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DIFFERENCES IN SINGING BEHAVIOR BETWEEN RUFOUS-COLLARED SPARROWS IN COSTA RICA AND NORTHWESTERN ARGENTINA[1]

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Key words: Zonotrichia capensis; *Rufous-collared Sparrow; song repertoire; countersinging.*

The Rufous-collared Sparrow (*Zonotrichia capensis*) is one of the most common passerine species in Latin America, ranging from southern Mexico to Tierra del Fuego. Although there are studies on the vocal behavior of this species from several locations across South America (see King 1974, Nottebohm 1975, Tubaro et al. 1993), most have concentrated on populations in northwestern Argentina (Nottebohm 1969, King 1972, Handford 1988, Lougheed and Handford 1992). Males within these populations sing songs that have two distinct parts: an introductory theme, consisting of one to five usually dissimilar whistles, and a terminal trill, made from a series of repeated, morphologically similar notes (Nottebohm 1975). In northwestern and west-central Argentina, song dialects in Rufous-collared Sparrows are defined by quantitative variation in trill rate (Nottebohm 1969), and map closely onto patterns of original natural vegetation (Nottebohm 1975, Handford 1988).

Based on studies in Argentina, Rufous-collared Sparrows have been characterized as having a repertoire of one song type per individual; that is, although song themes may vary considerably among individuals within a population, and trill rates may vary between populations in different habitats, there is little variation in the songs of a single individual. Nottebohm (1969) analyzed at least five songs (and occasionally up to 30 songs) from each of 523 Rufous-collared Sparrows from 29 populations in northern Argentina. He reported that only 19 birds (3.6%) sang more than one song type. Similarly, King (1972) studied song variation in three populations in northwestern Argentina and found that only five of 771 birds (0.6%) sang more than one song type. Other recent observations of Rufous-collared Sparrows in northwestern Argentina have also noted song stereotypy within individuals across a breeding season (S. C. Lougheed, pers. comm.).

Since studies investigating the vocal behavior of Rufous-collared Sparrows have almost exclusively concerned populations in northwestern Argentina, the generality of these observations is unknown. To determine if song stereotypy is common throughout their range, I recorded songs of Rufous-collared Sparrows from three localities in Costa Rica. My observations indicate that, unlike birds in northwestern Argentina, Rufous-collared Sparrows in Costa Rica commonly possess individual song repertoires and lack the terminal trill.

METHODS

I recorded songs from Rufous-collared Sparrows between 14–26 February, 1994, at three main sites in

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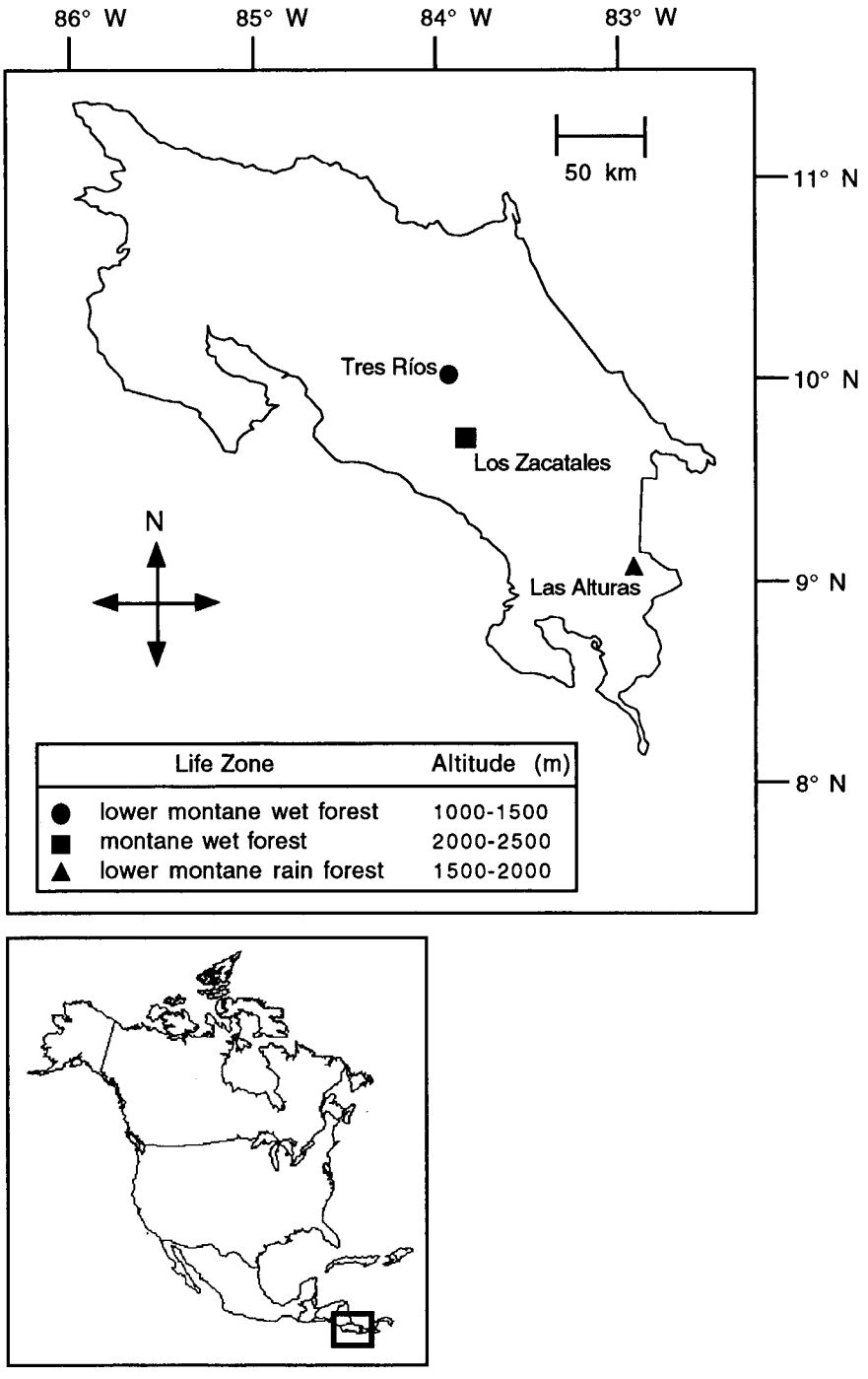

FIGURE 1. Location of Rufous-collared Sparrow recording sites in Costa Rica. Life zones are defined by native vegetation that would have corresponded to each recording site had that site been undisturbed (Janzen 1983).

Costa Rica: Tres Ríos, Los Zacatales, and Las Alturas (Fig. 1). Rufous-collared Sparrows breed throughout the year in Costa Rica, with a peak in breeding activity from February to April (Wolf 1969, Stiles and Skutch 1989). All of the individuals I recorded sang loud, stable songs and displayed territorial behavior; thus, they were assumed to be males. Songs were recorded from distances of 4–8 m using an Audio-technica 815a unidirectional microphone and a Sony Walkman Professional WM-D3 cassette recorder. I recorded between five and 20 songs from 34 individuals at Tres Ríos, 20 individuals at Las Alturas, and six at Los Zacatales. I also recorded one individual at Cerro Buenavista (northwestern highlands of Cordillera de Talamanca) and one individual at the Wilson Botanical Garden near San Vito.

All recordings were made in human-altered habitats. At Tres Ríos, birds sang from bushes or power lines along busy roadsides, and in urban yards. At Los Zacatales, I recorded birds in cattle pastures, urban yards and forest edge scrub. At Las Alturas, birds sang predominantly from fence posts along the perimeter of cattle pastures, as well as from roadside scrub vegetation, urban yards and banana plantations. The habitat surrounding each site and between sites was human-altered and generally open (although the pastures at Las Alturas border primary lower montane rain forest reaching westward into Panama; see Fig. 1), but it is not known whether the recording sites were part of a single continuous population.

I generated sonagrams from all recordings using a Kay Elemetrics DSP Sona-Graph Model 5500. I assessed song variation within individuals by simply identifying males that sang different song types. Song types were defined by the qualitative structure and sequence of their notes. Different theme notes were classified into four categories: *Type 1*—level, or close to level inflection; *Type 2*—rising inflection; *Type 3*—falling inflection; and *Type 4*—rising then falling (from Handford and Lougheed 1991).

I quantified song diversity within each site by dividing the total number of different theme types by the number of birds recorded. When calculating the number of theme types at a site, I considered only the first five songs recorded from each bird so that variation in the number of songs recorded per individual would not affect measures of song diversity. I compared song diversity between sites in Costa Rica and northwestern Argentina using data reported by Nottebohm (1969).

RESULTS

Of the 62 Rufous-collared Sparrows recorded in Costa Rica, 17 individuals (27%) sang more than one song type. Individuals with more than one song type changed only the theme note types and sequence between songs. Three birds were recorded singing four different song types, four sang three song types, and ten sang two song types. At least one individual from each of the three sites was recorded singing different song types (see Fig. 2). The individual recorded near San Vito also sang two song types.

Several of the birds employed a repertoire of different song types during the course of countersinging with other males. Of the 62 birds, twelve (six duos) were recorded while engaged in countersinging bouts (where one individual consistently sang immediately following the song of his neighbor). Individuals engaged in countersinging changed their song to a type that differed from that sung by the other male, or matched the song type of the other male, or both (e.g., Fig. 3). Although no systematic measures of breeding density were made, the density of singing birds appeared greater at Tres Ríos than at Los Zacatales or Las Alturas.

Of the six individuals recorded at Los Zacatales, and of the 20 individuals recorded at Las Alturas, none had songs with a terminal trill (e.g., Fig. 2b, c). Males recorded at Cerro Buenavista and San Vito also lacked a trill. Instead, all songs consisted of long, whistled notes, that were otherwise similar to those found in song themes reported in northwestern Argentina. In contrast, the 34 individuals recorded in Tres Ríos had songs with an introductory theme and a terminal trill (e.g., Fig. 2a), that were qualitatively similar to many of the songs recorded in Argentina.

Song diversity measured 0.53 at Tres Ríos, 1.00 at Los Zacatales, 0.65 at Las Alturas, and ranged from 0.04–0.52 at 13 sites in Argentina (data from Nottebohm 1969). Song diversity was greater at the Costa Rican sites than in northwestern Argentina (Mann-Whitney U; $z = -2.96$, $P = 0.009$).

DISCUSSION

My estimate of the incidence of multiple song repertoires in Costa Rica (27%) is probably conservative, considering that only five to 20 songs were recorded on one day from each individual. Past studies of this species in northern Argentina have generally reported within-individual song stereotypy using recordings of at least five songs from each bird. In Costa Rica, 13 of the 62 birds (21%) sang more than one song type within the first five songs recorded, and the other four individuals with song repertoires sang two song types within the first nine songs recorded. The method I used to assess repertoire size of Rufous-collared Sparrows from Costa Rica was similar to that used for studies in Argentina (e.g., Nottebohm 1969, 1975; King 1972). This suggests that songs from individuals within Argentina populations are indeed more stereotyped than songs from Costa Rican birds.

Bird song is generally thought to function as a mate attraction signal and/or a territory defense signal. Most studies of Rufous-collared Sparrows in Argentina have focused on the importance of song in assortative mating (e.g., Nottebohm 1975, Lougheed and Handford 1992). My observations of countersinging between males in Costa Rica suggest that song in this species may also serve in territorial defense. If countersinging is related to successful territory defense, then the incidence of song repertoires may be affected by the diversity of songs in a community; that is, males who live in communities where conspecifics sing different songs may need a repertoire of songs in countersinging. Perhaps songs from individuals within Argentine populations are more stereotyped than songs of Costa Rican individuals because song diversity is greater at Costa Rican sites than in northwestern Argentina. Other factors, such as breeding density, could affect repertoire

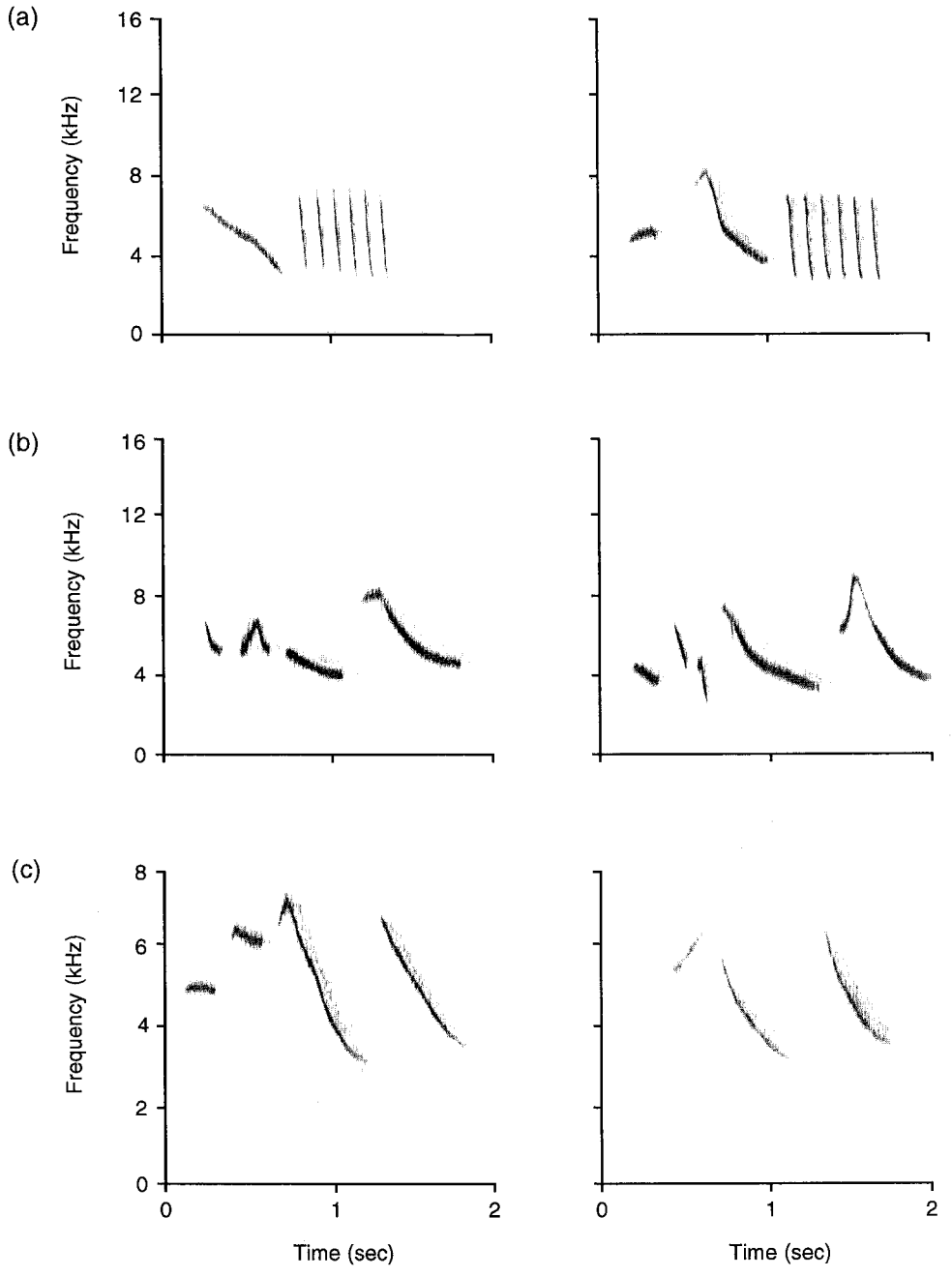

FIGURE 2. Song type variation of Rufous-collared Sparrows in Costa Rica. (a) Individual 18 at Tres Ríos sang two different song types: one with theme note 3, and one with theme note sequence 2–4. All birds at Tres Ríos sang songs with both a theme and a trill. (b) Individual 6 at Los Zacatales sang two different song types: one with a theme note sequence 3-4-3-4, and one with theme note sequence 3-3-3-3-4. All individuals at Los Zacatales lacked a terminal trill. (c) Individual 1 at Las Alturas sang two different song types: one with a theme note sequence 1-3-4-3, and one with theme note sequence 2-3-3. All birds at Las Alturas also lacked a terminal trill.

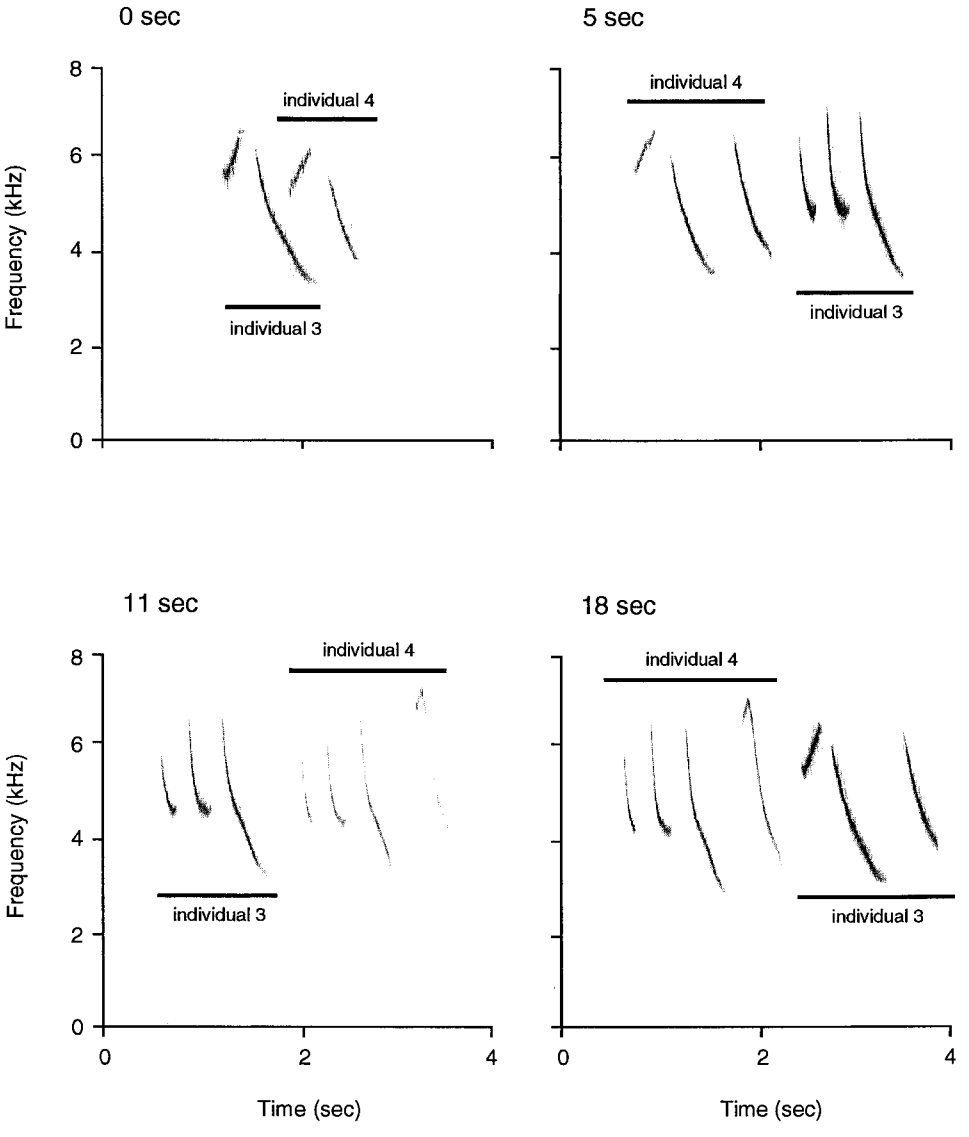

FIGURE 3. Countersinging by Rufous-collared Sparrows in Costa Rica. In this 18 sec. excerpt from a vocal exchange that lasted approximately 240 sec, individuals 3 and 4 each sing three different song types. The remaining 222 sec of countersinging between these two individuals consisted of 39 vocal exchanges in which individual 4 sang note type sequence 3-3-3-4 and individual 3 immediately followed with note type sequence 2-3-3 (as in the exchange at 18 sec). Countersinging was observed at all three sites.

size in a similar way; however, these were not measured for sites in Costa Rica.

At two of the three Costa Rican sites (Los Zacatales and Las Alturas), none of the individuals ($n = 26$ birds) used a terminal trill (males recorded at Cerro Buenavista and San Vito also sang songs without a trill). Nottebohm (1975) recorded Rufous-collared Sparrows at Cerro de la Muerte in Costa Rica and reported that they also sang songs without a terminal trill. The terminal trill of the birds from Tres Ríos was the only song feature that characterized this population; there were no other systematic differences among the songs I recorded at any other site. The Tres Ríos birds (with a relatively fast trill) were living at a lower altitude (Fig. 1) and apparently at a higher population density than birds that omitted the terminal trill (from Los Zacatales and Las Alturas). This pattern is consistent with that found by Nottebohm (1975) in his cross-continent study of patterns of song variation in Rufous-collared Sparrows. Still, while vocal dialects in northwestern Ar-

gentina have been defined by patterns of variation in trill morphology, the terminal trill is absent at two of the three Costa Rican study sites. Handford and Lougheed (1991) report that some males recorded in Monte desert habitat in northwestern Argentina sang languid, whistled songs with no trill (or a very slow trill), yet these birds were exceptional. A more comprehensive survey of Rufous-collared Sparrows from Central America is now needed to determine whether the birds in this study were also exceptional.

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INTRACLUTCH VARIATION IN EGG VOLUME OF GREAT CRESTED GREBES[1]

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Key words: Great Crested Grebes; Podiceps cristatus; *egg volume; hatching asynchrony.*

Grebes start incubating their eggs before the clutch is complete (Cramp and Simmons 1977). Grebe broods therefore hatch asynchronously and hatching asynchrony creates age and size hierarchies within broods. An often-cited hypothesis concerning the selection pressure to start incubation before the clutch is complete suggests that hatching asynchrony is adaptive because it facilitates a selective elimination of the younger offspring if food is short after hatching (Lack 1954). Slagsvold et al. (1984) suggested that variation in egg size within clutches is adaptive too, through its influence on hatching hierarchies (young hatching from larger eggs are heavier and survive better, at least in the short term), and used the relative size of the last-laid egg as a measure of intraclutch variation in egg size. Birds following a "brood-reduction" strategy are expected to have a relatively small final egg to accentuate the size hierarchy within the brood arising from asynchronous hatching.

Few have studied intraclutch variation in egg size of grebes. Fugle and Rothstein (1977) and Forbes and Ankney (1988) examined two and six clutches of the Pied-billed Grebe (*Podilymbus podiceps*), respectively,

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