

in measured ground speeds. Flying at minimum power velocity (Vmp) or maximum range velocity (Vmr) may be of less importance to birds flying at or near the nest area with abundant resources, than to birds on migration.

Non-migratory flight speed is determined by behavioral activities of birds and delimited by morphologic, physiologic, and aerodynamic constraints. Determination of flight speeds of birds in their daily habitat is necessary for closer examination of energetic costs of flight.

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Song variation within and among populations of Red-winged Blackbirds.—Evolution of micro-geographic song variation (e.g., dialects) and sizes of song repertoires continues to be a major interest, and comparative data from different populations of widespread species can help us understand the forces that produce such song variation. Because Simmers (1975) found no obvious differences in song of Red-winged Blackbirds (*Agelaius phoeniceus*) among New England sites, and because differences in song form and repertoire size are not substantial among northern, mostly migratory populations (e.g., Smith and Reid 1979, Yasukawa et al. 1980, Yasukawa 1981, Brenowitz 1983), we tested whether vocal behavior in two more southern and perhaps more sedentary populations, one in Florida and one in California, differed from northern populations.

Methods.—We recorded Red-winged Blackbirds at several sites. Our most intensive efforts were at Carr Lake, near Tallahassee, Florida, 22–29 April 1987. Most males had been banded with distinctive combinations of colored and aluminum bands. One male (male 17; see

Table 1) was recorded again five years later, on 21 April 1992. Supplemental recordings were made at three additional locations in Florida during April and May 1987 and April 1992: (1) St. Marks National Wildlife Refuge, about 60 km south of Carr Lake; (2) Orlando; and (3) Naples. Males were recorded in central California at three locations: (1) San Luis National Wildlife Refuge (near Los Banos), (2) Grizzly Island Wildlife Area (Fairfield), and (3) Gray Lodge State Wildlife Area (Gridley). Males at these secondary locations in Florida and California were not banded but were identified readily by their singing locations over a period of several hours.

We made most recordings with a Nagra IS-DT tape recorder and Sennheiser 106 microphone mounted in a 60-cm aluminum parabolic reflector. Supplemental recordings at Carr Lake and Naples and all of the recordings from Orlando were made with cassette tape recorders (Marantz PMD-221, Sony WMD6, or Realistic CTR-85) and a Sennheiser 816 shotgun microphone or Sony condenser microphone in a 33 cm Sony parabola. Occasional playback of a single song from a cassette recorder was used to stimulate singing from the males.

In the laboratory, song repertoires were analyzed with a Kay Elemetrics DSP5500 spectrum analyzer. Because males typically repeated a given song form several times before advancing to the next, males themselves provided a convenient measure for distinguishing variation within song types from variation among song types. Songs of a given male occurred as discrete types, with no continuous variation among the types, and repertoires could be identified. Each occurrence or series of a given song type, when separated by 10 or more songs of other types, was called a "bout," i.e., one "independent" occurrence of that particular song type.

To quantify differences in song among our Florida samples, we measured the rate of delivery of repeated units in the "trill" portion of the song. For most songs, the repeated units were discrete "syllables" clearly separated by silence from adjacent syllables (e.g., in Fig. 1; 9A, 9B, 11A), but in other songs the trill consisted of a rapid train of amplitude and/or frequency modulated pulses (in Fig. 1; 11B, 9C, 11D). For simplicity, we refer to this measure of repeated units as "syllables/second."

Results.—At Carr Lake, Florida, our estimates for song repertoires for 22 males ranged from four to eight types. Most males (12 of 22) sang five different types, and five males sang six types ($\bar{x} = 5.2$; see Table 1, Fig. 1). The number of sampled bouts for each male was sufficiently large that our repertoire estimates were largely independent of the sample size of total bouts recorded. Data from one male indicated that a song repertoire can be maintained intact from year to year. In April 1987, bird 17 used six song types; five years later, during April 1992, he was singing the same six types. In 11 recorded bouts during 1992, he used five types twice and his sixth one once. We could detect no between-year changes in the complex, multi-parted songs of this male.

We had fewer recordings from California, but the data suggested that repertoire sizes in California and Florida were not markedly different from each other. The four California males with the largest number of sampled bouts (12–16) each had four or five song types. Samples of only 12 bouts from each of the 22 Florida males also yielded four or five song types for 18 of the 22 males.

We found striking differences in the Red-winged Blackbird songs between two neighboring locations in Florida. A graph of one simple measure, the number of repeated syllables/sec in the song, was highly bimodal at Carr Lake. Of 122 different songs from the combined repertoires of all males (five songs were from males not listed in Table 1), 31 contained 8–18 syllables/sec (a "slow trill") and 89 contained >102 syllables/sec. Only two songs fell between these two groups, one at 62 and one at 72 syllables/sec. These distinctive "slow trill" songs comprised about one quarter of all song forms at Carr Lake and were sung by

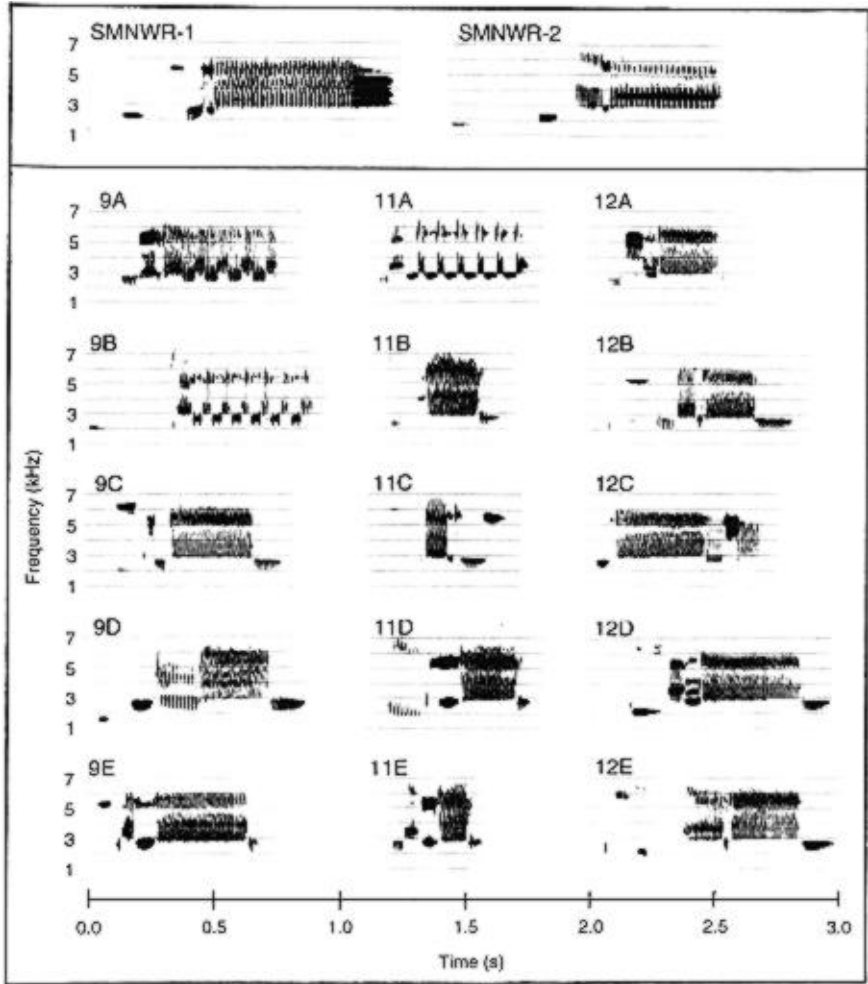


FIG. 1. Typical song repertoires for three male Red-winged Blackbirds (A–E for males 9, 11, 12) at Carr Lake, near Tallahassee, Florida, together with song types from two males at St. Marks National Wildlife Refuge (1 and 2, SMNWR), 60 km to the south. Carr Lake males typically had at least one or two song types with a relatively slow rate of syllable repetition (see 9A, 9B, 11A), but rates of syllable repetition in other songs were far more rapid. Many St. Marks refuge songs, however, such as the two illustrated here, had intermediate rates. Sonograms were produced on a Kay Elemetrics DSP5000 sonograph, with transform size of 100 pts (comparable to “wide-band” 300 Hz analog filter).

most (e.g., 18 of 22 intensively recorded males) of the birds there. At St. Marks Refuge, only 60 km south of Carr Lake and on the coast of the Gulf of Mexico, however, the structure of songs and the distribution of syllables/sec was markedly different (see Fig. 1). Of 38 recorded songs from about 25 individuals at St. Marks, six contained 8–18 syllables/sec

TABLE 1
SAMPLING EFFORT AND REPERTOIRE SIZE FOR 22 RED-WINGED BLACKBIRDS AT CARR
LAKE, TALLAHASSEE, FLORIDA

Bird ^a	Number of bouts in which each song type was recorded ^b								Number of bouts recorded
1	7	7	6	4					24
2	17	10	9	7					43
3	15	13	12	11					51
4	6	5	3	3	2				19
5	4	3	3	3	2				15
6	6	5	5	4	2				22
7	10	10	7	7	6				40
8	7	6	5	5	4				27
9	10	9	8	8	7				42
10	12	10	8	7	6				43
11	19	9	8	8	6				50
12	16	12	10	9	5				52
13	10	7	6	6	5				34
14	8	7	5	3	1				24
15	10	8	8	7	5				38
16	5	4	4	3	3	1			20
17	6	6	4	3	2	2			23
18	6	6	4	4	2	2			24
19	9	9	6	6	4	4			38
20	6	5	4	4	3	3			25
21	4	3	2	2	1	1	1		14
22	10	9	8	8	8	7	7	2	59

^a Birds listed in order of increasing repertoire size.

^b Numbers of bouts for each male's song type (i.e., the number of independent occurrences for each type), listed in decreasing order. Thus, bird 1 sang four song types in 24 bouts; two types occurred on seven different occasions, one on six occasions, and one on four occasions.

(16% at St. Marks, 25% at Carr Lake), 23 contained 28–89 syllables/sec (61% at St. Marks, 2% at Carr Lake), and nine contained >100 syllables/sec (24% at St. Marks, 73% at Carr Lake).

Our recordings from other locations in Florida also revealed population differences in song. Of 20 songs from Orlando and 26 from Naples, none contained the characteristic slow trills found at Carr Lake and, to a lesser extent, at St. Marks. Of the 84 total recorded songs at locations other than Carr Lake, most songs (53, or 63%) contained 38–92 syllables/sec, thus falling between the two peaks of syllable repetition for Carr Lake males.

California males produced a greater variety of song forms than did the Florida birds, but discrete song types from each male could readily be identified. Some of the distinctive Grizzly Island songs (e.g., A and B, Fig. 2), for example, lacked a trill of identifiable repeated units and consisted largely of a few introductory notes together with a long nasal sound (E. S. Morton, unpubl. data). Some songs consisted of a series of relatively pure tones without a distinctive concluding trill, some contained a complex series of introductory notes with only an abbreviated concluding trill (C and D, Fig. 2), and still others contained two well-developed trills (E and F, Fig. 2). Each song form was given repeatedly and consistently, with the same kind of delivery as that used by males of other populations. We therefore

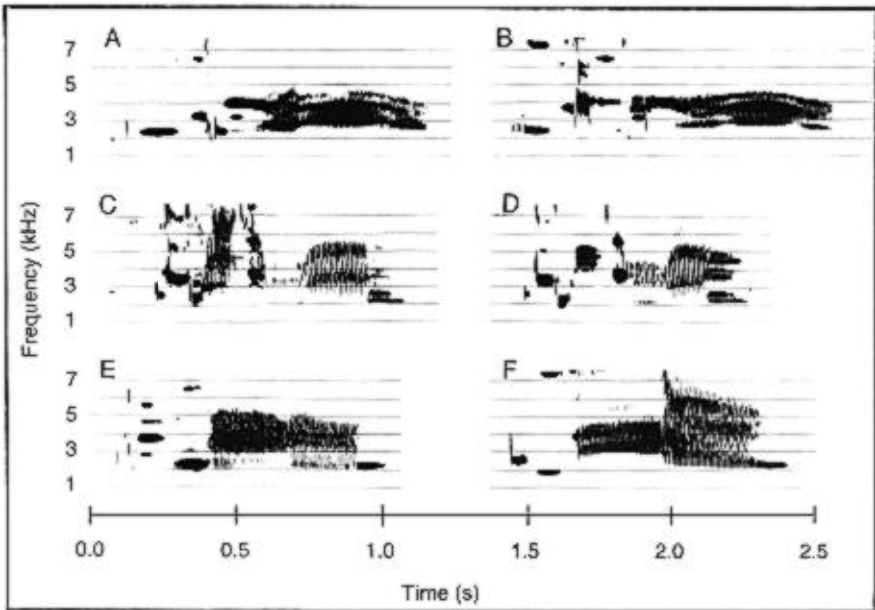


FIG. 2 Geographic variation of songs in California populations. Males within a given population shared similar songs (A and B from Grizzly Island, Fairfield; C and D, E and F from San Luis National Wildlife Refuge, Los Banos), thus resulting in local dialects.

classified each of these song forms as a type within a male's repertoire (cf Morton, unpubl. data).

Although the variable structure of songs prevented us from consistently using features such as syllable rates to demonstrate geographic variation within California, qualitative differences in the songs from location to location were obvious, even to the unaided ear. As in our Florida populations, neighboring males within California populations often shared similar song types (see Fig. 2). Additional surveys by Morton (unpubl. data) in some of these areas revealed abrupt changes in song form over distances of less than 1 km.

Discussion.—The average or median repertoire size of songs of males in local populations of Red-winged Blackbirds seems to be four or five. The two largest samples of published repertoires are from central Indiana, where males sing two to eight song types ($\bar{x} = 3.9$, median = 4, $N = 49$ males; Yasukawa et al. 1980), and from southeastern New York, where males sing three to eight types ($\bar{x} = 4.8$, median = 5, $N = 34$ males; Yasukawa 1981). The majority of Florida birds, and probably California birds also, had repertoires of four or five types.

Most authors (e.g., Kim et al. 1989) have inferred that Red-winged Blackbirds are "open-ended learners" and can change the composition or increase the size of their repertoire with age, but our data from one Florida male suggest that additional data are needed on this topic. In the laboratory, first and second year males are able to learn songs (Marler et al. 1972, Kroodsma, unpubl. data), but males typically do not breed until they are two years old (Orlans 1980). In the field, older breeding males seem to have larger song repertoires than do younger breeding males (Yasukawa et al. 1980), but this difference could arise

without learning if birds with larger repertoires have greater survival rates (Lambrechts and Dhondt 1986, Hiebert et al. 1989). Field data from Carr Lake male 17 reveal that a repertoire of six songs can be maintained intact over a period of five years. Stability in song form from year to year was also reported by Simmers (1975).

We are not able to compare the extent of micro-geographic song variation in our Florida and California samples with those of more northern populations. Although the basic form of the *konk-la-reeee* song pattern seems relatively constant over broad areas of the eastern United States (Marler et al. 1972, Simmers 1975, Smith and Reid 1979, Yasukawa et al. 1980, Brenowitz 1983), no quantitative survey such as we used in Florida has been attempted. Song forms in the eastern United States certainly do not change as dramatically over distance as do the songs of California males (Morton, unpubl. data; Brenowitz 1983), but changes nevertheless might occur, perhaps in more subtle aspects of the song.

The apparent local differentiation in songs among populations in California and Florida in relation to that of more northerly populations may be a consequence of the fact that northern populations are highly gregarious in winter. Migratory red-wing populations undoubtedly mix in migration and in the massive southern winter roosts formed mostly by males (Burt and Giltz 1977, Dolbeer 1978). Although adults can be highly site faithful from one season to the next (Yasukawa et al. 1980, Beletsky and Orians 1987), the extensive mixing of populations from different breeding sites probably contributes both to relatively high dispersal distances, perhaps especially by first-year male birds (Knittle et al. 1987), and to a relatively high gene flow among populations (Cox and James 1984, Ball et al. 1988, Gavin et al. 1991). Males do sing in these large flocks (pers. obs., and Brenowitz 1981), and any song learning by first or second year males (Marler et al. 1972), and especially by adults, would lead to song similarities over the breeding range represented by the flock. Birds of our Florida and California sites flock less in winter than do those blackbirds of most previous studies. In northern Florida, data from measurements of birds in both breeding season and winter suggest that males are sedentary, although females migrate (James et al. 1984). Birds of central California also appear to be resident the year round (Van Rossem 1926). The more sedentary behavior of the males would lead to increased vocal isolation of populations and an increased degree of local song variation.

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Nest site selection by birds in Acacia trees in a Costa Rican dry deciduous forest.—Little is known about the criteria that tropical birds use to choose nest sites because the spatial complexity of tropical forests allows birds to conceal nests effectively (Skutch 1976). Nests in dry forests are easier for researchers to find and identify than those in wet forests because