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

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 (≥ 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.

F

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 10e15 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

season; young from second broods hear few or no males singing after fledging. Because individual males vary widely in how often they sing (see below), natal neighbours that are particularly vocal may have a disproportionate influence on song learning (Nelson 1992). There may be advantages in learning from natal neighbours (and from breeding-year neighbours), assuming that Savannah sparrows are like other species in which females prefer natal dialects in selecting a mate (O'Loghlen & Rothstein 1995; Hernandez & MacDougall-Shackleton 2004). A complicating factor in separating the influence of natal neighbours versus genetic fathers is that most genetic fathers are also natal neighbours (Freeman-Gallant et al. 2005).

B

By the time most 1-year-old males return from migration in late April or early May to breed for the first time, older males have already reclaimed their territories and are using song to defend them and attract mates. By this age the classical sensitive period of songbirds studied under laboratory conditions has long since passed (Marler 1970). None the less, at least some 1-year-old Savannah sparrows do not crystallize their songs until 1e2 weeks after arriving at the breeding ground (N. T. Wheelwright & H. Williams, unpublished data), so a young male could adopt the songs of breeding-year neighbours through direct imitation or selective attrition of songs heard earlier in life (Nelson & Marler 1994). Young males of many passerine species incorporate elements of the songs of breeding-year neighbours into their own songs (Payne 1996; Liu & Kroodsma 1999, 2006; Nordby et al. 2001; Kroodsma 2004). The ability to sing a current local song (as opposed to a song learned in a previous year) may be favoured if it improves a male's chances of attracting a local mate or reducing aggression from neighbouring males (Hernandez & MacDougall-Shackleton 2004). Because older birds (after-second-year, ASY) arrive earlier and are socially dominant (at least at the beginning of the breeding season), we predicted that a young male would be more likely to copy these males than he would his 1-year-old peers (second-year, SY) (Payne 1996). Note, however, that in populations with strong breeding philopatry, ASY breeding-year neighbours would also have been natal neighbours for young males that re-

section as the portion of the song containing information about individual identity.

Evidence that song is learned rather than innate and is learned on the breeding grounds rather than on the wintering grounds comes from the observation that Savannah sparrow populations have distinctive dialects over even small spatial scales, independent of population

(a) SR.B

1994

1995

1996

1997

( ) R .

2004

2006

(c)   B. R

2004

2006
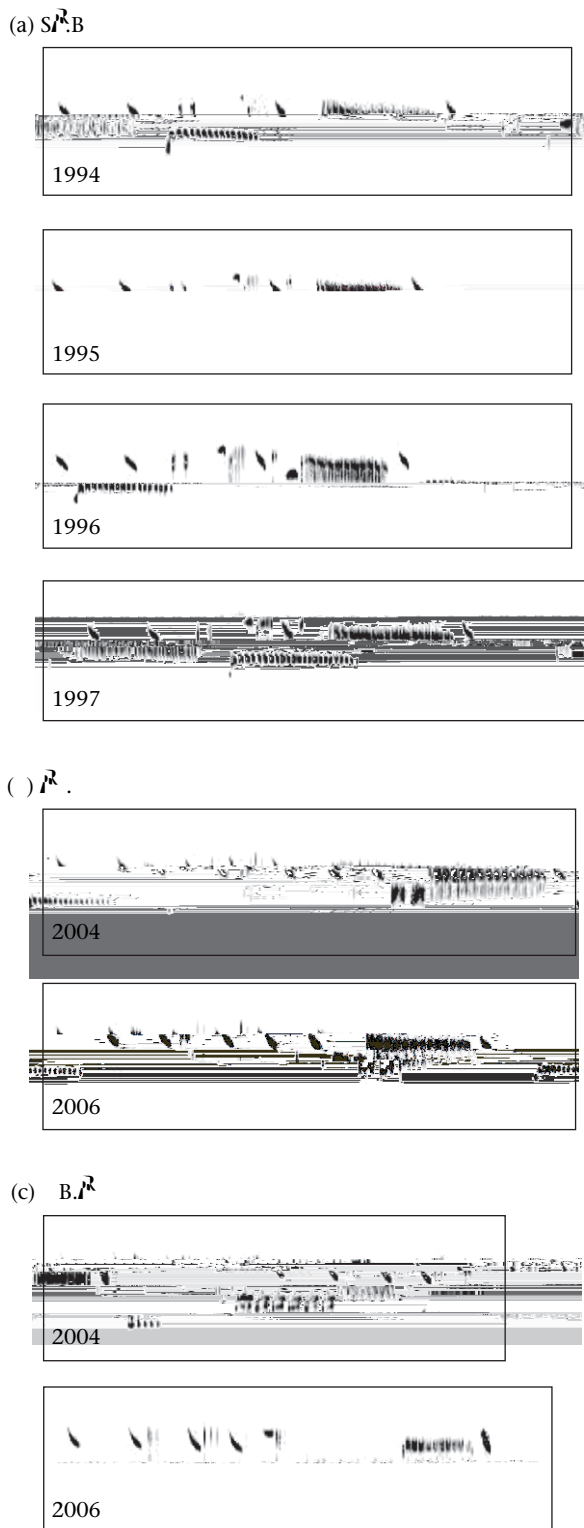
F   2. Consistency of song over the course of a Savannah sparrow's life. (a) Male SR.B was banded as an adult (probably a 1-year-old) when he first bred on the main study area in 1994; his song was identical in 3 subsequent years. Males (b) RL.Y and (c) NB.R were banded as nestlings in 2003 and recorded as 1-year-olds in 2004; their songs did not change when they were 2-year-olds in 2005 (not illustrated) and 3-year-olds in 2006. NB.R is an example of a 'stutterer' (note extra Ch notes).

and then declined steeply between 3 July and 21 July (r_{14}^2 0.59, $P < 0.0009$). Singing rates on 2 July were more than 14 times higher than those on 21 July, when 90% of birds were silent. By the last week in July, almost all males had ceased singing.

We recorded songs over an 18-year period, including about 10% of males breeding in the study site in 1988 and 1989, 90% in 1993e1998, 100% in 2003e2004 and 90% in 2005. In total we recorded 189 males. Of those, 98 had been banded as nestlings, 39 as independent juveniles (and therefore known to have been raised outside the study site but within the archipelago) and 52 as adults (known to have been raised outside the study site and possibly outside the archipelago and presumed to be SY males on the basis of primary feather shape and breeding philopatry; Wheelwright & Mauck 1998). For 69 of the 98 males banded as nestlings, we had also recorded their social fathers and at least one natal and breeding-year neighbour, and for 57 we also had complete recordings of at least two natal neighbours and two breeding-year neighbours. Extrapair fertilizations are common in the population (45% of all offspring; Freeman-Gallant et al. 2003, 2005). We determined genetic paternity for 24 males that had hatched between 2001 and 2004; 11 were extrapair offspring, so we were able to compare their songs to those of both their social and their genetic fathers. Sample sizes in the following analyses vary because of differences in the amount of information available for different males (e.g. social and genetic parentage, number of natal and breeding-year neighbours recorded).
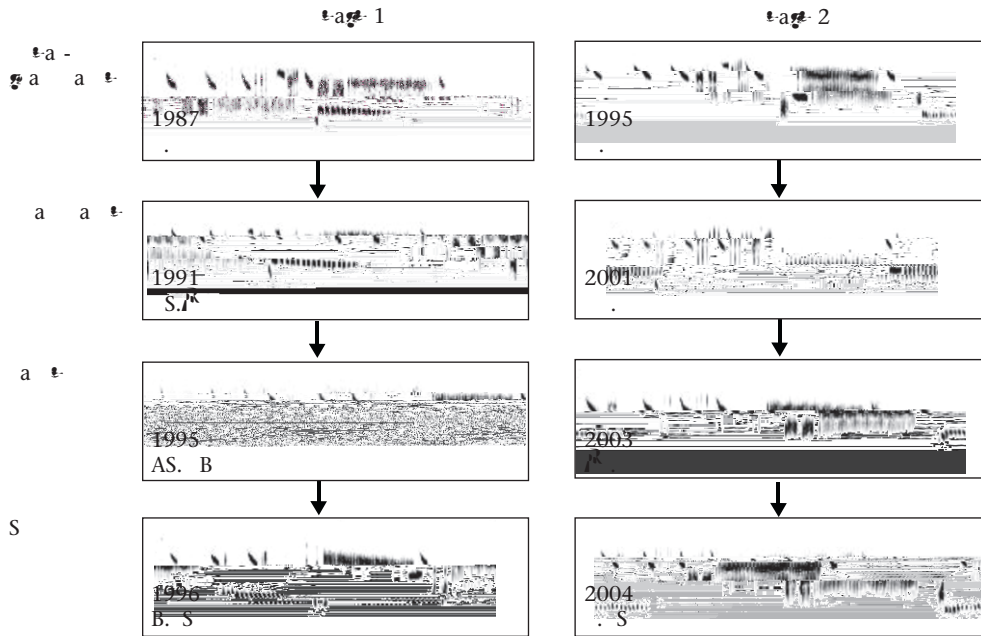
Songs were recorded in the field using a Sony TCM 5000EV recorder with Gibson parabolic microphone (1980s), a Marantz PMD recorder with either a Sennheiser ME66 shotgun microphone or a Telinga Pro II microphone with a parabolic reflector (1993e2004) and a Sony MZ-N707 Mini-Disc or a Marantz PMD670 digital recorder with Sennheiser ME66 shotgun microphone (2001e2006). Because the minidisk recorder used a compression algorithm, we compared 2003 recordings and uncompressed 2004 recordings of the same males to verify that the algorithm did not affect measurements and song similarity scores. As described below, visual similarity scores were based on the sequence, presence or absence, frequency and duration of song elements, all features that could be characterized independent of type of recording device or spectrogram. For Sound Analysis software score (Tchernichovski & Nottebohm 1998; Tchernichovski et al. 2000; see below), we confirmed that there was no effect by quantitatively comparing 2003 and 2004 recordings of the same individual (H. Williams, unpublished data).

Recordings were opportunistically made at all times of day. On Kent Island, Savannah sparrows have a distinct predawn chorus, but otherwise song rates vary relatively little during the day, with peak singing as likely to occur in late morning or midafternoon as at other times (N. T. Wheelwright, unpublished data). The vast majority of songs were recorded during the seasonal peak of singing

(mid- to late June), although we recorded some songs as early as early May and others as late as mid-July. By early August, Savannah sparrows on Kent Island have stopped singing entirely, and by late August (when fledglings from second broods are only 30e50 days old), most adult males have departed on their southbound migration. Typically we recorded 6e10 songs of a male per recording session and recorded males on multiple days throughout the breeding season. Twenty-three per cent of males were recorded in more than 1 year, 60% of whom were recorded in both their first and their last years of life; 7% were recorded in 3 or more years (Fig. 2).

For songs recorded in the 1980s and 1990s, spectrograms (sonagrams) were produced by a Kay Elemetrics Corp. DSP Sona-graph 5500; song characteristics (frequency, duration, sequence and presence or absence of elements) were measured directly from spectrograms. Beginning in 1999, Canary and Raven software for the Macintosh (Cornell Bioacoustics Lab, Ithaca, NY, U.S.A.) was used both to produce spectrograms and to measure song characteristics. Most measurements were done on spectrograms produced using standard default settings, except for poor-quality recordings or recordings of distant birds, in which case we adjusted settings to maximize temporal and frequency resolution to improve measurement accuracy and repeatability. Spectrograms generated by SoundEdit (Macromedia, San Francisco, CA, U.S.A.) and spectral derivatives generated by Sound Analysis software were used to prepare figures.

For each song we measured nine variables: mean

F   4. Transmission of Savannah sparrow songs between generations. The two lineages shown here illustrate the songs of birds that were banded as nestlings between 1987 and 2004. Each lineage represents four generations; arrows link (social) fathers and sons. Some males had songs that closely matched those of their fathers (e.g. B.LS, Lineage 1), while other males' songs had little in common with their fathers' (e.g. RL.Y, Lineage 2).
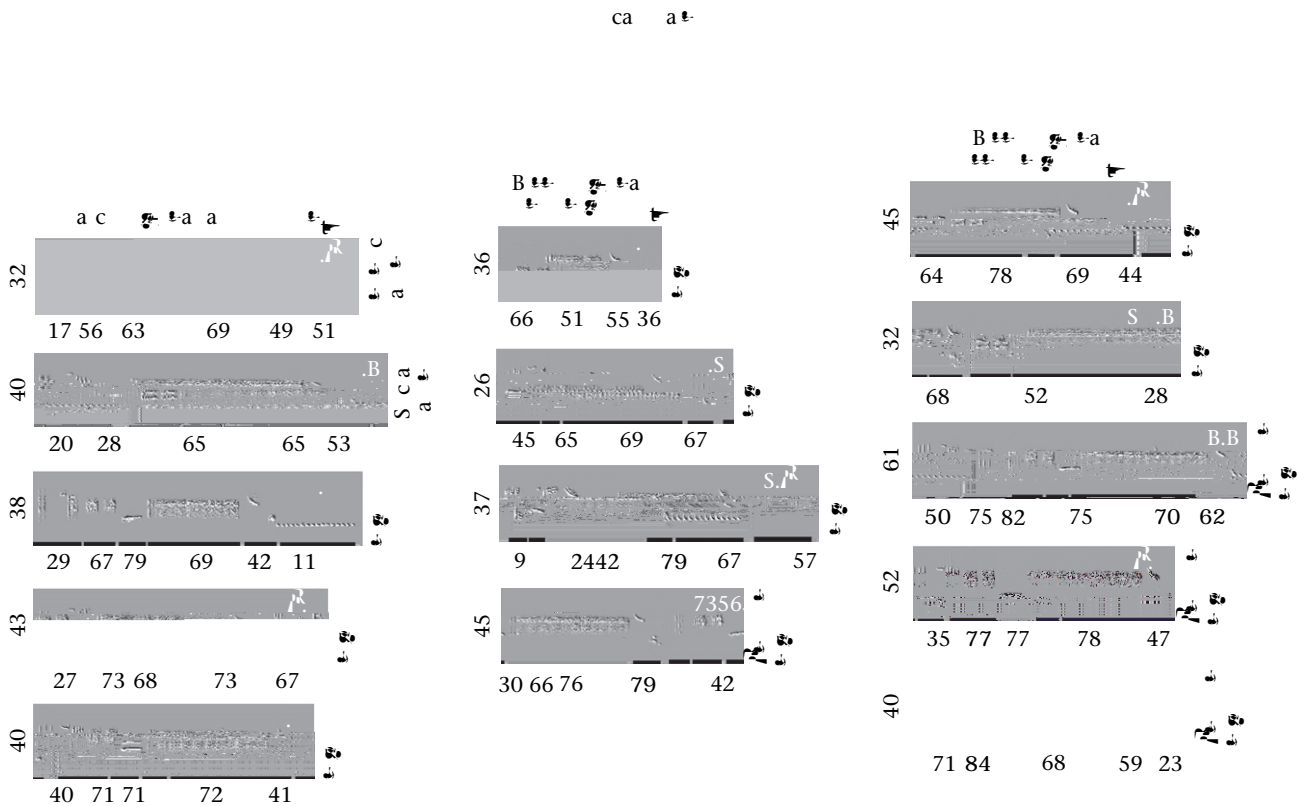
tape recordings from the 1980s and 1990s in addition to later digital recordings. Three observers with extensive experience distinguishing songs by ear in the field and analysing Savannah sparrow spectrograms (N.T.W., M.B.S. & I.I.L.) independently scored the similarity of all pairs of spectrograms on a scale from 0 (both recognizably Savannah sparrow songs but very different in syntax and having few specific elements in common) to 6 (songs so similar in frequency, timing and syntax that they could almost have been the same recording). Scoring was done blindly with respect to social and genetic relationships between males. Correlations between scores assigned by all pairs of observers were strongly positive (correlation coefficients: $0.67\ominus0.71$; all $P < 0.0001$). Visual similarity scores from the three observers were then averaged to produce a mean score for each comparison. Note that although we use the term 'visual' similarity scores, songs with very similar-looking spectrograms also sounded very similar, at least to the human ear.

Second, we compared digitized songs using Sound Analysis software (Tchernichovski & Nottebohm 1998; Tchernichovski et al. 2000). Recordings were saved as 16-bit, 44-kHz WAVE files and filtered digitally using Sound Edit to eliminate all energy outside the frequency range of Savannah sparrow song ($3.5\ominus10$ kHz; Fig. 1). The clearest example of each male's song was selected for analysis. Because the frequency range of Savannah sparrow songs is higher than that used by Sound Analysis ($0\ominus8$ kHz), the pitch of songs was digitally reduced to 67% of that of the original. Similarity scores were calculated for the entire song and separately for the Ch notes, buzz and terminal trill sequences using sound similarity analysis based on spectrogram cross-correlation (Tchernichovski et al. 2000separate and spectrogram analysis from

distinctive song (N 189 adult males recorded and observed throughout the breeding season). For four 1-year-old males recorded in the first week of May and then recorded later in the season and in subsequent years, songs were completely crystallized within 2 weeks after arriving on the breeding ground. Based on analyses of the spectrograms of 43 males whose songs were recorded in more than 1 year (including 26 males recorded in the last year

on song variation came from two cases where two males shared the same social father but had different genetic fathers and had relatively low Sound Analysis similarity scores (0.11 and 0.24). In two other cases, where two males had different social fathers but shared the same genetic father, their similarity scores were slightly higher (0.28 and 0.45), although small sample sizes did not permit a meaningful test of significance.

Natal neighbours

In 20 of 57 cases (35%) the highest visual similarity score was between a young male and one of his natal neighbours. In 8 of 24 cases (33%) where we had digitized recordings, the highest Sound Analysis score was between a young male and one of his natal neighbours. There was also a positive correlation between the frequency of the terminal trill in a young male's song and the average trill frequency of the songs of his natal neighbours (linear regression: r^2_{64} 0.05, P 0.04). On the other hand, we found no difference in the songs of siblings raised together (same social father and natal acoustic environment) versus apart (same social father but different natal acoustic environment), although small sample sizes limit the power of the analysis. The mean visual similarity score of the songs of siblings raised in the same nest (2.7, N 3) was no greater than that of siblings raised in different nests in the same year (3.2, N 6) or in different years (2.9, N 11; ANOVA: $F_{2,17}$ 0.19, P 0.83). Singing rates of natal neighbours had no apparent influence on the probability that they would be imitated: a young male was no more likely to copy a natal neighbour with a high song rate than a neighbour with a low song rate (linear regression of a young male's natal neighbour's song rate against Sound Analysis scores comparing their songs: N 47, r^2 0.05, P 0.12). Thirteen of the20uld te14F39tchm3ouo2-575293(3f9-70py)-c-1(5-539om3ou318c727crnis-c-1(55h3)n4

fledglings would have heard their songs repeatedly. None the less, their distinctive songs were never imitated (at least in their entirety) by any other male.

DISCUSSION

This study establishes the following features of Savannah sparrow song on Kent Island. Each male has a song repertoire that consists of a single song that is individually distinctive (or, in unusual cases, two individually distinctive songs). Males sing the same song their entire lives, as in other 'age-limited' song learners (Nordby et al. 2002). Males crystallize their song within 1e2 weeks of arriving at the breeding ground at the age of 9e11 months. Based on comparisons between the songs of birds on Kent Island and those of other populations (Chew 1981; Bradley 1994; Burnell 1998; Wheelwright & Rising 2007), Savannah sparrow songs are composed of a relatively small set of shared elements across the range of the species, although there are clear differences between populations in the frequency, duration and sequence of specific elements, and different populations have distinct dialects, even over short distances (Sung 2004). In each of these respects, Savannah sparrows are very similar to other well-studied sparrows (e.g. Liu & Kroodsma 2006). However, on the fundamental questions of at what age, under what conditions and from whom a young male learns his song in the wild, our results were equivocal and quite different from those of other related species.

We began our analyses by testing the simplest model of song learning, namely that young males imitate the complete song of a particular tutor (as opposed to incorporating song elements from the songs of a variety of tutors). We also followed the convention of assuming that, of all potential tutors, the individual whose song was most similar to a focal male's song is the individual from whom the focal male learned his song (Nordby et al. 1999; Liu & Kroodsma 2006). Unexpectedly, however, we found almost no evidence for imitation of entire songs, unlike in other sparrows (Nelson 1992; Nordby et al. 1999; Liu & Kroodsma 2006). It was rare to find a precise match (visual similarity score 6) between the complete songs of a young male and those of any other male in the population; similarity scores of the best-matched tutor (of all the males of the five possible tutor types) averaged only about 4.4, compared to 2.8 for random males. Not every natal and breeding-year neighbour's song was recorded for every young male, so it is conceivable that we overlooked a few tutors in some cases. Moreover, young males, especially birds that wandered away from their natal territory while adult males were still singing, may occasionally have heard the songs of non-neighbours. None the less, the paucity of close matches of entire songs despite large sample sizes and complete recording of all potential tutors in several years of our study argues against learning of songs in their entirety.

We also found wide variation among individuals in the age at which songs were apparently learned and in the type of tutor that had the greatest influence. Our results are unambiguous in ruling out a male's social father as the most important song tutor. In only 12% of cases was the closest match for a male's song his social father. Contingency table analyses demonstrated that distinctive song elements were distributed independently among males and their social fathers. Siblings raised in the same nest typically sang songs that did not closely resemble their father's song (or each other's songs). In this regard, Savannah sparrows are quite unlike one of the model organisms for song learning, zebra finches, *Taeniopygia guttata* (Williams 1990; Riebel et al. 2002; Terpstra et al. 2006). It is unclear whether this reflects phylogenetic differences between the species or an artefact of the way zebra finches learn song under laboratory conditions. However, Savannah sparrows also differ from a more closely related group of birds that have been well studied in the wild, Galapagos finches (*Geospiza scandens, Geospiza fortis*). Galapagos finches, like zebra finches, learn their songs mainly from their fathers (Grant & Grant 1989, 1996).

Our study, one of the first to apply paternity analysis to the question of song learning in the wild, also rules out an overwhelming influence of genotype on individual variation in song learning in Savannah sparrows. In the case of offspring produced by extrapair fertilizations, a male's song was no more likely to resemble the songs of his genetic father than the song of his social father.

Judging by similarity of entire songs, about half of the young males in this study appear to have based their songs on those of adult models heard during their first summer (social fathers and natal neighbours). The other half were influenced more by songs of models heard at

The absence of a song tutor can extend the duration of the sensitive phase for song learning in some species (Eales 1985; Livingston & Mooney 2001). If this were the case in Savannah sparrows, we should have found that males that hatched late in the season would be more likely to develop songs similar to those of breeding-year tutors than to those of hatching-year tutors because few adults would have been singing during the young males' presumed 20- to 60-day sensitive period. None the less, we found no relationship between when a male Savannah sparrow had hatched and when it appeared to learn its song (hatching year versus first breeding year). This suggests that a late-hatching male needs to be exposed to only a very few songs as a nestling or fledgling to memorize songs or that males that hatch early in the season are as strongly influenced by breeding-year tutors as by hatching-year tutors. Other evidence that a male's early acoustic environment is a poor predictor of his adult song came from the absence of a relationship between age of banding and song characteristics and from the dissimilarity in most cases of the songs of siblings raised in the same nest. We also found no support for the prediction that males that are developmentally disadvantaged as nestlings develop distinctive songs or are more likely to learn from a particular tutor type. Whether a male's song was most like that of his father, natal neighbours or breeding-year neighbours were unaffected by his size or condition at fledging. Because we observed fledglings only within the normal size range (as opposed to severely stressed nestlings), these results do not directly address the developmental stress hypothesis (Nowicki et al. 2002; Buchanan et al. 2003).

Although this is the first study to examine the influence of a bird's social father, genetic father, natal neighbours, older breeding-year neighbours and 1-year-old breeding-year neighbours on song learning, we were unable to consider three other possible types of song tutors: birds heard during autumn migration, birds heard on the wintering grounds and birds heard during spring migration. None the less, as described above, it appears unlikely that Savannah sparrows learn their songs during the nonbreeding season, given the paucity of song during the autumn and winter (Wheelwright & Rising 2007, personal observation) and the fact that birds that breed on Kent Island sing a distinctive local dialect despite overwintering along the length of the Atlantic coast from Maine to Georgia (U.S. Geological Survey Bird Banding Laboratory, unpublished data).

The infrequency of close matches between the entire songs of young males and those of all likely tutors in the population leads us to hypothesize that a Savannah sparrow develops his song by learning specific song elements sung by a variety of other males during his hatching (and perhaps his first breeding) year. These components are then recombined during a male's first breeding year, perhaps somewhat haphazardly, to create a song that does not deviate too much from songs currently in the local dialect yet that is also individually distinctive. Significant correlations in linear and multiple regressions between focal males and particular tutor types for certain elements of song suggest the possibility that different portions of Savannah sparrow songs may be preferentially learned from different tutors at different times of life, as in nightingales, *Luscinia megarhynchos*, and zebra finches (Hultsch & Kopp 1989; Hultsch & Todt 1989; Williams 1990; Williams & Staples 1992). At the same time, our finding that components of Savannah sparrow song are not independent of each other (e.g. males that included a dash note in their song tended to have shorter and lower-pitched terminal trills) implies that there are limits to the ways in which elements learned from different males can be recombined.

Our results cannot explain why some young males appear to learn more from hatching-year models whereas others are influenced more by breeding-year models, however, or why specific song elements might be acquired in different years. We were also unable to identify the characteristics that make an adult male a particularly influential tutor, although we could rule out his size, origin (based on banding age), longevity and lifetime reproductive success. Nor did a young male's hatching date, natal nest area or size at fledging help predict when or from whom he learned his song.

Despite drawing from a relatively small set of elements within the constraints of a simple overall song structure, Savannah sparrows sing individually distinctive songs. Conceivably, inbreeding avoidance is one of the advantages of individual recognition, which could partially explain the absence of father–daughter matings in the population (Wheelwright et al. 2006). Another consequence of the flexible song-learning system of Savannah sparrows is that it can result in rapid cultural evolution. Song elements can be omitted, duplicated, modified or shifted in sequence, and the frequency and duration of individual song elements can show significant directional trends within less than a decade (N.T.W. & I.I.L., unpublished data).

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