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Song repertoires of the White-browed Blackbird.—The vocal behavior of the White-browed Blackbird (*Leistes superciliaris*), a locally common species in grassland and pastures of Argentina, Uruguay, Paraguay, Bolivia, southeastern Brazil, and Peru has been studied poorly. The taxonomic status of *L. superciliaris* is uncertain, as the bird appears to form a superspecies with the Red-breasted Blackbird (*L. militaris*; Short 1975). The latter replaces *L. superciliaris* northward, and they occupy open areas in the Amazon river region from Peru to the state of Para in northern Brazil (Meyer de Schauensee 1982). Like most other species in this genus, *L. superciliaris* is generally terrestrial, gregarious during the nonbreeding season, and sexually dimorphic in coloration. In the Argentine pampas, the breeding season lasts from September to February, and it is during this period that males sing. Here, I describe in detail the flight song (FS) and the perched song (PS) of *L. superciliaris* in the Argentine pampas. Also, I present evidence on the sharing of FS features among neighboring males.

Methods.—From September to December 1989, songs from 23 adults of *L. superciliaris* were recorded at the University of Luján Campus, Partido of Luján, northeast Buenos Aires Province, Argentina. Eight other neighboring males were recorded on 12 October 1990. Luján Campus is a typical agro-ecosystem with a dominant open herbaceous vegetation and several scattered introduced tree species (e.g., *Eucalyptus* sp.). Although birds were not banded, the chance of recording the same subject twice in the same day was negligible because simultaneous observation of several territorial neighbor males was possible. In addition, to avoid including the effect of possible song variation during the study period, I restricted the analysis of syllable sharing to those small neighborhoods where all males were recorded on the same day.

Recordings were made with a Uher 4000 Report-L at a speed of 9.5 cm/sec, using a directional hypercardioid Lec 970 LEEA microphone. Only best quality recordings were sonographed (total = 196 songs, ranging from 1 to 16 songs/individual) using a Kay Electric

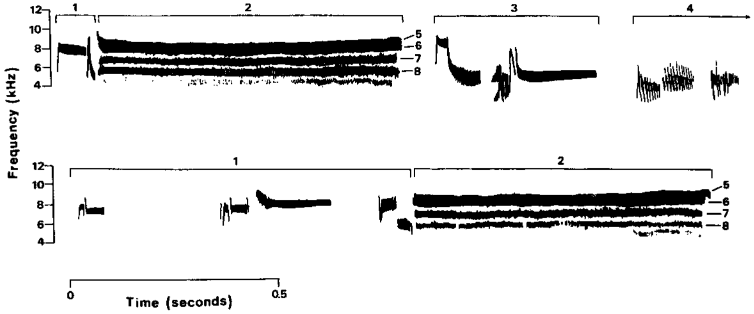


FIG. 1. Sonograms of the flight song (top) and perched song (bottom) of *L. superciliaris.* Parts of the respective vocalizations are as follows: (1) introductory phrase; (2) harsh central note; (3) ending phrase; (4) "chirp" notes; (5) and (6) principal bands; (7) and (8) first and second accessory bands.

Sonagraph 7029-A, set for wide band filters and the 160–16000 Hz frequency range. The terminology used to describe song follows Kroodsma (1974), except that I define syllable as a note or group of notes that can be recognized as a unit in the song of the same or different individuals. On each sonogram, I measured total duration, and maximum and minimum frequencies of the complete song and of each of the song phrases. For the quantitative description of the song, only the clearest sonogram of each song type of each individual was considered. Additionally, a catalog of the FS syllable types was compiled, and the sharing of syllable types among males was analyzed employing the isogloss method (for a detailed description of this method and its application in birds, see Mundinger 1982). Due to the small and scattered distribution of males whose PS were recorded, the isogloss analysis of the PS could not be performed.

Results.—The song repertoire of the White-browed Blackbird is composed of the FS and the PS, differing both in their acoustical structure and associated behavior (Fig. 1). The FS is composed of three phrases: a brief ($\bar{x}$ = 137 msec, SD = 79 msec, N = 31) introductory series of one to three syllables, a long ($\bar{x}$ = 633 msec, SD = 90 msec, N = 31) harsh central note, and a final phrase (lasting a mean of 381 msec, SD = 154 msec, N = 31) of two to four syllables. Next to this last phrase there is a series of complex "chirp" syllables.

The FS is broadcasted at the top (6–12 m of height) and during the descending part of a flight display. This typically consists of an oblique ascending flight leading into a brief and fast ascent in an almost vertical trajectory followed by a short drop and a descending flight. Only rarely was the FS sung at the top of a tree (one of the 31 subjects [3.2%] studied) or during a "multipeak flight display" (two subjects [6.4%]). In this last case, the flight display consisted of two or three successive peaks, each one accompanied by an utterance of a FS.

The perched song (Fig. 1) is always sung from a perch, usually near the ground (up to 1.5 m of height). In contrast to the FS, the PS lacks the final phrase and "chirp" syllables. For seven males in which both PS and FS were tape-recorded, the PS introductory phrase was significantly longer ($\bar{x}$ = 826 msec, SD = 185) and was more complex ($\bar{x}$ = 5.29 syllables, SD = 1.11 syllables) than the FS' counterparts ($\bar{x}$ = 162 msec, SD = 84; $\bar{x}$ = 2.43 syllables, SD = 0.51 syllables; Wilcoxon matched pair sign-ranked tests $t = 0$, df = 7, $P < 0.02$, two-tailed). In addition, the harsh central note was longer in the PS ($\bar{x}$ = 746 msec, SD = 133 msec) than in the FS ($\bar{x}$ = 645 msec, SD = 102 msec), but this difference was not statistically significant ($t = 3.5$, df = 7, $P > 0.05$). FS and PS did not differ in frequency, both ranging between 2.8 and 9.5 kHz ($t \geq 9$, df = 7, $P > 0.05$).

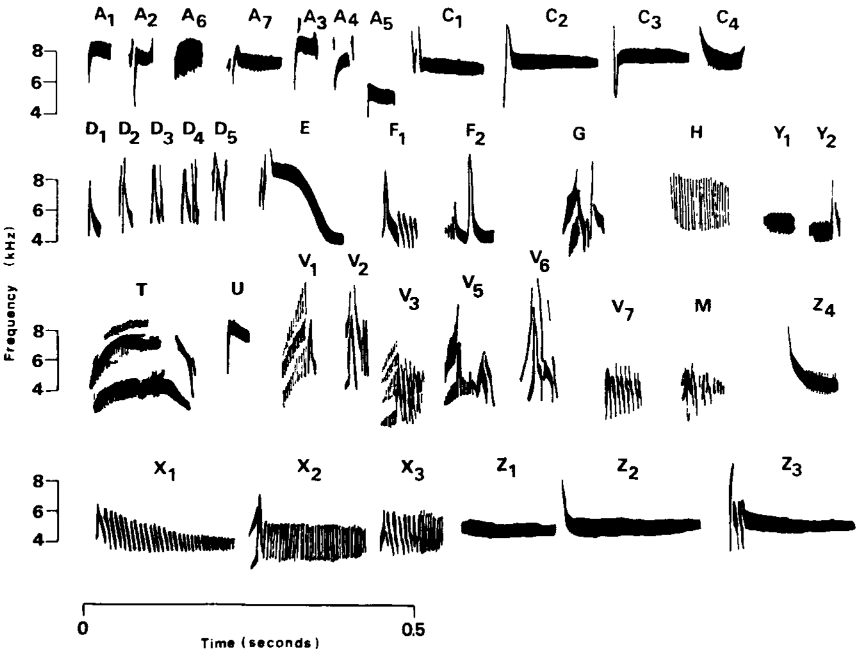


FIG. 2. Catalog of syllable types and minor variants found in the introduction and ending phrase of the flight song of *L. superciliaris*. Syllable types are identified with letters and minor variants within each category with numbers. Syllables A to H are introductory syllables, and the rest correspond to the ending phrase. Syllables V_7 and M are the "chirp" notes that usually follow the ending phrase.

The complex structure of the harsh central note (HCN) includes a wide range of frequencies, from 4 to 9.5 kHz, but energy is mostly concentrated in a number of narrow bands of steady frequency. Typically, there are two "principal" bands of high frequency and amplitude, and two "accessory" bands of low frequency and amplitude (Fig. 1). The two principal bands contact in the frequency axis, and they are separated at regular intervals from the accessory bands. The number of bands of emphasized frequency also exhibit some degree of inter-individual variation. Three of the 31 subjects (9.7%) studied had only one principal band, and only one of them (3.2%) also had one accessory band. In addition, in at least one individual, the HCN contained more than two accessory bands. Although these bands of emphasized frequency could represent harmonic tones of a low fundamental, they may also be the product of a two voice phenomenon (Gaunt 1983). Unfortunately, on the basis of sonograms alone, it is impossible to determine in this case the exact nature of the HCN.

Excluding the HCN, 39 FS syllable types and variants were defined (Fig. 2). Table 1 shows that individuals differ in the number, type, and sequence of syllables employed in FS.

To illustrate the geographic distribution of the syllable types and variants, isoglosses were drawn. Fig. 3 depicts this analysis in two song neighborhoods. Neighboring males usually share the same syllabic variant, and there is concordance among the distribution of the different variants. This concordance is reflected by the existence of small groups of neighboring males (of up to three or four individuals) having almost identical song patterns (e.g.,

TABLE 1

SEQUENCE OF SYLLABLE TYPES IN THE FLIGHT SONG OF WHITE-BROWED BLACKBIRDS

Bird syllable sequence[a]	Bird syllable sequence	Bird syllable sequence
S_1[b] C_4F_1H-HCN-V_6Z_1	S_{11} HA_1D_1-HCN-X_3Z_1	S_{21} EA_1D_3-HCN-V_3Z_1
S_2 D_2-HCN-$Y_2V_3UX_2$	S_{12} A_3D_4-HCN-V_3Z_3	S_{22} EA_1D_3-HCN-V_3Z_1
S_3 $C_1A_2A_5$-HCN-$Y_1V_3Z_1$	S_{13} A_1D_4-HCN-V_3Z_3	S_{23} A_1G-HCN-$TV_3X_3Z_1$
S_4 A_6D_3-HCN-$V_6Z_1X_1$	S_{14} A_2G-HCN-$TV_3X_3Z_2$	S_{24} A_1D_1-HCN-$UZ_4V_5Z_2$
S_5 A_6D_3-HCN-$V_6Z_1X_1$	S_{15} A_2F_2-HCN-V_2Z_2	S_{25} A_1D_4-HCN-V_3Z_3
S_6 ED_2-HCN-V_5Z_1	S_{16} $A_4C_2D_5$-HCN-$Y_1V_1Z_2X_2$	S_{26} A_1D_1-HCN-$UZ_4V_5Z_2$
S_7 $A_4C_3D_5$-HCN-$Y_1V_1Z_2X_2$	S_{17} ED_2-HCN-V_5Z_1	S_{27} A_1D_4-HCN-V_3Z_3
S_8 A_3D_4-HCN-V_3Z_3	S_{18} $A_4C_2D_5$-HCN-$Y_1V_1Z_2X_2$	S_{28} A_1D_4-HCN-V_3Z_3
S_9 A_1D_3-HCN-V_3Z_3	S_{19} A_1D_1-HCN-UZ_4Z_2	S_{29} A_1D_3-HCN-V_5Z_1
S_{10} A_1D_4-HCN-V_3Z_3	S_{20} A_6D_3-HCN-$V_6Z_1X_1$	S_{30} C_4F_1H-HCN-V_6Z_1
		S_{31} A_1G-HCN-$TV_3X_3Z_1$

[a] Syllable types as indicated in Fig. 2. Hyphens separate flight song phrases.

[b] Subjects S_1 to S_{23} recorded during 1989, and S_{24} to S_{31} recorded during 1990.

subjects S_{16} and S_{18}; S_{24} and S_{26}; S_{25}, S_{27} and S_{28}; in Fig. 3). A similar situation has been found in the House Finch (*Carpodacus mexicanus*) by Bitterbaum and Baptista (1979).

Discussion.—This study shows that the White-browed Blackbird has a repertoire of two song types, the FS and PS. These types differ in acoustical structure and associated behavior. The FS is more complex than the PS and has an ending phrase followed by a series of chirp notes. The PS lacks this end phrase and chirp notes, and it has an introduction longer than the FS. Besides, the PS is almost always broadcasted at a low perch, while the FS is emitted during the descendent part of a conspicuous flight display.

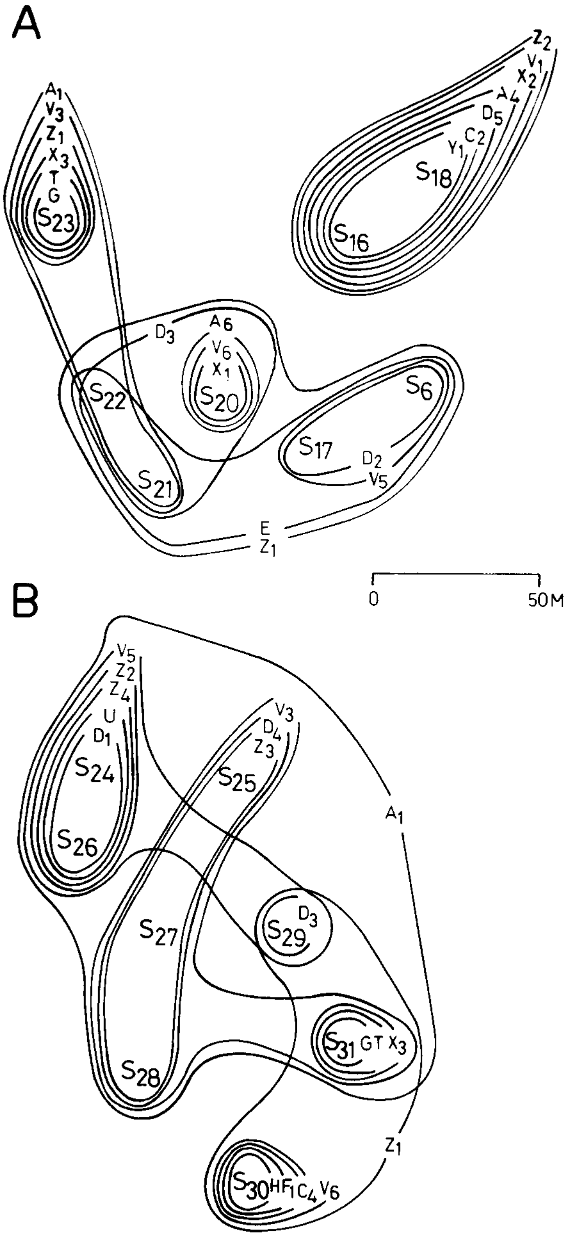
Although each male has distinctive flight and perched songs, it is possible to establish the existence of syllable sharing among neighboring males. Syllable and song sharing has been reported in a variety of Icterids: Eastern and Western Meadowlarks (*Sturnella magna* and *S. neglecta*; Lanyon 1957); Yellow-rumped Cacique (*Cacicus cela*; Feekes 1977, Trainer 1989); Red-winged Blackbird (*Agelaius phoeniceus*; Marler et al. 1972); Bobolink (*Dolichonyx oryzivorus*; Avery and Oring 1977); and Brown-headed Cowbird (*Molothrus ater*; Dufty 1985), but the presence of FS dialects (i.e., song variants characteristic of local groups of males, separated by well defined boundaries) has only been described for the latter (see "flight whistle" dialects in Rothstein and Fleischer [1987]).

Whether FS sharing among neighboring White-browed Blackbird males represents a dialect system is a matter of debate, but if true, it is clear that it differs from the flight whistle dialects in the Brown-headed Cowbird. These differences include the number of individuals sharing the "dialect" and its temporal stability, both features being smaller in the former than in the latter. During 1990, I looked for song neighborhood "A" (Fig. 3), but this area was found empty, as well as many other sites occupied by this species during 1989. Despite the lack of temporal stability of song neighborhoods, the clumped distribution of syllables and song patterns in *L. superciliaris* suggests that vocal imitation among neighboring males plays a role in song development.

Why does *L. superciliaris* fly during singing? In open habitats, temperature and wind gradients could refract sound, creating a shadow zone for the horizontal propagation of sound above the ground (Morton 1975, Wiley and Richards 1982). Singing at a greater height increases the active space of the song (i.e., distance from the source over which signal amplitude remains above the detection threshold of potential receivers), since the distance along the ground to the shadow zone increases with the square root of the singer's height (Wiley and Richards 1982). In addition, singing at a greater height also has the advantage of increasing the bird's visual conspicuousness and minimizing the acoustical interference generated by orthopteran songs emitted on or near the ground. In the absence of elevated song perches, it could be useful to fly during singing.

The presence of flight song displays is widespread among bird species living in open habitats (Armstrong 1963, Morton 1975, Miller 1983). The occurrence of flight display varies among *Leistes* and *Sturnella* species, indicating a possible relationship between the lack of elevated song perches and the presence of this behavior. Thus, while *L. superciliaris, L. militaris,* Lesser Red-breasted and Peruvian Red-breasted Meadowlarks (*S. defilippi* and *S. bellicosa*) live in open grasslands and exhibit a flight display during which the FS is emitted, Long-tailed Meadowlarks (*S. loyca*) which inhabit shrub areas with abundance of song perches, lacks a flight display (Hudson 1920, Gochfeld 1979).

Why do the flight song and perch song of the White-browed Blackbird differ in structure? In addition to the possible differences in their communicative function, it is tempting to relate the structural differences between the PS and FS to those existing in the acoustical properties of the pathways in which they are broadcasted. Shiovitz (1975) and Richards (1981) suggested that song introduction could function as an alerting element, thus facilitating the detection of the biologically significant part of the signal by removing the uncertainty


A
Z_2
V_1
X_2
A_4
D_5
C_2
Y_1
S_{18}
S_{16}
A_1
V_3
Z_1
X_3
T
G
S_{23}
D_3
A_6
V_6
X_1
S_{20}
S_{22}
S_{21}
S_6
S_{17}
D_2
V_5
E
Z_1
0
50M
B
V_5
Z_2
Z_4
U
D_1
S_{24}
S_{26}
V_3
D_4
Z_3
S_{25}
A_1
S_{27}
D_3
S_{29}
S_{31} G T X_3
S_{28}
Z_1
S_{30} H F_1 C_4 V_6

about its time of arrival. Interestingly, the PS has a longer and comparatively more complex introduction than the FS, just as would be expected for a signal emitted in a heavily interfered channel. In addition to the song shadows produced by the thermal and wind gradient, the acoustical interference of orthopteran songs mainly affects PS, because it is sung from low perches near the ground. These facts could make necessary the use of a long tonal introduction which could result in an improvement of receiver detection.

Even though the song introduction could function as an alerting element, the structural differences between the flight and perched song introductions could be explained in a different way. The visual conspicuousness of the ascending flight, previous to the FS start, could alert receivers about the incoming acoustical signal, avoiding the need to include additional alerting elements in the FS introduction.

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FIG. 3. Isogloss analysis of the *L. superciliaris* FS. Capital letters with subscripts indicate the syllable type and variant mapped by the isogloss (following the nomenclature of Fig. 2). The letter "S" with subscript identify the position of different males. Neighborhoods "A" and "B" were recorded during 1989 and 1990, respectively.

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Social organization in Snow Geese: family size and individual behavior.—Great importance has been given to the family and its role in goose and swan societies (Raveling 1970, Prevett and MacInness 1980, Scott 1980, Lamprecht 1986, Black and Owen 1989). The social hierarchy of wild geese may be based on the family (or social unit) rather than on the individual (Boyd 1953, Hanson 1953, Raveling 1970, Black and Owen 1989), and individual ranks may not be independent from each other. For example, if individual "A" obtains rank 1, no other individual can obtain that rank. Moreover, the ranks of unit members are dependent on each other, that is, a juvenile cannot obtain a higher rank than its father or mother. Therefore, if a family gander has a low rank, all the members of its family have low ranks. The assertion that the behavior and characteristics of the individuals comprising these social units is unimportant compared to the social unit has not been unequivocally demonstrated, however. Although it was first thought that the number of individuals in a unit was the major determinant of rank (Boyd 1953, Hanson 1953, Raveling 1970, Black and Owen 1989), Lamprecht (1986) found in Bar-headed Geese (*Anser indicus*) that the rank of a family is determined mainly or solely by the behavior of the gander. Furthermore, events happening during hierarchy formation may also influence the dominance status eventually attained by a family.

We determined the relative importance of the nature and size of the social unit on the one hand, and the characteristics and behavior of individual birds composing these units, on the other, in the establishment and maintenance of the nested hierarchy in Greater Snow Geese (*Chen caerulescens atlantica*). The present study was conducted at La Pocatière, 100 km northeast of Québec city, Canada, between May and August 1988. Geese were cannon-netted, sexed, and fitted with numbered plastic neck collars. Age was determined as: (1)