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The influence of different tutor types on song learning in a natural bird population

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Male Savannah sparrows, *Passerculus sandwichensis*, sing a single, individually distinctive song their entire life, which they presumably learn from other males in the same population. We took advantage of a strongly philopatric, known-age and known-parentage island population to examine the influence of five tutor types on song learning: a bird's social father, genetic father, natal neighbours, older breeding-year neighbours and 1-year-old breeding-year neighbours. Of 57 males banded as nestlings, there was wide variation in the tutor type with the greatest influence on song learning. Based on pairwise visual comparisons of spectrograms of all co-occurring males plus quantitative measures of similarity of digitized songs, only 12% of males sang songs that were most strongly influenced by their social father, as inferred by overall similarity of entire songs. About 45% of males were the product of extrapair paternity, but no male sang a song that was most similar to his genetic (versus social) father. Thirty-five per cent of males produced songs that were most similar to those of natal neighbours, 26% sang songs most like older breeding-year neighbours and 26% sang songs most like 1-year-old breeding-year neighbours. Neither a male's body condition at fledging nor his fledging date was related to tutor type, and tutors did not differ from nontutors in morphology, longevity or reproductive success. Savannah sparrows apparently draw upon a wide set of models heard in both their hatching and their breeding years, incorporating specific song elements into their own song rather than copying in its entirety any particular tutor's song.

Keywords: birds; developmental stress; Emberizidae; *Passerculus sandwichensis*; Savannah sparrow; song learning; tutor

In most species of oscine songbirds, males learn their songs from older males, showing a strong learning bias towards conspecific models (Beecher & Brenowitz 2005; Nowicki & Searcy 2005). At what age, under what conditions and from whom a young male learns his song in the wild remain open questions, especially in migratory species. Previous research has focused on three potential tutor types: a male's father, natal neighbours (adult males that held territories near the nest in which he hatched) and breeding-year neighbours (adult males that held territories near his own territory a year later, when the male was breeding for the first time). A common assumption is that close similarity between the songs of a male and those of a potential tutor is evidence that the male learned his song from that tutor (Nordby et al. 1999; Kroodsma 2004).

Laboratory experiments that demonstrate a relatively brief sensitive period during early development highlight the importance of tutors heard during a young male's hatching year (i.e. father, natal neighbours) (Marler 1970; Beecher & Brenowitz 2005; Phan et al. 2006). On the other

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hand, some field studies suggest that a young male's song is learned mainly from neighbouring males during his first breeding season (Kroodsma 1974; Payne 1996; Liu & Kroodsma 2006). Other studies emphasize the influence of both hatching-year and breeding-year tutors, with songs learned early in life but a bird's ultimate song repertoire modified later in life by selective attrition of some of those songs or the acquisition of new songs (Nelson & Marler 1994).

To complicate matters, one should distinguish between breeding-year neighbours of different ages. Older males ($\geq$2 years old, with previous reproductive experience) are likely to differ from peer males (1 year old, breeding for the first time) in the way they interact with young males. An additional complication is extrapair fertilizations. To the extent that there is a genetic component to individual variation in song (Nelson et al. 1995; Hernandez & MacDougall-Shackleton 2004), a male's genetic father (as opposed to his social father) could influence his song. No previous field study of birds has quantitatively examined the influences on song learning of all five classes of potential tutors: a young male's social father, genetic father, natal neighbours, older breeding-year neighbours and peer breeding-year neighbours. To explore how song learning occurs under natural conditions, we took advantage of a highly philopatric, known-age island population of Savannah sparrows, *Passerculus sandwichensis*, where spatial, social and genetic relationships between birds were known. The theoretical basis for predicting the influence of each tutor type is outlined below.

Social Father

In white-crowned sparrows, *Zonotrichia leucophrys*, swamp sparrows, *Melospiza georgiana*, and song sparrows, *Melospiza melodia*, most song learning occurs between the ages of 20 and 60 days (Marler & Peters 1987, 1988; Phan et al. 2006) and possibly as early as 10 days old (Marler 1987). In the Kent Island Savannah sparrow population, hatching does not begin until early to mid-June, and most males have stopped singing by mid-July and rarely sing again until spring migration (see below). Consequently, fledglings from second broods hear little or no conspecific song after the age of 10–15 days, and even fledglings from first broods hear little song after the age of 40 days, until the following spring.

If the sensitive period in Savannah sparrows is similar to that of other sparrow species, most young males probably hear the songs of their social father much more frequently and distinctly during the main phase of song learning than the songs of other males. During the breeding season, adult male Savannah sparrows spend most of their time on their territories, exclude other males from the vicinity of their nests and remain nearby with their offspring for a median of 2 weeks after fledging, until their offspring achieve independence at about 25 days old (Wheelwright et al. 2003). Males often sing immediately after they have fed their nestlings and fledglings and as their mates approach the nest, which means that associative learning (the linking of two stimuli: food delivery and song) could be an especially powerful proximate reinforcing mechanism of learning from one's social father (assuming that the sensitive period begins earlier than 25 days of age; Marler 1987).

From an ultimate perspective, natural selection in social species could conceivably favour learning the songs of one's father and other close relatives because of the benefits of recognizing and directing altruism towards kin (cf. McDonald et al. 2007). In Savannah sparrows such altruism has not been demonstrated and, given the absence of strong sociality, is improbable, although the ability to recognize kin and assess overall genetic similarity apparently does exist (Wheelwright & Mauck 1998; Freeman-Gallant et al. 2006; Wheelwright et al. 2006). However, if songs are the cues used to avoid inbreeding, there could actually be selection against learning one's social father's song because doing so would narrow a young male's mating opportunities if females avoid mating with close relatives.

Genetic Father

There is clearly a genetic basis to song learning at the species level in oscine songbirds: avian brains and sensory systems are innately more sensitive to and predisposed to learn the songs of their own species or even subspecies (Thorpe 1958; Marler & Peters 1977; Braaten & Reynolds 1999; Nelson 2000). Although it has never been demonstrated in a natural population, subtle differences in song between individuals could conceivably have a genetic basis, especially given that morphological traits tend to have high heritability and that the size of a bird's vocal apparatus has been shown to constrain aspects of song among species (Smith & Wettermark 1995; Podos 2001). If so, the songs of males produced by extrapair fertilizations would more clearly resemble those of their genetic father than those of their social father. None the less, any genetic effect underlying individual differences in song would probably be minor, given abundant evidence of phenotypic variability and plasticity in song (e.g. learning, rapid cultural evolution and geographical variation in dialects: Bradley 1994; Grant & Grant 1996; Payne 1996).

Natal Neighbours

Aside from the song of his social father, a young male is most likely to hear the songs of natal neighbours during the early sensitive period. Savannah sparrows' songs can be plainly heard over a distance of 50 m and, depending upon background noise and wind speed and direction, faintly heard for 100 m or more (based on casual observations: N.T.W., personal observation). At our study site, Savannah sparrow territories have a mean diameter of about 40 m, indicating that a typical nestling routinely hears the songs of three to eight natal neighbours, depending upon local territory density (N. T. Wheelwright & K. Oh, unpublished data). For 2 weeks after fledging, young males generally remain within 50–100 m of their natal nests, where they may hear the songs of additional males. This applies especially to young from broods that hatch early in the