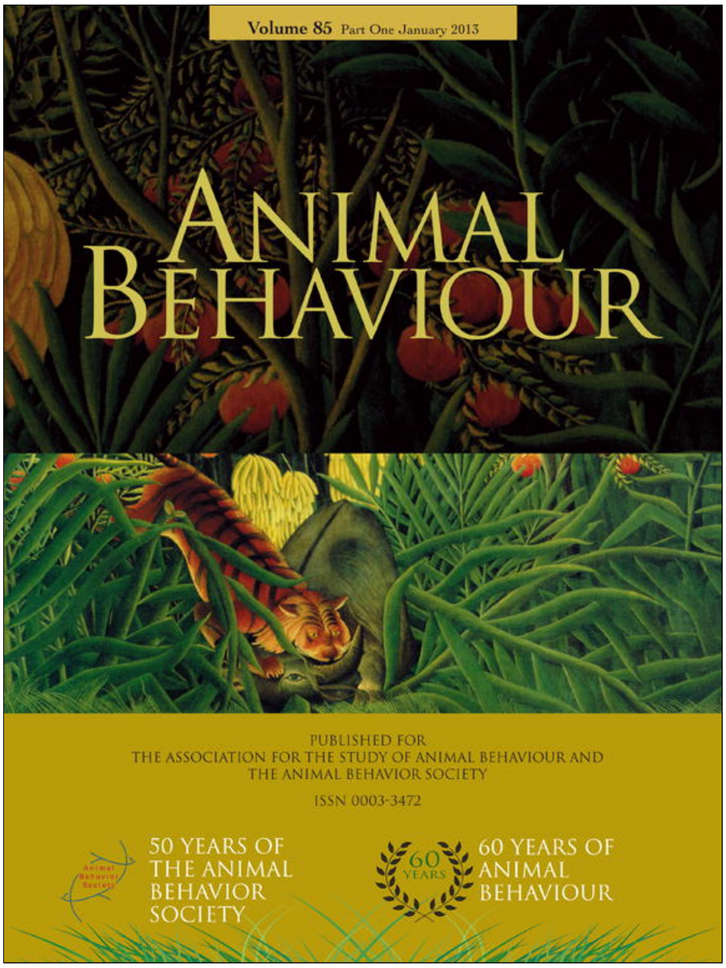
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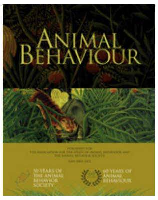

Three decades of cultural evolution in Savannah sparrow songs

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Cultural evolution can result in changes in the prevalence not only of different learned song types within bird populations but also of different segments within the song. Between 1980 and 2011, we examined changes within different segments of the single songs of male Savannah sparrows, *Passerculus sandwichensis*, in an island population. Introductory notes did not change. The buzz segment showed similar stability; although a rare low-frequency variant appeared and then disappeared, the buzz segments from 1980 and 2011 were essentially identical. The middle segment, made up of discrete notes assembled into several types, was variable. However, the form of the middle segment did not affect fitness and may serve to denote individual identity. The terminal trill decreased steadily in frequency and duration over three decades. Longer trills were associated with lower reproductive success, suggesting that trill duration was under sexual selection. The notes sung between introductory notes were also associated with reproductive success. A high cluster sung in 1980–1982 disappeared altogether by 2011, and was gradually replaced by click trains, which were associated with greater reproductive success. During the final decade of the study, more clicks were added to click trains. Longer click trains, which may require vocal virtuosity and so indicate male quality, were also associated with greater reproductive success. Both trill duration and the number of clicks increased in variance during the three-decade span of the study. We suggest that such increases in variance might be a signature of directional cultural selection. Within the Savannah sparrow's relatively short and simple learned song, cultural evolution appears to be mediated by different mechanisms for different song segments, perhaps because the segments convey different information.

Cultural evolution, defined broadly as the social learning of complex behaviours (see Bonner 1980; Whiten et al. 1999, 2011; Rendell & Whitehead 2001), can be considered to be similar to genetic evolution (Mundinger 1980; Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). There are two main hypotheses describing how socially learned traits, such as the songs sung by a population of oscine songbirds, change over time: (1) trait variability is due to neutral cultural processes analogous to genetic drift and mutation; and (2) traits evolve under selection. Where neutral processes define cultural evolution, changes in the pool of song forms within a population occur because of the addition of new forms via improvisation or copying errors during song learning ('mutation'), or when individuals that learned their songs elsewhere immigrate into the population ('meme flow'). Other forms that are neutral in their effects on fitness may be lost because of random events such as emigration of a male singing a rare form or when young males fail to learn a song form sung by the previous generation ('drift'; Kimura & Crow 1964; Bentley et al. 2004). The neutral model is consistent with the evolution of many cultural changes: the popularity of pottery types in Neolithic Germany (Bentley et al. 2007), chaffinch, *Fringilla coelebs*, songs in the Azore and Canary Islands (Lynch 1996), and the unaccented song types of chestnut-sided warblers, *Dendroica pensylvanica* (Byers et al. 2010). In contrast, cultural selection acts to stabilize certain learned forms or favour directional change. Accented song types of chestnut-sided warblers do not fit the neutral allele model, changing very little over space and time (Byers 1996; Byers et al. 2010), and low-frequency anthropogenic noise has resulted in directional selection for and stronger responses to higher-frequency song types of some urban songbird species (Slabbekoorn & Boer-Visser 2006; Cardoso & Atwell 2010; Luther & Derryberry 2012).

Previous studies have focused on neutral processes and selection as responsible for cultural evolution of song types. In this study we characterize cultural evolution in the Savannah sparrow, *Passerculus sandwichensis*, over three decades. In our study population

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males are likely to be subject to sexual selection via female choice, as 22.4% of the variance in male reproductive success is attributable to the degree of polygyny (Freeman-Gallant et al. 2005). We use reproductive success, as inferred from the total number of young fledged from the nest of males' social mates, to relate fitness to the cultural evolution of song. Because the songs of many species have multiple parts that may serve different functions, it is possible that different mechanisms might be responsible for the independent evolution of different segments within a song. Indirect evidence for this idea is provided by the finding that, within the songs of white-crowned sparrows, *Zonotrichia leucophrys*, the trill, which encodes dialect identity, changes more slowly over time than do note complexes, which encode individual identity (Nelson et al. 2004; Nelson & Poesel 2009). Similarly, the biphonic calls of North Pacific killer whales, *Orcinus orca*, which are used for group identification and localization, are less diverse than the monophonic calls, which are thought to be important in denoting individual identification (Filatova et al. 2012). The songs of Savannah sparrows include segments such as the introductory notes that do not vary across wide geographical areas, while the buzz segment varies little within populations and may serve as a dialect marker, and still others, such as the middle section, vary substantially within a population and may serve to denote individual identity (Chew 1981; Bradley 1994; Sung & Handford 2006). We predicted that (1) change over time would be less evident in song segments characteristic of the species and population, and (2) where cultural evolution occurs, it may be driven by neutral processes for markers of individual identity and by selective processes for song segments associated with male quality.

METHODS

Study Site and Savannah Sparrow Population

A population of Savannah sparrows has been studied at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada, since the 1960s, first by Dixon (1978) and, beginning in 1987, by Wheelwright and colleagues (Wheelwright et al. 1992; Freeman-Gallant et al. 2005; Mitchell et al. 2012). During many of these years, and continuously since 1987, all of the individuals nesting within a 10 ha study area (ca. 40–50 pairs each year) have been banded with distinctive colour band combinations. Kent Island Savannah sparrows show strong natal and breeding philopatry (Wheelwright & Mauck 1998), and birds hatched on the study site represent 40–80% of those recruited to the study site, although they are part of a larger population inhabiting Kent Island and two smaller adjacent islands. Because of the systematic banding programme, the hatching year for all males with songs recorded in 1989 and thereafter is known.

Songs and Song Recordings

Male Savannah sparrows sing only one song type (fewer than 2% sing two different song types), crystallize that song early in the first breeding season, and only very rarely (<1%) change their songs thereafter (Wheelwright et al. 2008). Thus, a recording of a male at any point during or after the first breeding season can be taken to represent the song used throughout the life span. A series of high-quality recordings of males allowed us to compare songs spanning a period of 32 years. Clara Dixon used a Nagra tape recorder to record songs from the study population extensively in 1980 and 1982. Recordings in 1988–1989 were made using a Sony TCM 5000EV recorder and a Gibson parabolic microphone. Systematic recordings of breeding males were made using a Marantz PMD cassette recorder with either a Telinga Pro II or a Sennheiser ME-66 shotgun microphone (1993–1998), Sennheiser ME-66 and ME-67 microphones and a Sony MZN707 digital recorder (2003), or a Marantz PMD (670 or 660) digital recorder (2004–2011). Savannah sparrows have a life expectancy of about 1.5 years but can live for up to 8 years (Wheelwright & Rising 1993), and so to avoid pseudoreplication, we focused upon songs sung at intervals of 5–7 years: in 1980–1982 ($N = 60$), 1988–1989 ($N = 16$), 1993 ($N = 26$), 1998 ($N = 38$), 2004 ($N = 36$) and 2011 ($N = 39$). Except for 1988–1989, the sample sizes represent recordings of between 75% and 95% of the males present on the study area. Although the 1988–1989 sample is smaller than that for other intervals, these songs are included for the insight they provide into the timing of changes. The lowest-quality recordings, in terms of signal:noise ratio, were also those from 1988–1989; nevertheless, all song features, including click trains, were discernable and measurable in those recordings. Three birds were present during two sample intervals. For convenience, we will refer to each interval as a 'year', but the two earliest sample intervals covered two different years.

Analogue recordings were digitized using SoundEdit16 (Macromedia, San Francisco, CA, U.S.A.), and one to three representative songs with a high signal:noise ratio from each bird were chosen for analysis. Test tones from the tape recorders as well as incidental recordings of the nearby White Head Island foghorn (300 Hz) allowed us to confirm that different recording regimes did not introduce any systematic errors of timing or frequency that would compromise analysis across years. Digital files of the 28 songs depicted in Fig. 2 are available in the online repository Dryad (http://dx.doi.org/10.5061/dryad.34jb6).

Song Analysis

The songs of Kent Island Savannah sparrows consist of four main segments (Fig. 1). The song opens with the 'introduction': a series of three to seven loud, high-frequency downswept (frequency-modulated) 'introductory notes', between which softer notes, such as clicks, high whistles and fast trills, may be sung, often in the form of a 'high cluster' immediately before or after the final introductory note. The next segment is the 'middle', which consists of a combination of short, loud notes; the most common of these are 'Ch' notes, so called because of their percussive sound, and the 'dash', a relatively unmodulated tonal note. The third song segment is a long (median 0.59 s) broadband 'buzz'. The buzz is separated from the final segment, the 'trill', by a note essentially identical to the introductory notes. The final trill is a series of repeated tonal notes; the first note in the series often differs in phonology and frequency from the remainder of the trill. To the human ear, the middle and trill segments are the most individually distinctive portions of the song, but sonagrams reveal important differences in the introduction, primarily in the pattern of softer notes falling between the introductory notes.

To analyse song characteristics that might have changed over time, we used the following measures.

Presence of a high cluster

A high cluster, found at or near the end of the introductory segment, included at least four notes and one or more note types not present in other introductory intervals.

Presence of a click train and number of repeated click notes within a click train

The song depicted in Fig. 1 includes two click trains between introductory notes; each is composed of three clicks. A few songs varied in the number of click notes within trains; in such cases, the larger number was used.

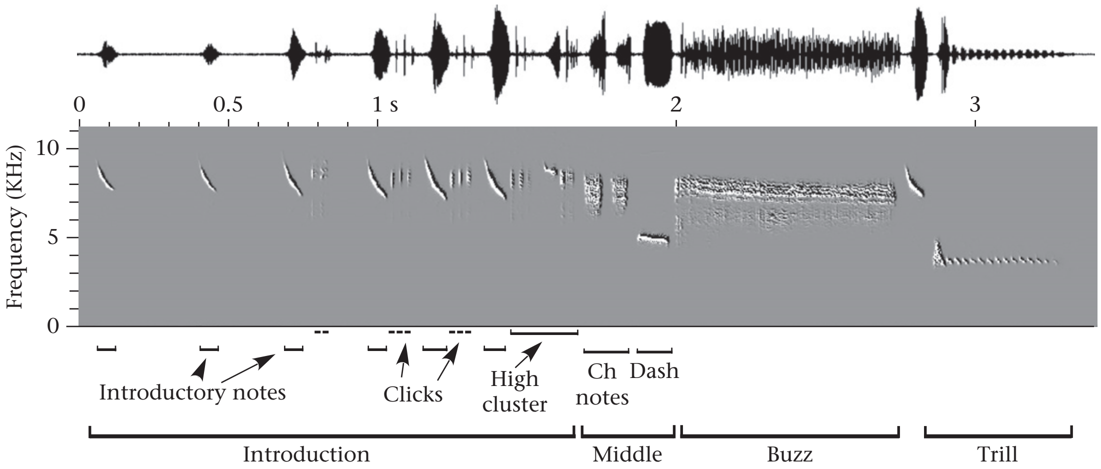

Figure 1. Kent Island Savannah sparrow song features. Waveform and sonagram of a typical song, composed of four segments. The song begins with an ‘introduction’ composed of an accelerating series of descending introductory notes and, in the intervals between those notes, softer sounds including clicks, and, at the end of the sequence, a cluster of short, relatively soft high notes. The ‘middle’ segment usually consists of one or more broadband ‘Ch’ notes, and sometimes, as here, a tonal ‘dash’. A high-frequency ‘buzz’ follows, and the song concludes with a terminal ‘trill’.

Number of introductory notes and Ch notes

These were scored as a simple count for each song.

Position of the dash note

Dash notes were scored as absent, present in the initial or final position within the middle segment, or as the sole note in the middle segment.

Middle segment type

Songs were assigned to one of five categories (see Fig. 2 for examples): (1) two Ch note songs; (2) stutter songs, with more than two Ch notes; (3) dash + Ch songs, with one dash and one or two Ch notes; (4) dash + short notes songs, usually including at least three short notes; and (5) songs with middle segments consisting of a single note (typically Ch note in 1980–1982 and a dash thereafter). Only seven of the 215 songs in the sample did not fall into one of these categories.

Duration and frequency of introductory notes, Ch notes, dashes, buzzes and trills

SoundAnalysisPro (ofer.sci.ccny.cuny.edu/sound_analysis_pro) was used to measure the mean frequency and duration of each note type and segment in each bird’s song. FFT window size was set at 10 ms and the advance between windows at 2 ms. Measurements were taken by using cursors placed at the beginning and end of the segment to be measured. Duration resolution was 2 ms increments, and mean frequency resolution was 3 Hz for 100 ms segments.

Because multiple variables were tested for change over time, we used the Bonferroni correction to set the level of statistical significance at $P = 0.00357$. The distribution of all parametric song measures was tested for fit to a normal distribution to determine whether an ANOVA test was appropriate. Two variables (buzz frequency and trill duration) failed this test, and for these measures we used a Kruskal–Wallis test to assess the significance of changes over time. Two additional variables (introductory note duration and buzz length) fit a normal distribution after a single outlier had been removed; in one such case, the recording of the introductory notes was of particularly poor quality, and in the case of the buzz outlier, the entire song was decidedly unusual for the population.

Some measures showed changes over time in variability. The coefficient of variation (CV) was used as a metric for assessing such changes, and significance was assessed by calculating the 95% confidence interval of the CV.

Reproductive Success

We estimated reproductive success by locating all successful nests in the study area. The adult male that defended the nest territory, guarded the female incubating the eggs and fed the nestlings was designated the (social) father for that nest. Nestlings were measured and banded at day 8 posthatch, and the number and identity of fledglings was subsequently noted (for details, see Wheelwright & Mauck 1998). Although there is substantial extrapair paternity (EPP) in this population (47% of nestlings in 2002–2004), the number of offspring that fledged from a male’s nest is nevertheless a good predictor of his overall genetic reproductive success (Freeman-Gallant et al. 2005), and the number of fledglings produced in a male’s nests is positively correlated with the total number of fledglings sired (Pearson correlation: $r_{77} = 0.654$, $P < 0.0001$; C. Freeman-Gallant & N. T. Wheelwright, unpublished data). Thus, as EPP information was available only for 2002–2004, we used the total number of fledglings as an index of a male’s fitness.

Because reproductive success was higher in older males (ANOVA: $F_{1,137} = 4.10$, $P = 0.045$) and varied between years (ANOVA: $F_{4,137} = 3.156$, $P = 0.016$), we used age and year as covariates in linear models to examine whether particular song traits influenced the number of young fledged from a male’s nests. We used both the raw measure for the song variable (as a linear variable) and also divided the measurements for each year into quintiles (a nominal variable). Quintiles were used because (1) selection might have been stabilizing rather than directional and so would not be captured by a linear regression, and (2) any fitness effects would have occurred in relation to the other males and song types present in a given year. Only the song variables that showed significant changes over the course of the study were assessed for effects on fitness, and a Bonferroni correction set the threshold for significance at $P < 0.00625$.

Ethical Note

All procedures were carefully considered with respect to their effects on the birds, were reviewed and approved by the Bowdoin College Research Oversight Committee (2009-18 r2011), the Williams College Institutional Animal Care and Use Committee (WH-D-

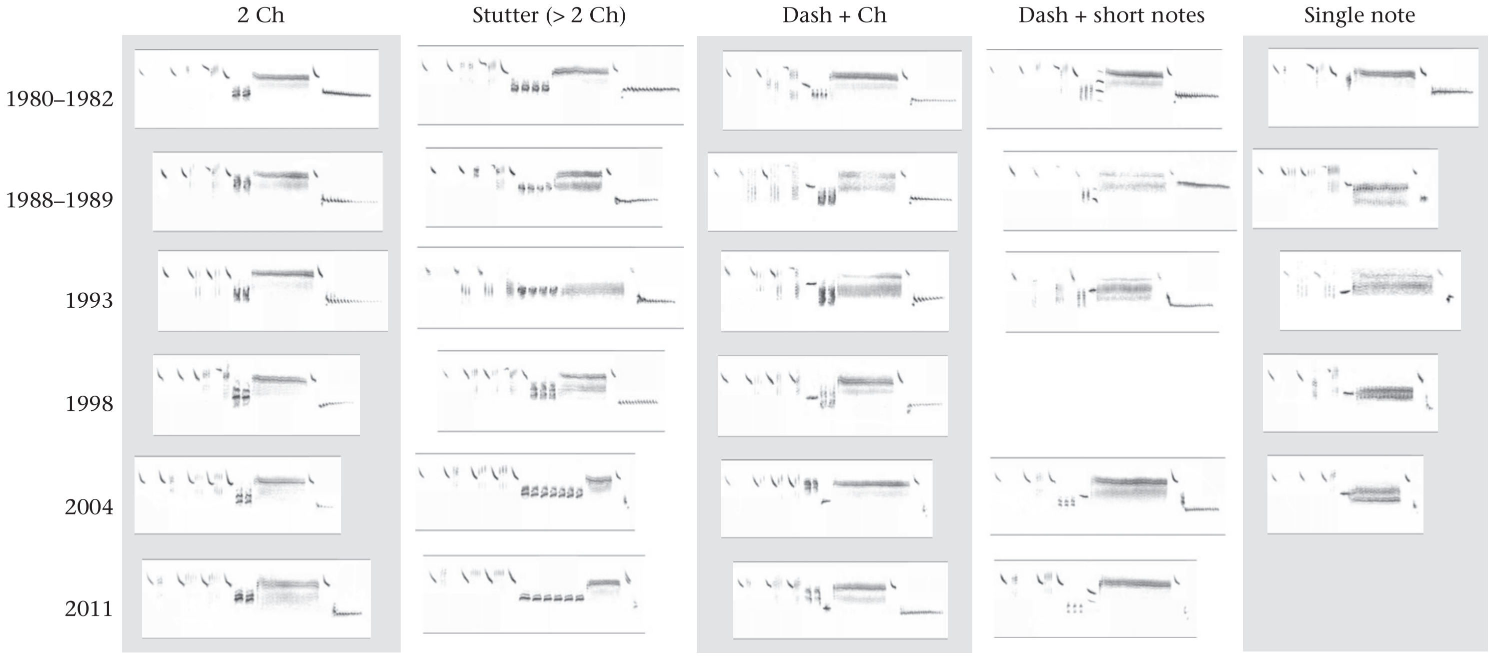

Figure 2. Examples of song types of male Savannah sparrows. Song types are classified here by the middle section of the song, which is characterized by a combination of discrete notes. Stutter songs are defined as songs including a sequence of three or more Ch notes. In the first two decades of this study, the dash note in ‘dash + Ch’ note usually occurred before the Ch notes, but in the 2000s, it occurred after the Ch notes. Single Ch-note songs were common in 1980–1982, but only one bird sang this song type thereafter; single dash note songs were sung in the 1990s and early 2000s, but not in 2011. One or more introductory notes were trimmed from the beginning of some songs shown here, but all notes sung between introductory notes were retained.

09), the University of Guelph Animal Care Committee (08R601), and were carried out as specified by the U.S. Fish and Wildlife Service (banding permit 02109) and the Canadian Wildlife Service (banding permit 10789D).

RESULTS

Introductory Segment

Over the three-decade period of the study there were notable changes in the duration, frequency and structure of the primary components of Kent Island Savannah sparrow song (Fig. 3). Introductory notes did not fluctuate much over the span. Frequency did not vary significantly (ANOVA: $F_{5,208} = 1.94$, $P = 0.055$; the criterion for significance after applying the Bonferroni correction is 0.00357 for this series of tests) and, although introductory notes varied in average duration across years (ANOVA: $F_{5,209} = 19.24$, $P < 0.0001$) and were shorter in 1988–1989 and 1993 than in other years (post-hoc $P < 0.001$), the mean values for 1980–1982 (73.6 ms) and 2011 (73.2 ms) were nearly identical. The number of introductory notes sung in each song did increase slightly, from a median of four to five in the first two decades to a median of five or six in the 2000s (ANOVA: $F_{5,209} = 12.41$, $P < 0.0001$; Fig. 4a).

In contrast to the introductory notes themselves, the softer notes sung between introductory notes changed substantially over time. The proportion of songs with high note clusters at or near the end of the introductory segment was 90% or greater in the 1980s, but decreased in the 1990s and early 2000s, reaching 0% in 2011 (logistic regression: $R^2 = 0.36$, $P < 0.0001$). Click trains were not sung in the early 1980s, but were present in 42.9% of songs in 1988–1989 and then became more common; in 2011, click trains were sung by more than 90% of males (logistic regression for 1988–1989 through 2011: $R^2 = 0.15$, $P < 0.0001$; Fig. 4c). Some males sang both high clusters and click trains, most notably in 1998 (44.7%) and 2004 (27.0%), and 5.6% of males sang neither click trains nor high clusters. As click trains were sung in more songs, the number of clicks in these trains also increased (ANOVA: $F_{3,131} = 17.29$, $P < 0.0001$; Fig. 4b). In 1988–1989 and 1993, all trains consisted of either two or three clicks; in 1998, one male sang a train with four clicks; in 2004, six males sang four-click trains; and in 2011, 23 males sang trains with four or more clicks (two males sang seven-click trains). Thus, between 1980–1982 and 2011 one feature of the introductory segment, high clusters, decreased and then disappeared altogether, while another, click trains, appeared, became nearly fixed within the song population, and shifted systematically towards including more clicks.

Middle Segment

The duration, frequency and sequence of the primary middle segment notes (Ch and dash) varied across years, but not in a systematic fashion (Fig. 3). The duration of both dash (ANOVA: $F_{5,93} = 6.40$, $P < 0.0001$) and Ch notes (ANOVA: $F_{5,193} = 6.34$, $P < 0.0001$) differed significantly across years, as did the frequency of Ch notes (ANOVA: $F_{5,193} = 4.912$, $P = 0.0003$), but no consistent pattern of change was evident (see Fig. 3). The frequency of dash notes did not change (ANOVA: $F_{5,93} = 1.07$, $P = 0.39$). The large fluctuation in the span of Ch note duration was related to the presence or absence of short Ch notes. In years when dash + short note middle segments were sung in more than 5% of the songs (1980–1982, 1988–1989 and 2011), the coefficient of variation (CV = SD/mean) of Ch note duration was 0.39 (lower bound of 95% confidence interval = 0.34); when fewer than 5% of the songs included this type of middle segment (1993, 1998 and 2004), the CV was 0.18 (upper bound of 95% confidence interval = 0.22).

The organization of notes within the middle segment shifted over the three-decade span. Stutter songs, with more than two Ch notes in succession, were sung in all years (Fig. 5c). The number of Ch notes within stutter songs increased over time, from a median of either three or four between 1980–1982 and 1998 to a median of 6.5 in 2004 and 2011, but this increase failed to meet the criterion for significance after applying the Bonferroni correction (ANOVA: $F_{5,18} = 4.35$, $P = 0.009$; Fig. 5a). Across years, dash notes were sung in as few as 33% of songs (in 2011) and in as many as 66% of songs (in 1998). The position of the dash note within the middle segment varied over time. In 1980–1982, more than 90% of dash notes occupied the final position in the middle segment, but a shift to the initial position occurred in the 1990s, with 65% of dash notes being sung as the first note of the middle segment in 2004. Songs with middle segments consisting only of dash notes were also sung between 1988 and 2004. In 2011 all dash notes occurred in the final position within the middle segment (Fig. 5b).

During the three-decade span, the most common and consistent type of middle segment was the two-Ch type (25–50% of all songs). Stutters were also present in all years, making up 7–16% of middle sections. Other middle segment types varied more substantially: 0–38% for dash + short note, and 3–42% for dash + Ch. Single Ch notes, which accounted for 23% of middle sections of songs sung in 1980–1982, essentially disappeared thereafter (only sung by a single bird in 2004), and songs with a middle segment composed of a single dash note were present in 1998–1989 through 2004, but not in the first or last years of the study. Although the types of middle segments that were present or dominant within the population varied, diversity was constant: at least four of the six distinct types were sung by two or more males in every year recorded.

Buzz Segment

Buzzes were remarkably consistent over the long term (Fig. 3). There was no variation across years in the average buzz duration (ANOVA: $F_{5,208} = 2.714$, $P = 0.23$). Buzz frequency varied somewhat across years, but not significantly so (Kruskal–Wallis test: $H_5 = 10.069$, $P = 0.06$). The variation in buzz frequency can be attributed to a low-pitched variant, with a frequency of approximately 5.5 kHz (2 kHz lower than the population average), that first appeared in 1988–1989 (see the songs for 1988–1989, 1998 and 2004 in the 'single note' category in Fig. 2). Low-frequency buzzes were sung by 25% of males in 1998–1989, 15.4% in 1993, 15.8% in 1998 and 8.3% in 2004. By 2011, the low-frequency buzz had disappeared.

Trill Segment

In contrast to the buzz segment but like the middle segment, the trill segment varied substantially over the course of three decades (Fig. 3). Trills became significantly shorter over time (Kruskal–Wallis test: $H_5 = 65.461$, $P < 0.0001$); some of the shorter trills are illustrated in Fig. 2. Trill frequency also decreased significantly over the three-decade span (ANOVA: $F_{5,206} = 12.86$, $P < 0.0001$), and the trills sung in 2004 and 2011 were lower-pitched than those sung previously (post-hoc $P < 0.05$). Both of these trends were monotonic and gradual; where recordings for intervening years existed, they were aligned with the overall trend illustrated in Fig. 3.

Song Characteristics and Reproductive Success

Only two song segments, the introduction and the trill, showed an association with reproductive success in an analysis that included the age of the male and the year the song was sung

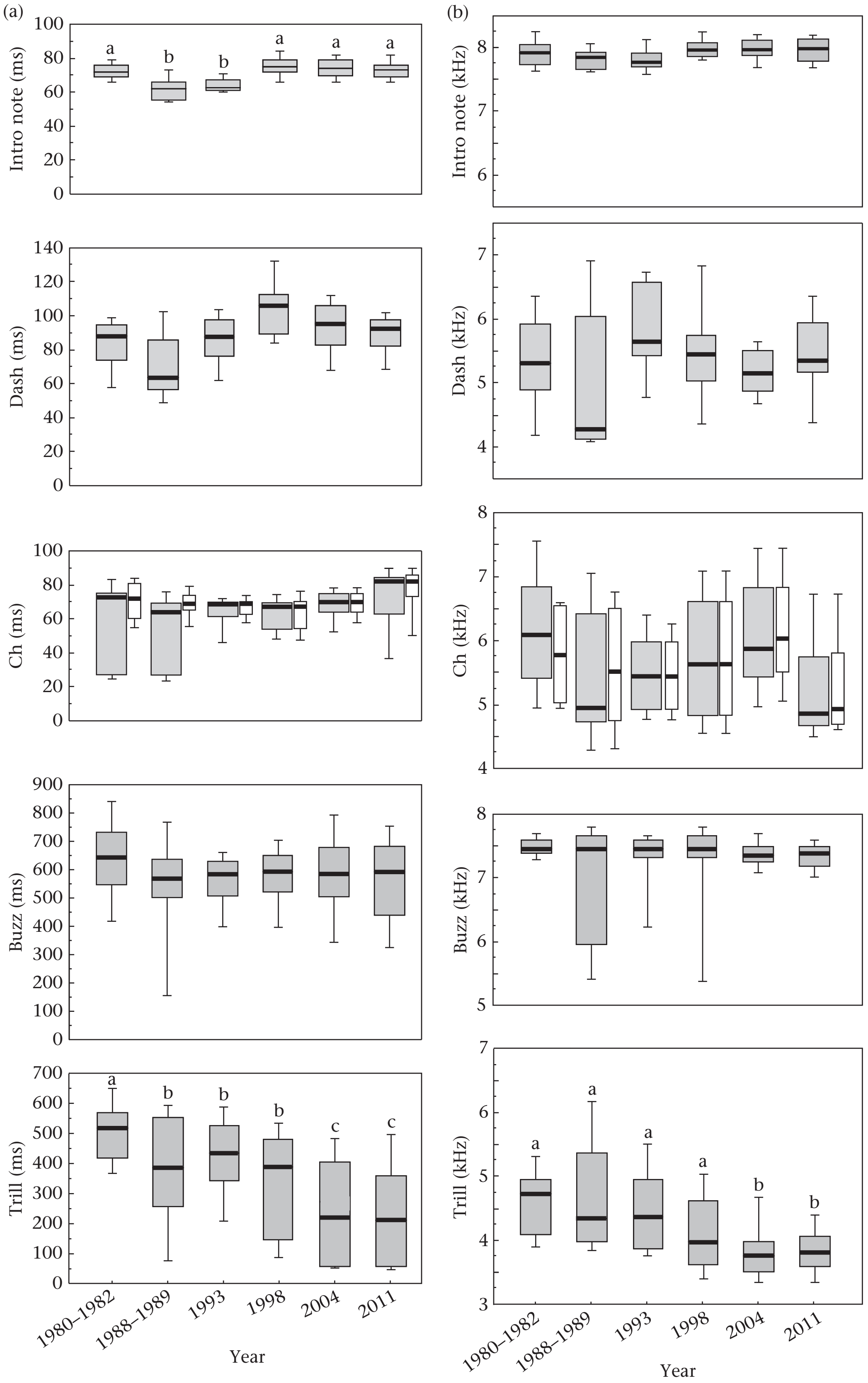

Figure 3. Duration and frequency of male Savannah sparrow song elements. (a) Duration (ms) of introductory notes, dash and Ch notes, and buzz and trill segments. (b) Frequency (kHz) of the same notes and segments. Upper and lower boundaries of each box are the 75th and 25th percentiles, central bar marks the median value for all songs, and error bars are the 10th and 90th percentiles. Different letters above box plots denote a significant difference between means (post-hoc $P < 0.05$). Open bars exclude ‘short Ch notes’, found only in one type of middle section.

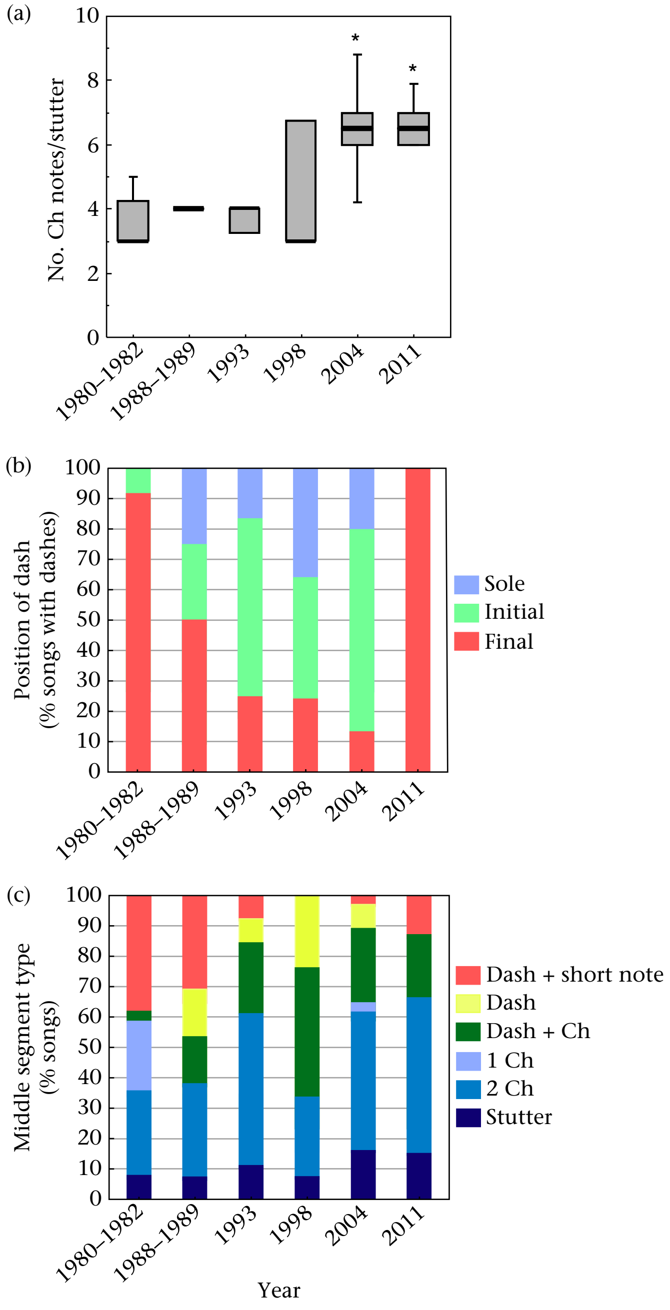

Figure 5. Changes in composition of the middle segment of male Savannah sparrow song. (a) Number of Ch syllable repeats within stutter songs. Upper and lower boundaries of each box are the 75th and 25th percentiles, central bar marks the median value, and error bars are the 10th and 90th percentiles. Asterisks denote years in which songs had significantly more Ch notes than those sung before 1998 (post-hoc $P < 0.05$). (b) Position of dash notes within middle sections shifted over time. (c) Distribution of middle segment types across three decades of recordings.

(Fig. 6a, b). There was a trend for longer trills to be associated with decreased reproductive success (ANOVA: $F_{4,130} = 2.51$, $P = 0.045$; coefficient for the longest quintile $= -1.9$ fledglings). The presence of a click train within the introductory segment was associated with

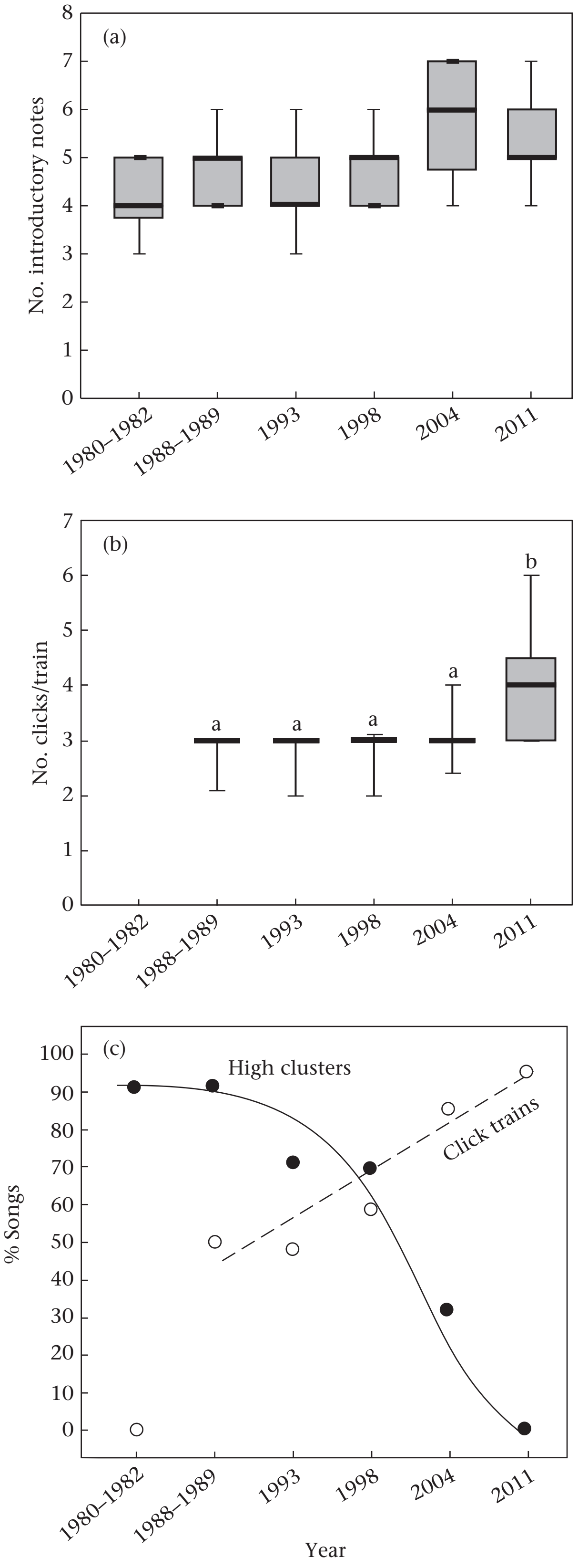

Figure 4. Changes in composition of the introductory segment in male Savannah sparrow song. (a) Number of introductory notes in songs recorded in a specific year. Upper and lower boundaries of each box are the 75th and 25th percentiles, central bar marks the median value, and error bars are the 10th and 90th percentiles. (b) Number of clicks sung within click trains. Different letters above box plots denote a significant difference between means (post-hoc $P < 0.05$). (c) Percentage of songs with high note clusters (solid circles) and click trains (open circles) within the introductory segment.

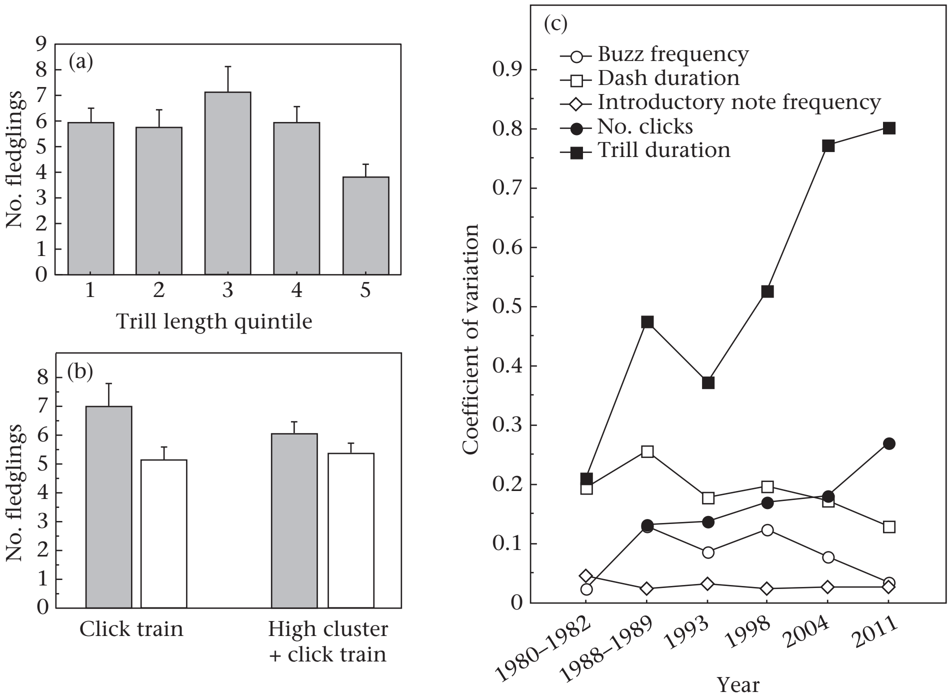

Figure 6. Reproductive success and changes in song features of male Savannah sparrows. (a) Relation between male trill length and the number of fledglings produced in a given year. (b) Relation between the number of fledglings produced and the presence (grey bars) or absence (open bars) of click trains and of high clusters or click trains in male song. (c) Relation between the coefficient of variation (CV) of measured song traits during the study period that were (solid symbols) or were not (open symbols) associated with increased reproductive success.

a significant increase in reproductive success (ANOVA: $F_{1,136} = 8.75$, $P = 0.004$; coefficient for the presence of click trains = +1.04 fledglings). Among songs that included click trains, a larger number of clicks was associated with greater reproductive success (ANOVA: $F_{1,136} = 6.32$, $P = 0.013$; coefficient for each additional click = +0.54 fledglings).

Decreasing trill length and increasing click train prevalence and number of clicks within trains could represent a trade-off, as production of click trains at the beginning of the song might impair a bird's ability to produce a long trill. If such a trade-off exists, then the number of clicks should be negatively correlated with trill length and a statistical model including both variables should result in a decrease in explanatory power of one of the variables. However, using only the 2004 and 2011 data when the number of clicks and the trill lengths were most variable and thus any correlation was more likely to be apparent, the number of clicks and trill length were not significantly correlated (Pearson correlation: $r_{71} = 0.08$, $P = 0.49$). Including both variables in a model to explain reproductive success increased the strength of the effects for both trill length ($F_{4,129} = 3.05$, $P = 0.019$) and number of clicks in click trains (ANOVA: $F_{1,129} = 8.26$, $P = 0.005$), indicating that effects of the two song segments on fitness were independent.

Trill length and number of clicks in click trains both showed gradual monotonic changes over the course of the study and were related to reproductive success, suggesting that they were under directional selection. One signature of directional selection on quantitative genetically transmitted characters is a decrease in variation (Futuyma 1997, pp. 418–422). However, as trill length decreased, the coefficient of variation (CV) for this measure increased, from 0.20 in 1980–1982 to 0.80 in 2011 (Fig. 6c); the 1980–1982 variation was significantly less than that in other years, and the 2004 and 2011 variation in trill length was significantly higher than that in other years (falling outside 95% confidence intervals). The CV for the number of clicks in click trains showed the same trend, increasing from 0.13 in 1988–1989 to 0.27 in 2011; variation in 2011 click train length was significantly greater than that in 2004, which was in turn higher than that for previous years. Traits such as buzz duration and introductory note frequency that were constant over the three-decade span and were not associated with reproductive success did not show these systematic changes in variation.

DISCUSSION

Over the course of three decades, three of the four segments of Kent Island Savannah sparrow song showed rapid and substantive cultural evolution. Introductory sequences lost high clusters, added click trains and increased the number of clicks in a train; middle sections shifted in their note composition and the position of the dash note changed; and trills became shorter and decreased in frequency.

In contrast, the buzz segment remained relatively constant over the three decades of the study period (apart from the introduction of a low-frequency variant in the late 1980s, which was never sung by more than one-fourth of the population, and disappeared altogether by 2011). Long-term stability of the buzz segment may reflect a role for that segment in defining the species or dialect of the singer, just as the terminal trills of white-crowned sparrow songs remained constant within populations over 25 years while other portions of the songs changed (Nelson et al. 2004). Such stability could be maintained by a learning bias for the most common form heard by juveniles. Even weak biases that favour regularity in human language can give rise to strong systematic rules favouring one grammatical form rather than two (Kirby et al. 2007; Reali & Griffiths 2010).

The middle segment of Savannah sparrow song is composed of distinct note types that form a set of discrete categories. The number of different middle segment types in the population remained relatively stable during the course of the study; the four most common types always accounted for more than 90% of the song types sung in a given year. However, the identity of the most common middle segment type changed substantially from year to year, as did the ordering of the notes, exemplified by the position of the dash note. Neither the middle segment type, the order of the notes, nor the duration and frequency of the notes were associated with reproductive success. Changes in this segment of the song thus appear to fit the neutral allele model, where a combination of mutation, immigration and drift defines the turnover rate and distribution of variants in a learned trait (Slater & Ince 1979; Lynch 1996; Bentley et al. 2004, 2007). Such a model explains the changes in popularity of the names given to babies in the U.S. (Hahn & Bentley 2003). It may be that middle section types, with their discrete and relatively distinctive characteristics, serve, like human baby names, as markers of individual identity and evolve rapidly but have no direct association to fitness.

Over the 30-year span of this study, the trill segment became substantially shorter and lower-pitched. A population-wide shift in the frequency of birdsong can occur in response to changes in environmental or anthropogenic noise (Slabbekoorn & Boer-Visser 2006; Bermúdez-Cuamatzin et al. 2009; Cardoso & Atwell 2010), and this is one potential explanation for the frequency shift of the trill section of Savannah sparrow song, which was not associated with reproductive success. This explanation would presume that there was less low-frequency environmental noise during the 1990s, when the average trill frequency showed the most marked decrease. However, there is no evidence for such a shift in environmental noise. On Kent Island, wave action on the shore and anthropogenic noise from fishing boats and foghorns do not appear to have changed appreciably during the period spanned by the recordings, and these sources of environmental noise have peak energies at lower frequencies than do the trill segment of the song. It also seems unlikely that low-frequency environmental noise (e.g. due to automobile traffic) declined on the sparrows' southerly wintering grounds or migration routes. Thus, the adaptive significance (if any) and the mechanism responsible for the population shift in trill frequency are unknown. In contrast, the halving of the average trill length over the course of three decades may be associated with differences in reproductive success; males with the longest trills produced, on average, 1.9 fewer fledglings per year, suggesting that sexual selection, operating either via female choice or through a competitive advantage for males with shorter trills, has selected against long trills.

The introductory segment includes two main note types: loud, descending introductory notes and softer notes composed of click trains and high clusters, which are sung between introductory notes. The frequency and temporal structure of introductory notes was remarkably stable (although frequency was lower in two recording years, notes from the early 1980s and 2000s were indistinguishable). Over the 30-year span of this study, the number of introductory notes increased, but no introductory note feature was associated with reproductive success. It is possible that the accelerating sequence of introductory notes serves as a culturally stable species-specific marker and a prelude to the song that draws attention to the more distinctive (and presumably more informative) portions of the song; it is certainly a distinctive feature for these purposes to the human ear.

In contrast to the stability of the introductory notes, the softer notes intercalated between them underwent substantial changes. The high cluster, included in the songs of more than 90% of males in the 1980s, disappeared by 2011, and click trains, absent in 1980–1982, were sung by an ever-higher proportion of males beginning in 1998–1989. By 2011, click trains were sung by more than 90% of males, effectively replacing high clusters. As click trains became the dominant feature sung between introductory notes, the number of clicks in a train also increased. Both of these trends were associated with increased reproductive success. Interestingly, males that sang both high note clusters and click trains had slightly greater reproductive success than did those that sang only one or neither feature, suggesting that although high note clusters were not themselves associated with a fitness advantage, they might add to the advantage that a male gained by singing a click train and that the two song features might play a similar role, perhaps as an indicator of male quality.

A number of features of learned song and the performance of that song have been related to male quality. Nowicki et al. (2002) found that female swamp sparrows, *Melospiza georgiana*, choose males based on the accuracy of song learning, which is related to an individual's ability to weather developmental stresses. Males' performance of the songs they learn may also be an indicator of quality. The degree of consistency across songs sung by individual males of several species increases with age (Byers 2007; Botero et al. 2009; de Kort et al. 2009), indicating that consistency may be difficult to acquire, particularly for sounds that are vocally challenging. For many species, series of closely spaced frequency-modulated notes (trills) are performed near the limit of what the vocal system can produce (Podos 1997; Suthers & Zollinger 2008; Podos et al. 2009). Acoustic features that place a premium on the learning and performance ability of the singer may thus serve as reliable indicators of a male's quality, and so might provide both direct and indirect benefits to females that choose males based on such song features. In Savannah sparrows, both high clusters and click trains are composed of multiple notes sung in rapid succession, features that may require a degree of vocal virtuosity from the singer. Such a 'vocal virtuoso' hypothesis might also explain sexual selection for the increasing number of clicks within click trains.

One question raised by this scenario is how increased fitness of a male that sings more clicks is translated into longer click trains in the next generation's songs. Savannah sparrows learn their songs not only from their social or genetic fathers but also from neighbouring males in both their natal and first breeding years (Wheelwright et al. 2008). Furthermore, young males' songs often included more clicks than did those of males singing during the preceding year. Thus, simple transmission of longer click trains from older to younger males cannot account for the cultural evolution of longer click trains. However, social learning through observation of others' responses to an individual's own performance or to other individuals learning a song is an important component of song acquisition in several species (King & West 1983; West et al. 2003; Bertin et al. 2007; Williams 2008). Because adults often produce two broods per season, Savannah sparrow males that fledge early in the year have the opportunity to observe adult male songs and female responses during renesting. Hence, they could learn about responses to features of several males' songs and then use what they learn to subsequently shape their own songs. When yearling males return the following spring, they often do not crystallize their songs immediately but continue to produce late plastic song for 1–2 weeks while interacting with adult males that are also singing (H. Williams, personal observation). If producing long click trains requires vocal virtuosity, the number of clicks a young male sings might be influenced by behavioural responses to his own and to other males' songs, and such responses might favour longer click trains.

A long-standing problem for evolutionary biologists is how genetic diversity can be maintained in the face of directional or stabilizing selection, as such selection eliminates outliers for the trait under selection and so reduces variability (see Lande 1975). Thus, one might predict that cultural evolution would also cause song traits that changed substantially over a decade or more and were related to reproductive success to show decreased variation. However, as click trains grew longer and trills grew shorter on average, variation in these culturally transmitted traits increased, although it did not change for other song features for which there was no evidence of selection. We suggest that such a seemingly contradictory increase in variation may be a signature of ongoing directional cultural selection. Lande noted that variability of genetically transmitted traits can only be maintained by mutation rates that counter the loss of variation due to directional selection. In contrast to genetically determined characters, learned traits have the potential for much higher rates of mutation. Individuals are not restricted to reproducing traits present in their father's song or even those sung by other males within the population. Instead, they are able to improvise and sing song characters that fall outside the distribution of those sung by the previous generation. In addition, the 'mutation rate' for learned traits may not be independent of selection. A young male, observing successful older males singing more clicks, may copy the larger number of clicks, but as that young male is not restricted to singing only what he heard in the songs of other males, he may in fact sing more clicks than were sung in any of the model songs. Thus the rate of change for learned traits (1) is potentially many times higher than that for genetically determined traits and (2) is itself subject to selection. Directional 'cultural' selection, favouring ever-more extreme forms of a learned trait, may result in a 'mutation rate' that exceeds the reduction in variation due to selection and so results in increased variance in the trait such as that observed in click train length in our study.

Strong links between cultural evolution of songs and fitness have proven difficult to demonstrate. In the medium ground finch, *Geospiza fortis*, Gibbs (1990) found that minority song types tended to displace majority song types over time. Although males singing minority songs were likely to survive longer and were more likely to have sons recruited into the population, there were no significant effects of song type on overall fitness. Payne & Payne's (1993) long-term study of indigo buntings, *Passerina cyanea*, found that age, which was strongly correlated with plumage colour and date of arrival, strongly influenced young males' choices of adult male song models; once those factors were accounted for, an adult male's fitness did not predict whether his song would be learned by first-year males. Although, in our study, two song characters showed a link to fitness, several other aspects of song that changed over time were not related to reproductive success. It may be that a strong link between reproductive success and cultural evolution exists in other species, and the relative rarity of studies that assess both song and fitness over a long period has affected the ability to find such a strong relationship. However, it is equally possible that, because some features of learned song are either (1) under stabilizing selection or (2) fit the null model of random variation, relationships between other song features and fitness may be obscured when the entire song is considered as a single unit.

Our results suggest that different portions of Savannah sparrow song, which are likely to serve different purposes, change at different rates and may be affected by different evolutionary mechanisms. The series of introductory notes and the buzz segments are common to most populations across the species' range (Chew 1981; Bradley 1994; Burnell 1998; Sung & Handford 2006), and may serve mainly to identify the species. Such a function is consistent with the stability over time that we observed in these song segments. The middle segment, although highly variable, appeared not to influence fitness; instead, it has characteristics such as discrete note types and multiple combinations that are likely to be useful in distinguishing individuals. A neutral model could account for regular change in the middle segment. The substantial variation present in the trill segment may also allow that song segment to convey information about individual identity, but the systematic changes in both frequency and duration over the span of three decades and the possible fitness advantage of shorter trills suggest that selective pressures, probably sexual, but perhaps also related to survival, drove the cultural evolution of the trill segment. The softest and shortest notes, those that fall between introductory notes, appear to be an indicator of male quality and may have been the most strongly influenced by selection over the course of the 30 years covered by this study. Thus, within the single simple learned song a Savannah sparrow male sings, each segment evolves culturally at different rates, is likely to communicate different types of information and appears to be subject to different selective pressures.

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