Three decades of cultural evolution in Savannah sparrow songs

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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

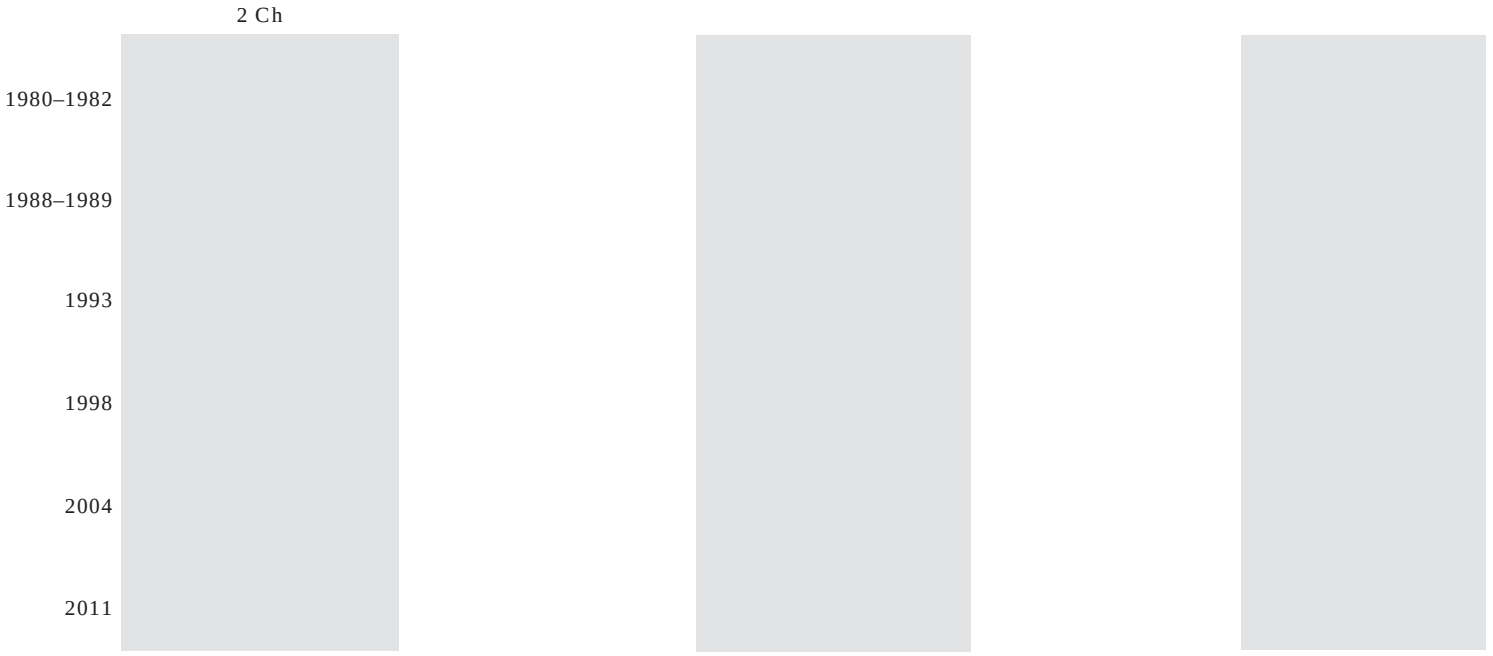
These were scored as a simple count for each song.

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.

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.

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.

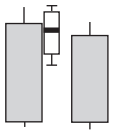
Because multiple variables were tested for change over time, we used the Bonferroni correction to set the level of statistical significance at

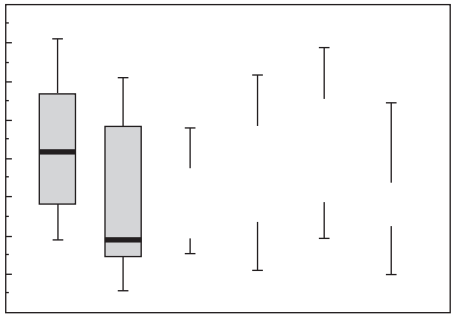

2 Ch
1980–1982
1988–1989
1993
1998
2004
2011

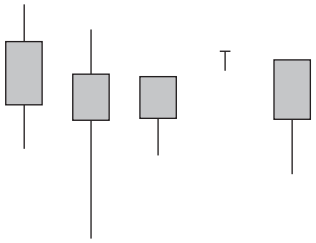
09), the University of Guelph Animal Care Committee (08R601), and were carried out as specified by the U.S. Fish and Wildlife Service (banding permit 02109) and the Canadian Wildlife Service (banding permit 10789D).

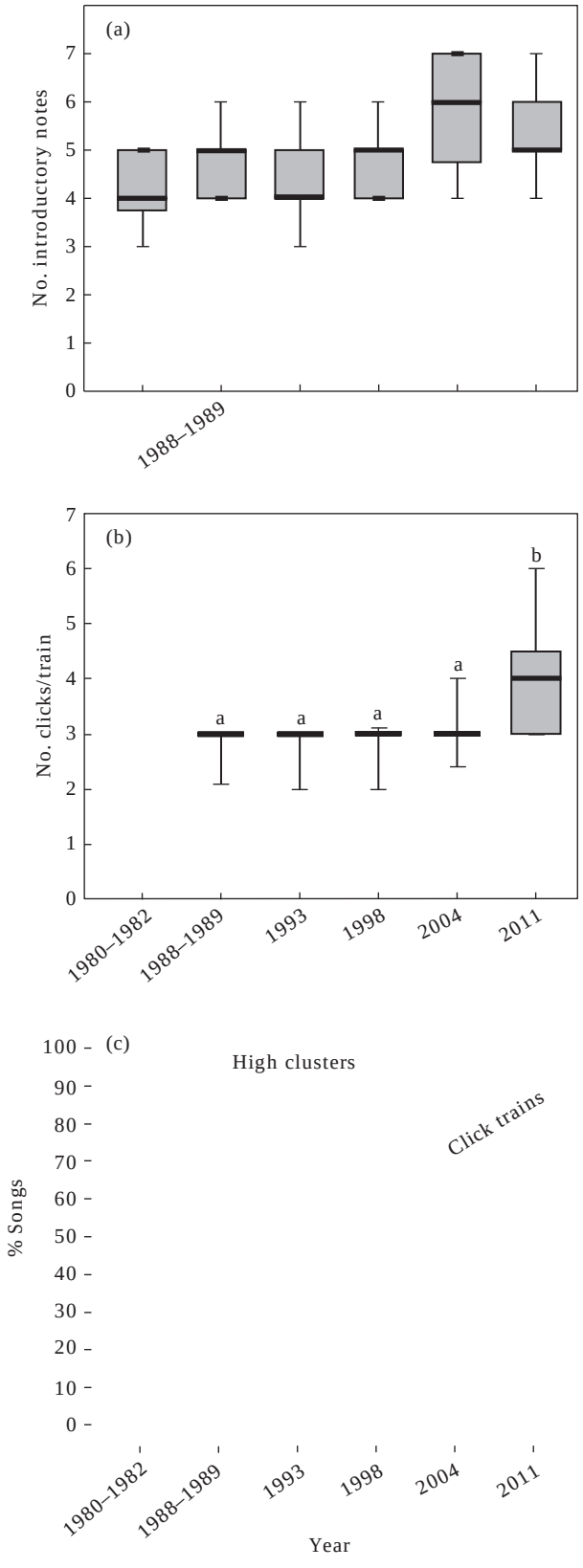
RESULTS

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: $_{5,208} = 1.94$, $= 0.055$; the criterion for signifi









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

a significant increase in reproductive success (ANOVA: $_{1,136} = 8.75$, $= 0.004$; 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: $_{1,136} = 6.32$, $= 0.013$; 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: $_{71} = 0.08$, $= 0.49$). Including both variables in a model to explain reproductive success increased the strength of the effects for both trill length ($_{4,129} = 3.05$, $= 0.019$) and number of clicks in click trains (ANOVA: $_{1,129} = 8.26$, $= 0.005$), 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

remained relatively stable during the course of the study; the four most common types always accounted for more than 90% of the

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.

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