	35	18.8	7.3	-1	1	O	1	113	170	
ANWC	14421	021271	KOSC	NSW	12.0	65	35	17.9	7.6	-1	1	C	1			
ANWC	38575	301084	TABL	NSW	11.0	64	35	18.6	7.8	1	1	O	1			
ANWC	19190	060881	PARR	NSW		62	33	18.8	7.3	1	1	C	1			
ANWC	36971	0981	TABL	ACT	1	60	32	18.8	6.8	1	1	C	1			
ANWC	14365	140971	TABL	ACT	12.0	64	35	18.7	7.4	1	1	C	1			
ANWC	38591	311084	TABL	ACT	11.5	62	31	18.3	7.0	1	1	O	1			
ANWC	38590	311084	TABL	ACT	11.5	63	37	18.6	7.4	1	1	O	7			
ANWC	38180	081183	TABL	ACT	11.7	64	34	18.2	7.2	-1	1	O	1			
ANWC	6622	181067	CANB	ACT	11.0	65	32	19.0	7.7	1	1	O	1			
ANWC	11197	091068	SNOW	NSW	10.5	67	36	20.3		1	1	O	2			
ANWC	19957	121077	TABL	ACT	13.0	64	36	18.9	7.4	1	1	S	1			
ANWC	15040	080972	FROM	SA	10.0	63	37	19.1	7.3	1	1	O	6			
ANWC	19710	181077	WILU	WA	11.5	65	34	19.5	8.4	1	1	S	1			
ANWC	36423	110778	TABL	ACT		66	37	19.7	8.1	1	1	O	1			
ANWC	17537	110784	ALIC	NT	11.0	63	32	18.9	7.5	-1	1	O	7			
ANWC	170	011259	CANB	ACT	12.0	63	35	18.8	8.0	1	1	SO	1	110	190	
ANWC	16669	280878	STUR	NSW	11.5	63	34	20.0	8.4	-1	1	S	7			
AM	058276	070979	DRAK	NSW	12.2	64	33	20.0	7.6	1	1	S	1			
AM	029954	110811	BRIN	NSW		64	34	18.7	7.5	1	1	O	6			
AM	013681	001004	CARD	NSW		67	34	20.4	7.5	1	1	O	1			
AM	01233	001087	DUBB	NSW		65	32	19.5	7.6	1	1	O	6			
AM	022870	000865	CARD	NSW		66	34	20.0	6.3	-1	1	S	7			
AM	045834	031076	TIBO	NSW	6.0	63	33	19.3	7.4	1	1	O	7		96	
AM	044772	071173	CAMP	NSW	12.5	62	33	19.1	8.4	1	1	S	1	105		
AM	044678	150873	FINL	NSW	16.0	64	34	20.0	7.7	1	1	O	6	112		
AM	01227	001087	DUBB	NSW		66	34	20.3	7.3	1	1	O	2			
AM	041757	100865	PARR	NSW	12.7	65	34	20.6	7.5	1	1	O	2	98		
AM	046466	000977	WAGG	NSW	12.0	65	34	20.7	8.1	1	1	S	1	113		
AM	039726	090957	BOOL	NSW		62	33	19.3	8.1	1	1	S	6			
AM	057903	200783	SYDN	NSW	15.0	69	36	19.8	7.5	1	1	Y	1	116		
AM	033140	101232	MURR	NSW		63	34	20.5	7.8	1	1	O	7			
AM	029946	001004	BATH	NSW		64	35	19.6	8.2	1	1	O	1			
AM	029945	001004	BATH	NSW		66	36	18.7	7.1	1	1	O	2			
AM	044773	071173	CAMP	NSW	13.5	64	33	20.0	6.9	1	1	O	2	107		
AM	047071	230778	CONC	NSW		67	34	18.8	6.9	1	1	OS	6	105		
AM	045804	031076	TIBO	NSW	7.0	60	32	18.4	7.7	1	1	OS	6	94		
AM	194147	070979	DRAK	NSW	11.9	65	33	20.5	7.1	1	1	Y	1			

AM	033139	121032	MURR	NSW		65	36	18.5	8.4	1	1	O	7	
SAM	B34254	241181	BIGH	SA	13.0	60	34	20.3	8.0	1	1	O	7	
SAM	B34254	231181	SEYM	SA	13.5	65	36	21.2	8.4	1	1	S	1	
SAM	B25409	100888	EMUC	SA		62	34	19.6	7.8	1	1	O	7	
SAM	B2973	031019	BELM	NSW	11.8	65	32	18.7	7.7	1	1	O	6	105
SAM	B21225	170993	EPPI	VIC		64	33	19.0	8.4	1	1	OS	2	103
SAM	B24214	191051	KANG	SA		65	33	19.2	8.0	-1	1	O	7	104
SAM	B28434	180821	BELT	SA		64	33	19.8	8.0	-1	1	O	7	
SAM	B26824	181163	MTCR	SA		63	33	19.2	7.4	-1	1	O	7	
SAM	B26966	031263	LAKE	SA		63	32	20.2	7.5	1	1	O	6	
SAM	B34264	251181	BOOL	SA	11.5	60	32	19.0	7.3	1	1	O	4	
SAM	B26825	181163	MTCR	SA		65	33	18.9	7.7	1	1	O	7	
SAM	B22399	280820	DULK	SA		65	32	18.8	7.3	1	1	O	7	
SAM	B26969	031263	LAKE	SA		63	33	19.5	7.6	1	1	SO	7	
SAM	B37167	171282	PADT	SA		63	34	19.9	7.7	1	1	O	6	
SAM	B27584	251266	BELA	SA		63	35	18.5	8.2	1	1	O	6	
SAM	B27583	191066	MURB	SA		66	32	18.8	6.9	1	1	O	7	
SAM	B5243	161124	FLIN	SA		58	29		8.1	1	1	O	6	
SAM	B2974	061019	BELM	NSW	12.0	63	32	18.0	6.9	1	1	O	7	105
SAM	B26821	181163	MTCR	SA		64	32	17.4	6.7	1	1	S	7	
SAM	B22404	001016	BOWH	SA		64	32	19.2	8.0	1	1	O	6	
SAM	B26820	101263	HAMI	VIC		63	30	18.2	7.5	-1	1	O	7	
SAM	B24213	241051	KANG	SA		62	33	18.3	7.1	-1	1	O	6	102
SAM	B6905	200826	MILD	VIC		66	34	18.5	7.2	1	1	O	7	
SAM	B352	070812	KALL	SA		64	31	18.6	7.2	1	1	O	7	
SAM	B34259	241181	BIGH	SA	13.0	66	34	20.3	8.8	1	1	S	7	
SAM	B2409	281018	KING	SA		64	33	19.5	7.5	1	1	S	7	
SAM	B34257	241181	BIGH	SA	12.0	64	32	18.7	7.8	-1	1	O	6	
SAM	B16923	070833	BLAC	SA	11.5	62	34	19.7	7.0	1	1	S	7	103
SAM	B26831	171063	BLAN	SA		67	34	20.0	8.1	-1	1	S	7	
SAM	B34256	241181	BIGH	SA	11.5	61	32	20.3	7.2	1	1	O	6	
SAM	B38278	100882	MILD	VIC		66	32	18.4	7.3	-1	1	O	6	
SAM	B21231	101216	BROK	NSW		62	31	19.2	8.0	-1	1	O	7	96
SAM	B21228	080901	BROK	NSW		64	32	18.7	7.9	1	1	O	3	94
SAM	B4469	180823	DONA	SA	9.3	63	32	17.9	7.3	1	1	O	7	102
SAM	B21230	101216	BROK	NSW		64	32	19.6	7.5	-1	1	O	6	102
SAM	B34261	251181	BOOL	SA	12.5	62	35	19.0	7.8	1	1	O	6	
SAM	B25410	210858	COOP	SA		64	32	18.3	7.1	1	1	O	7	
SAM	B21227	170993	EPPI	VIC		64	34	18.5	7.3	1	1	O	1	109
SAM	B8941	140802	DONA	SA		64	35	18.4	7.9	-1	1	O	7	
SAM	B26823	181163	MTCR	SA		62	34	18.3	8.0	1	1	O	6	
SAM	B37166	201182	PADT	SA		63	32	18.7	8.0	1	1	O	7	
SAM	B8930	001006	COPM	NSW		60	30	18.4	7.4	0	0	S	6	
NMV	B5704	011250	PHIL	VIC		63	32	18.4	7.7	1	1	O	1	
NMV	B5580	020754	BENE	VIC	12.5	62	34	18.0	7.0	1	1	O	6	100
NMV	B8495	220962	WARR	VIC		69	36	19.1	8.7	1	1	O	2	105
NMV	B12244	290975	CROY	VIC	12.0	66	34	17.2	7.1	1	1	SO	4	103
NMV	B5696	290949	OUYE	VIC		65	32	18.7	7.9	1	1	O	6	100
NMV	B5703	091149	BRIG	VIC		63	34	17.6	7.3	1	1	O	2	
NMV	B2371	161141	EMUV	QLD		63	32	17.9	7.8	0	0	OS	7	
NMV	B13147	101179	PORT	VIC	11.3	63	32	19.7	7.5	1	1	O	1	
NMV	B13152	281179	TERA	VIC	11.4	63	33	19.8	7.6	1	1	C	1	

NMV	B13144	241179	HEYW	VIC	12.2	62	32	18.6	8.5	1	1	O	1	
NMV	B7611	080959	RUTH	VIC	15.0	63	35	19.2	7.8	1	1	S	6	114
NMV	B2369	101141	WARW	QLD		62	35	18.4	8.3	-1	1	S	7	
NMV	B16048	251254	WAKO	NSW	13.0	65	34	20.7	7.3	1	1	O	7	100
NMV	B2367	081141	WARW	QLD		62	35	17.4	7.5	1	1	S	1	
NMV	B2370	111141	WARW	QLD		64	33	19.2	7.1	-1	1	S	6	
NMV	B5700	210850	BEND	VIC		65	32	21.0	8.2	-1	1	O	7	
NMV	B5702	091152	MILD	VIC	10.0	63	31	18.0	7.5	-1	1	O	6	110
NMV	B12253	080875	CHIL	VIC	13.0	66	36	17.2	6.8	1	1	S	1	109
NMV	B6491	191053	FRAN	VIC	17.0	63	34	17.4	6.9	1	1	S	1	107
NMV	B5694	290950	GISB	VIC		67	36	19.0	7.8	1	1	S	2	100
NMV	B5701	200850	BEND	VIC		63	31	20.1	8.0	1	1	O	7	100
NMV	B952	190995	BEND	VIC		67	35	19.0	7.6	1	1	S	7	
NMV	B5695	290949	OUYE	VIC		64	31	17.2	6.5	-1	1	O	6	98
NMV	B10686	190869	OUYE	VIC	12.0	63	34	18.7	7.3	1	1	O	6	
NMV	B10687	190869	OUYE	VIC	12.0	63	32	19.1	7.9	-1	1	O	6	
NMV	B5693	270950	GISB	VIC		62	32	20.5	7.4	1	1	S	1	105
NMV	B986	040940	MILD	VIC		65	35	20.1	7.5	-1	1	O	7	
NMV	B5697	220751	TOOL	VIC		62	34		6.9	1	1	O	7	96
NMV	B13146	241179	HEYW	VIC	12.2	65	31	17.9	8.0	1	1	O	6	
NMV	B13148	051179	WEDD	VIC	11.8	62	31	18.2	7.2	-1	1	O	7	
NMV	B13141	051179	WEDD	VIC	10.8	61	31	18.0	7.7	1	1	O	7	
NMV	B13140	071179	GOKO	VIC	12.5	62	32	20.2	7.9	1	1	S	7	
NMV	B13150	271179	MORT	VIC	12.7	67	33	18.7	7.5	-1	1	O	6	
NMV	B13149	271179	MORT	VIC	12.4	65	32	20.2	8.3	1	1	O	6	
NMV	B13153	281179	TERA	VIC	11.5	64	34	19.2	7.4	1	1	S	7	
NMV	B13143	241179	HEYW	VIC	11.8	65	32	19.8	7.8	1	1	O	1	
WAM	A19958	241085	PYRA	WA	11.0	63	32	19.5	7.3	-1	1	O	4	110
WAM	A19965	281085	CLYD	WA	11.5	61	31	18.2	7.8	1	1	O	6	108
WAM	A19967	291085	DERA	WA	11.0	60	33	17.1	7.4	-1	1	O	7	110
WAM	A19386	041084	MTLU	WA	10.0	63	33	19.3	7.5	-1	1	O	6	100
WAM	A18247	160983	BONN	WA	11.0	63	31	19.8	7.8	1	1	O	6	109
WAM	A19963	271085	SHEO	WA	11.5	63	33	19.0	8.2	1	1	O	7	108
WAM	A19968	291085	DERA	WA	11.0	65	33	18.6	7.0	-1	1	O	7	107
WAM	A19969	051185	BOIN	WA	11.0	64	32	16.8	7.0	-1	1	O	7	112
WAM	A18584	030984	EURA	WA	12.0	64	31	19.5	7.9	1	1	O	7	111
WAM	A18571	111084	RAVE	WA	9.4	60	32	16.8	6.8	1	1	O	6	102
QM	018095	101079	ROCW	QLD	10.5	61.0	30.1	18.2	7.8	0	1	C	6	
QM	018096	101079	ROCW	QLD	10.5	62.0	31.7	16.2	8.0	0	1	S	6	
QM	101079	101079	ROCW	QLD	11.0	60.0	32.5	18.0	7.9	0	1	S	6	
QM	018078	011079	MURP	QLD	10.4	63	31.4	17.2	8.0	0	-1	C	6	
QM	018079	011079	MURP	QLD	10.2	60	30.1	17.5	8.0	-1	1	C	6	
QM	018080	011079	MURP	QLD	10.1	61	31.2	18.0	8.0	-1	1	C	6	
QM	018091	051079	ELLI	QLD	12.0	64	31.1	18.3	8.4	0	-1	C	6	
QM	018092	061079	ELLI	QLD	10.6	62	31.9	17.7	7.1	0	1	C	6	
QM	018094	061079	ELLI	QLD	10.3	62	31.8	17.7	7.5	0	-1	C	4	
QM	018089	170979	EMUC	QLD	11.8	63	32.5	18.3	8.3	0	1	CS	6	
QM	018090	170979	EMUC	QLD	11.2	61	30.2	17.9	7.0	0	-1	C	7	
QM	018083	180979	ORPH	QLD	11.0	62	32.0	17.2	7.0	0	1	C	7	
QM	018081	180979	ORPH	QLD	11.0	65	33.0	17.4	7.8	0	0	C	7	
QM	018082	180979	ORPH	QLD	10.1	60	34.0	16.9	8.1	0	-1	S	7	
QM	018085	190979	ORPH	QLD	10.8	63	33.1	17.0	7.9	0	1	OS	7	
QM	018087	200979	ORPH	QLD	10.3	61	30.6	17.1	7.6	-1	-1	SO	7	
QM	018088	210979	ORPH	QLD	10.8	60	31.5	17.6	7.7	0	-1	SO	7	
QM	018086	200979	ORPH	QLD	10.9	59	31.7	16.9	8.1	0	0	S	7	

AMNH	824914	271179	MORT	VIC	12.5	64	33.2	17.7	7.4	1	1	O	1
AMNH	824915	271179	MORT	VIC	12.4	64	33.5	18.6	8.2	1	1	SO	1
AMNH	824920	201179	TYRE	VIC	11.6	62	33.1	18.5	7.3	1	1	S	2
AMNH	824912	201179	TYRE	VIC	12.8	65	33.5	18.6	7.8	1	1	S	6
AMNH	824919	201179	TYRE	VIC	11.8	62	33.0	17.2		1	1	SO	6
AMNH	824906	061179	MITR	VIC	11.2	64	32.5	18.9	7.9	1	1	S	3
AMNH	824907	061179	MITR	VIC	11.9	63		18.5	7.8	1	1	O	6
AMNH	824908	061179	MITR	VIC	12.7	66	33.0	18.3	8.0	1	1	SO	6
AMNH	824913	251179	HEAT	VIC	12.2	66	34.1	18.2	7.8	1	1	SO	2
AMNH	824917	251179	HEAT	VIC	13.2	67	33.5	18.2	7.9	1	1	S	7
AMNH	824910	261179	HEAT	VIC	12.0	64	33.2	18.8	7.7	1	1	SO	6
AMNH	824918	261179	HEAT	VIC	12.0	63	33.0	18.4	7.3	1	1	O	7
AMNH	461403	070854	LAWR	QLD		60.9	31.8	16.5	6.8	0	0	C	6
AMNH	461404	070854	LAWR	QLD		61.0	28.0	16.6	7.1	0	-1	C	6
AMNH	699027	010789	ROCH	QLD		63.8	30.9	17.0	6.8	0	0	C	6
AMNH	815978	060979	BLAC	NSW	12.5	64	35.1	18.2	6.9	1	1	C	2
AMNH	815975	060979	BLAC	NSW	12.5	61	32.6	17.2	7.4	1	1	S	6
AMNH	815972	060979	BLAC	NSW	11.1	61	32.1	17.7	6.9	1	1	S	7
AMNH	815977	060979	BLAC	NSW	12.3	64	33.0	16.9	7.3	1	1	S	1
AMNH	815974	110979	TABU	NSW	10.0	60	30.8	17.8	8.1			SC	4
AMNH	703258	280840	BUNY	QLD	11.2	62.0	33.0	18.2	7.8	0	1	S	6
AMNH	703260	250940	BUNY	QLD	10.8	62.0	32.5	18.2	8.4	0	0	S	6
AMNH	703262	050941	EMUV	QLD		64	33.7	18.2	7.6	-1	1	OS	6
AMNH	703263	230941	EMUV	QLD		61	30.0	17.9	7.2	0	1	O	6

WING LENGTH:

LOC	N	MEAN	SD	MIN	MAX	SE	VAR	CV
BEND	3	65.0	2.00	63.0	67.0	1.15	4.00	3.08
HEYW	3	64.2	1.73	62.4	65.5	1.00	3.00	2.71
MILD	4	65.2	1.41	63.5	66.3	0.71	2.00	2.18
OUYE	4	63.7	0.96	63.7	65.5	0.48	0.92	1.50
BIGH	4	62.7	2.75	60.2	66.1	1.38	7.58	4.39
MTCR	4	63.5	1.29	62.6	65.5	0.65	1.67	2.03
MURR	6	63.7	2.16	60.4	66.4	0.88	4.67	3.39
TABL	12	64.1	2.02	60.6	67.8	0.58	4.08	3.15

TAIL LENGTH:

LOC	N	MEAN	SD	MIN	MAX	SE	VAR	CV
BEND	3	32.7	2.08	31.3	35.1	1.20	4.33	6.37
HEYW	3	31.7	0.58	31.2	32.4	0.33	0.33	1.82
MILD	4	33.0	1.83	31.0	35.0	0.91	3.33	5.53
OUYE	4	32.3	1.26	31.2	34.6	0.63	1.58	3.90
BIGH	4	33.0	1.15	32.0	34.8	0.58	1.33	3.50
MTCR	4	33.2	0.82	32.4	34.4	0.41	0.67	2.47
MURR	6	33.8	1.33	32.5	36.6	0.54	1.77	3.93
TABL	12	34.7	1.78	31.9	37.8	0.51	3.15	5.12

TARSUS LENGTH:

LOC	N	MEAN	SD	MIN	MAX	SE	VAR	CV
BEND	3	20.0	1.00	19.3	21.2	0.58	1.00	5.00
HEYW	3	18.8	0.96	17.9	19.8	0.55	0.92	5.12
MILD	4	18.7	0.93	18.0	20.1	0.46	0.86	4.94
OUYE	4	18.4	0.84	17.2	19.1	0.42	0.70	4.55
BIGH	4	19.9	0.80	18.7	20.3	0.40	0.64	4.02
MTCR	4	18.4	0.79	17.4	19.2	0.40	0.63	4.30
MURR	6	19.1	0.79	18.3	20.5	0.32	0.62	4.14
TABL	12	18.7	0.50	17.9	19.7	0.14	0.25	2.66

CULMEN LENGTH:

LOC	N	MEAN	SD	MIN	MAX	SE	VAR	CV
BEND	3	7.93	0.31	7.60	8.20	0.18	0.09	3.85
HEYW	3	8.10	0.36	7.80	8.50	0.21	0.13	4.45
MILD	4	7.37	0.15	7.20	7.50	0.08	0.02	2.03
OUYE	4	7.40	0.66	6.50	7.90	0.33	0.44	8.96
BIGH	4	7.95	0.66	7.20	8.80	0.33	0.44	8.31
MTCR	4	7.45	0.56	6.70	8.00	0.28	0.31	7.47
MURR	6	7.97	0.41	7.40	8.50	0.17	0.17	5.19
TABL	12	7.52	0.41	6.80	8.10	0.12	0.17	5.41

WEIGHT:

LOC	N	MEAN	SD	MIN	MAX	SE	VAR	CV
HEYW	3	12.1	0.23	11.8	12.2	0.13	0.05	1.91
BIGH	4	12.4	0.75	11.5	13.0	0.37	0.56	6.06
MURR	4	12.4	0.25	12.0	12.5	0.13	0.06	2.02
TABL	10	12.0	0.87	11.0	14.0	0.28	0.76	7.25

APPENDIX VII

Calculations which were used to quantify some mtDNA results are given in this section.

Haplotypic Diversity, G, as defined by Nei (1987), was calculated as follows:

$G = (n / n-1)\ (1 - \sum f_i^2)$, where f_i is the frequency of the ith mtDNA haplotype in a sample of n individuals.

The proportion of shared bands between pairs of haplotypes, $\hat{F}$, was calculated for all pairs within and between localities using the formula of Nei and Li (1979):

$\hat{F} = 2n_{xy} / (n_x + n_y)$, where n_x and n_y are the number of fragments in a composite of the two haplotypes, and n_{xy} is the number of fragments common to both haplotypes.

The average number of nucleotide substitutions per site, $\hat{\delta}$, for each pair of haplotypes was calculated using the formula of Upholt (1977). Nei and Li (1979) calculated δ in a different manner, but Upholt's method is simpler and gives identical values (Quinn and White 1987):

$\hat{\delta} = 1 - [(-\hat{F} + (\hat{F}^2 + 8\hat{F})^{1/2}) / 2]^{1/r}$, where r is the number of base pairs recognized by the endonuclease.

Estimates of nucleotide diversity, π, for northern, central, and southern samples of individuals were made using the formula of Nei and Li (1979), with the correction for small sample sizes of Nei and Tajima (1981):

$\hat{\pi}_A = \sum_{ij} A_i A_j \hat{\delta}_{ij}$, where A_i is the frequency of the ith composite haplotype in population A, and $\hat{\delta}_{ij}$ is the number of nucleotide differences per nucleotide site between the ith and jth composite haplotype; the value of $\hat{\pi}_A$ is then multiplied by $n/(n-1)$, where n is sample size.

The average nucleotide diversity among populations, π_{AB}, was then estimated by:

$\hat{\pi}_{AB} = \sum_{ij} A_i B_i \hat{\delta}_{ij}$, where A_i and B_i are the frequencies of the ith composite haplotypes in populations A and B.

The net nucleotide difference, $\hat{\delta}_{net}$, between northern and southern samples was estimated by:

$\hat{\delta}_{net} = \hat{\pi}_{AB} - (\hat{\pi}_A + \hat{\pi}_B) / 2$

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