Behav Ecol Sociobiol (1981) 8:203–206

Behavioral Ecology and Sociobiology

Vegetational Correlates of Variation in the Song of *Zonotrichia capensis*

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Received July 30, 1980 / Accepted February 20, 1981

Summary. 1. Geographical variation in the song of *Zonotrichia capensis*, the Rufous-Collared Sparrow, in northwestern Argentina is discussed. Boundaries between song 'dialects' appear to have been stable for at least 10 years. 2. The pattern of song change previously described on a transect across the Aconquija mountains is shown to be duplicated on similar transects elsewhere in these mountains. The association of song types with features of the environment is supported.

Introduction

It has been reported (Handford and Nottebohm 1976; Nottebohm 1969; 1975; Nottebohm and Selander 1972) that the rate of the trill in the song of *Zonotrichia capensis* changes gradually, or not at all, in areas of uniform habitat. However, in regions where habitat variables change rapidly, for example in mountain ranges, sharp dialect boundaries are often found, and some environmental correlates of this variation have been considered (Handford and Nottebohm 1976; Nottebohm 1975). The present report lends support to the idea that there are consistent associations between habitat and dialect type, at least in the northwest of Argentina.

Materials and Methods

In *Zonotrichia capensis*, dialects are defined by abrupt changes in the rate of the trill, which is the latter portion of the complete song (see Handford and Nottebohm 1976; King 1972; or Nottebohm 1969 for description of the structure of the song).

The material derives from tape recordings and observations made between October 1972 and February 1974, from observations made in January and February 1979 and from the works of King (1972) and Nottebohm (1969, 1975). Recordings were made at 9.5 cm/s with a Nagra III recorder and Sennheiser MKH 804 'shotgun' microphone. Observations utilized the field notation described by Nottebohm (1969) and King (1972). The song is very simple and, with experience, the major features of its frequency and temporal structure may be rendered unambiguously. From earlier fieldwork, I am assured of the reliability of the notation through comparison with sound spectrograms made later. In assessing trill rate, I agree with King's (1972) designation of 'able to count' and 'too fast to count'. Also, my extensive listening experience with these birds in the field and with sound spectrograms has permitted me to assign songs to classes on a comparative basis (e.g. a song may be "very similar to those of Tafí village" and therefore have a trill interval of approximately 60 ms).

Sample size is very variable and often small, especially in the 1979 season. Samples are also irregularly distributed in space, since many collections were made whilst travelling, with a 10–30 min stop at various points on highways. However, trill rates are sufficiently consistent at a location to make small samples of value (see also Nottebohm 1975) especially when the localities are in a more or less continuous series, as are most of those considered here. Except in the areas studied in detail, all songs were observed well into the local nesting season, and I am therefore confident that birds were members of the local breeding population. The vegetation, geography and topography of northwestern Argentina is considered by Mares et al. (1981).

Results

The climate and vegetation of northwestern Argentina are complex. The flat chaco and the agricultural region around Tucumán abut pre-Andean mountain ranges whose eastern flanks are covered by subtropical rain forest between 600 and 1,300 m, with alder woodland above to approximately 1,850 m. Higher levels are covered by grassland, or by puna vegetation above approximately 3,700 m. Between these front ranges and the main Andean massif further west is a series of deep basins and north-south valleys, which are often extremely arid and support the northernmost extents of the Monte phytogeographic province (Morello 1958). This arid zone extends up the western flanks of the Sierra de Aconquija, and along the ridge of this front range one finds an abrupt transition from the dense grassy vegetation of the eastern slopes to the scattered scrub and cacti of the western slopes. A simplified map of these ecological zones is given in Fig. 1. Also shown are localities at which record-

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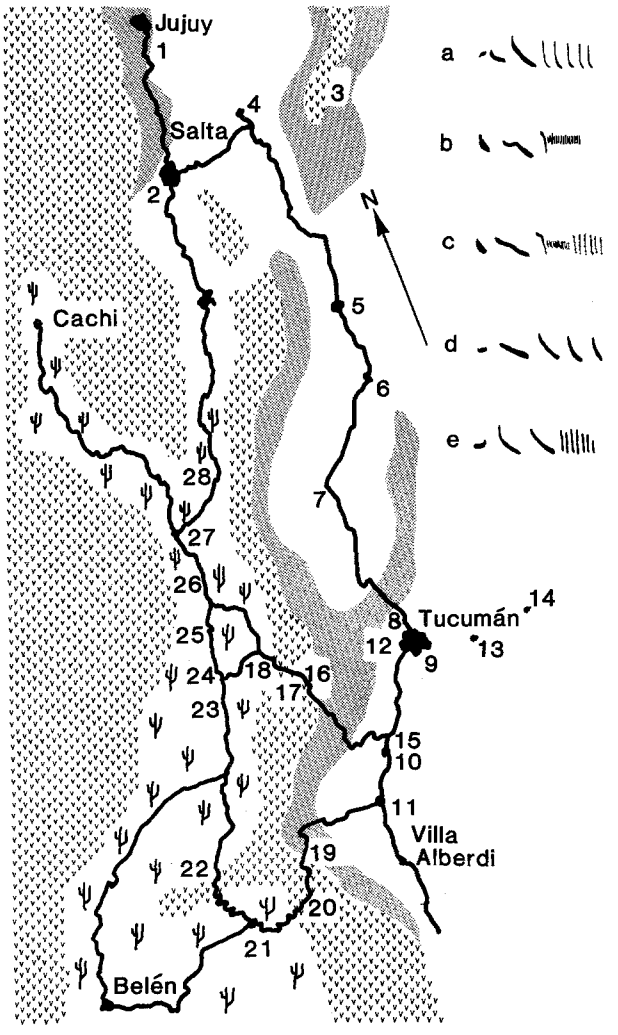

Fig. 1. Schematic map of northwestern Argentina, including parts of the provinces of Jujuy, Salta, Tucumán and Catamarca, showing major vegetation types, numbered roads and numbered sampling localities. Some localities have been visited by Nottebohm (FN) and King (JK) and further information may be obtained from their referenced publications. Those places at which tape recordings have been made are indicated by an asterisk. *1, 2* Outskirts of the cities of Jujuy and Salta in house gardens, roadside hedgerows and pastures. **3* Finca El Rey. In bushes and scrub bordering fields near National Park buildings. Natural vegetation is transition woodland/forest grading into rain forest at higher altitudes. *4–11* Outskirts of: General Martin M. de Güemes (*4*), Metán (*5*), Rosario de la Frontera (*6*), Trancas (*7*), El Cadillal (*8*), Tucumán city (*9*), Monteros (*10*) and Concepción (*11*). Along roadsides on the fringes of towns; in suburban gardens; at several roadside stops on the road between Tucumán and Acheral (*15*). **12* Horco Molle (JK 1972). The lowest slopes skirting the Aconquija mountains to the west of Tucumán city. King worked between the University residences at Horco Molle, in partly cleared forest habitat, and Acherál (*15*). **13* Los Ralos (JK 1972). Chaco scrub with some cultivation. **14* Las Cejas (JK 1972). Chaco scrub in the main. **15–18* Transect A. Described in detail in Handford and Nottebohm (1976) and Nottebohm (1975). From Acheral (*15*) through Tafí del Valle (*16*), and the pass of El Infiernillo (*17*) to Amaicha (*18*) in the arid Santa María valley. See text. *19–21* Transect B. From Concepción through rain forest and alder woodland via the Cuesta del Clavillo (*19*) to grassland at Las Estancias (*20*), dropping via the Cuesta de la Chilca to Andalgalá (*21*) on the northern fringes of the Bolsón de Pipanaco, which is dominated by monte vegetation. See text. *22* Minas Capillitas. A mine camp at about 3,000 m in dry rocky scrub and grasses. **23–27* Various points along RN 63 and RN 40 between Capillitas (*22*) and Cafayate (*27*): San José (*23*), Santa María (*24*), El Bañado (*25*) and Colalao del Valle (*26*). The region is in monte scrub dominated by *Larrea*. FN has made tape recordings between El Bañado (*25*) and Amaicha (*18*) (Nottebohm 1975). *28* Valles Calchaquíes. Various points along highway RN 68. Rising from Cafayate (*27*) to Salta (*2*) the road passes from monte vegetation into the more mesic chaco scrub forest. Also shown are representations of songs showing trill types typical of various areas: *a* montane forest and woodland: sites *3, 19, 15* to *16*; *b* and *c* high mountain bunchgrass: sites *17* and *20*; *d* monte scrub: sites *18, 22–28*; *e* chaco, village and suburban: sites *1, 2, 4–11, 13, 14, 16*. Key to shading: *unshaded* chaco scrub; *dense stipple* montane forest and woodland; v v v v v high mountain bunch-grass; ψ monte desert

ings or observations on song have been made, and the geographical distribution of song types is indicated.

Handford and Nottebohm (1976) and Nottebohm (1975) described trill variation along Transect A (15–18) as follows: slow, easily countable trills (80–100 ms) in the well-watered agricultural zone and lower foothills; very slow trills (120–180 ms) in the montane rain forest and alder woodland above; moderate trills (40–60 ms) from the woodland border through the environs of Tafí village (16) to the burned and grazed grassy hills above; extremely rapid trills (20–25 ms) in the *Festuca* bunchgrass from about 2,800 m to Infiernillo (17); extremely slow trills (300–480 ms) from Infiernillo to the Santa Maria valley (23–25). King (1972) adds measures of approximately 60 ms for trills from the chaco region east of Tucumán (13, 14).

My second transect (Transect B) passes through a very similar sequence of vegetation and trill types. On entering the forest zone, the fairly slow trills of the agricultural flats give way to very slow trills, particularly so in the alder woods. At 1,700–1,800 m one issues into open scrub and grassland. At once the trills are moderately rapid, most only doubtfully, or not, countable. This means that the trill interval here is in the order of 40–50 ms, very similar to those of the zone of similar vegetation below the village of Tafí (16). The land continues to rise gradually to the large, flat basin of Las Estancias (20) at about 1,900 m. The vegetation is *Festuca* bunchgrass, typical of the levels about 1,000 m higher on Transect A. Here, the trills are very rapid and, at least on the day in question, over half of the 23 birds heard were giving the double-trill songs commonly heard between 2,800 and 3,000 m on Transect A. Continuing westwards, the terrain becomes more arid, and beginning

the descent into the Pipanaco basin, xeric scrub gives way to bajada vegetation. During this descent, no *Z. capensis* were heard.

In the village of Andalgalá (21), in the surrounding agricultural fields, and along the thickly vegetated, permanent River Andalgalá, *Z. capensis* is abundant and gives songs with trills that are countable, or nearly so. Their character is very much that of the songs of Tucumán city gardens or of the village of Tafí and environs (16), that is, a trill interval of 60–70 ms.

In two days working in the monte desert outside Andalgalá (21) (altitude approx. 1,000 m) no *Z. capensis* were seen or heard, and they were next encountered at about 3000 m in scrub and sparse grass near Minas Capillitas (22). During two days in this region, the birds were singing vigorously, yet the songs were very short, comprising a two-note theme and a two- or three-element very slow trill. Such extremely slow trill songs are found all along the road (RN 63) leading north from Capillitas and from Santa Maria (24) to Cafayate (27).

From Cafayate (27) to Salta (2) the terrain changes from sparsely vegetated, arid monte into the more mesic chaco scrub-forest zone. Here vegetation is quite tall and thick. Somewhere in this vegetational transition, between the villages of La Viña and Alemania, the extremely slow trills of the monte return to trills which are countable or nearly so (approx. 60 ms). Such trills are to be heard from here north through Coronel Moldes to Salta (2). I have found, between Salta and Tucumán (via RN 34, 55 and 9), that *Z. capensis* songs, though they do show some variability, always appear close to the borderline between countable and not countable (trill interval approx. 60 ms). Similar trills are also to be heard on the southern outskirts of the city of Jujuy (1) to the north of Salta. I tentatively conclude that throughout this chaco and chaco-transition zone *Z. capensis* trills are of this type, and the conclusion is lent some weight by King's (1972) observations and recordings between Tucumán and Las Cejas (14) (see above). A similar picture emerges from the few birds that I observed south of Tucumán along the road leading through Simoca, La Madrid, and Frias.

Discussion

Within the Salta-Tucumán region of northwest Argentina there appears to be a clear association between trill types and vegetational zones: chaco/village/suburban (approx. 60 ms), humid agricultural/transition forest (approx. 100 ms), montane forest and woodland (120–180 ms), high *Festuca* grassland (20–25 ms), and arid monte (300–480 ms). It is probable that more detailed analysis will show the chaco group to be more heterogeneous than it appears at present. Indeed, in the chaco both south (personal observation) and east (King 1972) of Tucumán there are patches where birds show slow trills (90–100 ms) and Morello and Adámoli (1968) have shown that the chaco vegetation consists of a complex mosaic of distinct plant assemblages. But the forest, *Festuca,* and monte song types appear well-defined, fairly uniform and stable over at least 10 years.

There is opportunity in this region for further testing of this association, as there are negotiable tracks and roadways that permit replicate transects to be made. For example, north of Transect A, one may cross the Aconquija from Trancas (7) via San Pedro de Colalao to Colalao del Valle (26), or one may travel from Villa Alberdi over the mountains to Andalgalá. I would predict the same sequence of song types as that described here.

It seems clear now that song type is associated with vegetation type rather than altitude per se, evidenced by the occurrence of the very rapid trills, often a double trill, in *Festuca* grassland regardless of altitude on Transects A and B. Other transects could help establish the proposed association, and in this regard it is interesting to note that Nottebohm (1969, Fig. 11:X, Y, Z) reports double-trill songs of very similar form in the grasslands at about 1,200 m in the Sierras Grandes de Córdoba in central Argentina.

It is clear then, as Nottebohm (1975) has observed, that dialects in *Z. capensis* are geographically nonrandom; indeed this is the only case in which it has been possible to associate specific dialect types with any aspect of the environment. Nevertheless, we are a long way from an understanding of the significance and rationale of these associations. Nottebohm (1975) has shown that one cannot account for all that we know about trill-rate by using arguments (e.g. Morton 1975) from attenuation and distortion of vocal signal information in different habitats. For example, although frequency-modulated elements (whistles) do occur prominently in the songs of *Z. capensis* from closed woodland and forest habitats, such whistled trills are also typical of the arid monte, which is a habitat often as open as grassland, where rapid trills are the rule.

Handford and Nottebohm (1976) suggested the possibility that, rather than dialects being related to the type or structure of the vegetation per se, they may be related to the avifauna of the vegetation zone, which often changes its composition more markedly than does the physical structure of the vegetation itself. They point out some very suggestive resemblances between the songs of *Z. capensis* and other species of bird from the same areas and considered these similarities in a context of convergence under the stimulus of interspecific communication.

I feel that the proposition that *Z. capensis* is matching its trill to some elements of the local avifauna deserves serious attention, since there appear to be no morphological or genetical differences clearly associated with dialect boundaries (Handford and Nottebohm 1976), since observations are inconsistent with expectations from hypotheses derived from the physics of sound transmission and since the similarities in trills are often impressive, especially to the ear. A program for the evaluation of this suggestion would include a cataloguing of the distribution of relevant bird species along a series of transects such as described and advocated here, together with an investigation of the form (and possible variability) of the vocalizations of these species. Comparison of the song-form and distribution of these birds with the distribution of *Z. capensis* dialects would permit the identification of species that, on a song-convergence hypothesis, should interact (say, through territoriality) with *Z. capensis* significantly more than the other species do.

Acknowledgements. The early field work was carried out with the support of NSF Grant GB 38344 to Fernando Nottebohm. I am grateful variously to Rubén Barquez, Oscár Éscobar, Jorge Goane, Peter Leahy, Mike Mares, Tony Nastase, Fernando Nottebohm, Claes and Gunilla Olrog, and Abraham Willink for help, hospitality, discussion and companionship.

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