INDIVIDUAL VARIATION IN SONGS OF DARK-EYED JUNCOS

LAIDLAW WILLIAMS†

AND

MICHAEL H. MacROBERTS

The study of bird vocal behavior has advanced to the point where a large body of information exists on intraspecific and intrapopulation variation (Borror 1961, Mulligan 1966, Thielcke 1969, Thorpe 1961). However, less attention has been focused on variation within the song repertoire of the individual, which is requisite to a complete description of specific and geographical variation (Marler and Isaac 1960). As Thompson (1970:58) has said, "for a fuller understanding of a behavioral characteristic, just as in the case of a morphological feature, it is important to study the kind and amount of variation within a single population and, especially for behavior, within a single individual."

This paper describes the song repertoires of individuals in one population of Dark-eyed Juncos (*Junco hyemalis*), together with inter-individual variation within that population, and compares these variations with those of Yellow-eyed Juncos (*Junco phaeonotus*) in Durango, Mexico (Marler and Isaac 1961) and Dark-eyed Juncos in Berkeley, California (Konishi 1964a, b).

METHODS AND PROCEDURE

This study was conducted between 1972 and 1975 at Carmel Highlands, Monterey County, California. The study area was approximately 10.9 ha in extent and was located 1.6 km S of Point Lobos State Reserve headquarters. The habitat is hilly pine-oak woodland (*Quercus agrifolia* and *Pinus radiata*) with *Rhamnus* and *Heteromeles* as understory and *Arctostaphylos* and *Ceanothus* as adjacent chaparral. The area is partially suburban with a few houses and gardens.

Birds were banded with individual color combinations or were otherwise individually recognizable and were followed for as many years as they were present. The ten best-known individuals form the basis of this paper. We attempted to record all songs in a bird's repertoire and to determine if any changes occurred in the repertoire in successive years.

Songs were recorded at 7½ ips on a Uher 4000 Report-L tape recorder using a 60-cm parabolic reflector and an Electro-voice microphone (dynamic model 636). Song playbacks often were used to stimulate singing. Recorded songs were analysed on a Kay Electric Co. Sonograph (wide band) and by listening to playbacks.

TERMINOLOGY AND GENERAL DESCRIPTION OF SONG

Junco songs have been the subject of several previous studies; on this basis it is clear that the songs of the Highlands juncos differ in some respects from those of juncos in other localities. Consequently, a description of song and singing behavior is given here along with definitions of terms used.

The basic terms used are *song*, *songbout* or *bout*, *syllable*, and *subsong*. The definition of syllable used here is the same as that used by Marler and Isaac (1961) and Konishi (1964b), i.e., a single continuous noise or group of noises forming a more or less coherent unit. The syllable, therefore, although often consisting of a number of discontinuous parts ("notes" in Konishi's 1964b terminology), is not fragmented further by the bird using it. The different syllables used by the ten birds in the present study are shown in figure 1. In the Highlands population, syllable duration varies from .01 to .32 sec, and intersyllable duration varies from .02 to .06 sec (table 1).

A song is any temporal grouping of syllables that is broken by intervals longer than the intersyllable interval. In the Highlands population, songs are made up of from 5 to 27 syllables and vary in duration from .86 to 1.70 sec. Most songs are monosyllabic and consist of the same syllable repeated. Some songs are bisyllabic, consisting of two different syllables. Bisyllabic songs usually consist of several repetitions of a syllable of one type followed by several repetitions of a syllable of another type. The interval between these syllables is no greater than that between individual syllables in a monosyllabic song. In addition we recorded one trisyllabic song, one with five different syllables, and one highly variable song. These three song types are discussed later.

Konishi (1964a:94) also working with Dark-eyed Juncos, found "an inverse correlation between the duration of syllable and the number of syllables contained in a song or in

The Condor 79:106–112, 1977

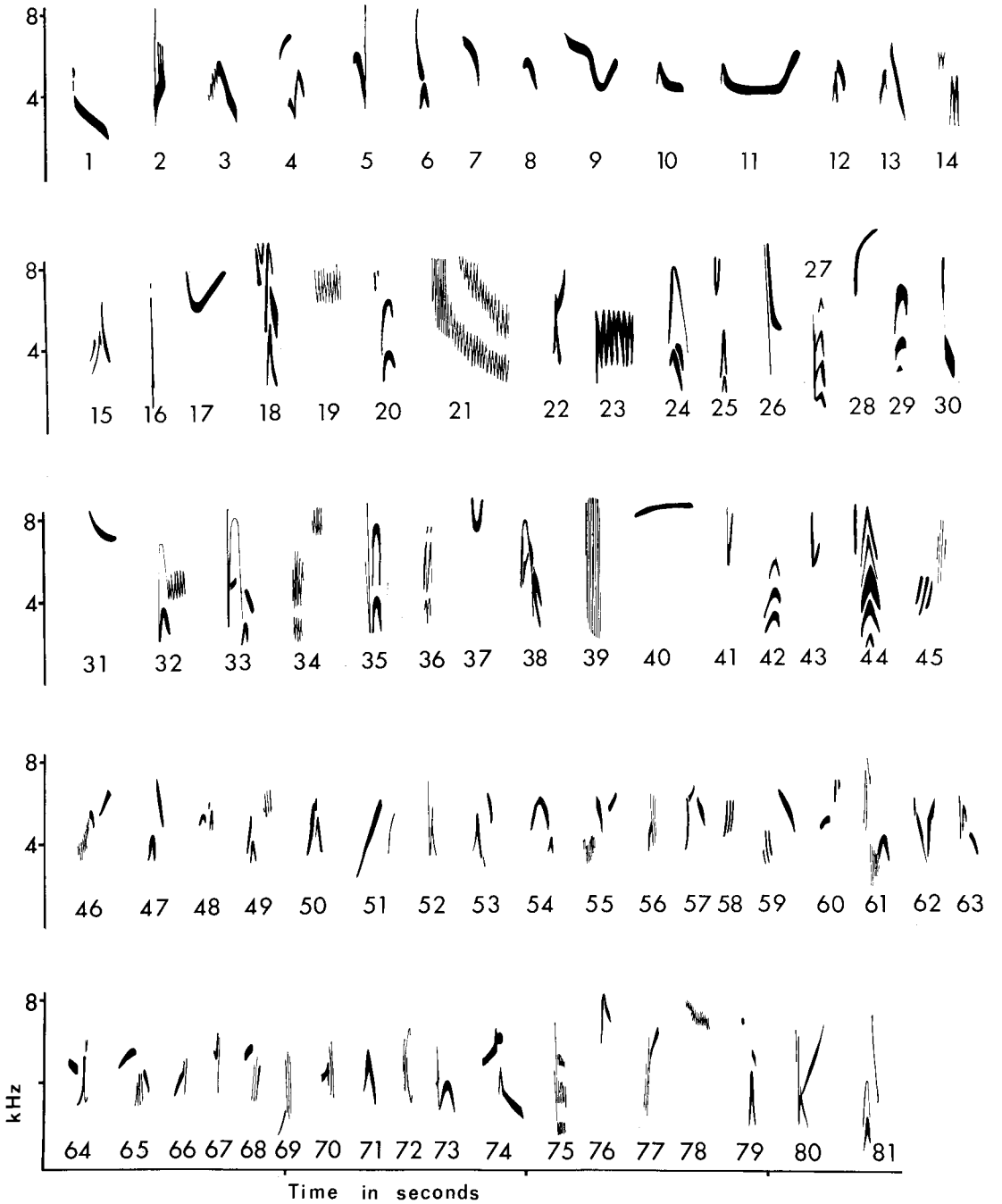

FIGURE 1. Syllables used by ten Dark-eyed Juncos from the Carmel Highlands population. Syllables 1 to 74 were used in song. Bird B's subsong (see text) consisted of syllables 15–17, 19–22, 24–28, 30–33, 40–41, 43, 61, and 75–81.

a unit of time. The longer the syllable the smaller the number of syllables. On the other hand, the total duration of song is for the most part constant, it being relatively independent of variations in syllable duration, intersyllable interval, and in the number of syllables in a song or per unit of time." Konishi (1964b:432) continued: "hence, we can conclude that the relative constancy of song duration within a population, in the face of wide differences in the number of syllables, is achieved only by varying the syllable duration." Konishi's findings apply also to the Highlands juncos.

Songs are given in bouts. A bird usually sings from an exposed, elevated perch and

TABLE 1. Comparison of song repertoires of Dark-eyed and Yellow-eyed Juncos.

Species	Dark-eyed (Berkeley)[a]	Dark-eyed (Highlands)	Yellow-eyed (Durango)[a]
No. of syllables in song	14.1 ± 4.38[b] (31.10)	13.8 ± 4.77 (34.56)	10.1 ± 2.9 (28.70)
Song duration (sec)	1.49 ± .203 (13.60)	1.31 ± .19 (14.50)	1.63 ± .29 (17.80)
Intersyllable interval (sec)	.036 ± .009 (25.60)	.031 ± .01 (32.25)	—
Syllable duration (sec)	.080 ±.029 (36.60)	.087 ± .054 (62.07)	.138 ± .077 (55.80)
Sample size in song types	77	50	67

[a] Data from Konishi (1964b).
[b] Mean ± standard deviation, with coefficient of variation (S.D. × 100)/$\bar{x}$ in parentheses.

repeats the same song from one to as many as 120 times in regular succession. The time between successive songs in a bout varies between 2 and 7 sec. Occasionally a bird may switch from one song type to another, the interval between the last song of the first series and the first song of the new series being the same as the interval between songs of one series. More usually, a bird moves to another perch, or performs some other activity, before changing song type. However, a bird may move or interrupt singing with another activity and then resume its next bout with the same song type. A male tends to exhaust its repertoire in a relatively short time. In a typical case, one bird sang six of its seven song types in a two-hour observation period.

Each individual tended to sing all of its song types at a constant rate. There were short, medium and long duration singers. For example, one bird had five song types that ranged from .86 to 1.05 sec, another used seven song types that ranged from 1.05 to 1.28 sec, and another had six song types that ranged from 1.36 to 1.66 sec.

In agreement with Konishi (1964b), we found by comparing the coefficients of variation that syllable duration is the most variable parameter examined (table 1).

In this paper we mention subsong only because one of Bird B's five song types showed many similarities to subsong. Subsong differs from normal song in several respects. It is rambling, lacks a standard duration, and may last up to 5 or 6 sec. It consists of varied series of up to 45 syllables given quietly, usually on or near the ground. Many different syllables (Bird B used at least 27 different syllables) are given in what appears to be random order. (We use "random" only in a general sense here; we have not examined the ordering of syllables in subsong in detail.) The number of different syllables used is far greater than in normal song, and many of the syllables are never used in normal song. Subsong does not appear to be confined to any particular age class. Bird A, at least in his fourth year, and Bird B, in at least his second year, frequently uttered long series of subsong in spring and summer. Intervals between successive subsongs are variable.

RESULTS

Below we present individual vignettes of each of the ten birds selected from the study population. Table 2 summarizes some of the data discussed below.

Bird A was banded 12 March 1972 and observed on the same territory every year of the study. This bird had seven song types, five of which were unique to it. Five of its song types were monosyllabic (consisting of syllables 3, 4, 5, 6, and 12), one bisyllabic (syllables 1 and 2), and one pentasyllabic (syllables 7–11). This bird used 12 different syllables, 3 of which were used by other individuals. Two of its song types (one consisting of syllable 3, the other consisting of syllable 12) were identical with song types of another individual (Bird B). The other syllable (no. 2), held in common with another bird (Bird C), was part of Bird A's bisyllabic song type in which the other syllable (no. 1) was unique to Bird A. Bird A's five-syllable song type mimicked a Brown Creeper (*Certhia familiaris*). Figure 2 compares this song type with that of a Brown Creeper recorded within Bird A's territory.

Bird B was banded 19 October 1973 and observed on the same territory in each of the two succeeding years. This bird had five song types; four were monosyllabic (syllables

TABLE 2. Comparison of song and syllable repertoires of individual juncos from the Carmel Highlands population.

Bird	Song Types						Syllables		
	No. songs/ repertoire	No. unique to indiv.	No. diff. syll./song type				No. syll./ repertoire	No. shared	Present in repertoire (nos. as in) (fig. 1)
			1	2	3	>3			
A	7	5	5	1		1	12	3	1–12
B	5	2	4			1	34	6	3, 12–44
C	4	3	4				4	2	2, 45–47
D	4	3	4				4	2	13, 48–50
E	5	3	4	1			6	4	51–56
F	3	2	2	1			4	1	57–60
G	4	1	4				4	3	15, 47, 50, 61
H	6	4	6				6	2	15, 62–66
I	5	4	5				5	1	63, 67–70
J	7	4	4	2	1		11	7	36, 38, 51, 52, 54, 55, 57, 71–74
Total	50	31	42	5	1	2			

3, 12, 14, and 15), and one was highly variable (syllables 13–44). This bird used 34 different syllables, six of which were used by other birds. Three of its monosyllable songs were identical to the songs of other individuals. Syllable 15 was shared with Birds G and H, and syllables 3 and 12 were shared with Bird A. The other syllables held in common with other birds were part of B's variable song type. Additionally, two of the syllables used in B's monosyllabic songs (syllables 14 and 15) were also incorporated into B's variable song type. The variable song type differed from all songs in the sample in that it consisted of many different syllables. In this respect it resembled subsong except that subsong lacks a stereotyped duration and is always given quietly. Bird B, when singing the variable song might give one song that consisted of one syllable only and then incorporate that syllable with others in the next song of the bout. Thus, in a single bout, Bird B might sing in the following manner: song 1: monosyllabic, song 2: bisyllabic, song 3: eight different syllables randomized; and so forth. Individual songs of B's variable song type consisted of up to eight different syllables, but in the aggregate of all utterances of this song type, 32 different syllables were used. The order of syllable presentation appeared random, or nearly so. B's variable song type was far more common in 1974 than in 1975.

Bird C was banded 17 April 1974 and was last seen on 29 May 1974. It was recorded for only two hours on 19 April 1974. Consequently, its entire repertoire may not have been recorded. This bird had four monosyllabic songs (syllables 2, 45–47). Two of its syllables (2 and 47) were shared with other birds, but only one of its song types (that involving syllable 47) was identical to the song type of another bird (Bird G). Bird C used syllable 2 as a monosyllabic song while, as we have pointed out above, Bird A used syllable 2 as part of a bisyllabic song.

Bird D was banded 16 March 1972 and observed on the same territory until 15 April 1974. This bird had four monosyllabic songs (syllables 13, 48–50). Syllables 13 and 50 were shared with Birds B and G, but only one song type was identical. Syllable 13 was shared with Bird B but was used by B only as a part of its variable song type.

Bird E was banded 14 June 1972 and was observed on the same territory until 5 April 1973. This bird had five song types, four monosyllabic (syllables 53–56) and one bisyllabic (syllables 51–52). Bird E used six different syllables, four of which were shared with other birds. Two of its monosyllabic songs (syllables 54 and 55) were identical with two song types of Bird J. The other two syllables held in common were those constituting this bird's bisyllabic song type. Both Birds E and J had bisyllabic songs made up of syllables 51 and 52, but they differed in several respects. First, although each bird's bisyllabic song type began with syllable 51

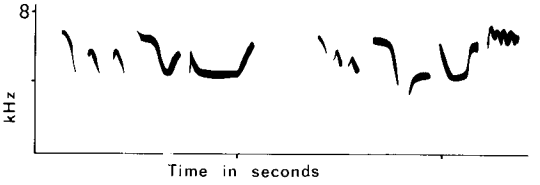

FIGURE 2. Bird A's five-syllable song (left) and Brown Creeper song (right).

and ended with syllable 52, E averaged 4.8 (R = 4–5) repetitions of syllable 51, while J averaged 7.7 (R = 7–9) repetitions of this syllable. E averaged 14.6 (R = 6–22) repetitions of syllable 52 and J averaged 5.7 (R = 2–10) of syllable 52. Second, both birds interspersed monosyllabic song types consisting only of syllable 51 within bouts of the bisyllabic song. Bird E did this at a rate of about one monosyllabic song type to 25 bisyllabic ones, while J did this at a rate of about three monosyllabic to one bisyllabic song type. Thus, although the two birds had song types made up of the same two syllables, their performance could be distinguished easily.

Bird F was banded 24 January 1973 and observed on the same territory until 19 May 1973. This bird had three song types, two monosyllabic (syllables 57 and 60) and one bisyllabic (syllables 58 and 59). It shared one song type (syllable 57) with Bird J.

Bird G was banded 26 January 1973 and observed on its territory through the 1974 breeding season. This bird had four monosyllabic song types (syllables 15, 47, 50, and 61) of which only one (syllable 61) was unique to it. One song type (syllable 15) was shared with two birds (B and H), and two song types (syllables 47 and 50) were shared with one bird each (C and D, respectively).

Bird H was banded 18 February 1973 but an unbanded bird with an identical vocal repertoire was tape recorded on the same territory in the previous year. Bird H was observed through June 1973. This bird had six monosyllabic songs (syllables 15, 62–66). Two of its song types were identical with those of other birds. One (syllable 15) was shared with Birds B and G, and one (syllable 63) was shared with Bird I. One feature of this bird's singing behavior deserves special note. Most junco singing bouts, as we have noted earlier, consist of the bird delivering between one and 120 repetitions of the same song type. The bout is usually not broken by other song types. Bird H had the unusual characteristic of alternating song types during singing bouts. For example, he might alternate song types A, B, A, B regularly, or A, A, A, B, B, A, B, B, B, A irregularly. He characteristically alternated specific song types (consisting of syllables 62 and 63; 64 and 65; and 15 and 66). Alternation of song type is uncommon, but it was tape recorded from one other junco in the study area in 1974.

Bird I was banded 3 February 1974 and observed until June 1974. This bird had five monosyllabic songs (syllables 63, 67–70). One song type (syllable 63) was identical to that of Bird H.

Bird J was not banded but was individually recognizable by plumage peculiarities. It was observed and tape recorded for only 9 hours on 6 days in 1975. It had seven song types consisting of 11 different syllables. Four song types were monosyllabic (syllables 54, 55, 57, and 71), two were bisyllabic (syllables 51 and 52, and 36 and 74), and one was trisyllabic (syllables 38, 72 and 73). Three of its monosyllabic song types were identical to those of other birds (syllables 54, 55, and 57: Birds E and F). The similarities and differences between one of this bird's bisyllabic songs and one of Bird E's bisyllabic songs, which was also made up of syllables 51 and 52, are compared under Bird E's vignette above. The other bisyllabic song type and the trisyllabic song type shared syllables with other individuals, but they also contained unique syllables and were, therefore, distinct.

To summarize, ten Dark-eyed Juncos used from three to seven song types each, for a total of 50 song types. These song types were made up of 74 different syllables. Forty-two of the songs were monosyllabic, 5 were bisyllabic, 1 was trisyllabic, 1 was pentasyllabic, and 1 consisted of 32 different syllables. Thirty-one of the song types were unique to one individual, 8 were shared by two individuals, and one was shared by three individuals. Therefore, in this sample there were 40 distinct song types. No two birds shared the same complete repertoire.

DISCUSSION

The song repertoire of individual birds observed over two or more years did not change except in one case. Bird B's variable song type, which as we noted above was common in 1974, was almost absent in 1975. This finding differs from that of Marler et al. (1962) who found that hand-raised juncos frequently change song types.

The degree of stereotypy of song repertoire of juncos falls between the extremes of the Song Sparrow (*Melospiza melodia*) and the White-crowned Sparrow (*Zonotrichia leucophrys*). In the former species, "structural variation in the song is extensive, involving a large repertoire, a great variety of syllable types peculiar to each individual, and relatively wide variation in successive repetitions of the same song type" (Mulligan 1966:17). In the latter species, "all the members of a restricted population sing the same song,

with only slight variation" (Mulligan 1966: 17).

In the Highlands area, each male junco has a repertoire of up to seven song types most of which are individually distinct. Additionally, most song types are highly stereotyped. By this we mean that the variations that occur are slight and consist mainly of the number of syllables used in each song. However, J's trisyllabic song type, A's pentasyllabic song type, and B's variable song type showed some distinct variations. J's trisyllabic song usually consisted of 4 to 5 repetitions of syllable 72, followed by one syllable 73, then 5 to 7 repetitions of syllable 38, ending with one syllable 73. Four irregular patterns were noted. The song occasionally lacked the final syllable, or repeated the final syllable twice, or added syllable 38 once or twice to the end of normal song, or added one syllable 38 and one more syllable 73 to the end of normal song. Of 133 songs recorded, 28 were irregular. In 970 recordings of Bird A's pentasyllabic song type, 842 were regular (fig. 2), but 128 were irregular with syllable 10 added once or twice between syllables 9 and 11 or with another syllable 11 added at the end of the song.

Bird B's variable song type was unique and in many respects resembled subsong. This bird's subsong and its variable song shared many if not all syllables. In two subsongs of which sound spectrograms were made, 19 of the 32 syllables used in variable song were found. An additional 8 syllables were present in B's subsong (syllables 61, 75–81; fig. 1) including one (syllable 61) that was characteristic of Bird G. A more detailed examination of this bird's subsong undoubtedly would reveal more different syllables. Additionally, variable song, like subsong, consisted of "randomized" syllables. The only differences between this bird's subsong and variable song were in loudness of singing and duration of songs in a bout. The bird delivered variable song as loudly as normal song and in the form of normal song bouts. In one singing bout, for example, although each song might differ in the syllables used and order of their use, most of the syllables would be used, some only once, some repeatedly. It seems clear, then, that variable song was simply subsong sung from normal perches, at normal volume, and in the normal bout pattern.

Variation in song types among individuals within the Highlands population was such that we could identify an individual in most cases on the basis of only one song. In cases of shared song types we could specify with certainty that the singer was one of two individuals, or in one case, one of three individuals. With the inclusion of other information (e.g., location of singer), individual recognition in the latter cases became more likely. Finally, because a bird seldom sang one song type for long, it was highly probable that its next song would be either individually distinct or a combination of shared song types unique to it.

Marler and Isaac (1961:195) described Yellow-eyed Junco songs from Durango, Mexico. They found that "each male has a repertoire of several song patterns, two or three being an average estimate from field observations." In addition, they found that the number of syllable types per song usually ranged from two to five. They observed no monosyllabic songs. In their sample of 67 songs from 63 males they found no two individuals with identical songs and apparently with no identical syllables. However, at least some Yellow-eyed Juncos from the Chiricahua Mountains, Arizona, have monosyllabic songs (Konishi 1964a).

Konishi (1964a, b) described songs of Dark-eyed Juncos from Berkeley, California. Most songs were monosyllabic, but a few (4 of 77) were bisyllabic. Also, individuals did not share syllables. Even between "subpopulations" some distance apart "there appear to be no local differences in the form of syllables or notes and no noticeable homogeneity within subpopulations" (Konishi 1964b:429). The exact size of repertoires of individual Berkeley juncos was not determined, but it appears that at least some individuals may have had several song types (Marler et al. 1962, Konishi 1964b).

Clearly, then, the Highland juncos are similar to yet different from both Berkeley and Durango juncos. In the Highlands, individual juncos have more song types than do Berkeley birds, and they may have more than the Durango birds. The Highlands birds certainly have more multisyllabic songs than do Berkeley juncos but fewer than Durango juncos. The Durango juncos use more different syllables in their total repertoire than do the Highlands birds, but the latter use more than the Berkeley birds. The Highlands juncos share syllables and song types with other population members, while Durango and Berkeley birds do not. Finally, the duration of syllables, intersyllables, and songs are essentially the same in all three localities, although Yellow-eyed Juncos appear to use more long syllables and have longer songs than do Dark-eyed Juncos (table 1).

Bird A obviously mimicked the Brown Creeper in its five-syllable song (fig. 2). This song was an integral part of A's repertoire and was used similarly to his other songs. Unfortunately, the ontogeny of this is unknown. The only other evidence of mimicry came from A's bisyllabic song, which consisted of one utterance of syllable 1 followed by about 17 repetitions of syllable 2. This song type was similar to songs of local Rufous-sided Towhees (*Pipilo erythrophthalmus*), but not as obviously as in the case of the song similar to the creeper's (see spectrograms in Borror 1975 and Kroodsma 1971). Mimicry is not common in juncos although it may occur in hand-raised individuals exposed early in life to the songs of other species, including those of Rufous-sided Towhees (Marler et al. 1962).

SUMMARY

The song repertoire of ten Dark-eyed Juncos at Carmel Highlands, Monterey County, California, is described and compared with that of Dark-eyed Juncos from Berkeley, California, and Yellow-eyed Juncos from Durango, Mexico.

Each individual in the Highlands population had a repertoire of between 3 and 7 song types. Most songs were monosyllabic consisting of one repeated syllable, but some were multisyllabic. Each bird had some song types that were unique, but each also shared syllables and song types with other individuals in this population. Most individuals' repertoires were stable over time. Most song types were highly stereotyped.

A number of dialectal differences exist between the Durango, Berkeley, and Highlands juncos. The Highlands juncos share syllables and song types. Durango and Berkeley juncos do not. The Highland juncos are intermediate between the Durango and Berkeley juncos in many respects, notably in the number of multisyllabic songs making up individual repertoires. In general, however, the Highlands juncos are more similar to Berkeley juncos than they are to Durango juncos.

A number of unusual song types and singing patterns are noted including one definite case of interspecific mimicry and one case of an individual singing subsong as a normal song type.

ACKNOWLEDGMENTS

We wish to express gratitude to L. F. Baptista and R. Tenaza for making the sound spectrograms, B. R. MacRoberts for drawing the figures, E. Loung for assistance in the field, J. Davis for many favors, and A. L. B. Williams for assistance in all phases of the work.

LITERATURE CITED

BORROR, D. J. 1961. Intraspecific variation in passerine bird songs. Wilson Bull. 73:57–78.

BORROR, D. J. 1975. Songs of the Rufous-sided Towhee. Condor 77:183–195.

KONISHI, M. 1964a. Effects of deafening on song development in two species of juncos. Condor 66:85–102.

KONISHI, M. 1964b. Song variation in a population of Oregon Juncos. Condor 66:423–436.

KROODSMA, D. E. 1971. Song variations and singing behavior in the Rufous-sided Towhee, *Pipilo erythrophthalmus oregonus*. Condor 73:303–308.

MARLER, P., AND D. ISAAC. 1960. Physical analysis of a simple bird song as exemplified by the Chipping Sparrow. Condor 62:124–135.

MARLER, P., AND D. ISAAC. 1961. Song variation in a population of Mexican juncos. Wilson Bull. 73:193–206.

MARLER, P., M. KREITH, AND M. TAMURA. 1962. Song development in hand-raised Oregon Juncos. Auk 79:12–30.

MULLIGAN, J. A. 1966. Singing behavior and its development in the Song Sparrow *Melospiza melodia*. Univ. California Publ. Zool. 81:1–76.

THIELCKE, G. 1969. Geographic variation in bird vocalizations, p. 311–339. *In* R. A. Hinde [ed.], Bird vocalizations. Cambridge Univ. Press, Cambridge, England.

THOMPSON, W. L. 1970. Song variation in a population of Indigo Buntings. Auk 87:58–71.

THORPE, W. H. 1961. Bird-Song. Cambridge Univ. Press, Cambridge, England.

Address of second author: 740 Columbia St., Shreveport, Louisiana 71104. Accepted for publication 23 June 1976.