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Song development in the grasshopper sparrow, *Ammodramus savannarum*

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Adult male grasshopper sparrows sing two structurally and functionally distinct songs: buzz song and warble song. To investigate how these songs develop, we tutored three groups of young males in the laboratory: one with recordings, one with live adult tutors and one with no song (isolate birds). We used visual scoring of spectrograms, principal components analysis of acoustic measures and spectrogram cross-correlation to analyse the results. Tape-tutored and live-tutored birds developed structurally normal buzz songs and largely normal warble songs. Isolate birds developed moderately normal buzz songs along with one or two more atypical songs. Neither buzz songs nor warble songs were accurately imitated by any of the tape-tutored birds. Live-tutored birds imitated buzz songs, but not warble songs, more closely than did tape-tutored birds. We also examined buzz songs in a population of grasshopper sparrows in the field. Comparisons of buzz songs of yearling males with those of their social fathers and with those of their first-breeding-year territorial neighbours indicate that sons do not imitate songs of their social fathers, and imitate songs of their immediate territorial neighbours only to a limited degree. Overall our results suggest that grasshopper sparrow song does not develop by imitation but that exposure to conspecific song is important for normal song development. Differences in development of the two song types may relate to both acoustic structure and function of these songs.

Studies of songbird vocal development have documented considerable variation across species in what is learned in song, and when. Examples of features of song learning that vary across species include the extent to which songs are imitated versus improvised or invented, the tendency to mimic other species, the number of songs that are learned, and the stages of life at which song learning occurs (e.g. Kroodsma 1988; Slater 1989). Broadly, these song-learning features are thought to vary because each species has a unique evolutionary history and set of life history traits. Birdsong ethologists are interested in understanding this variation in a functional sense. Selection is expected to optimize the relationship between ecological or life history features and the specific mechanisms by which song learning proceeds.

The extent of imitation in song development may be correlated with breeding site fidelity, and thus the likelihood that an individual bird will interact with the same neighbours through time (Kroodsma et al. 2002). In *Cistothorus* wrens, for example, male North American sedge wrens, *C. platensis*, display low breeding site fidelity within and between years, share few song types with neighbours (Kroodsma & Verner 1978), and have been found to improvise or invent songs when tutored in the laboratory (Kroodsma et al. 1999a). Two other species, the marsh wren, *C. palustris* (Verner 1976) and the Merida wren, *C. meridae* (Kroodsma et al. 2001) show higher breeding site fidelity and greater song sharing between neighbouring males, suggesting that song develops by imitation in these two species. Indeed, when tutored in the laboratory, marsh wrens were found to imitate song models (Kroodsma & Pickert 1984). Populations of sedge wrens in Central and South America, which are sedentary, also show neighbour song sharing and microgeographical song variation and thus are presumed to learn song by imitation (Kroodsma et al. 1999b, 2002). In combination, these studies indicate that among *Cistothorus* wrens, song develops by means other than imitation only in populations of wrens with low breeding site fidelity.

The grasshopper sparrow, *Ammodramus savannarum*, shows low breeding site fidelity in much of its range in North America (Vickery 1996). If a correlation between breeding site fidelity and song imitation holds generally across songbird families, this species would be expected to develop song by improvisation or invention. Investigating this question was one of our goals in the current study.

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Grasshopper sparrows and their song are interesting in several additional respects. First, songs of this species are unusually high-pitched (6–10 kHz) and contain an extremely rapid sequence of frequency- and amplitude-modulated notes (Fig. 1a). We investigated whether such high, rapid songs are learned by imitation, and if so, how accurately. Second, grasshopper sparrows are unusual among emberizids in that adult males sing two song types that differ in both structure and function (Vickery 1996). The primary song, identified here as the 'buzz song', consists of two to four very brief introductory notes at different frequencies, followed by a high-pitched, rapidly modulated sequence of notes (here, the buzz 'segment') lasting approximately 1 s (Fig. 1a). Buzz song is thought to serve both inter- and intrasexual territorial advertisement functions, based on (1) when it is produced in the season and breeding cycle (Smith 1959), (2) evidence that unpaired territorial males produce only this song type (B. Lohr, personal observation) and (3) the observation that the majority of songs given by males in response to song playback are buzz songs (Vickery 1996).

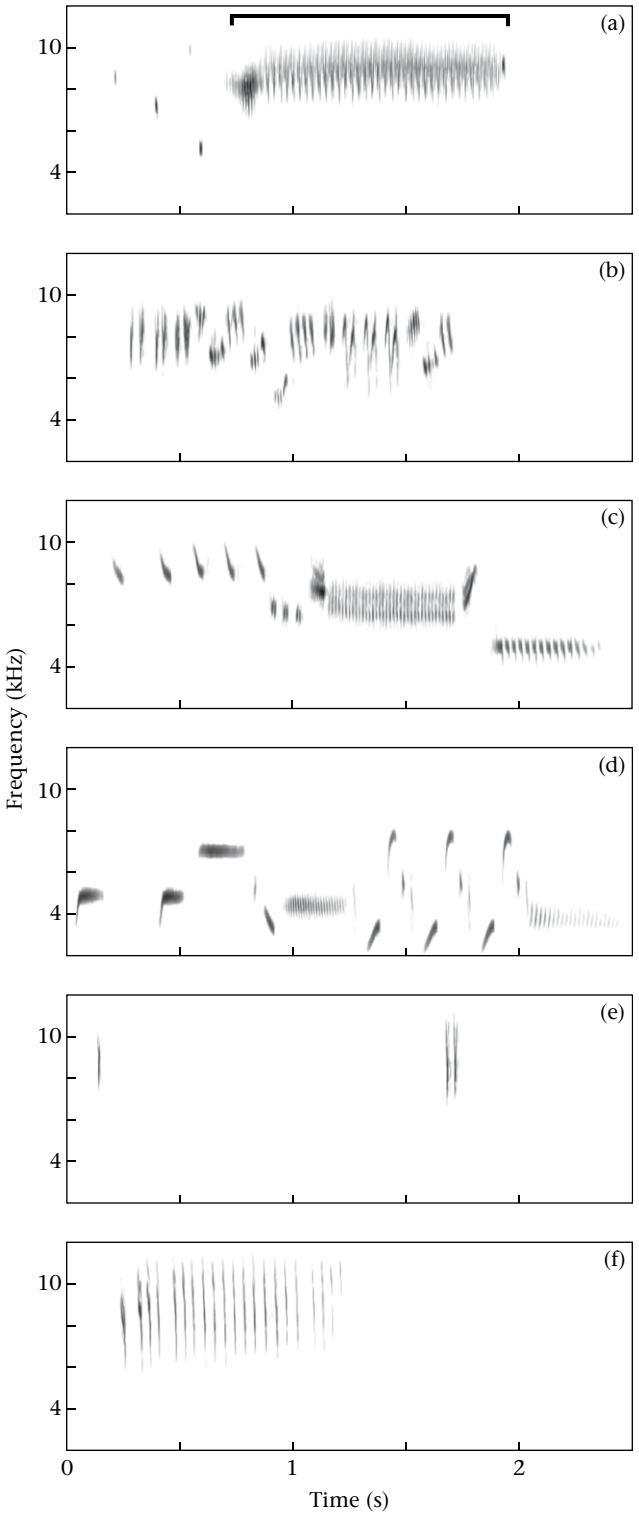

Figure 1. Six stimulus types used in laboratory experiments with young grasshopper sparrows: (a) grasshopper sparrow buzz song, with buzz segment indicated by bracket, (b) grasshopper sparrow warble song, (c) Savannah sparrow song, (d) song sparrow song, (e) grasshopper sparrow tic–tillic call, (f) grasshopper sparrow trill call. All six types were used in the early vocal response test. Types (a)–(d) were used as tutor models in the tape-tutoring experiment.

The second song type, or 'sustained song' of Vickery (1996), identified here as 'warble song', contains multiple short notes of variable structure (Fig. 1b). Some of these notes are repeated twice or more in sequence before the next note is produced, and the entire sequence may be repeated two or more times. The buzz and warble songs are often sung separately, but are also commonly produced with the buzz song immediately preceding the warble song. Because males sing the warble song much more frequently after pairing (Vickery 1996), and because a female call (the 'trill') and male warble songs may be produced in response to one another (Smith 1959), this song type may have female-directed functions such as pair bond maintenance or female reproductive stimulation. Each male grasshopper sparrow has an individually distinctive repertoire of one buzz song and one warble song (Smith 1959; Vickery 1996), both of which appear to remain stable over the course of a male's life.

The production of two functionally distinct song types is unusual in sparrows. While some sparrows produce 'flight songs' in addition to territorial signals (e.g. swamp sparrows *Melospiza georgiana*: Nowicki et al. 1991), the two song types in the grasshopper sparrow may be more analogous to the functionally distinct song categories produced by some New World warblers. In chestnut-sided warblers, *Dendroica pensylvanica*, for example, songs in one category are thought to serve as intrasexual signals and songs in the other as intersexual signals (Byers 1996a). Byers & Kroodsma (1992) documented differences in how chestnut-sided warblers learn songs of the two categories. In particular, they found that development of the intrasexual song was dependent on social interaction, while learning of the intersexual song was not. We wanted to investigate whether differences exist in learning of the two grasshopper sparrow song types, and if so, whether they parallel those observed in the chestnut-sided warbler, to the extent that the functional categories may be similar in these two species. We began by investigating early recognition of song types by fledgling grasshopper sparrows to determine whether we could find evidence for a predisposition to attend to one or both types of conspecific song for memorization. We then analysed the songs developed in a controlled laboratory setting using tape tutors, live tutors and isolate birds having no exposure to song. Finally, we assessed song imitation in a field setting with a banded population of grasshopper sparrows under long-term study, where both territorial neighbours and social fathers of second-year (SY) males could be identified.

METHODS

Subject Rearing and Care

Birds were collected as nestlings in 2004 and 2005 (details below), syringe-fed Kaytee Exact® Hand-Feeding Formula (Kaytee Products, Inc., Chilton, WI, U.S.A.) hourly during daylight for the