



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.

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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 (≥ 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

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'Loughlen & 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).

Breeding-year Neighbours

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 1–2 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 return to their natal site to breed, which makes it difficult to pinpoint the age at which songs are learned, even if specific tutors can be identified (Nordby et al. 1999).

Other Factors

Hatching date could affect when and from whom a young male learns his song. We predicted that males that hatched early in the season would be more likely to be influenced by their social father and natal neighbours, whereas males that hatched late in the season, when few adults are still singing (see *Methods*), would be more likely to be influenced by their breeding-year neighbours. A young male's condition at fledging could also affect song learning. The developmental stress hypothesis predicts that the song that a male sings as an adult reflects in

part the circumstances under which he was raised (Nowicki et al. 1998; Buchanan et al. 2003). Males that were underfed as nestlings would be predicted to be hindered or delayed in song learning, as evidenced by simpler, or at least distinctive, adult songs as a result of poorer condition at fledging. Finally, certain adult males may be more attractive tutors than others. For example, males that sing especially frequently (Nelson 1992) or that are larger, in better condition, locally reared, longer-lived or reproductively more successful would be expected to have a stronger influence on song learning.

METHODS

Savannah Sparrow Song

Throughout their North American range, Savannah sparrows sing a characteristic short (2–4 s), high-pitched, buzzy, insect-like song that consists of a relatively small set of elements in a characteristic sequence (Bradley 1977, 1994; Chew 1981; Burnell 1998; Sung 2004). The song can be considered to have four parts: an introduction, a middle section, an elongated buzz and a terminal trill (or pair of trills) (Fig. 1). The introduction consists of three to eight high-pitched 'introductory' or 'A notes' (mean frequency = 8.0 kHz). The final few introductory notes are often separated by clusters of 'clicks' ('pulses' in Chew 1981), which are not clearly audible to the human ear but give a scratchy quality to the sequence. Some males end the introduction with a single higher-pitched note (8.5–9.5 kHz), which we call the 'high note'. Following the introduction is the middle section, which is the most individually distinctive in terms of the sequence and presence or absence of elements (Bradley 1977; Burnell 1998; Figs 1–5). Most males produce two short (~100 ms) broad-frequency notes, which we call 'Ch notes' because of their sharp, staccato sound ('short buzzes' in Bradley 1977). Ch notes are sometimes preceded, followed or replaced by a short whistle, which we call a 'dash' because of its appearance in spectrograms. The third part of the song, present in all males' songs, is an extended broad-frequency 'buzz' (mean frequency = 7.2 kHz) ('primary trill' in Chew 1981). Typically a single A note and a very short lower-frequency (3–4 kHz) note ('chirp') follow the buzz. The final part, which we call the 'terminal trill' ('terminal flourish' in Bradley 1977, 1994), is made up of notes with little or no frequency modulation (mean frequency = 4.0 kHz). The length of the trill ranges from as few as three repeated notes (less than 0.1 s, producing a raspy sound) to as many as 30 repeated notes (0.8 s, mean = 0.4 s, producing a more musical trill). Female Savannah sparrows produce various vocalizations but do not sing.

Early studies listed Savannah sparrows as a probable example of a species in which the repertoire of each male consists only of a song 'of one pattern' (Borror 1961). Bradley (1977), Chew (1981) and Burnell (1998) documented differences in songs between individual Savannah sparrows in populations from California, Ontario and Nova Scotia, respectively, and highlighted the middle

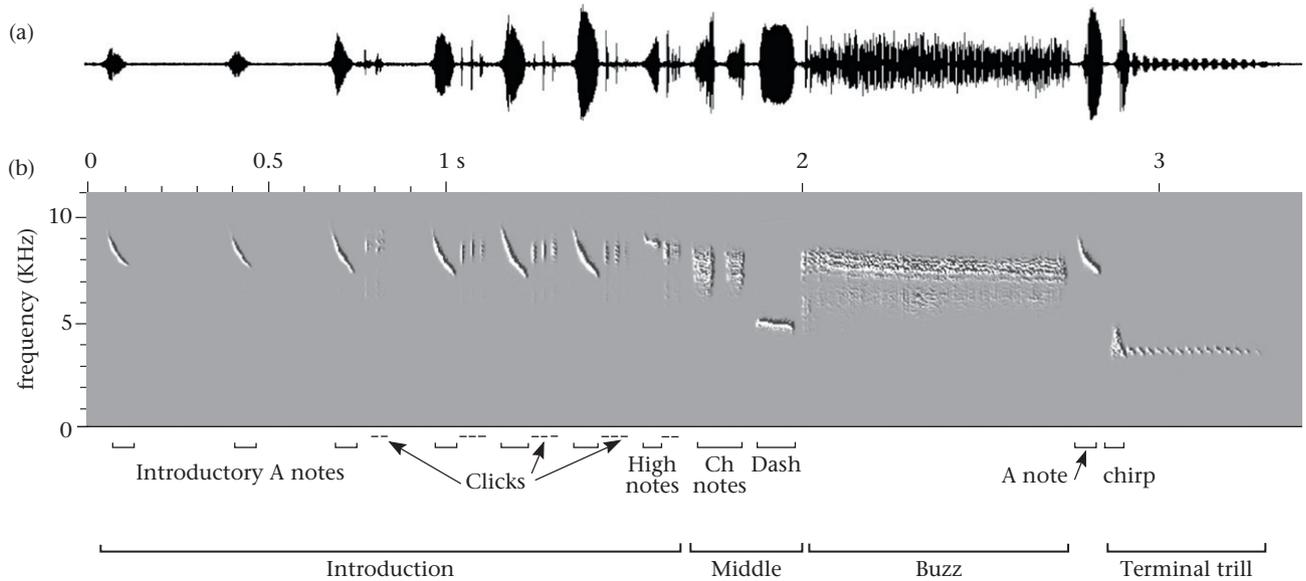


Figure 1. Savannah sparrow song. (a) Waveform (oscillogram) showing amplitude versus time. (b) Spectral derivative (derivative of traditional spectrogram) showing change of power over time and across frequency.

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 genetic structure (Pitocchelli 1981; Sung 2004; N.T.W., unpublished data; see Freeman-Gallant 1996). On a continent-wide scale, geographical variation in songs is even greater but, as with local dialects, it does not necessarily parallel genetic differences between populations (cf. Fig. 1 and spectrograms in Chew 1981; Bradley 1994; Zink et al. 2005). Experimental studies of acoustically isolated nestlings, the definitive test of whether song is innate, have never been conducted in Savannah sparrows. However, in a study of migratory orientation, Savannah sparrow nestlings were removed from the wild 1–3 days after hatching, held in captivity in groups and deprived of the opportunity to hear typical Savannah sparrow songs after that age. In their first spring, some of these males produced songs that ‘bore resemblance to wild Savannah sparrows but were very deficient’. Specifically, pitch and tonal quality of individual elements were similar to those of normal adults, but patterning of notes was variable and abnormal (K. Able, personal communication).

Study Site and Species

We studied Savannah sparrows breeding on Kent Island, New Brunswick, Canada (44°35'N, 66°46'W), site of the Bowdoin Scientific Station. Kent Island (80 ha) is the largest island in the Three Islands Archipelago, located 9 km from Grand Manan Island and isolated in the Bay of Fundy by more than 20 km from the mainland. The study site comprises 10 ha of open shoreline and fields within

which 40–50 Savannah sparrow males hold territories each year; the habitat has been undisturbed for 60 years but has seen little successional change because of the cool climate. Every Savannah sparrow adult in the study area was banded with a U.S. Fish and Wildlife Service aluminium band and a unique, randomly determined combination of three plastic colour bands. Morphological measurements (all made by N.T.W.) included wing length, tarsus length, mass, bill depth and bill length (Wheelwright et al. 2003). All successful nests within the study site were found and their fledglings banded. Beginning in 2001, blood samples were taken from all adults and nestlings for paternity analysis, and genetic as well as social fathers were identified for 96% of all offspring (Freeman-Gallant et al. 2005). Kent Island Savannah sparrows show strong natal and breeding philopatry: 11% of nestlings return as yearlings to breed within the study site, and surviving adults (annual mortality = ca. 50%) reclaim the same territories between years, with a mean distance of only 28 m between nests in successive breeding seasons (Wheelwright & Mauck 1998; E. Minot, R. Mauck & N. T. Wheelwright, unpublished data). As a result, we were able to compare songs of the same individuals over their entire lifetimes and songs of different individuals within lineages across as many as five generations. The ages of all males in the population were known (in many cases to the day), which allowed us to differentiate between ASY and SY males as potential song tutors.

On Kent Island, Savannah sparrows sing only sporadically during pair formation and egg laying (late May–early June). Singing rates actually peak a month later, during the laying of replacement and second clutches and when average temperatures have risen 5–10°C. In 2003 we quantified singing rates for 30 males on 46 days each between 28 May and 21 July during 3- to 6-h censuses (see below). Mean daily singing rates increased between 28 May and 2 July (linear regression: $r_{31}^2 = 0.55$, $P < 0.0001$)

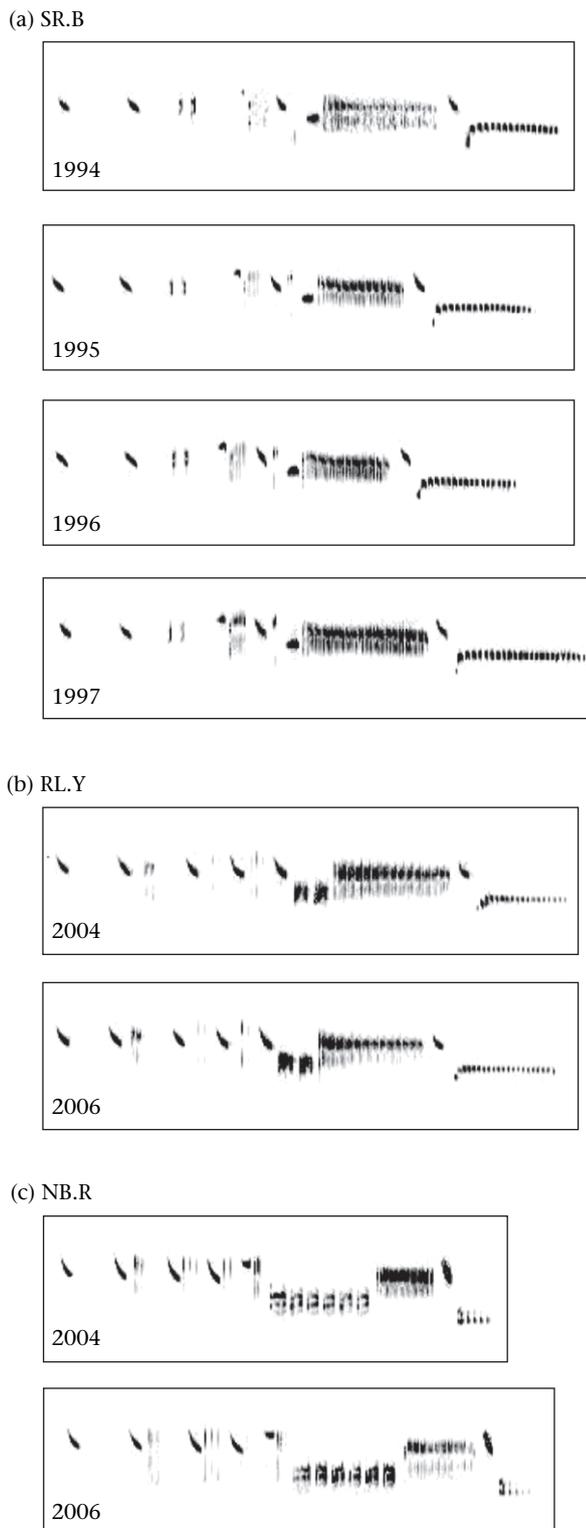


Figure 2. Consistency of song over the course of a Savannah sparrow's life. (a) Male SR.B was banded as an adult (probably a 1-year-old) when he first bred on the main study area in 1994; his song was identical in 3 subsequent years. Males (b) RL.Y and (c) NB.R were banded as nestlings in 2003 and recorded 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).

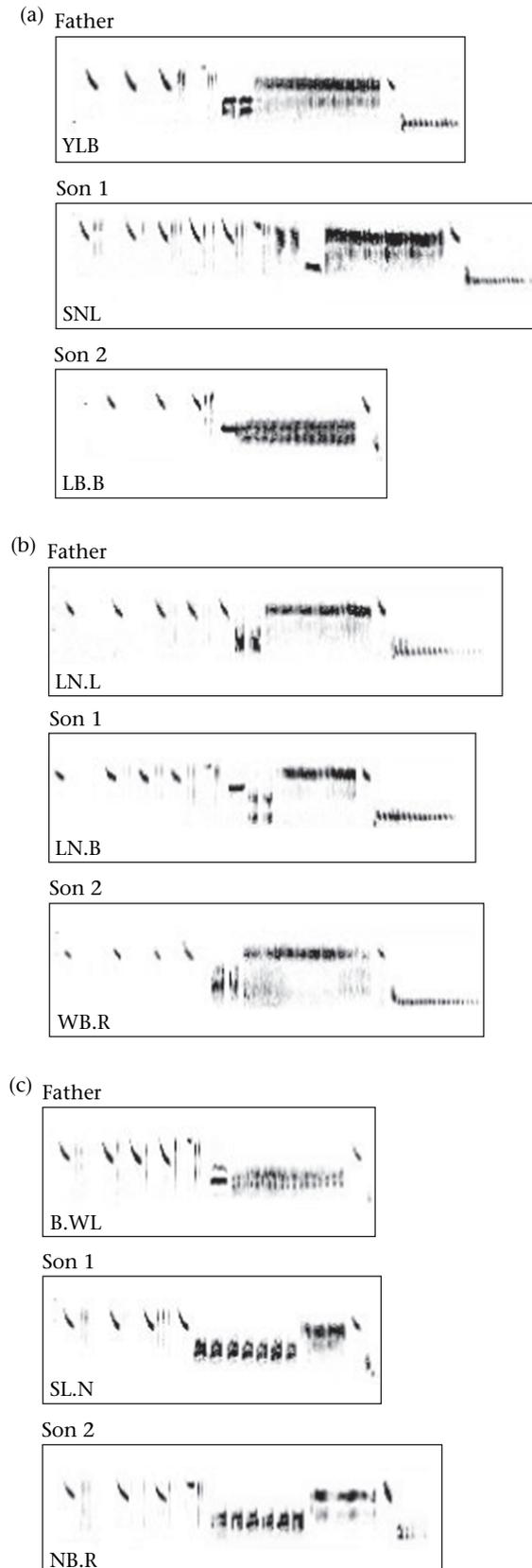
and then declined steeply between 3 July and 21 July ($r^2_{14} = 0.59$, $P < 0.0009$). Singing rates on 2 July were more than 14 times higher than those on 21 July, when 90% of birds were silent. By the last week in July, almost all males had ceased singing.

Recordings

We recorded songs over an 18-year period, including about 10% of males breeding in the study site in 1988 and 1989, 90% in 1993–1998, 100% in 2003–2004 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 (1993–2004) and a Sony MZ-N707 Mini-Disc or a Marantz PMD670 digital recorder with Sennheiser ME66 shotgun microphone (2001–2006). 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 pre-dawn 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 30–50 days old), most adult males have departed on their southbound migration. Typically we recorded 6–10 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).

Song Measurements

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 frequency (average of maximum and minimum frequencies, in kHz) of introductory notes, buzz and terminal trill; duration (s) of buzz and terminal trill; presence or absence of dash and high introductory note; and number of Ch notes. Principal component analysis (PCA) was performed on normalized data. The model explaining the greatest proportion of the variance in PC1 (60%) included only three of the variables: duration and frequency of the terminal trill and frequency of the buzz. Statistical analyses were conducted using Statview 4.5.1 (SAS Institute, Cary, NC, U.S.A.).

Song Similarity Analyses

We used three methods to quantify the similarity between the songs of a young male and those of all potential tutors for whom we had recordings. First, we visually compared spectrograms of the songs of all co-occurring males, which allowed us to take advantage of

Figure 3. Three examples of two male Savannah sparrow siblings raised in the same nest showing song variation within the same brood. None of the males closely matched his father's song (although WL.R's song resembled his father's), and, in most cases, siblings' songs were unlike (a, b). One pair of siblings (SL.B and NB.R) developed songs that were similar to one another, although quite unlike their father's song (c).

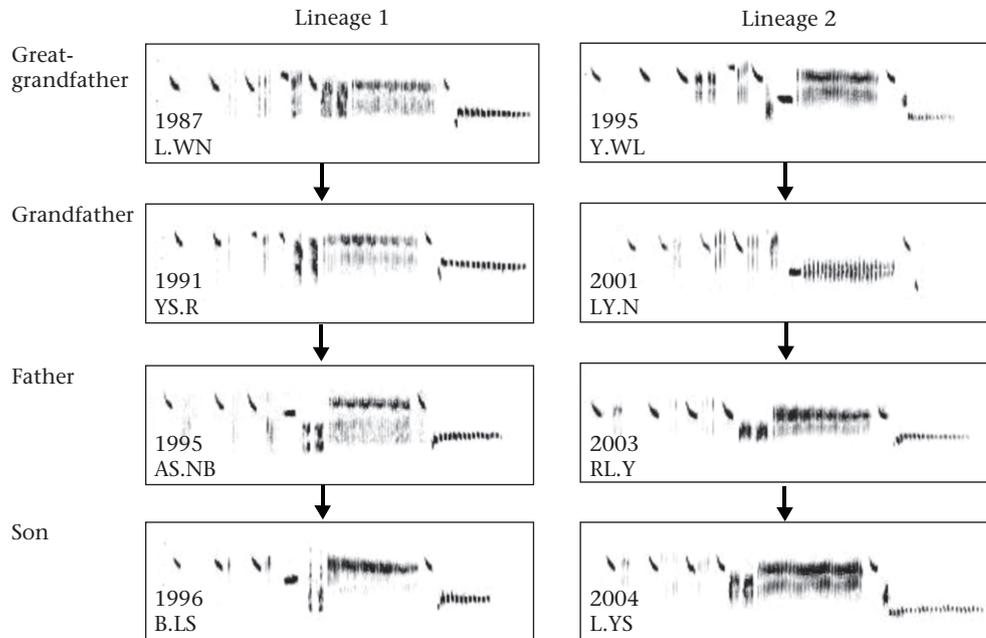


Figure 4. Transmission of Savannah sparrow songs between generations. The two lineages shown here illustrate the songs of birds that were banded as nestlings between 1987 and 2004. Each lineage represents four generations; arrows link (social) fathers and sons. Some males had songs that closely matched 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).

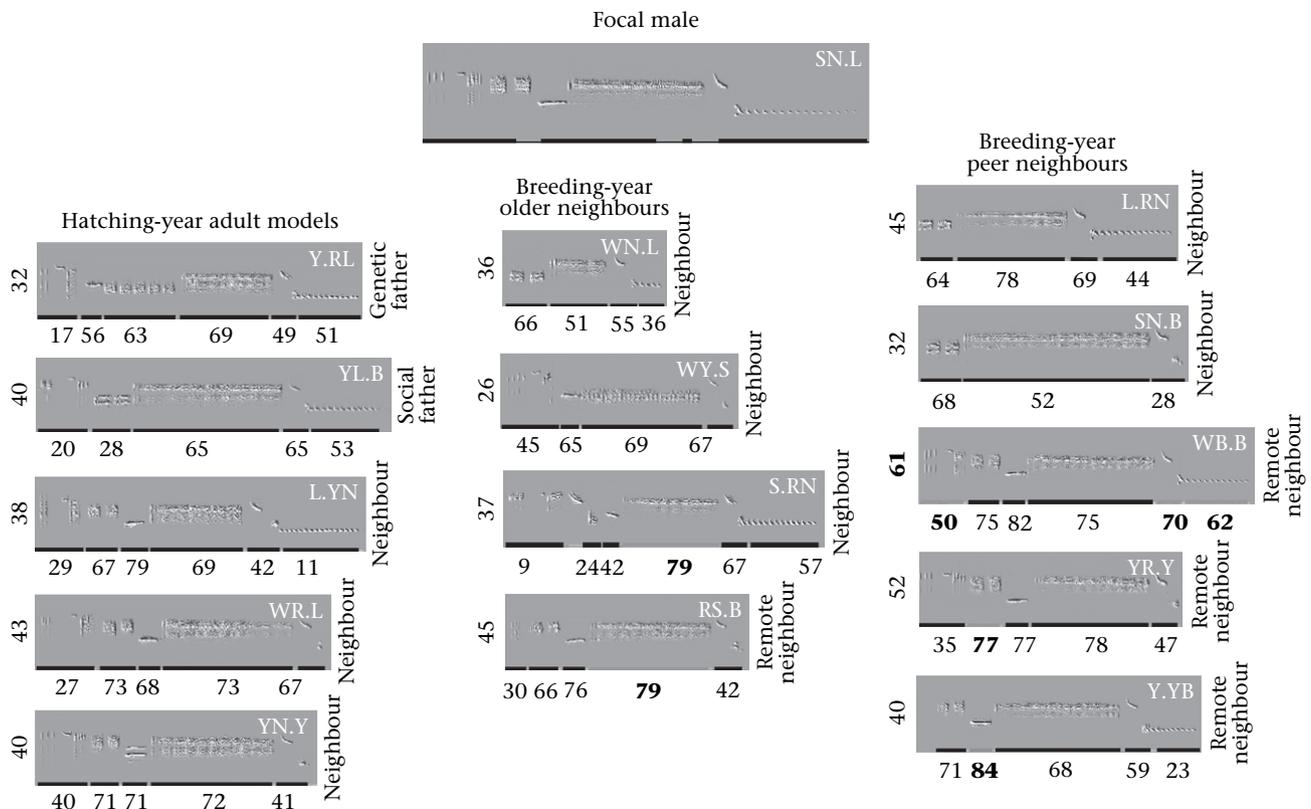


Figure 5. Example of the song of a young male and his most likely models from all five tutor types. The focal male, SN.L (uppermost spectral derivative), hatched in a nest that was attended by YL.B, his social father. Paternity analysis showed that his genetic father was Y.RL, who was also a natal neighbour. Three other adult males sang in neighbouring territories. When SN.L returned a year later to breed for the first time, his breeding-year neighbours included four ASY males and five SY males. To the left of the spectrogram of each possible song model is a number denoting the overall Sound Analysis similarity score between the model's song and that of the focal male. In this example, the best overall match was a breeding-year peer neighbour (WB.B). Similarity scores for each portion of the possible models, illustrate the possibility that different components of song could be learned from different tutors at different times. Values in bold denote high similarity between the focal male and the model. For example, the model whose dash note most closely resembled that of the focal male was a breeding-year peer neighbour (Y.YB; similarity score = 84).

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: 0.67–0.71; 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 (3.5–10 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 (0–8 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. 2000). Each pairwise score was calculated twice, using each song as the reference song in turn, and the minimum of the two scores was used. Visual and Sound Analysis similarity scores for the subset of recordings for which we had both spectrograms and digital files were strongly correlated ($r^2 = 0.46$, $N = 297$ pairwise comparisons, $P < 0.0001$).

Third, we used linear regressions and chi-square tests to test for associations between young males and potential song tutors in the frequency, duration or presence of specific elements of the songs (e.g. stuttering, dash, raspy terminal trill).

We focused on five potential types of song tutors. Social fathers were defined as males that were socially paired to a young male's mother and that mate-guarded her, defended an exclusive territory around her nest and provided parental care to the young male when he was a nestling and fledgling (Wheelwright et al. 2003). Genetic fathers were identified using microsatellites (Freeman-Gallant et al. 2005). Natal neighbours were adult males whose territories included at least one nest located within 75 m of a young male's natal nest (based on GPS coordinates). On average, each focal male had 4.8 natal neighbours whose songs had also been recorded. Breeding-year neighbours were adult males whose territories included at least one nest located within 100 m of a focal male's first nest when he was 1 year old (as opposed to the nest in which he had hatched the year before). We

used a greater distance criterion for breeding-year neighbours than for natal neighbours because as a 1-year-old a young male is not tied to the immediate vicinity of his nest, unlike when he was a nestling or fledgling. Thus, a male is exposed to more potential song tutors as a 1-year-old than as a juvenile. Among breeding-year neighbours, we distinguished between ASY and SY males as potential tutors. ASY males generally returned from migration and established territories a week or more before SY males. They also averaged 1.6% larger in wing length and mass and tended to dominate SY males in social interactions (Wheelwright & Rising 2007). On average, each focal male had 5.0 ASY and 4.2 SY breeding-year neighbours whose songs we recorded. The mean number of natal, ASY breeding-year and SY breeding-year neighbours per focal male did not differ (ANOVA: $F_{2,168} = 1.30$, $P = 0.28$).

Quantifying Singing Rates

In 2003 and 2004 we developed a simple measure of singing rate to test the hypothesis that natal neighbours that sang frequently would have a stronger influence on song learning than males that rarely sang (Nelson 1992). Singing rates of all natal neighbours were calculated for each young male when he was 14–28 days of age. The beginning of the period (14 days) was chosen because it included fledging and the presumed first part of the sensitive phase (Marler & Peters 1987, 1988); the end of the period (28 days) was chosen because it corresponded to the time when most juveniles had achieved independence, dispersed from their natal territory and joined juvenile flocks, which made it more difficult to identify potential tutors (Wheelwright et al. 2003). However, as described above, only birds that hatch early in the season hear much singing after the age of 28 days; late-hatching birds would be unlikely to hear any songs at all by the time they reached independence. A daily score of 0 was assigned to males for whom we heard no songs during a day of censusing, a score of 1 to males that sang only infrequently (generally fewer than 3 songs/h), a score of 2 to males that sang at intermediate rates (typically several song bouts per hour, at rates of 3–6 songs/min) and a score of 3 to unusually active singers (almost constant song during many periods of the day, at rates of >6 songs/min). Daily scores were assigned at the end of the day based on a consensus of field notes of one to three observers who each spent several hours in the field, incidentally assessing the singing behaviour of individual males while searching for nests, mapping territories, mist-netting birds, etc. Each male's daily scores were then averaged over the 2-week period to give an overall estimate of his potential influence on song learning of young males from nests within 100 m.

RESULTS

Repertoire Size

The repertoire of 96.8% of the Savannah sparrows on Kent Island consisted of just a single, individually

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 they were seen), each male sang the same song, with virtually no change between years, for his entire life (see examples in Fig. 2). Visual similarity scores comparing songs of the same male recorded in 2 successive years averaged 5.6 ± 0.7 on a scale of 0–6 ($N = 21$). For males recorded in 3 successive years, scores comparing songs of the same male recorded as a yearling and then as a 3-year-old averaged 5.7 ± 0.5 ($N = 15$; paired t test: $t_{35} = 0.67$, $P = 0.51$). By comparison, scores comparing songs of random males averaged just 2.8. Only 0.2% of comparisons of the songs of random males received a score of 6, versus 72.0% of between-year comparisons of the songs of the same male ($N = 2396$). Sound Analysis scores comparing songs of the same male recorded in successive years averaged 0.50 ± 0.10 ($N = 14$), versus only 0.18 ± 0.11 for the songs of random males ($N = 475$) ($P < 0.0001$).

There were only a few exceptions to the observation that a male Savannah sparrow sings only one song over the course of his lifetime. Four males (2.1%) sang two songs that differed in their terminal trills, and two males (1%) sang two quite distinct songs. Minor variations in the number or length of certain elements (although not in the frequency or sequence of elements) were not uncommon, however. For example, the number of introductory notes within a male's song often ranged from 3 to 6. 'Stutterers' (males that sang three to eight Ch notes instead of the normal two) occasionally added or deleted one or two extra Ch notes. The length of the buzz or terminal trill also varied slightly from song to song, particularly late in the season. Depending upon whether a male was broadcasting his song in territorial defence or 'whisper-singing', amplitude also varied.

Different song characteristics were not independent. Males that sang high-pitched buzzes also tended to sing high-pitched introductory notes and terminal trills and to have longer terminal trills (linear regressions: $r_{140}^2 = 0.03, 0.08$ and 0.31 , $P = 0.03, 0.0005$ and 0.0001 , respectively). Males that sang two Ch notes had longer and higher-pitched terminal trills and higher-pitched buzzes than 'stutterers' or birds that sang zero or only one Ch note (ANOVAs: $F_{3,137} = 15.0, 3.5$ and 69.0 , $P = 0.0001, 0.02$ and 0.0001 , respectively). Males that included a dash in their song had shorter and lower-pitched terminal trills and lower-pitched buzzes (paired t tests: $t_{139} = 3.1, 2.2$ and 3.7 , $P = 0.003, 0.03$ and 0.0003 , respectively; for examples, see Figs 1–5).

When and From Whom Does Song Learning Occur?

Our data do not support a simple model of song learning, with songs copied in their entirety and learning

occurring only in either a young male's hatching or his first breeding year. Below we present the evidence for and against the influence of each potential tutor type.

Social father

In only 7 of 57 cases (12%) where we had spectrograms from all five types of tutors was the highest visual similarity score between a young male and his social father. In only 1 of 24 cases (4%) where we had digitized recordings (i.e. songs recorded after 2001) was the highest Sound Analysis score with a social father. Although siblings reared in the same nest had shared the same social father and early acoustic environment, in most cases they ended up singing quite different songs (Fig. 3). In terms of specific components of the song, there was no significant correlation between the songs of young males and those of their social fathers in the frequency or duration of buzzes or terminal trills (linear regressions: $r_{67}^2 = 0.002$ and 0.04 , $P = 0.69$ and 0.09 , respectively). Nor was there any relationship between young males and their social fathers in the presence or absence of distinctive characteristics such as dashes, 'stuttering' or raspy terminal trills (see Comparisons of potential song tutor types, below). Over several generations, spectrograms of sons and their social fathers were as likely to demonstrate dissimilarity as similarity within lineages (Fig. 4). The best evidence for the influence of social fathers on song learning was a positive correlation between PC1 scores for young males and their social fathers (linear regression: $r_{68}^2 = 0.08$, $P = 0.009$). The correlation was no longer significant when we considered only the subset of social father–son pairs that were digitally recorded, however ($r_{12}^2 = 0.05$, $P = 0.45$), and may have been an artefact of temporal autocorrelation in PCA scores and cultural evolution (N. T. Wheelwright & I. I. Levin, unpublished data).

If song is transmitted across generations through imitation of one's social father, young males should sing songs that are more similar to the songs of their paternal grandfathers than to those of their maternal grandfathers. There were five cases where we had recordings of both types of grandfathers. In one case, a young male's song strongly matched the song of his paternal grandfather but not his maternal grandfather, in one case the reverse was true and in the remaining cases the male's song resembled neither grandfather.

Genetic father

There were no cases where a young male's genetic father had the highest visual or Sound Analysis similarity score ($N = 24$). We compared the similarity of a male's song to that of his social father and his genetic father for 11 young males whose social and genetic fathers were different individuals. In four cases, a young male's song was more similar to his social father's song than to his genetic father's song, in five cases the reverse was true and in two cases his songs were equally similar to his social and his genetic father's song. Paired t tests showed no difference in similarity scores between a male and his social versus genetic father (visual: $t_{10} = 0.36$, $P = 0.73$; Sound Analysis: $t_{10} = 0.06$, $P = 0.95$). The only hint of a genetic influence

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: $r_{64}^2 = 0.05$, $P = 0.04$). 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 the 20 natal neighbours identified as likely tutors survived to the following year, so it is possible that their influence on a young male's song learning occurred during his first breeding year.

Breeding-year neighbours

Among the potential types of song tutor, breeding-year neighbours accounted for the most cases of the highest visual similarity score (30 of 57 cases, 53%) and the highest Sound Analysis score (15 of 24 cases, 63%; $\chi_3^2 = 33.3$ and 24.3, respectively, $P < 0.0002$). A young male was equally likely to sing a song that was similar to the song of an SY neighbour as that of an ASY neighbour: 15 of 57 of the highest visual similarity scores (26%) and 10 of 24 of the highest Sound Analysis scores (42%) were with SY breeding-year males, whereas 15 of 57 of the highest visual similarity scores (26%) and 5 of 24 of the highest Sound Analysis scores (21%) were with ASY breeding-year males. For at least one song component (buzz frequency), there was a significant positive correlation between the young males and their SY (but not ASY) breeding-year neighbours (linear regression: $r_{62}^2 = 0.09$, $P = 0.01$).

The similarity in song between some young males and their SY breeding-year neighbours was unlikely to have been due merely to their having been exposed to the same songs as nestlings and fledglings. Males banded as

nestlings within the study area shared a more similar early acoustic environment than males first banded as juveniles or adults because the latter had been raised in different locations outside the study site and possibly outside the archipelago. Yet the similarity of a young male's song to that of his SY breeding-year neighbours did not depend upon the age at which SY breeding-year neighbours had been banded (ANOVA: visual: $F_{2,247} = 0.08$, $P = 0.93$; Sound Analysis: $F_{2,104} = 0.73$, $P = 0.49$). In general, song characteristics were independent of age of banding (Table 1; chi-square tests: $P > 0.05$).

Comparisons of potential song tutor types

Breeding-year neighbours (ASY and SY) tended to be overrepresented and social fathers underrepresented among the best matches for young males across the tutor classes (visual: $\chi_3^2 = 13.1$, $N = 57$, $P = 0.001$; Sound Analysis: $\chi_3^2 = 12.2$, $N = 24$, $P = 0.002$). (Genetic fathers were not included in this analysis because the genetic paternity of males was determined for only 4 years of the study and because our results showed no evidence of genetic effects on song variation between individuals.) However, the average young male had twice as many breeding-year neighbours as natal neighbours in the sample (because of the greater distance criterion, 100 m versus 75 m), and more than nine breeding-year neighbours per social father. Correcting expected values for the increased probability of finding the best match among tutor types with larger sample sizes, the significant difference between tutor types disappeared ($\chi_3^2 = 3.7$, $P = 0.29$).

When we considered the entire sample of pairwise visual similarity scores, there was no difference between tutor types or between hatching-year tutors collectively (social and genetic fathers plus natal neighbours) versus breeding-year tutors collectively (ASY plus SY neighbours) (ANOVA: $F_{4,936} = 0.99$, $P = 0.41$; $F_{1,664} = 1.52$, $P = 0.22$). In comparisons of Sound Analysis scores, SY breeding-year neighbours had the highest mean (0.33, out of

Table 1. Effect of banding age on song traits in Savannah sparrows*

Trait	$F_{2,186}$	P
Frequency of introductory notes (kHz)	0.13	0.13
Number of Ch notes	1.94	0.39
Duration of buzz (s)	0.73	0.48
Frequency of buzz (kHz)	0.64	0.53
Duration of terminal trill (s)	0.82	0.44
Frequency of terminal trill (kHz)	0.08	0.93
PC1	0.20	0.81
	χ_2^2	P
Presence of 'stutter'	1.92	0.41
Presence of dash	5.74	0.06
Presence of raspy terminal trill	0.09	0.96

*Males banded as nestlings within the study area had shared the same acoustic environment during their hatching year, but males banded as juveniles and especially males banded as adults had been exposed to different early acoustic environments. The frequency, duration, number and presence or absence of specific song elements were independent of banding age (P values based on ANOVA and chi-square tests; $N = 189$ males).

a possible score of 1.00 for a perfect match), followed by natal neighbours (0.27), ASY breeding-year neighbours (0.24), social fathers (0.18) and genetic fathers (0.17) (ANOVA: $F_{4,112} = 7.75$, $P < 0.0001$). SY breeding-year neighbours had significantly higher Sound Analysis scores than ASY breeding-year neighbours and social and genetic fathers, and natal neighbours had significantly higher Sound Analysis scores than social and genetic fathers (Fisher's PLSD: $P < 0.0001$).

In an attempt to parse the influence of different tutor types and explore the possibility that distinct song elements are learned from different tutors, we performed stepwise multiple regressions between specific components of young males' songs and the songs of potential tutors, averaging across tutor classes. (Genetic fathers were not included in the analysis; see above.) For duration of the buzz and frequency of the terminal trill, only natal neighbours significantly entered into the model ($P = 0.04$). For frequency of the buzz, only the effect of SY breeding-year neighbours was significant ($F_{1,43} = 4.07$, $P = 0.005$). For PC1, only social father was significant ($F_{1,43} = 4.94$, $P = 0.007$). For duration of the terminal trill, none of the tutor types was significant. In general, these results were in accord with the simple linear regressions reported above.

An analysis of uncommon song traits illustrates the difficulty in pinpointing the most influential song tutor. Of 69 young males whose social father's song and at least one natal and breeding-year neighbour's songs were known, four (6%) developed a 'stutter'. Two of the young stutters were siblings from the same nest who had had a stuttering natal neighbour (neither their social nor their genetic father was a stutterer). As yearlings, the two stuttering siblings established territories next to each other, and within 150 m they had another SY breeding-year neighbour and an ASY breeding-year neighbour who were also stutters. Thus, their unusual song could have been learned from their stuttering natal neighbour, from their ASY or SY breeding-year neighbour, or from each other. Of the other two young males who developed a stutter, one had been exposed to only a single potential tutor who stuttered, an ASY breeding-year neighbour. The other young stutterer had no stuttering models among his social father or natal or breeding-year neighbours and therefore either learned to stutter from a non-neighbour or produced his stutter through improvisation. At the least, these limited data provide no support for the learning of stuttering from one's social father ($\chi^2_1 = 0.26$, $P > 0.99$). The same was true of other distinctive song elements. Forty of 69 young males included a dash in their song and 16 ended their song with a raspy terminal trill. In neither case was there an association between the young males and their social fathers in the presence or absence of the distinctive traits ($\chi^2_1 = 0.22$ and 1.28 , $P = 0.83$ and 0.46 , respectively).

Other Factors

We had predicted that young males that hatched late in the season would be less likely than males that hatched

early in the season to learn their songs from natal neighbours because few adults are still singing late in the season. However, males whose songs most resembled that of a natal neighbour were no more likely to have hatched early in the season than males whose songs most resembled the song of a breeding-year neighbour (ANOVA comparing mean hatching date: $F_{1,22} = 0.09$, $P = 0.77$). The 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 disappeared when we examined only males that had hatched early in the breeding season (linear regression: $r^2_{37} = 0.05$, $P = 0.10$). Moreover, there was no difference in the mean hatching date of males that adopted a song more similar to that of one of their hatching-year neighbours versus males that adopted a song more similar to that of a breeding-year tutor ($t_{48} = 0.64$, $P = 0.53$).

We tested the prediction that males that fledged at a lower mass or smaller size than average would be more likely to show a delay in song learning (and hence would be more likely to learn from a breeding-year tutor) or at least would sing distinctive songs. However, males whose song was most similar to that of a breeding-year tutor did not differ at 7 days of age in wing length, tarsus length, mass or condition (mass/wing length) from males whose song was most similar to that of a hatching-year tutor ($t_{48} = 0.61$, 0.95 , 0.14 and 0.45 , $P = 0.55$, 0.34 , 0.89 and 0.66 , respectively). Neither condition nor any measure of size (wing, tarsus, mass) at fledging was correlated with any song characteristic (linear regressions of size and condition at fledging against the frequency and duration of the buzz and terminal trill: $P > 0.05$).

Of 189 males whose songs were recorded, 43 individuals were identified as the most likely tutors for at least one young male, based on the highest visual similarity score among the tutor classes. Each of the identified tutors influenced a mean \pm SE of 1.3 ± 0.7 young males (range 1–5). Males that apparently served as tutors did not differ in any aspect of morphology from males that were not identified as tutors (t tests on wing length, tarsus length, mass, bill length and bill depth: $t_{122-186} = 0.26$, 0.48 , 1.31 , 0.75 and 1.10 , $P = 0.79$, 0.63 , 0.19 , 0.46 and 0.27 , respectively). Nor did tutors differ from nontutors in traits such as longevity or lifetime number of nests, fledglings or recruits ($t_{186} = 0.40$, 0.57 , 0.45 and 0.17 , $P = 0.69$, 0.57 , 0.65 and 0.86 , respectively). The age at which a male was first banded (nestling, juvenile or adult, which is an indication of where he was raised) also had no effect on whether a male was an apparent tutor ($\chi^2_2 = 0.92$, $P = 0.63$). The only characteristic that differed between tutors and males that did not serve as tutors (based on overall similarity of song) was lifetime number of mates (tutors: 2.7 ± 4.2 ; nontutors: 2.1 ± 3.7 ; $t_{186} = 2.11$, $P = 0.04$), but even this result was not significant after Bonferroni correction for multiple comparisons.

The songs of some birds were apparently intrinsically less likely to be imitated than others. For example, three males with song types quite different from any other in the population collectively produced 121 fledglings and seven male recruits over the course of their lifetimes (7, 8 and 8 years). More than 1000 neighbouring nestlings and

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 1–2 weeks of arriving at the breeding ground at the age of 9–11 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 beginning of their first breeding season a year later. Using the criterion of similarity of entire songs, vertical transmission (Cavalli-Sforza et al. 1982) of songs heard during a male's hatching year (i.e. copied from the social father) accounted for the songs of about one-eighth of young males. Oblique transmission from an older neighbour heard either during a male's hatching year (about one-third of young males) or during his first breeding season a year later (about one-fourth of young males) accounted for most song learning. One-fourth of all males developed songs that were most similar to the songs of SY breeding-year neighbours, which suggests convergence among yearlings on the same songs under the influence of similar tutors heard in either their hatching or their first breeding year. An alternative explanation, learning from peers (horizontal transmission), seems less probable. There is no indication that Savannah sparrows or other sparrow species learn from peers on the wintering ground or during migration. In light of the existence of local dialects, such a model would require birds from the same population to remain together during the nonbreeding season, a behaviour not supported by the limited banding returns from Kent Island. Moreover, the songs of 1-year-old males are not crystallized by the time they arrive on the breeding grounds, at which point older males are already established and using song to attract females and defend their territories. Other studies have documented that young males learn preferentially from older males (e.g. Payne 1996; Liu & Kroodsma 2006).

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.L.L., unpublished data).

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