SYSTEMATICS OF THE TAWNY-BELLIED SEEDEATER (*SPOROPHILA HYPOXANTHA*). I. GEOGRAPHIC VARIATION, ECOLOGY, AND EVOLUTION OF VOCALIZATIONS

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Abstract. Geographically isolated populations diverging in vocalizations and habitat use are prime candidates for diversification along the speciation/differentiation continuum. The Tawny-bellied Seedeater (*Sporophila hypoxantha*) is relatively widespread, thus potentially variable across its range. We investigated geographic variation in vocalizations, habitat use, and migratory behavior, identifying five regiolects (song variants encompassing extensive subpopulations of a species and all individuals within this large range), which correspond with different patterns of habitat use but arose independently of migratory behavior. Given the low level of genetic divergence in the capuchinos, a subset of the genus *Sporophila* that includes *S. hypoxantha*, the phylogenetic potential for learning in the genus, the fast temporal changes evident within regiolects (chronolects), the existence of environmental sound assimilation, and the singing of subsongs by young males, we conclude that geographic variation is due mostly to learning, the genetic makeup of the various populations having little effect. The occurrence of allopatric habitat-related regiolects with little (if any) morphological differentiation, suggests that this constitutes a plausible step toward the evolution of new species in the capuchinos. These results highlight the importance of habitat use and vocalizations in understanding the evolutionary differentiation and diversification of the seedeaters and suggest that their explosive radiation has been strongly influenced by the interplay of habitat choice, migratory behavior, and vocal differentiation.

Key words: capuchinos, chronolect, evolutionary radiation, habitat, regiolect, migration, speciation, Sporophila hypoxantha, *vocalization.*

Sistemática de *Sporophila hypoxantha*. I. Variación Geográfica, Ecología y Evolución de las Vocalizaciones

Resumen. Las poblaciones que se encuentran aisladas y que exhiben variación en sus vocalizaciones y en el uso del hábitat son candidatas a diversificación a lo largo del continuum especiación/diferenciación. *Sporophila hypoxantha* es una especie con una distribución relativamente amplia, y por eso probablemente exhiba variación geográfica. Investigamos la variación geográfica en sus vocalizaciones, uso de hábitat y comportamiento migratorio. Reconocimos cinco regiolectos (variantes de canto encontradas en subpoblaciones de una especie en una gran extensión y en todos los individuos dentro de este gran rango), que se corresponden con diferentes patrones de uso de hábitat, pero que aparecieron independientemente de la presencia del comportamiento migratorio. Dada la escasa divergencia genética entre los capuchinos, un grupo dentro del género *Sporophila* que incluye a *S. hypoxantha*, el potencial filogenético para el aprendizaje en el género, los cambios rápidos dentro de regiolectos (cronolectos), la existencia de asimilación acústica ambiental y la grabación de machos jóvenes con sub-cantos, concluimos que la variación geográfica se debe principalmente al aprendizaje, con poco efecto del trasfondo genético de las diferentes poblaciones. La presencia de regiolectos alopátricos vinculados a hábitats, con poca (o ninguna) diferenciación morfológica, sugiere que esto constituye una etapa hacia la evolución de nuevas especies en los capuchinos. Este trabajo resalta la importancia del uso de hábitat y de las vocalizaciones para entender la diferenciación evolutiva y la diversificación en *Sporophila*, y sugiere que su radiación explosiva ha sido fuertemente influenciada por la interacción entre los procesos de selección de hábitat, comportamiento migratorio y diferenciación vocal.

INTRODUCTION

Speciation is a process so is amenable to separation in arbitrary stages. If speciation in various lineages is not closely synchronized, then various stages of speciation should be represented at any given time. Since it may be a long process, it is usually analyzed a posteriori by comparison of snapshots of the speciation of closely related organisms (Mayr and Diamond 2001). With time following speciation, the accumulation of evolutionary changes blurs the distinction between traits relevant and those not directly responsible for the generation of the reproductive discontinuities that define speciation.

Where speciation is recently completed or still continuing, detailed evolutionary, ecological, and biogeographical studies of young evolutionary radiations can contribute substantially to the understanding of the mechanisms of speciation (Grant and Grant 2008, Price 2008). Specifically, a comparison of intraspecific geographic variation in features that usually influence interbreeding among different closely related species in a young evolutionary radiation should provide insights into the evolutionary mechanisms underlying speciation and differentiation of the group.

Vocalizations and habitat specificity have long been considered important cues for species recognition in birds (Marler 1957, Cody 1985, Kroodsma 1996). One of the possible evolutionary outcomes of divergence in vocalizations and habitat use is speciation (Slabbekoorn and Smith 2002, Davis and Stamp 2004). Thus geographically isolated populations diverging in vocalizations and habitat use are prime candidates for diversification along the speciation/differentiation continuum (Slabbekoorn and Smith 2002, Patten et al. 2004). In general terms, two hypotheses, not mutually exclusive, can explain the existence of discrete macrogeographic variants in voices: vocal learning (Thorpe 1954, Marler and Peters 1982, Hultsch and Todt 2004) or genetic differentiation (Kroodsma 1984, Lanyon 1978, Lindell 1985, Isler et al. 2005, Brumfield 2005). The capacity to learn songs is the basic substrate for the appearance of essentially nongenetic geographic variation in voices, and different genetic composition is regarded as the main influence on geographic variation when voices are not learned (Baker and Cunningham 1985, Baptista 1996, Kroodsma 2004). Likewise, imprinting on a habitat may play a crucial role in the generation and maintenance of habitat preferences in birds (Davis and Stamp 2004, Beltman and Haccou 2005) and could result in assortative mating within the preferred habitat. In turn, the magnitude of ecological divergence can also play an important role in reproductive isolation independent of genetic differentiation of two populations (Funk et al. 2006, Nosil et al. 2009).

The grasslands of subtropical South America harbor a most interesting group of tiny seedeaters known as *capuchinos* or *caboclinhos*, a subset of the genus *Sporophila*. Their small size notwithstanding, they pose huge enigmas to ornithology: their taxonomy is tremendously complex; many species are austral migrants, but their migration patterns and winter ranges are basically unknown; they seem to be genetically extremely similar, yet they differ strikingly in plumage, habitat use, and vocalizations (Sclater 1871, Hellmayr 1904, 1938, Sabel 1990, Ouellet 1992, Sick 1997, Silva 1999, Lijtmaer et al. 2004, Areta 2008, Areta et al. 2011). When taken together, available data suggest that the capuchinos represent a very young evolutionary radiation (Campagna et al. 2009, Areta et al. 2011).

In the capuchinos, macrogeographic vocal variation has been so far reported only in the Dark-throated Seedeater

(*S. ruficollis*) (Areta et al. 2011, but see also Areta 2010 for a wider analysis of variation in the capuchinos), while of other species of *Sporophila* the Lined Seedeater (*S. lineola*) is the only one whose geographic variation in voice has been studied (Schwartz 1975, Silva 1995, Neto and Vasconcelos 2007, Areta and Almirón 2009). The Tawny-bellied Seedeater (*S. hypoxantha*) is one of the most widespread capuchinos, ranging from central-eastern to northwestern Argentina through Uruguay, southeastern to southwestern Brazil, Paraguay, and eastern Bolivia (Ridgely and Tudor 1989). This fairly large distribution is not continuous, the species being present only in suitable grassland. Hence *S. hypoxantha* has the potential for geographic variation in habitat use and vocalizations, two features important for evaluation of species limits in the capuchinos (Areta 2008, Areta et al. 2011). Data on geographic variation in *S. hypoxantha* would provide crucial information for understanding how diversification within a species proceeds in the young evolutionary radiation of the capuchinos.

Here, we describe patterns of geographic and temporal variation in vocalizations, patterns of habitat use, and migratory behavior of *S. hypoxantha* across its breeding range. On the basis of these data we asked (1) is geographic and temporal variation in vocalizations of *S. hypoxantha* due to vocal learning?, (2) is geographic variation in vocalizations related to migratory behavior in different breeding populations?, (3) how can our findings on patterns of geographic variation in vocalizations, habitat use, and migratory behavior within *S. hypoxantha* contribute to the understanding of the evolutionary radiation and differentiation of other capuchinos?, (4) what is the specific status of *S. hypoxantha*?, and (5) how does geographical variation in vocalizations and habitat use affect the taxonomic treatment of *S. hypoxantha*?.

METHODS

GEOGRAPHIC AND TIME COVERAGE

We searched for capuchinos during seven breeding seasons from October 2003 to April 2009. Sampling effort totaled 227 days in the field, with 33 days at 11 locations in Entre Ríos (Argentina), 28 days at 7 locations in Corrientes (Argentina), 3 days at 2 locations in Santa Fé (Argentina), 2 days at 1 location in Formosa (Argentina), 3 days at 2 locations in Paysandú (Uruguay), 3 days at 3 locations in Rocha (Uruguay), 3 days at 2 locations in Santa Cruz (Bolivia), 3 days at 1 location in Beni (Bolivia), 85 days at 10 locations in Rio Grande do Sul (Brazil), 70 days at 5 locations in Santa Catarina (Brazil), and 4 days at 1 location in Paraná (Brazil) (Fig. 1).

BIRD VOCALIZATIONS

We recorded vocalizations with various microphones (Audio-Technica 815b, Sennheiser ME-67 protected with a Rycote 6 Kit [shock-mount, windshield, and windjammer], Sennheiser ME-62 mounted on a Telinga Universal parabola or on a 60-cm
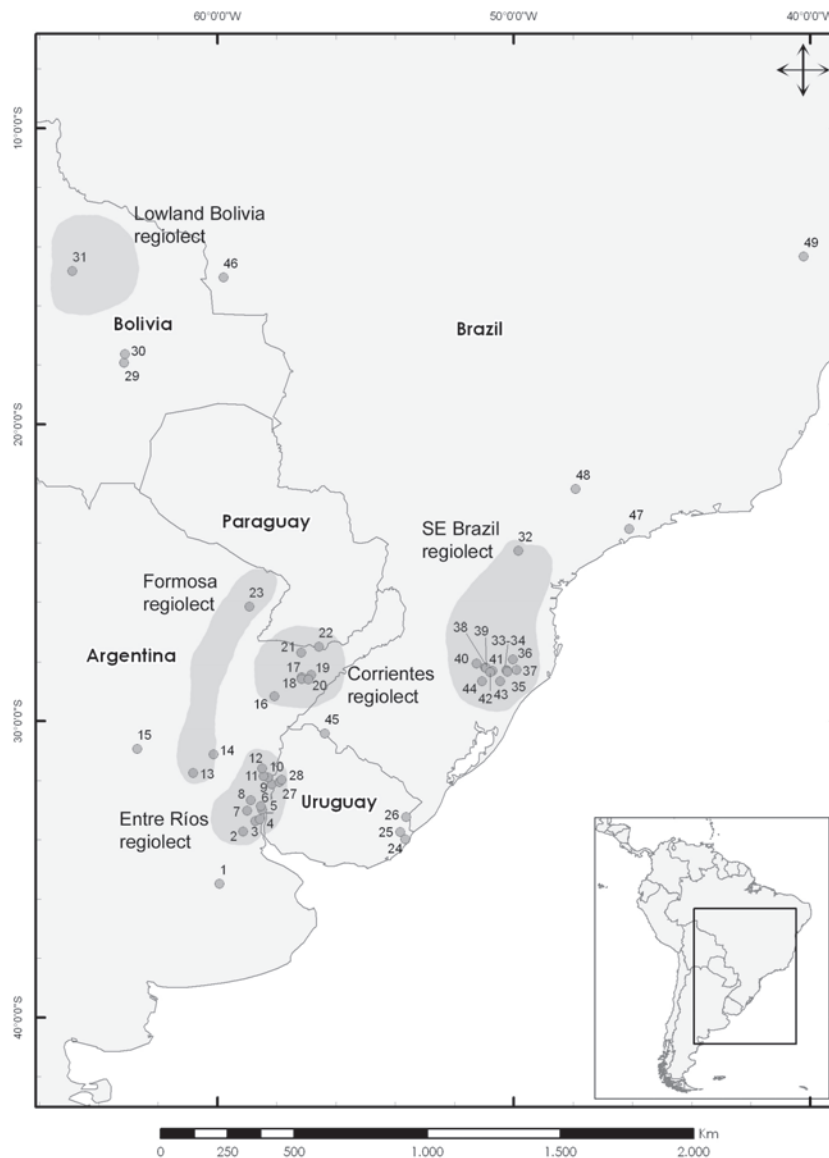
FIGURE 1.   Approximate distribution of regiolects of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) and locations of sites visited during this study (numbers). See Appendix 1 for localities where birds were recorded. **Argentina, Buenos Aires**: 1, Saladillo (59º 56′ W, 35º 30′ S). **Entre Ríos**: 2, Ibicuy (59º 09′ W, 33º 44′ S); 3, Arroyo Ñancay (58º 44′ W, 33º 23′ S); 4, Estancia La Marita (58º 35′ W, 33º 20′ S); 5, Gualeguaychú (58º 30′ W, 33º 00′ S); 6, Las Piedras (58º 33′ W, 32º 53′ S); 7, Larroque (59º 00′ W, 33º 02′ S); 8, Urdinarrain (58º 53′ W, 32º 41′S); 9, Pto. Liebig and Arroyo Caraballo (58º 11′ W, 32º 09′ S); 10, Parque Nacional El Palmar (58º 18′ W, 31º 55′ S); 11, Arroyo Baru (58º 27′ W, 31º 52′ S); 12, San Salvador (58º 30′ W, 31º 37′ S). **Santa Fé**: 13, Sauce Viejo (60º 50′ W, 31º 46′ S); 14, Campo del Medio (60º 08′ W, 31º 08′ S). **Córdoba**: 15, Laguna Mar Chiquita (62º 43′ W, 30º 57′ S). **Corrientes**: 16, Mercedes (58º 05′ W, 29º 10′ S); 17, Estancia Rincón del Socorro (57º 10′ W, 28º 32′ S); 18, Colonia Pellegrini (57º 10′ W, 28º 35′ S); 19, Cambá Trapo (56º 51′ W, 28º 27′ S); 20, Cuenca del Río Aguapey (56º 56′ W, 28º 36′ S); 21, Estancia San Juan Poriahú (57º 11′ W, 27º 42′ S)/Parque Nacional Mburucuyá (58º 05′ W, 28º 00′ S); 22, Rincón Santa María (56º 35′ W, 27º 30′ S). **Formosa**: 23, Estancia El Bagual (58º 56′ W, 26º 10′ S). **Uruguay, Rocha**: 24, Laguna Negra (53º 40′ W, 34º 00′ S); 25, Bañados de la India Muerta (53º 50′ W, 33º 45′ S); 26, Cebollatí (53º 38′ W, 33º 15′ S). **Paysandú**: 27, Lorenzo Geyres, Quebracho (57º 55′ W, 32º 04′ S); 28, Queguayar (57º 50′ W, 32º 00′ S). **Bolivia, Santa Cruz**: 29, Lomas de Arena (63º 10′ W, 17º 56′ S); 30, Pampas de Viru-Viru (63º 08′ W, 17º 39′ S). **Beni**: 31, Trinidad-Mamoré (64º 54′ W, 14º 50′ S). **Brazil, Paraná**: 32, Fazenda Chapadão–Rio das Perdizes (49º 51′ W, 24º 17′ S). **Santa Catarina**: 33, Coxilha Rica/Estancia do Meio (50º 15′ W, 28º 18′ S); 34, Cerro Negro (50º 52′ W, 27º 50′ S); 35, Rio São Mateus (50º 13′ W, 28º 21′ S); 36, Pedra Branca (50º 02′ W, 27º 55′ S); 37, São Joaquim/Lages (49º 55′ W, 28º 17′ S). **Rio Grande do Sul**: 38, Capão Alto (50º 58′ W, 28º 12′ S); 39, São Pedro (50º 56′ W, 28º 13′ S); 40, Capão Bonito (51º 16′ W, 28º 04′ S); 41, Antiga Estação Férrea–Bom Jesus (50º 44′ W, 28º 19′ S); 42, Fazenda Socorro/Rio Santana (50º 48′ W, 28º 22′ S); 43, Cachoeira dos Baggio (50º 28′ W, 28º 40′ S); 44, Guacho (51º 05′ W, 28º 40′ S); 45, Distr. Areal-Quaraí (56º 23′ W, 30º 26′ S). **Mato Grosso**: 46, Campos do Encanto–Vila Bela da Santíssima Trindade (59º 48′ W, 15º03′ S). **São Paulo**: 47, Mogi das Cruzes (46º 07′ W, 23º 33′ S); 48, Estação Ecológica Itirapina (47º 55′ W, 22º 12′ S). **Bahia**: 49, Boa Nova (40º 13′ W, 14º 21′ S).

parabola), and tape recorders (Marantz PMD-222, PMD-661, and Sony TC-D5M). We prepared spectrograms with Syrinx 2.1 (J. Burt, www.syrinxpc.com). Additional recordings were provided by other investigators (see Appendix 1). All of our recordings are archived at the Macaulay Library of Natural Sounds (MLNS, Cornell Lab of Ornithology, Ithaca, NY).

The songs of the capuchinos include many different, non-repetitive, and morphologically complex notes. To examine differences and similarities among populations, we first characterized notes that we could identify unambiguously, on the basis of shape (including duration and frequency distribution) and relative position in the songs, despite variation among individuals. We then compared the frequency of occurrence of these notes in an individual's repertoire within and among populations. Our analysis was limited to sexually mature males. To evaluate changes within regiolects through time, we compared recordings from 1971 housed at the MLNS to those made by us from 2006 to 2009 in southeastern Brazil. We sought potentially homologous elements by applying the criteria of position and special similarity (Wenzel 1992).

HABITAT USE

To characterize habitat use on a regional scale, we assigned the habitat of each territorial bird to one of 13 broad categories within three basic types: (A) Dry grasslands. (1) *Caraguatal–cardal* is a dry grassland of generally flat areas with large stands of sawgrass known as *caraguatá* (*Eryngium horridum*) and *cardos* or naturalized thistles (*Carduus* spp.), isolated *chilca* (*Baccharis* spp.) shrubs, and occasional *espinillo* (*Acacia caven*) and *ñandubay* (*Prosopis affinis*) trees. (2) Undulating grassland includes dry grasslands on the ridges, valleys, and slopes of the mesopotamian grasslands of Entre Ríos and Corrientes and near the Uruguay River in Paysandú, Uruguay. Typical features of this habitat include rocky outcrops, sandy soils, diverse grasses (e.g., *Paspalum*, *Bromus*, *Piptochaetium*), and occasionally *yatay* palms (*Butia yatay*). (3) Depressed pampas grasslands are dry grasslands of *Paspalum quadrifarium* and *Spartina densiflora* with occassional sawgrass (*Eryngium* sp.) growing on salty soils, encountered only in Buenos Aires province. (4) Dry grasslands of *Elionurus muticus* and *Imperata brasiliensis* or *Andropogon lateralis* ("*campos altos*"). (5) Shrubby dry grasslands of many species of grasses, growing on well-drained soils with frequent small woodlands of *espinillo* trees and *chilca* shrubs. A salient feature of shrubby grasslands is the common presence of *tacurús*, large nests of dried mud built by the ant *Camponotus mirabilis*. (6) *Flechillares* are upland grasslands characterized by numerous grasses of the genus *Stipa*, accompanied by species of *Briza*, *Schizachyrium*, *Paspalum* (e.g., *P. notatum*), *Axonopus* (e.g., *A. affinis*). Several *chilcas* (*Baccharis trimera* and *B. chordifolia*) and *Eupatorium* shrubs are common on drier soils, while in more humid areas *sauce criollo* (*Salix humboldtiana*) and ceibo (*Erythrina crista-galli*) trees can be found in low

density or in small groves. (7) Valley shrubby grasslands are dry and dense grasslands generally located between 700 and 900 m above sea level, usually growing on steep slopes with rocky outcrops in the region of the Campos da Cima da Serra and Campos Gerais of Paraná state (southern Brazil), and characterized by *Piptochaetium montevidensis*, *Sorghastrum setosum*, *Saccharum angustifolium*, *Eragrostis* sp., *Paspalum plicatulum*, *Andropogon macrotrix*, *Setaria parviflora*, several shrubs of the genera *Baccharis* (*B. trimera*, *B. articulata*), *Eupatorium*, and *Vernonia*, and *Eryngium horridum*. (8) The Llanos de Moxos include several habitats, of which two grassland types could be relevant for *Sporophila hypoxantha*: the "*altura*" dry savanna of the bunchgrass *Trachypogon*, with *Trachypogon plumosus*, *Leptocoryphium lanatum*, and *Paspalum ionanthum*, and the dry mounds of seasonally flooded grassland communities, "*sertanejales*," which floristically resemble the moist *altura* but include other grasses such as *Aristida torta*, *Sacciolepis myuros*, and *Sorghastrum stipoides*. The *sertanejales* have frequent ant nests, much like the *tacurús* of the shrubby grasslands.

(B) Wet grasslands. (9) Wet grasslands of *Paspalum intermedium* and *Sorghastrum setosum* ("*campos bajos*"). (10) Lowland marsh or wet grasslands, including any grass- or sedge-dominated plant community regularly flooded during the rainy season or with permanent water. Plants characterizing this habitat include diverse grasses (e.g., *Paspalum* and *Panicum*), cattails (*Typha*), and bulrushes (*Scirpus*). (11) Highland wet grasslands on humid or inundated soils with *Eryngium pandanifolium*., *Eleocharis* sp., *Andropogon lateralis*, and sparse *Bacharis* spp. shrubs. (12) Bogs and *caraguatá* wetlands with abundant sawgrasses (*Eryngium pandanifolium*, *E. elegans*), turf (*Sphagnum* spp.), Cyperaceae, and, in the transition to drier areas, other species of grasses, situated in soaked, undulating terrain without rocks, generally above 1000 m above sea level in the Campos da Cima da Serra in southern Brazil.

(C) Annual crops and other anthropogenic habitats. (13) Annual crops, including soy (*Glycine max*), rice (*Oryza sativa*), and corn (*Zea mays*), are grown on a large scale throughout the sampled area.

These habitat types are widely distributed at the geographical scale and may coexist as a mosaic within a small area (i.e., several habitats may interdigitate at the same locality). Although the broad habitat categories we used may mask subtle differences that could be a basis for habitat segregation of sympatric forms at a finer scale, we designed them to apply over a wide area over which more detailed descriptions of habitats would have precluded the discovery of any pattern of habitat use because many features unique to each site would have masked the sites' overall similarities (see sampling localities in Appendix 2).

In most areas we visited the birds were not marked, so to avoid pseudoreplication we included only data from territorial males that were spatially or temporally segregated or had been

banded previously. For areas visited more than once, we included only one record per territory. We consider each contact to be an independent sample appropriate to evaluation of habitat preference. We evaluated habitat preference by comparing the frequency of occurrence of males of each population in each habitat. We defined preferred habitat as the habitat in which we found at least 65% of the territorial males singing each regiolect.

MIGRATORY BEHAVIOR

We evaluated the migratory status of populations on the basis of our field work and that of others spanning all the months in all the regions, examination of museum specimens, and the literature (especially Silva 1999, Di Giacomo 2005).

RESULTS

VOCALIZATIONS

We documented the existence of four essentially allopatric macrogeographic song variants, defined by note types, in Argentina and Brazil, with a possible fifth variant in Bolivia. These variants can be considered regiolects ("song variants encompassing extensive subpopulations of a species and all individuals within this large range," Martens 1996:221), or institutions ("regional populations of lexical variants," Mundinger 1982:195). We found no evidence of intermediate vocalizations that could suggest the existence of any link between these regiolects.

On the basis of their known breeding ranges, we named the regiolects Formosa (regiolect 1), Corrientes (regiolect 2), Entre Ríos (regiolect 3), and southern Brazil (regiolect 4) (Table 1). A fifth regiolect seems to exist in the lowlands of Bolivia (regiolect 5), but our data are insufficient to delimit it clearly (Table 1).

We found essential differences in all note types defining each regiolect. No regiolect was the product of recombination of note types from other regiolects, so we could not evaluate syntactic differences, there being no shared note types from which different syntaxes could be derived. Within each regiolect, the sequence of note delivery was fairly stereotyped, although occasionally an individual altered the order and

sequence of some notes, departing from the more common sequence. All the note types identified were parts of a song or were uttered as isolated elements.

In the Formosa regiolect (regiolect 1, Fig. 2, Table 2), we identified an introduction and 15 note types from the 19 adult males sampled. In the Corrientes regiolect (regiolect 2, Fig. 3, Table 2) we identified an introduction and 13 note types from the 24 adult males sampled. In the Entre Ríos regiolect (regiolect 3, Fig. 4, Table 2) we identified an introduction and 15 note types from the 12 adult males sampled (one female was excluded from the analysis). In the southern Brazil regiolect (regiolect 4, Figs. 5, 6, Table 2) we identified an introduction and 22 note types from the 33 adult males sampled. The comparison of two birds recorded in 1971 and those recorded 2004–2009 revealed that 17 of 22 note types were homologous (Figs. 5, 6, Table 2). Morphological changes of note types from 1971 to 2004–2009 involved shifts in frequency range, duration, and overall shape, making recognition of homologies difficult. In the understudied regiolect of the lowlands of Bolivia (regiolect 5, Fig. 7, Table 2) we identified an introduction and six note types from at least two adult males.

HABITAT USE

In general terms, for breeding, *S. hypoxantha* favors dry grasslands with shrubs (60%, $n = 107$). A minority of birds was found in other habitats such as marsh or wet grasslands (40%, $n = 71$). The species evidently avoids *caraguatal–cardal*, undulating grassland, depressed pampas grasslands, bogs, or annual crops, where we found none breeding (Table 3).

Both the physiognomy and floristic composition of preferred habitats varies geographically in a manner congruent with the regiolects (Tables 1, 3). Birds singing the Formosa, Corrientes, and Entre Ríos regiolects clearly preferred one habitat each (Table 3), while those singing the southern Brazil regiolect occurred in similar proportions in two habitats (Table 3). We could not evaluate habitat use of birds in the lowlands of Bolivia, but presumably habitats suitable for breeding occur in the grasslands of the Llanos de Moxos (Table 3).

TABLE 1. Summary of features characterizing the five regiolects of the Tawny-bellied Seedeater (*Sporophila hypoxantha*). See Discussion for details on the overlap of Formosa and Entre Ríos regiolects.

Regiolect	Voices	Distribution	Habitat	Migration
Formosa	Fig. 2	Formosa, extending into Santa Fé and Entre Ríos	*Campos altos* and *campos bajos*	Resident
Corrientes	Fig. 3	Corrientes	Shrubby grasslands	Migratory
Entre Ríos	Fig. 4	Entre Ríos, extending into Santa Fé	*Flechillares*	Migratory
Southeast Brazil	Figs. 5, 6	Southeastern Brazil	Campos de Cima da Serra	Migratory
Lowland Bolivia	Fig. 7	Bolivian lowlands	Llanos de Moxos (*altura and sertanejales*)	Resident?

TABLE 2. Types and percentages of notes by regiolect of individual adult male Tawny-bellied Seedeaters (*Sporophila hypoxantha*) whose songs included those notes. Letters correspond to spectrograms in Figures 2–7 and indicate notes homologous through time within the southeast Brazil regiolect but do not imply homology of notes of different regiolects.

Note	Regiolect (*n*)					
	Formosa (19)	Corrientes (24)	Entre Ríos (12)	SE Brazil (33)	SE Brazil 1971 (2)	Lowland Bolivia (2)
Introduction	78.9	79.2	100	93.9	50.0	×
a	78.9	79.2	91.7	78.8	100	×
b	89.5	70.8	100	72.7	100	×
c	89.5	70.8	100	66.7	100	×
d	78.9	70.8	75.0	90.9	100	×
e	78.9	79.2	83.3	90.9	100	×
f	84.2	54.2	83.3	75.8	100	×
g	84.2	58.3	75.0	33.3		
h	78.9	33.3	91.7	81.8	100	
i	36.8	62.5	91.7	84.8	100	
j	47.4	66.7	91.7	84.8	100	
k	42.1	41.7	66.7	78.8	100	
l	10.5	12.5	41.7	66.7	100	
m	15.8	29.2	75.0	39.4		
n	10.5		66.7	57.6	50	
o	15.8		50	66.7	50	
p				24.2	100	
q				21.2	50	
r				57.6		
s				9.1		
t				36.4	100?	
u				24.2		
v				6.1	100	

We found syntopy of two regiolects at two localities. On 20 February 2006, in the Campo del Medio, Santa Fé, we recorded one individual singing the Entre Ríos regiolect together with two individuals singing the Formosa regiolect. A pair was feeding fledglings in this area, but the male was silent, so we could not ascertain its regiolect. On 12 December 2003, at Estancia La Marita, Entre Ríos, we recorded a single male calling in the Formosa regiolect with breeding birds of the Entre Ríos regiolect. We did not confirm breeding of this male of the Formosa regiolect.

MIGRATORY BEHAVIOR

We found geographic variation in the migratory behavior of *S. hypoxantha*, with one population, that singing the Formosa regiolect, largely resident, the others migratory (Table 1). Although birds singing the Formosa regiolect breed territorially and overwinter in large flocks in the same area (El Bagual, DiGiácomo 2005; Fig. 1), our data on vocalizations suggest that at least a few birds of the Formosa regiolect are migratory, and that the birds resident at El Bagual may be augmented during winter with others of the same regiolect that breed in farther south. Completely migratory populations encompass the Corrientes, Entre Ríos, and southern Brazil regiolects, which occupy their breeding grounds roughly from October/November to March/April. We could not evaluate the migratory status of the regiolect of the lowlands of Bolivia thoroughly, but that population might be resident in the area (Davis 1993, Joseph 1996; pers. obs.) or engage in medium-distance seasonal migration (Q. Vidoz in litt.).

DISCUSSION

Our data demonstrate four regiolects of *S. hypoxantha* in Argentina and Brazil and apparently a fifth in the lowlands of Bolivia. The strong differences in vocal data are accompanied by less drastic but concordant changes in habitat use and are independent of migratory behavior (Table 1).

GEOGRAPHIC STRUCTURE OF VOCAL VARIATION

During the breeding season, the distributions of most regiolects of *S. hypoxantha* are allopatric, but because most
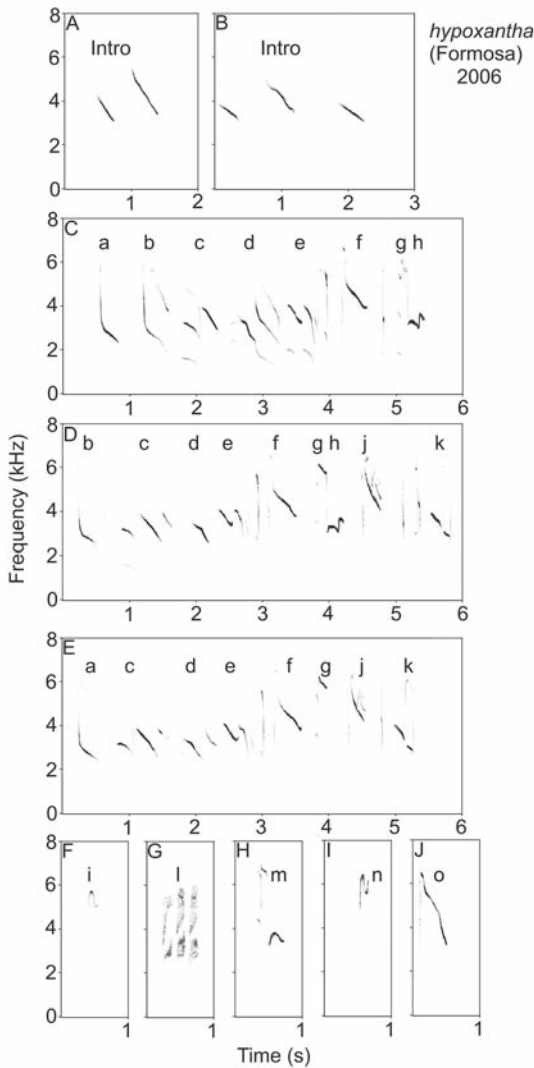
FIGURE 2. Representative spectrograms of vocalizations of the Formosa regiolect of the Tawny-bellied Seedeater (*Sporophila hypoxantha*; *n* = 19). Numbers in parentheses correspond with the recorded bird's identification number in Appendix 1. Locality name and locality number as in Fig. 1 are also included here to facilitate comparison of similarity of regiolects. (A) Introduction (47, El Bagual, 23), (B) introduction (52, El Bagual, 23), (C) song (47, El Bagual, 23), (D) song (52, El Bagual, 23), (E) song (52, El Bagual, 23), (F) note i (50, El Bagual, 23), (G) note l (50, El Bagual, 23), (H) note m (50, El Bagual, 23), (I) note o (50, El Bagual, 23), and (J) note o (56, El Bagual, 23). See Table 2 for frequency of each note type in the Formosa regiolect.

FIGURE 3. Representative spectrograms of vocalizations of the Corrientes regiolect of the Tawny-bellied Seedeater (*Sporophila hypoxantha*; *n* = 24). Numbers in parentheses correspond with the recorded bird's identification number in Appendix 1. Locality name and locality number as in Fig. 1 are also included here to facilitate comparison of similarity of regiolects. (A) Introduction (14, Mercedes, 16), (B) introduction (17, Colonia Pellegrini, 18), (C) introduction (24, Estancia Rincón del Socorro, 17), (D) introduction (24, Estancia Rincón del Socorro, 17), (E) song (25, Estancia, Rincón del Socorro, 17), (F) song (14, Mercedes, 16), (G) song (27, Estancia Rincón del Socorro, 17), and (H) note m (20, Estancia Rincón del Socorro, 17). See Table 2 for frequency of each note type in the Corrientes regiolect.

populations migrate, spatial overlap of regiolects is expected during migration or in winter. The syntopy of the Formosa and Entre Ríos regiolects in Campo del Medio, Santa Fé, may be ephemeral, since birds of the Entre Ríos regiolect are thought to migrate through the area, while the birds of the Formosa regiolect may breed there. The brief time that we spent in this locality does not allow a definite answer concerning
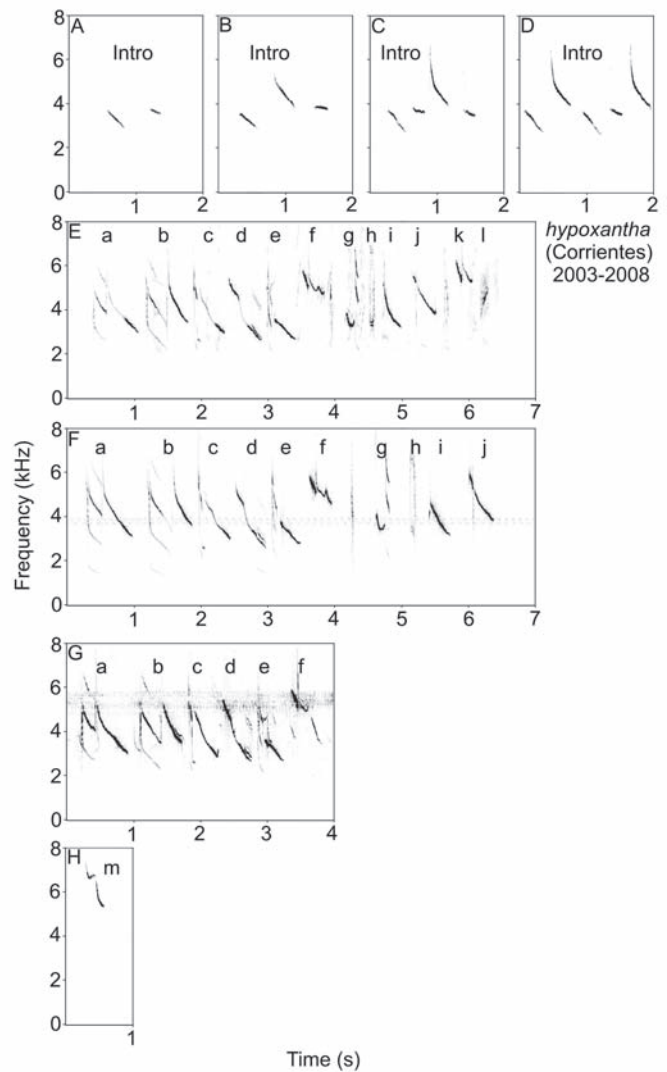
the meaning of syntopy of these vocal types or the migratory status of birds in Campo del Medio. On the other hand, the overlap of these two regiolects at Estancia La Marita, Entre Ríos, occurred within the breeding range of the Entre Ríos regiolect. These data show that the barriers between regiolects are not absolute and could be leaky. Although the occasional overlap of the Formosa and Entre Ríos regiolects shows the
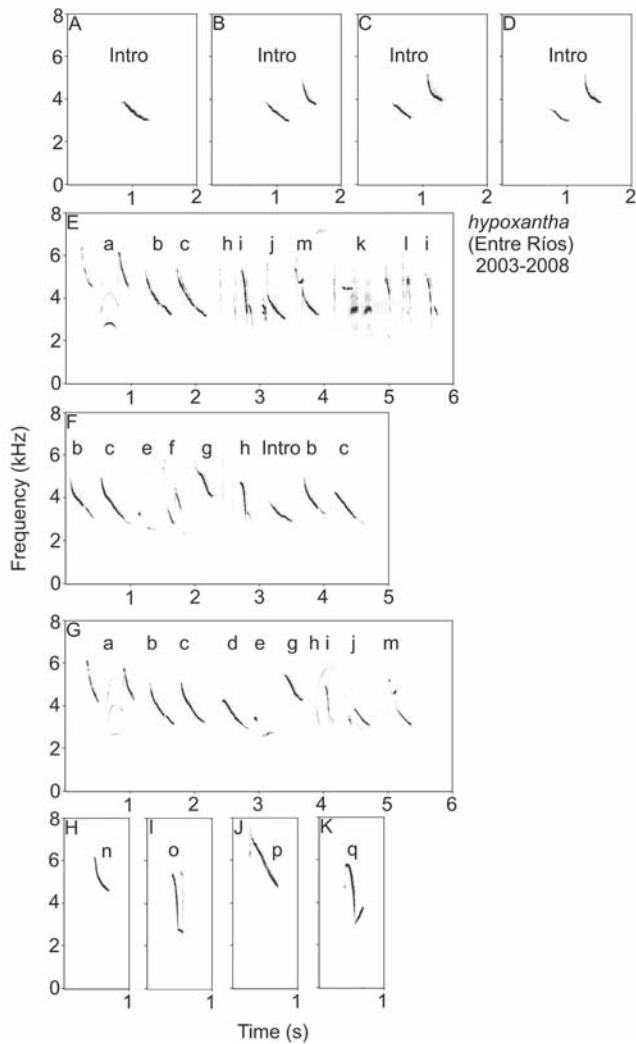
FIGURE 4. Representative spectrograms of vocalizations of the Entre Ríos regiolect of the Tawny-bellied Seedeater (*Sporophila hypoxantha; n* = 13). Numbers in parentheses correspond with the recorded bird's identification number in Appendix 1. Locality name and locality number as in Fig. 1 are also included here to facilitate comparison of similarity of regiolects. (A) introduction (32, Estancia La Marita, 4), (B) introduction (32, Estancia La Marita, 4), (C) introduction (33, Estancia La Marita,4), (D) introduction (38, Campo del Medio, 14), (E) song (32, Estancia La Marita, 4), (F) song (33, Estancia La Marita, 4), (G) song (38, Campo del Medio, 14), (H) note n (32, Estancia La Marita, 4), (I) note o (32, Estancia La Marita, 4), (J) note p (35, Estancia La Marita, 4), and (K) note q (38, Campo del Medio, 14). See Table 2 for frequency of each note type in the Entre Ríos regiolect.

FIGURE 5. Representative spectrograms of vocalizations of the southeast Brazil regiolect of the Tawny-bellied Seedeater (*Sporophila hypoxantha; n* = 43). Numbers in parentheses correspond with the recorded bird's identification number in Appendix 1. Locality name and locality number as in Fig. 1 are also included here to facilitate comparison of similarity of regiolects. (A) Introduction (115, Capão Alto, 38), (B) intro (101, Coxilha Rica, 33), (C) introduction (119, Rio São Mateus, 35), (D) introduction (82, Fazenda Socorro, 42), (E) song (115, Capão Alto, 38), (F) song (116, Capão Alto, 38), (G) song (117, Capão Alto, 38), (H) note r (115, Capão Alto, 38), (I) note s (115, Capão Alto, 38), (J) note t (116, Capão Alto, 38), (K) note u (116, Capão Alto, 38), and (L) note v (106, Fazenda Chapadão–Rio das Perdizes, 32). See Table 2 for frequency of each note type in the southeast Brazil regiolect.

colonization potential of note types, for immigration to occur (i.e., the effective establishment of new note types) the new note types must not only reach but also succeed in the new environment. There is no evidence of immigration of note types between the regiolects of *S. hypoxantha*, and most vocal differences can be explained by the balance between mutation and extinction of note types in isolated subpopulations (Lynch et al. 1989, Lynch and Baker 1994). This lack of immigration
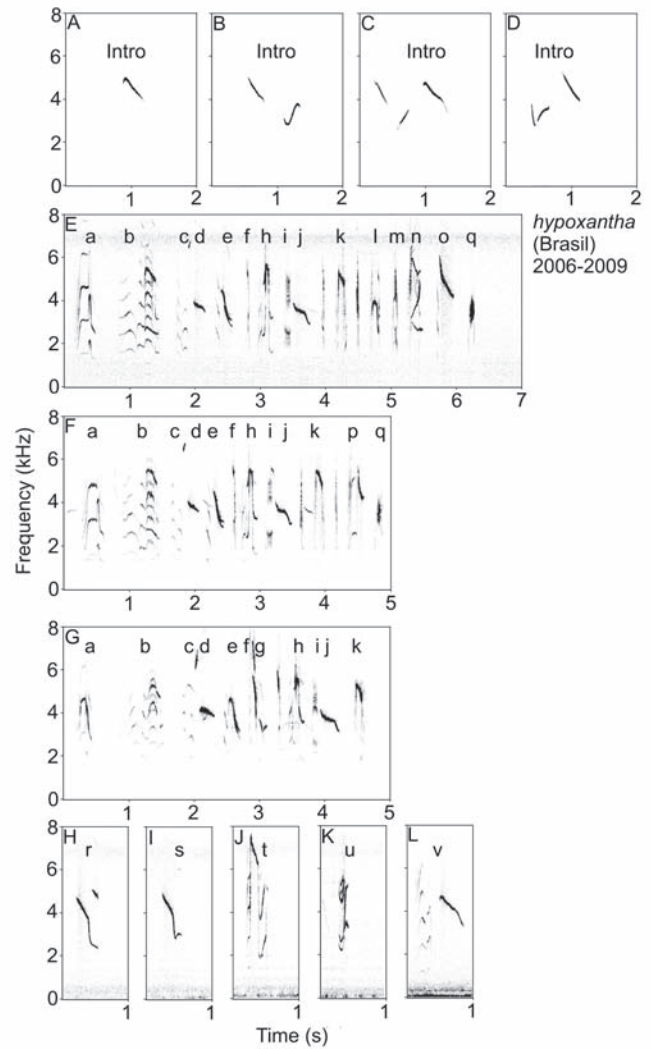
of note types (memes) suggests that the birds (carriers) of each regiolect are not exchanging genes either, although this remains unknown, and genetic flux could be decoupled from cultural transmission (Slabbekoorn and Smith 2002). The regiolect most divergent in note shape is that of southeastern Brazil, which suggest that it is either the most isolated regiolect or that it is more refractory to external influences than are the other regiolects.
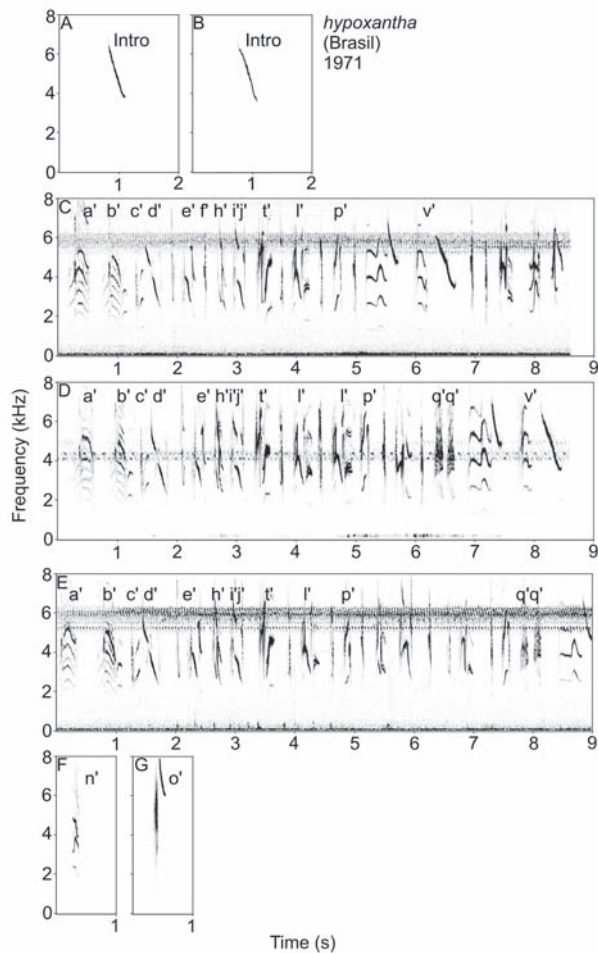
FIGURE 6. Representative spectrograms of vocalizations of the 1971 chronolect of the southeast Brazil regiolect of the Tawny-bellied Seedeater (*Sporophila hypoxantha*; *n* = 3). Numbers in parentheses correspond with the recorded bird's identification number in Appendix 1. Locality name and locality number as in Fig. 1 are also included here to facilitate comparison of similarity of regiolects. (A) introduction (PAS 123/MLNS 65796, Guacho/Vacaria, 44), (B) introduction (PAS 125/MLNS 65798, Guacho/Vacaria, 44), (C) song (PAS 124/MLNS 65797, Guacho/Vacaria, 44), (D) song (PAS 125/MLNS 65798, Guacho/Vacaria, 44), (E) song (PAS 124/MLNS 65797, Guacho/Vacaria, 44), (F) note n (PAS 124/MLNS 65797, Guacho/Vacaria, 44), and (G) note o (PAS1 25/MLNS 65798, Guacho/Vacaria, 44). See Table 2 for frequency of each note type in the southeast Brazil regiolect, 1971 chronolect.

NATURE AND NURTURE IN THE VOICES OF THE CAPUCHINOS

Four lines of evidence suggest that the current vocal differences within subpopulations of *S. hypoxantha* are due essentially to learning. First, the phylogenetic potential for learning is present in *Sporophila* (Sick 1963, 1979, 1997). A few species of *Sporophila* seedeaters are known to mimic or to incorporate voices of other sympatric bird species into their repertoires.
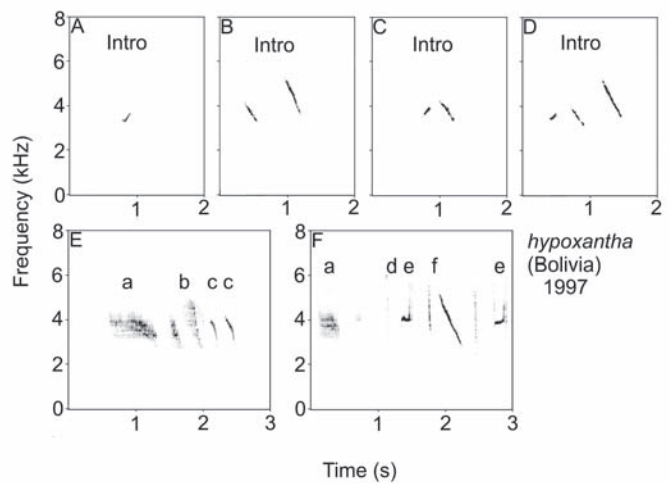

FIGURE 7. Representative spectrograms of vocalizations of the lowland Bolivia regiolect of the Tawny-bellied Seedeater (*Sporophila hypoxantha*; *n* = 2). Numbers in parentheses correspond with the recorded bird's identification number in Appendix 1. Locality name and locality number as in Fig. 1 are also included here to facilitate comparison of similarity of regiolects. (A) Introduction (SM 68, Trinidad, 31), (B) introduction (SM 68, Trinidad, 31), (C) introduction (SM 68, Trinidad, 31), (D) introduction (SM 68, Trinidad, 31), (E) song (SM 69, Trinidad, 31), and (F) song (SM 69, Trinidad, 31). See Table 2 for frequency of each note type in the lowland Bolivia regiolect.

For example, the Rusty-collared (*S. collaris*), Plumbeous (*S. plumbea*), White-throated (*Sporophila albogularis*) and Gray (*S. intermedia*) Seedeaters are known to mimic (Moschione 1989, Thomas 1996, Sick 1979, 1997; pers. obs.). No capuchino, however, is known to mimic (*n* = 270 individuals of all species in the *ruficollis* group, 44 individuals of *S. melanogaster*). Second, we recorded young of *S. hypoxantha* uttering subsongs, which are imperfect renderings of adult songs typical of species that need auditory feedback to produce a suitable output of their learned songs (Hultsch and Todt 2004). These presumed juveniles were singing the local regiolect, evidence of early learning of the natal regiolect. Third, changes in the voices of the closely related *S. palustris* and *S. cinnamomea* over 15 years are too fast to be attributable to genetic differences (Areta 2008), as are those in *S. hypoxantha* over 38 years (this study) and those observed in *S. melanogaster* (Areta 2010, Repenning et al. 2010b). The rapidity of change of note types in the capuchinos shows that each regiolect is in constant transformation (Areta 2008, Areta et al. 2011). This impressive dynamism seems to include the entire repertoire, and allochronic samples of the vocalizations in the same area through time (chronolects) show levels of divergence similar to those found between synchronic populations in different areas (regiolects). The fluidity of the chronolects makes their delimitation as such arbitrary, but their geographic boundaries are clear when they are considered as regiolects. Four, environmental sound assimilation in *S. hypoxantha* and

TABLE 3.   Habitat use of male Tawny-bellied Seedeaters (*Sporophila hypoxantha*) of different regiolects. See Methods for description of habitats.

Habitat	Regiolect (*n*)				
	Entre Ríos (22)	Formosa (25)	Corrientes (36)	SE Brazil (95)	Lowland Bolivia
Dry grasslands					
Caraguatal–cardal					
Undulating grassland					
Depressed pampas grassland					
Campos altos		72%			
Shrubby grassland			89%		
Flechillar	82%				
Valley shrubby grassland				41%	
Llanos de Moxos					(?)
Wet grasslands					
Campos bajos		28%			
Lowland wet	18%		11%		
Highland wet				59%	
Bogs					
Crops					

S. ruficollis provides direct evidence of local learning in different regiolects. We define environmental sound assimilation (Areta 2010) as the process by which, at some point in the learning process, a sound from the environment becomes part of the repertoire of a bird population or species without requiring acoustic contact with the initial model (i.e., primary mimicry followed by transmission within the species; see Saunders 1923, Baylis 1982, Kelley et al. 2008). The process of environmental sound assimilation differs fundamentally from regular mimicry (after the primary mimicry) in ontogeny (heterospecific vs. conspecific model), scope (population-wide vs. individual acquisition), and frequency (typical vs. atypical). The song of the Formosa regiolect includes a note (note J) that looks and sounds to the ear very similar to the short call of the Yellowish Pipit (*Anthus lutescens*), present in the area and the only pipit reported for the range of this regiolect (Di Giácomo 2005). Likewise, the song of the Entre Ríos regiolect includes a series of notes (notes B, C, and D) that resemble the local song dialect of the Rufous-collared Sparrow (*Zonotrichia capensis*). The song of the closely related *S. ruficollis* includes two notes (notes D, and E, see Areta et al. 2011) that sound very similar to the regular song of the Striped Cuckoo (*Tapera naevia*), and it seems to represent another case of environmental sound assimilation in the capuchinos.

On the other hand, the extremely shallow and inconsistent genetic differences among all the capuchinos (Campagna et al. 2009) provide evidence that the genetic makeup of the forms has little effect on their vocalizations (Areta 2008, Areta et al. 2010, this work). Nevertheless, continuing studies

of genetic differentiation in the capuchinos will test whether the learned vocal differences in the regiolects of *S. hypoxantha* have been accompanied by genetic divergence or not (Areta, unpubl. data).

EVOLUTIONARY ECOLOGY OF REGIOLECTS

Our data provide important insights into the evolution of the capuchinos. Birds singing three of the four well-studied regiolects of *S. hypoxantha* are completely migratory, vacating their breeding grounds from March/April to October/November but returning to the same areas to breed. Therefore, despite extensive opportunities for overlap and fusion, these regiolects seem to maintain integrity through space and time because of the birds' philopatry.

In *S. hypoxantha*, differences of regiolects are accompanied by habitat differences (and perhaps minor consistent plumage differences not evaluated in this study), suggesting that these traits have evolved in concert. Sick (1967) proposed habitat segregation as the most important isolating mechanism (isolating barrier) in the seedeaters. Given the contrast between the scant genetic differentiation and the habitat divergence of the capuchinos (Areta 2008, Areta et al. 2011), habitat segregation is evidently achieved by imprinting rather than by genetic factors. Therefore, we hypothesize that habitat choice and philopatry might be the product of a feedback loop in which an assortative mating system based on learned song and habitat preferences reinforces a more or less loose philopatry. Indeed, the capuchinos provide exceptional support in

favor of the importance of learning in speciation (Irwin and Price 1999, Areta et al. 2011).

Although there are at least five regiolects of *S. hypoxantha*, Areta et al. (2011) identified only two of *S. ruficollis*, and Areta (2008) identified none in *S. palustris* and *S. cinnamomea* over a large and partly overlapping area. Likewise, there is no geographic variation within the restricted range of *S. melanogaster* (Areta 2010, Repenning et al. 2010b). Therefore, the potential for evolutionary diversification of these closely related species seems different, and this difference in turn seems related to the geographic distribution of the species' preferred habitats, broadly defined: the more widespread shrubby dry grasslands favored by *S. hypoxantha* allow for a greater degree of population subdivision and vocal differentiation.

Our data on *S. hypoxantha* provide evidence that in the capuchinos geographically structured ecological and vocal variation can arise and be maintained through time without the need for intervening geographical barriers, supporting previous proposals that speciation and differentiation in the capuchinos have a strong ecological basis (Sick 1967, Areta 2008, Areta et al. 2011, Repenning et al. 2010a). The differences in songs between regiolects of *S. hypoxantha* are comparable to those found between different species in the group (Areta 2008, Areta et al. 2011), suggesting that the existence of allopatric habitat-related regiolects with little (if any) morphological differentiation might constitute an early step into the evolution of new species (Areta 2010).

SYSTEMATICS OF *SPOROPHILA HYPOXANTHA*

Previously treated with different spellings as *Loxia minuta* Linnaeus, 1758 (currently *Sporophila minuta*), *Sporophila hypoxantha* Cabanis, 1851, was finally described as a species on the basis of an adult male presumably held in the Berlin Museum at the time of the description, from either Montevideo, Uruguay (Cabanis 1851), or Brazil (Hellmayr 1938). Cabanis (1851) linked his *S. hypoxantha* to the 122 Pardo y canela of Azara (1802). The original specific epithet was taken by Cabanis from a label/manuscript name of Heinrich Lichtenstein, who informally named the bird as *Fringilla hypoxantha*. Unfortunately, the whereabouts of the type specimen are unknown (Claramunt et al. 2006).

The specific status of *S. hypoxantha* has been disputed in the literature. For many years, *S. hypoxantha* was considered a valid species (Lichtenstein 1854, Pelzeln 1871, Sclater 1871, Sharpe 1888, Hellmayr 1904), but Hellmayr (1938) and Meyer de Schauensee (1952, 1966), without explanation, treated it as a subspecies of *S. minuta*. Later, on the basis of its smaller size, lighter ventral coloration, and tawny instead of gray auriculars, Short (1969) raised *S. hypoxantha* to a full species, as originally proposed by Cabanis (1851). This treatment has been followed by most subsequent authors (Paynter and Storer 1970, Sibley and Monroe 1990, Belton 1994, Ouellet 1992, Sabel 1990, Sick 1997, Areta 2008, Areta et al. 2011, Remsen et al. 2009). Genetic data are also in agreement with species-level differences

between *S. hypoxantha* and *S. minuta*, in the otherwise genetically very uniform capuchino clade (Lijtmaer et al. 2004).

Other authors considered *S. hypoxantha* a variant of other species in the *ruficollis* group. Sharpe (1888:140) wrote that *S. cinnamomea* "would be identical with *S. hypoxantha*," Sclater (1871) and Sharpe (1888) considered *S. ruficollis* "allied to *S. hypoxantha*, of which it is perhaps the young bird" (Sharpe 1888: 140), and Short (1969, 1975) proposed that *S. hypoxantha* should be considered polymorphic, including *S. ruficollis* and *S. palustris* within it. However, the marked differences among these forms in preferred habitats, vocalizations, and plumages support full species status for each of them: Areta (2008) for *S. palustris* and *S. cinnamomea*, Areta et al. (2011) for *S. ruficollis*, this work for *S. hypoxantha*.

The correspondence between regiolects and habitat in *S. hypoxantha* raises an important question: should these regiolect populations of *S. hypoxantha* be considered different species under the recognition concept of species (Paterson 1985)? The answer to this question is not straightforward. Under a strict application of the recognition concept we might tentatively suggest that they are five different species. However, we believe this to be premature. First, birds of different regiolects may have minor plumage differences, but, if so, these differences are not as great as those of other forms considered species (Areta 2010). Second, there is no solid evidence of breeding syntopy/sympatry of regiolects, while valid sympatric species of capuchinos differ in plumage, vocalizations, and preferred habitats, broadly defined (Areta 2008, 2010). When compared against these adequate yardsticks, the regiolects of *S. hypoxantha* fail to pass the level of differentiation expected for good species. Geographic variation in vocalizations within *S. hypoxantha* should not be taken as evidence of multiple species, while geographical overlap of the regiolects of *S. hypoxantha* with other seedeaters distinct in plumage, ecology, and voice strongly supports their being different species. Regardless of the taxonomic treatment of the regiolect populations of *S. hypoxantha*, the taxonomic meaning of differences in voices and habitat use is much easier to interpret in sympatry, than in allopatry. In synthesis, we interpret the available data on vocal and habitat variation in *S. hypoxantha* as evidence for five regiolects, not five species, although the evidence demonstrates the existence of five somewhat different evolutionary trajectories. Our taxonomic conclusions under the recognition species concept (Paterson 1985) are the same as under the biological species concept (Mayr 1963), while those endorsing the phylogenetic species concept (Cracraft 1983) might prefer to treat the regiolect populations as species on the basis of their vocal diagnosability, despite the lack of a morphological diagnosis.

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APPENDIX 1.   Localities of birds recorded and identification of voices used in this study. Localities are shown in Figure 1. Numbers in brackets number of individuals per locality; numbers in parentheses, identification number of the individual in JIA database. All recordings by JIA and MR, except for SM = Sjoerd Maijer; PAS = Paul A. Schwartz.

Sporophila hypoxantha [102+]. Argentina, Entre Ríos regiolect [13]: Estancia La Marita [12] (1–5, 7, 32–37), Campo del Medio [1] (38). Formosa regiolect [19]: Estancia El Bagual [16] (43–58), Estancia La Marita [1] (6), Campo del Medio [2] (39, 40). Corrientes regiolect [25]: Colonia Pellegrini [5] (8, 9, 12, 13, 17), Cambá Trapo [2] (10, 11), Mercedes [4] (14–16, 28), Estancia El Socorro [14] (18–27, 29–31, 42). Bolivia, lowland Bolivia regiolect [2]: Trinidad [2+] (SM68–69, mixed species flock). Brazil, southeast Brazil regiolect [43]: Coxilha Rica [23] (89–90, 93–95, 97, 99–105, 108–113, 118, 120–122), Estância do Meio [4] (86, 91, 96, 98), Fazenda Socorro/Rio Santana [3] (80, 82, 88, 114), Lages [1] (64), Capão Alto [3] (85, 115–117), Capão Bonito [1, 127], São Pedro [2] (83–84), Cachoeira dos Baggio [1] (107), Rio São Mateus [1] (119), Guacho [2] (87, 92), Fazenda Chapadão–Rio das Perdizes [1] (106). 1971 chronolect: Guacho/Vacaria [3]. (PAS 123–125: MLNS 67596–67598).

APPENDIX 2.   Localities at which we obtained habitat-use information for this study. Localities are shown in Figure 1. Numbers in brackets, number of individuals or territories per locality.

S. hypoxantha [178]. Argentina, Entre Ríos regiolect [22]: Estancia La Marita [20], Campo del Medio [1], Arroyo Baru–San Salvador [1]. Formosa regiolect [25]: Estancia El Bagual [23], Campo del Medio [2]. Corrientes regiolect [36]: Colonia Pellegrini [18], Estancia Rincón del Socorro [18]. Southeast Brazil regiolect [95]: Fazenda Chapadão–Rio das Perdizes [2], Cerro Negro [4], Coxilha Rica [18], Estância do Meio [5], Rio São Mateus [4], Antiga Estação Ferrea–Bom Jesus [9], Fazenda Socorro/Rio Santana [11], Arroio Pessegueiros [15], Capão Alto [12], Capão Bonito [5], São Pedro [7], Cachoeira dos Baggio [1], Guacho [2].