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Differences in Song and Sexual Dimorphism between Cuban and North American Red-winged Blackbirds (*Agelaius phoeniceus*)

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In many species of birds, song is characteristic of the male (Nottebohm 1975). However, an increasing number of studies have also found that females sing (reviewed in Farabaugh 1982, Ritchison 1983). Usually, in such cases, male and female songs are distinctly different in structure but have similar functions, such as territory advertisement and defense (Armstrong 1963, Farabaugh 1982, Ritchison 1983). In temperate species, female song is relatively rare; however, it is more common in tropical species, where females often duet with their mates (Farabaugh 1982). Red-winged Blackbirds (*Agelaius phoeniceus*) are one of the few known species in which males and females sing different songs in temperate populations (Beletsky 1983, Searcy 1989a), whereas pairs duet in a tropical population (Farabaugh 1982, E. S. Morton pers. comm.). This intraspecific variation provides an opportunity to study the adaptive function of song and other sexually selected characteristics, such as plumage and body size.

We compared sexual differences in song, plumage and body size between temperate Red-winged Blackbirds in eastern North America (*A. p. phoeniceus*) and tropical Red-winged Blackbirds in Cuba (*A. p. assimilis*). Red-winged Blackbirds breed throughout most of North and Central America; the distribution of *A. p. phoeniceus* extends from north-central Ontario to northern Florida and from the Mississippi River to the Atlantic Ocean (Peters 1968, Power 1970), whereas *A. p. assimilis* is endemic to the western part of Cuba (Peters 1968, Garrido 1970, Bond 1985). In this paper we show that Cuban Red-winged Blackbirds exhibit relatively less sexual dimorphism in song, plumage and body size than North American Red-winged Blackbirds. We propose a hypothesis to account for these differences and suggest a possible test.

The songs of Cuban Red-winged Blackbirds were recorded in the Zapata Swamp at Treasure Lake (22°10′N; 81°50′W) during 9–10 April 1991. In Cuba, the birds were observed in bottle-brush trees (*Callistemon speciosus*) and tall grasses (*Phragmites* spp.) at the periphery of the lake. Two birds were observed carrying strips of vegetation, which suggested that April was the beginning of the breeding season for Cuban Red-winged Blackbirds. Temperate Red-winged Blackbird songs were recorded between April and June 1991 near Kingston, Ontario, Canada (44°33′N; 76°20′W). In Ontario, males were associated with breeding territories in cattail (*Typha* spp.) marshes, similar to other populations throughout North America (Nero 1956, Orians 1980).

Songs were recorded with an Audio-technica AT815a directional microphone and Sony Professional cassette recorder. Sonagrams were analyzed on a Kay Elemetrics DSP Sonagraph Model 5500, using a 16-kHz frequency axis with a 512-point transform (117-Hz band-pass filter) and a time axis of 2 s with a 200-point transform (300-Hz band-pass filter). We analyzed duets of pairs in Cuba and solo songs of individuals in Cuba and North America. We considered a duet as one pair of songs, one song produced by each sex, overlapping or less than 1 s apart, and given repeatedly in sequence (e.g. Farabaugh 1982; Fig. 1). Duets were performed by one male and one female perched 0.5 to 2.0 m apart. In most cases the male was perched above the female and they were facing each other. For simplicity we refer to a duetting male and female as a pair; however, it was not known whether the two individuals were mates. Songs given in sequence by the same individual, but not closely followed by the song of another individual, were considered solo songs. For solo songs the following
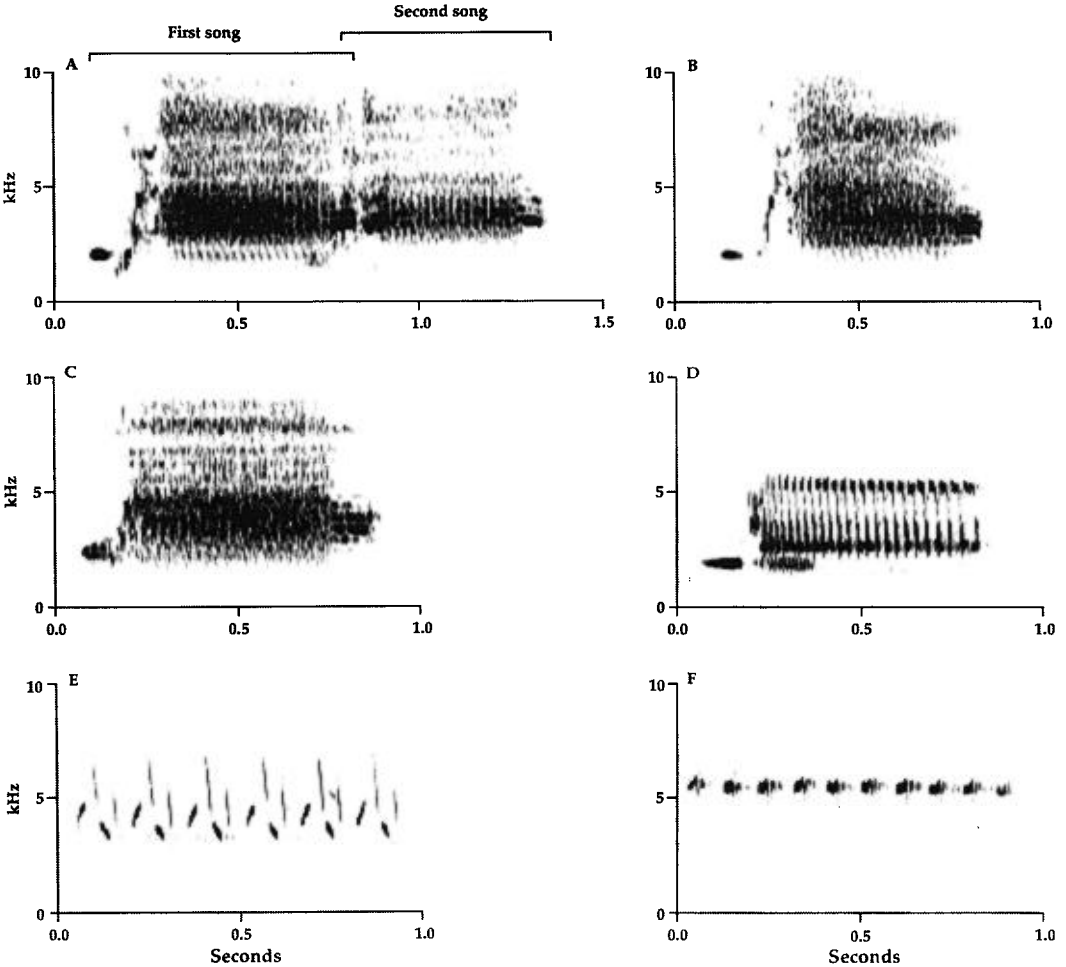
Fig. 1.   (A) Duet of Cuban Red-winged Blackbirds (*A. p. assimilis*). Either sex may produce the first or second song (female leading and male following shown here). Songs may overlap (shown here) or be separated by less than 1 s. Solo songs of Cuban Red-winged Blackbirds shown for (B) male and (C) female. Solo songs of North American Red-winged Blackbirds (*A. p. phoeniceus*) from Ontario shown for: (D) male; (E) female type 1; and (F) female type 2.

characteristics were determined: mean song duration, mean maximum frequency, mean minimum frequency, and mean frequency range (Beletsky 1983). For duets, the above characteristics were determined for both the male and female songs of the duet, as well as mean time between songs or mean song overlap, and interduet interval (the time between duets).

Duets of three different pairs were recorded in Cuba; however, only one pair produced a series of duets in which the male and female alternated in leading the duet. Thus, the examination of song characteristics in relation to leading sex was restricted to one pair, and the data for all duets included three pairs. We assumed that recordings made at different locations over 100 m apart were of different pairs. Solo songs and duets were not recorded from the same individuals.

In Ontario, songs recorded from 10 males and 20 females were used in the analysis. All males were color banded for individual identification. We were not able to identify females individually; therefore, we recorded only one female's song from each of 20 male territories and considered these different individuals.

At both sites, multiple recordings were made of the solo songs of each individual and the duets of each pair. To avoid pseudoreplication we calculated a mean value for each individual or pair. Thus, sample size (*n*) represents the number of individuals or pairs. Comparisons of song characteristics between groups were made with Mann-Whitney *U*-tests.

Observations of birds in the field and examination of specimens from museum collections were used to

TABLE 1. Characteristics ($\bar{x} \pm$ SE) of first and second songs of Cuban Red-winged Blackbird (*A. p. assimilis*) duets. Data for one pair in which female led six duets and male led three duets; and all pairs ($n = 3$ pairs).

	One pair when led by		All pairs
	Female	Male	
Song duration (s)			
First	0.65 ± 0.01	0.73 ± 0.01	0.67 ± 0.02
Second	0.74 ± 0.01	0.63 ± 0.01	0.66 ± 0.02
Maximum frequency (Hz)			
First	8,113 ± 110	8,055 ± 87	7,891 ± 133
Second	8,036 ± 79	8,013 ± 93	8,016 ± 126
Minimum frequency (Hz)			
First	1,393 ± 12	1,426 ± 13	1,510 ± 20
Second	1,540 ± 37	1,493 ± 109	1,567 ± 18
Range (Hz)			
First	6,720 ± 103	6,627 ± 96	6,336 ± 151
Second	6,496 ± 74	6,613 ± 87	6,503 ± 72
Time between songs			
within duet (s)	0.10 ± 0.01	0.07 ± 0.02	0.09 ± 0.01
Song overlap (s)	0.07	0.08	0.09 ± 0.01
Time between duets (s)	12.4 ± 1.6	10.8 ± 0.4	11.6 ± 1.3

examine sexual differences in plumage and body size between populations. Wing chord and tarsus length were measured to evaluate intrasexual differences in body size between populations and relative sexual dimorphism. We used the ratio of male-to-female tarsus length and wing chord as indices of sexual demorphism (i.e. Hughes and Hughes 1986). In addition, we compared body mass between *A. p. assimilis* (Olson 1985) and *A. p. phoeniceus* (L.A. Whittingham unpubl. data from Michigan).

Duets always included only two songs, one produced by each sex (Fig. 1A). We recorded nine, four and two duets from three pairs of Red-winged Blackbirds in Cuba. In one pair the female led six duets and the male led three duets. In the other two pairs the male led all duets. In general, male and female songs of duets were similar whether the male led and the female followed, or the female led and the male followed (Table 1). Maximum and minimum frequencies, and frequency range did not differ between the sexes regardless of which sex led the duet ($P > 0.40$). The time between the two songs of the duet ($U = 8, P > 0.20$) and between duets ($U = 12, P > 0.40$) also did not differ in relation to which sex led the duet. However, song duration was significantly shorter for females than males, when females were leading or following in the duet (leading, $U = 18, P < 0.02$; following, $U = 18, P < 0.02$).

Solo songs were recorded in Cuba from 3 males and 1 female, and in North America from 10 males and 20 females (10 females for each of two song types; Table 2). In Cuba, solo songs of both sexes (Fig. 1B, C and Table 2) were similar to songs in the duets (Fig. 1A and Table 1). Song duration, maximum and min-

imum frequencies, and frequency range were similar between solo and duet songs for both male and female Cuban Red-winged Blackbirds ($P > 0.30$). Compared with Cuban males, solo songs of North American males were significantly longer ($U = 27, P < 0.04$), lower in maximum frequency ($U = 30, P = 0.01$), and reduced in frequency range ($U = 30, P = 0.01$; Fig. 1B, D and Table 2). However, the minimum song frequency did not differ between North American and Cuban male songs ($U = 24, P > 0.10$).

Similar to Beletsky (1983), we found two distinct song types of North American females (Fig. 1E, F). Female songs in Cuba and North America were very different in structure (Figs. 1C, E, F). Songs of Cuban females were shorter, and had greater maximum frequency, lower minimum frequency and greater frequency range than North American female songs (Table 2). We never heard Cuban females sing either type of North American female song. If Cuban females used these vocalizations early in the breeding season (i.e. during nest building) with a frequency similar to North American females, then we would have expected to hear them during our recording sessions. Further observation will be necessary to determine whether the North American song types are present in the Cuban female's vocal repertoire.

In summary, the Cuban male and female songs were very similar to each other. The Cuban songs were similar in structure to North American male songs, although North American male songs were produced at lower frequencies. The songs of Cuban females were very different from either song type of North American females.

The plumage of Cuban and North American males

TABLE 2.   Characteristics of solo songs ($\bar{x} \pm$ SE) of male and female Red-winged Blackbirds from Cuba (*A. p. assimilis*) and North America (*A. p. phoeniceus*).

	Song duration (s)	Frequency (Hz)			No. individuals (*n*)	Songs/ individual
		Maximum	Minimum	Range		
Cuba						
Male	0.7 ± 0.05	7,930 ± 106	1,825 ± 10	6,105 ± 216	3	5, 4, 4
Female	0.6	7,733	1,387	6,376	1	3
North America						
Male	0.9 ± 0.03	5,506 ± 28	1,694 ± 62	3,812 ± 43	10	1
Female, type 1	1.9 ± 0.07	7,010 ± 44	2,986 ± 35	4,024 ± 48	10	1
Female, type 2	1.2 ± 0.1	5,688 ± 206	2,524 ± 168	3,164 ± 279	10	1

is similar. Males are uniformly jet black in color with scarlet lesser wing coverts (epaulet) and a narrow yellow margin at the lower edge of the epaulet. In both populations, males can conceal the epaulets with black scapular feathers. In North America, males display their epaulets in flight and in a song-spread display where the wings are arched and fanned out (Nero 1956). In Cuba, we only saw males display their epaulets in flight; males did not perform song-spread displays and always concealed epaulets while singing.

Female plumage varies greatly between Red-winged Blackbirds in Cuba and North America. North American females are brown and heavily streaked, and older females develop a small amount of pink or red color on the shoulders and chin (Crawford 1977). In contrast, Cuban females have uniformly coal-black plumage (Barbour 1943, Bond 1985, pers. observ.).

We examined 66 *A. p. assimilis* specimens from Cuba and 85 *A. p. phoeniceus* specimens from eastern North America (New York, Ontario and Michigan). For both sexes, wing chord was significantly longer in North American than in Cuban birds (Table 3). Conversely, tarsus length was significantly longer in Cuban than in North American birds for both sexes (Table 3). Cuban birds were less sexually dimorphic in wing chord (1.15:1) than North American birds (1.22:1), but similar in tarsus length (North American birds 1.10:1; Cuban 1.11:1). Body mass of Cuban males (50.6 ± SE of 0.7 g, $n = 10$) was significantly less than that of North American males (69.7 ± 0.6 g, $n = 49$; $U = 490$, $P < 0.001$). Similarly, body mass of Cuban females (39.4 ± 0.7 g, $n = 11$) was significantly less than that of North American females (44.4 ± 0.6 g, $n = 25$; $U = 253$; $P < 0.001$). The male-to-female body mass ratio was 1.28:1 in the Cuban population and 1.56:1 in the North American birds.

Song, plumage and body size were more similar between the sexes in Cuban (*A. p. assimilis*) than in North American (*A. p. phoeniceus*) Red-winged Blackbirds. In Cuba, both sexes sing a similar song as a duet and as solo songs, the plumage of both sexes is

entirely black, although the males have red epaulets, and both sexes are more similar in size. When singing, the males often concealed the entire epaulet and both sexes were essentially indistinguishable by song or plumage. Sex was easily determined only in flight when the male's red epaulets were exposed. In most other populations of Red-winged Blackbirds throughout North and Central America, females have streaked brown plumage and the sexes are easily distinguished (Power 1970, Dickerman 1974). However, similar to the Cuban population, females are uniformly dark (dark brown or sooty gray) in a central Mexican population, *A. p. gubernator* (Dickerman 1974).

Sexual dimorphism is often correlated with mating system. Populations studied throughout North and Central America are polygynous (e.g. Orians 1973, 1980). In contrast, the mating system of the Cuban population is virtually unknown. There is no evidence for polygony, but their vocal behavior suggests that Cuban Red-winged Blackbirds may be monogamous. For example, duets performed by one male and one female are generally associated with prolonged monogamous pair bonds (Farabaugh 1982). Within the family Icteridae, duetting has been described only for the Melodious Blackbird (*Dives dives*), which breeds

TABLE 3.   Wing chord and tarsus length (mm; $\bar{x} \pm$ SE) of adult male and female Red-winged Blackbirds from Cuba and North America.

	n	Wing chord	Tarsus length
Male			
North America	42	121.5 ± 0.5	27.4 ± 0.2
Cuba	29	108.8 ± 0.4	28.4 ± 0.2
t		18.0***	3.1**
Female			
North America	43	99.9 ± 0.5	24.8 ± 0.2
Cuba	37	94.4 ± 0.6	25.6 ± 0.1
t		7.4**	4.3**

**, $P < 0.01$; ***, $P < 0.001$.

monogamously (Orians 1983). Additional studies of individually marked birds will be necessary to describe the mating system of the Cuban Red-winged Blackbirds in detail.

Why should the sexes be so similar in Cuba and so different in North America? The similarity in breeding habitat between populations suggests that this is not a major factor influencing reduced sexual dimorphism in the Cuban birds. We suggest that the differences in sexual dimorphism may be related to the differences between populations in the roles of the sexes in territorial defense. In North America, aggressive interactions among conspecifics are intrasexual. Larger male than female body size is favored by intense competition among males to establish and defend territories throughout the breeding season (Searcy 1979). For males, the primary function of song is territorial defense (Yasukawa 1981, Searcy 1989b). North American females often sing during aggressive interactions with other females (Beletsky 1983), but do not defend territories per se (Searcy 1988). While aggressive interactions among females favor large body size, physiological constraints during the breeding season select for smaller body size in females (Langston et al. 1990).

In Cuba, duetting and reduced sexual dimorphism may be associated with more equal roles between the sexes in territorial defense throughout the year. In Melodious Blackbirds, duetting is associated with vigorous and prolonged defense of territories by resident pairs against paired intruders (Orians 1983). However, in this species each sex contributes different vocalizations to the duet. Duetting could also facilitate territorial defense by pairs in Cuban Red-winged Blackbirds; however, it still would not account for the similarity in song and plumage between the sexes. We suggest that, in addition to the defense of territories by pairs, the similarities between the sexes allow Cuban Red-winged Blackbirds to successfully defend the territory against individual intruders of either sex. This hypothesis can be tested by observing residents' responses to natural occurrences of paired and individual intruders, and by using model (taxidermic mount) presentations and song playbacks to simulate territorial intrusions by pairs and individuals. If the function of the duet and sexual similarities in song, plumage and size are related to territorial defense, then we would expect: (1) resident pairs to respond to paired intruders; and (2) residents of either sex to respond equally to individual intruders of either sex, rather than more strongly to intruders of the same sex.

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Intestinal Transit: How Can It Be Delayed Long Enough for Birds to Act as Long-distance Dispersal Agents?

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We recently described the rhythmic oscillating complex (ROC), a myoelectric/motor complex in avian small intestine (Clench et al. 1986, Clench and Mathias 1992). Because the gastrointestinal tract resumes fed-state motor activity after a ROC has occurred, we suggested that this motor event functions to recycle the small amount of food remaining in the gut of a bird that has been unable to continue feeding. In addition to its physiological importance, such a mechanism has ecological implications, especially in regard to how birds may disperse the propagules of other organisms.

In brief, we demonstrated in galliforms that after an individual has undergone a long fast and the proximal gut has emptied of food and become quiescent, ROCs begin to occur (Clench and Mathias 1992). The complex consists of rapidly moving bursts of spike potentials/ring contractions that propagate in alternating directions, orad and aborad—apparently a back-and-forth stripping motion that travels the entire length of the small intestine. ROC activity is prolonged, continuing for a mean of 7.6 min in chickens (*Gallus gallus*) and 15.4 min in a Ring-necked Pheasant (*Phasianus colchicus*). After a ROC has ended, fed-state motor activity resumes in the stomach and small intestine, indicating that food has been moved into the proximal tract for further digestion and absorption— seemingly recycled, probably from the distal part of the tract. As a bird continues to fast, ROCs also continue to occur periodically. How often the complex occurs is individually variable, but it is no more frequent than every 3 h and the intervals are often much longer. With each ROC, the distal gut is restimulated

into fed-state activity that lasts for shorter and shorter periods. A reasonable conclusion from this last observation is that in a long-fasting bird, after each successive ROC, less and less food remains in the tract to be recycled and thus the fed-state activity restimulated by the complex gradually diminishes.

The length of time required for food to move through the avian digestive tract ("transit time") has been measured in many species by using nondigestible, nonabsorbable physical markers or radioactive tracers (Duke 1986). Although many variables must be considered, food passage in birds is generally rapid compared with that of mammals (especially ruminants) or other vertebrates (c.f. data in Warner 1981, Karasov et al. 1986). For example, studies have shown that color-marked barium sulfate required only 22.9 to 69.4 min to move through the gut of passerines, based on data from about 700 individuals of more than 30 species (Herrera 1984, Jordano 1987). Although some of those measured transit times could have been unnaturally fast because barium ions stimulate intestinal tissue (Burnstock and Holman 1966, Daniel 1968), Herrera (1984) noted that fruit passage times he also recorded in some of the birds were often faster than those of the barium.

Some frugivorous species have been shown to have particularly rapid transit. Holthuijzen and Adkisson (1984) timed the passage of red cedar (*Juniperus virginiana*) cones and flowering dogwood (*Cornus florida*) fruits through fasted Cedar Waxwings (*Bombycilla cedrorum*) at means of 11.7 and 22.9 min, respectively. Walsberg's (1975) elegant study of Phainopeplas (*Phainopepla nitens*) demonstrated that desert mistletoe