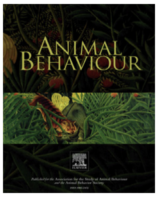
Animal Behaviour 155 (2019) 67–75

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Eavesdropping on adult vocal interactions does not enhance juvenile song learning: an experiment with wild songbirds

Daniel J. Mennill [a], [*], Stéphanie M. Doucet [a], Amy E. M. Newman [b], Heather Williams [c], Ines G. Moran [a], Ian P. Thomas [a], Bradley K. Woodworth [b], Mikayla M. K. Bornais [a], D. Ryan Norris [b]

[a] *Department of Biological Sciences, University of Windsor, Windsor, ON, Canada*
[b] *Department of Integrative Biology, University of Guelph, Guelph, ON, Canada*
[c] *Biology Department, Williams College, Williamstown, MD, U.S.A*

ARTICLE INFO

Article history:
Received 12 March 2019
Initial acceptance 23 April 2019
Final acceptance 24 May 2019

MS. number: A19-00186R2

Keywords:
birdsong
Passerculus sandwichensis
playback
Savannah sparrow
vocal learning

Animals often live within close proximity of multiple conspecific individuals, allowing them to eavesdrop on other animals' signalling interactions to guide their own social behaviours. For a young animal that is learning to vocalize, eavesdropping on vocal interactions between adults may provide a rich source of information: young animals might preferentially learn vocalizations that are commonly heard in interactions between adults or that are heard to be effective for attracting mates or defending resources. We used a multispeaker playback experiment with wild Savannah sparrows, *Passerculus sandwichensis*, to test the hypothesis that vocal learning is guided by eavesdropping. Over a 6-year period, we tutored young Savannah sparrows with experimental tutor songs; half of the tutor songs were broadcast in simulated vocal interactions between two tutors, and the other half were broadcast as noninteractive, stand-alone solo performances. If eavesdropping plays an important role in guiding vocal learning, we predicted that young birds would preferentially learn the vocalizations heard during interactions between tutors. In contrast to our prediction, young Savannah sparrows did not preferentially learn interactive tutor songs; birds were similarly likely to learn songs heard in an interactive context ($N = 13$) and in a noninteractive context ($N = 17$). Analysis of live adult tutors' reactions to the loudspeakers showed that they responded with similar vocal behaviour during interactive and noninteractive treatments, and therefore their vocal behaviour did not compromise the playback simulation. We conclude that eavesdropping on vocal interactions between tutors does not appear to be essential for vocal learning of wild Savannah sparrows.

Eavesdropping occurs when animals extract information from an interaction between other individuals without being directly involved in that interaction (McGregor, 1993). Many animals exhibit eavesdropping behaviour, including humans (Fox Tree, 2009; Jones, DeBruine, Little, Watkins, & Feinberg, 2011a), other mammals (Marshall-Pescini, Passalacqua, Ferrario, Valsecchi, & Prato-Previde, 2011; Valone, 1996), birds (Sprau, Roth, Amrhein, & Naguib, 2012; Wojas, Podkowa, & Osiejuk, 2018), fish (Doutrelant & McGregor, 2000; Webster and Laland, 2013) and invertebrates (Aquiloni, Buřič, & Gherardi, 2008; Clark, Roberts, & Uetz, 2012). Animal behaviourists recognize two separate forms of eavesdropping behaviour (reviewed in Peake, 2005). 'Interceptive eavesdropping' occurs when animals intercept signals intended for other receivers (e.g. a predator eavesdropping on the mating signals of its prey; Jones, Page, Hartbauer, & Seimers, 2011b). 'Social eavesdropping' occurs when animals extract relative information about other individuals engaged in an interaction, gathering information that could not be obtained outside the context of the interaction. In some birds, for example, females use information gained through social eavesdropping on the overlapping and pitch-matching interactions during male–male vocal exchanges to guide their reproductive decisions (Mennill et al., 2002, 2003; Otter et al., 1999), and males use information gained through social eavesdropping on overlapping interactions during male–male vocal exchanges to adjust their territorial behaviour (Mennill & Ratcliffe, 2004a,b; Naguib, Fichtel, & Todt, 1999; Toth, Mennill, & Ratcliffe, 2012).

Social eavesdropping provides a rich source of information that may guide vocal learning. At least six groups of social animals have evolved vocal learning, including three groups of birds (songbirds,

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[*] Correspondence: D.J. Mennill, Department of Biological Sciences, University of Windsor, Windsor, ON N9B3P4, Canada.
E-mail address: dmennill@uwindsor.ca (D. J. Mennill).

https://doi.org/10.1016/j.anbehav.2019.05.019
0003-3472/

hummingbirds, parrots) and at least three groups of mammals (humans, cetaceans, bats, and possibly pinnipeds and elephants; Jarvis, 2004; Poole, Tyack, Stoeger-Horwath, & Watwood, 2005; Reichmuth & Casey, 2014). In any vocal-learning animal, young individuals might listen to the interactions between nearby individuals to determine which sounds they should learn. They may use social eavesdropping to determine which sounds are produced most often during social interactions, to understand which sounds are effective at eliciting particular behaviours, or to infer the meaning of particular vocal signals. Vocal learning through eavesdropping has been documented most conclusively in humans: children as young as 18–24 months of age can learn novel nouns and verbs based on eavesdropping on interactions between adults (Akhtar et al., 2001; Floor & Akhtar, 2006). Beyond humans, the idea that social eavesdropping may be involved in vocal learning has only received little attention.

A few studies of learning through eavesdropping provide some experimental evidence that social eavesdropping may influence vocal learning in songbirds. In an aviary, two experimental studies showed that song sparrows, *Melospiza melodia*, preferentially learned songs from experimental tutors that they had overheard interacting with another young bird (Beecher, Burt, O'Loghlen, Templeton, & Campbell, 2007; Burt, O'Loghlen, Templeton, Campbell, & Beecher, 2007). The sample sizes for these studies were modest (7 and 8 juveniles, respectively, and 4 tutors in both studies), yet these results suggest that eavesdropping may be more important to vocal learning than direct one-on-one interactions with tutors, given that the juveniles were more likely to learn songs through overhearing a tutor than directly interacting with a tutor (Beecher et al., 2007; Burt et al., 2007). In a field setting, juvenile song sparrows approached two-speaker simulations of an interaction between potential tutors but did not approach single-speaker playback (Templeton, Akçay, Campbell, & Beecher, 2009), supporting the notion that social eavesdropping on interactions between adults may be important for young birds learning to sing in the wild.

In this study we test the hypothesis that young animals eavesdrop on the interactions between adults to guide the process of vocal learning. Studying a highly philopatric population of wild Savannah sparrows in eastern Canada, we used loudspeakers to simulate vocal tutors that broadcast novel sounds to young birds from the time they hatched until they left the island for autumn migration, and again when they arrived in spring to establish their first breeding territory. Half of the novel tutor songs were broadcast in an interactive context, simulating a countersinging exchange between tutors, and the other half were broadcast in a noninteractive context, simulating birds performing song bouts as stand-alone solo performances. Based on the social eavesdropping hypothesis for vocal learning, we predicted that birds would preferentially learn songs that they heard in an interactive context versus those heard in a noninteractive context. In a recently published study derived from the same experimental treatments, we showed that 30 wild Savannah sparrows from this population were able to learn songs from experimental tutors, that they passed those songs on to subsequent generations and that they preferentially learned songs heard during both their natal summer and their first breeding spring (Mennill et al., 2018). The current study addresses whether the interactive context of the simulated vocal tutors influenced the likelihood of wild birds learning specific tutor songs.

METHODS

General Methods

Between 2013 and 2018, we studied an individually marked population of Savannah sparrows at Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35′N, 66°46′W), a population well known for its high rate of natal site philopatry (Wheelwright & Mauck, 1998). This study population breeds at high densities in the grassy meadows across the island (densities of breeding adults ranged from 4.7 to 9.2 birds per ha during the study period; Woodworth, Wheelwright, Newman, & Norris, 2017). Each year, we banded all breeding adults in the central part of the island by outfitting each animal with a unique combination of coloured leg bands to facilitate identification. We monitored the behaviour of all birds, beginning with their arrival from spring migration (mid-April to mid-May), continuing throughout their breeding activities (late May to July) and concluding when birds began to depart for autumn migration (September). We mapped birds' territories, located and monitored the progress of their nests and banded their offspring using established protocols (Woodworth et al., 2017).

We collected recordings of the songs of all birds in the central part of the study site with a directional microphone (Sennheiser ME62/K6 mounted in a Telinga parabola) and a digital recorder (Marantz PMD660 or PMD661; 44.1 kHz sampling rate; 16-bit accuracy; WAV format). Recordings were collected on a daily basis between mid-April and late June of each year. In outlying parts of the study site, where focal recordings were impossible due to interference from abundant herring gulls, *Larus argentatus*, we collected recordings using automated digital recorders (Wildlife Acoustics Song Meter SM2; 44.1 kHz sampling frequency; 16-bit accuracy; WAC format). Only male Savannah sparrows produce song (Wheelwright & Rising, 2008); each male Savannah sparrow produces one song type (2% of males produce two song types) and each male's song types remain stable and consistent throughout his adult life (Mennill et al., 2018; Wheelwright et al., 2008; Williams, Levin, Norris, Newman, & Wheelwright, 2013). Therefore, the recordings we collected across the study site allowed us to build a library of the songs of all males on the island. Knowing the population-typical songs present in this population throughout the last three decades (Williams et al., 2013) and the songs of all adults on the island during each year of this study (Mennill et al., 2018), we were able to compare the songs of each young male to the population-typical songs of live tutors and the population-atypical songs of the interactive and noninteractive tutors.

Playback Apparatus

We used playback to simulate vocal tutors with songs containing distinctive acoustic elements. The playback apparatus consisted of 20 pairs of loudspeakers (modified FoxPro Scorpion speakers; power rating: 7 W) that were weatherproof (speakers were housed in weatherproof plastic containers), light-activated (a light sensor activated speakers at the first light of dawn and terminated playback with the last light of dusk) and capable of broadcasting tutor stimuli for months at a time (speakers were powered by rechargeable batteries and solar-powered batteries; Mennill et al., 2018). Each pair of speakers was separated by a 20 m stereo sound cable, so that the left channel of a stereo file could be broadcast through one loudspeaker and the right channel through another nearby loudspeaker. With this arrangement we could simulate two vocal tutors singing from two different, nearby locations; the two tutors could appear to be interacting with each other in simulated countersinging exchanges, or to be singing independently as noninteractive solo song performances. With a separation distance of 20 m between each pair of loudspeakers, this apparatus allowed us to simulate an interaction typical of two males perched near the edges of their territories, close to each other, but not yet embroiled in a fight.

Speakers were placed along the edges of birds' territories, and in small undefended spaces between territories, with a density of approximately four speakers per hectare (Fig. 1). From most

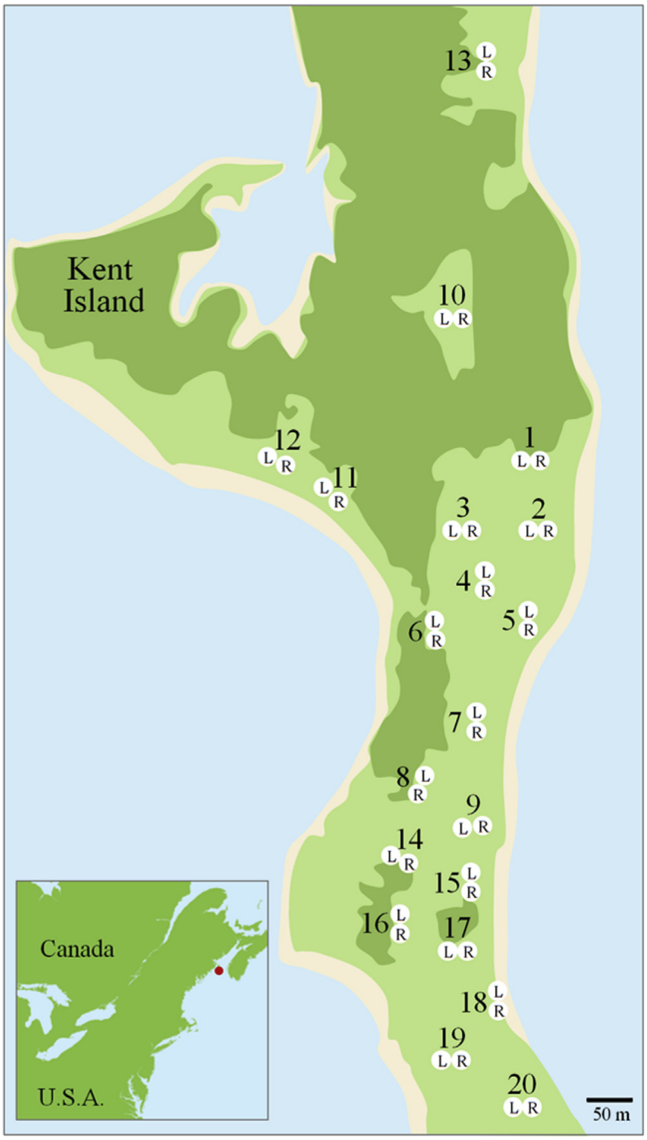

Figure 1. Map of Kent Island, New Brunswick, Canada, showing the location of 20 pairs of loudspeakers positioned within the fields on the study site (light green regions). The loudspeakers were used to simulate interactive or noninteractive tutors. Speakers were arranged in pairs so that the left (L) and right (R) channels of stereo sound files could simulate two tutors that either interacted with one another, or avoided interacting with one another. Inset map shows the location of Kent Island (red dot) in the Bay of Fundy in eastern North America.

locations on our study site, one or two pairs of speakers could be heard at a time. We designed the timing of playback so that the same simulated tutor could not be heard from more than one speaker at a time from anywhere on the study site (see Playback Stimuli below, for details). The amplitude of the speakers was set to 85 dB (measured at 1.0 m with a Caselli CEL-24X sound level meter; fast setting; C weighting), an amplitude that corresponded with our perceived amplitude of Savannah sparrows in the field and that has been used previously in studies of other sparrows (Ballentine, Searcy, & Nowicki, 2008; Searcy, Anderson, & Nowicki, 2006).

Playback Stimuli

We created tutor stimuli from sound files in the Macaulay Library of Natural Sounds (https://www.macaulaylibrary.org/) and the Borror Laboratory of Bioacoustics (https://blb.osu.edu/) using recordings of Savannah sparrows collected more than 2000 km from our study site. We selected recordings with distinctive spectrotemporal properties relative to all songs that we have recorded in our study population over the last three decades (Williams et al., 2013). We created a total of 46 simulated tutor songs that each had a distinctive acoustic signature and could be readily distinguished when viewed as spectrograms. In cases where the original recordings of tutor songs were highly similar to one another, we modified tutor songs in subtle ways by duplicating a song element or adding an element from another Savanah sparrow song (using the ‘copy’ and ‘paste’ features of Adobe Audition), by flipping the time axis of an individual song element (using the ‘reverse’ tool in Audition), or by making subtle transpositions in frequency of repeated elements (using the ‘transpose’ tool in Audition; sound spectrograms of all 46 simulated tutor songs are shown in Mennill et al., 2018).

We created playback stimuli by assembling tutor songs into 1 h stereo playback tracks. Each track featured two simulated tutors engaged in simultaneous bouts of interactive back-and-forth singing, or in alternating bouts of noninteractive independent singing (Fig. 2). The tutor stimuli were assigned randomly to an interactive or noninteractive context using a random-number generator implemented in Excel. The interactive and noninteractive stimuli were perfectly matched in terms of amplitude, duty cycle, output and broadcast time of day; the sole difference between the interactive and noninteractive stimuli was whether or not they were produced in a simulated countersinging exchange (see below).

Countersinging exchanges in songbirds often include both alternating and overlapping songs produced by the interacting animals (Mennill & Ratcliffe, 2004b; Todt & Naguib, 2000). The interactive exchanges that we created featured 92% alternating exchanges between the two simulated tutors (i.e. the song from one tutor was complete before the song from the other tutor began from the nearby speaker; the average time delay was 5.0 s between the start of one bird's song and the start of the second bird's song) and 8% overlapping exchanges (i.e. the song from one tutor began before the other tutor's song was complete). Within each 1 h block of interactive playback, each simulated tutor overlapped the other simulated tutor an equal number of times.

Between 2013 and 2015, we broadcast 10 tutor stimuli during each annual cycle (five interactive tutors, five noninteractive tutors), and between 2015 and 2018 we broadcast 18 tutor stimuli during each annual cycle (nine interactive tutors, nine noninteractive tutors), using a different set of songs in each annual cycle. Each of the 20 pairs of loudspeakers featured a different day-long playlist of 1 h playback tracks, with a change of tutors at each pair of loudspeakers during each subsequent hour (Table 1). The resident birds may have perceived our playback manipulation as though the tutors moved around the study site over the course of the day, or they may have perceived the manipulation as though multiple individuals at different locations sang the same unusual song at different times of day; in either case, the opportunity to hear songs in an interactive or noninteractive context was equivalent. By broadcasting the experimental tutors at different positions around the study site, we provided young birds on the study site with increased opportunity to hear all of the simulated tutors both while they were nestlings and fledglings, and again after they settled on territories as first-year breeders. In doing so we maximized the chance that all young birds could hear all of the experimental tutors regardless of the birds' positions on the study site. At each pair of speakers, an hour of interactive exchanges between two simulated tutors was followed by 1 h of noninteractive singing between two different simulated tutors (see Table 1). Half of the pairs of loudspeakers began the day simulating interactive tutors, and the other half noninteractive tutors. This pattern alternated across the day, so that half of the speakers were broadcasting interactive tutors and the other half were broadcasting noninteractive tutors at all times. The broadcast of each particular tutor was equally balanced across the 20 pairs of speakers, so that each tutor had the same level of song output across the study site each day. The interactive tutors were simulated to move around between loudspeakers, to interact with all other interactive tutors in all possible combinations, over the course of the day. To ensure balance, the noninteractive tutors moved around between loudspeakers in parallel fashion, appearing in all possible combinations with all other noninteractive tutors, although they were always broadcast in a noninteractive, solo context. To avoid any precedence effects, each simulated interactive tutor was simulated to produce the first song, or the second song, in an equivalent number of 1 h playback tracks across the study site.

Savannah sparrow vocal output varies with time of day, with higher output at dawn and dusk (Moran et al., 2019). We chose two levels of song output—a higher level of output at dawn and dusk, and a lower level of output for the periods between dawn and dusk—and used a song rate that was at the upper end of natural levels of song output at those two periods (Mennill et al., 2018). Between dawn and dusk, the duty cycle from each loudspeaker simulating a vocal tutor was 4 min of song followed by 16 min of silence (Fig. 2). At dawn and dusk the duty cycle of our simulated tutors was 10 min of song followed by 10 min of silence (Appendix, Fig. A1).

In summary, the playback stimuli were designed to simulate two types of tutor songs: some tutor songs were always broadcast in an interactive context and other tutor songs were always broadcast in a noninteractive context. Across all times of day and all times of year, within each 1 h block of playback, the simulated interactive tutor songs and the simulated noninteractive tutor songs had the same duty cycle and the tutor songs were matched for song rate and song amplitude. The sole difference between the interactive and noninteractive treatments was the relative timing of sounds broadcast out of the two nearby loudspeakers.

We conducted this experiment simultaneously with the study of seasonal timing of vocal learning described in Mennill et al. (2018). Our test of the eavesdropping hypothesis in the current study was

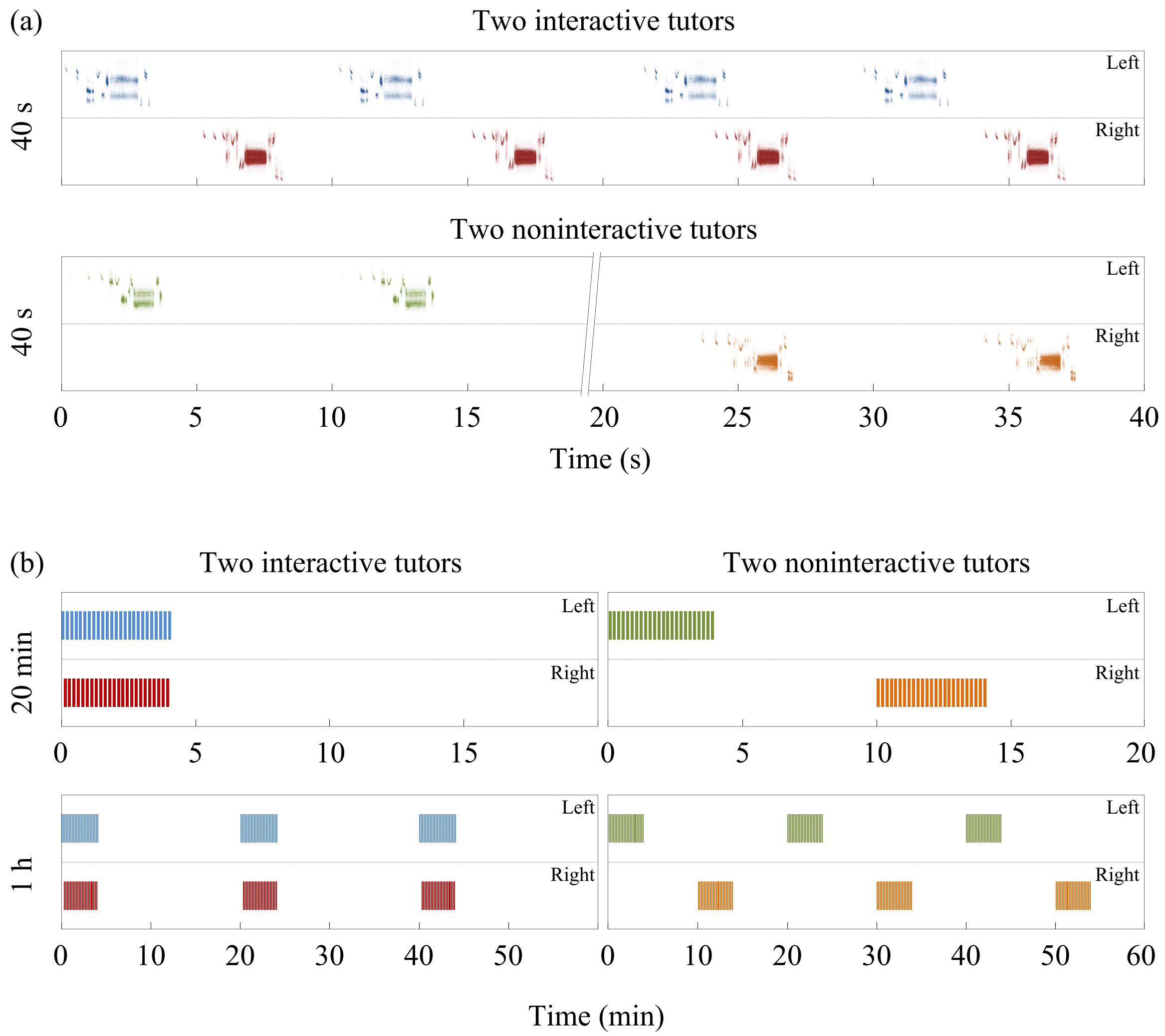

Figure 2. (a) Colour-coded sound spectrograms of playback stimuli used in an experiment designed to study eavesdropping and song learning in Savannah sparrows. The two-channel stimuli simulated two interactive tutors engaged in alternating and overlapping exchanges (blue and red tutors) or two noninteractive tutors engaged in stand-alone song performances (green and orange tutors) singing from different locations when broadcast through stereo loudspeakers. (b) Schematic representation of 20 min and 1 h of two-channel sound stimulus, where each vertical bar represents one song from each simulated tutor. Between dawn and dusk each day the simulated tutor song bouts were 4 min long (see Fig. A1 for a schematic representation of playback at dawn and dusk, when tutor song bouts were 10 min long).

embedded within the experiment described in Mennill et al. (2018) according to a balanced design (Appendix, Fig. A2).

Detecting Song Learners

We analysed recordings by visualizing songs as spectrograms using Syrinx-PC sound analysis software (J. Burt, Seattle, WA, U.S.A.). We assigned the song of each first-year male to a vocal tutor using visual comparison of spectrograms, as used in previous studies of Savannah sparrows (Wheelwright et al., 2008). This technique produces equivalent results to computation of similarity scores through sound analysis software (Williams et al., 2013). Across the five annual cycles, we detected 30 birds producing songs that matched the experimental stimuli (Mennill et al., 2018); these 30 males are the focus of the current study. It is noteworthy that birds could have learned from experimentally simulated vocal tutors or from live birds on the study site (the number of live tutors within the loudspeaker area ranged from 75 to 147 adult males across the years of the study). In addition to the 30 birds that learned songs from experimental vocal tutors, four birds produced songs they had learned from a previous year's experimentally tutored birds, and an estimated 60 birds produced songs that matched the songs of live tutors (Mennill et al., 2018; estimate based on the fact that one-third of banded nestlings learned experimentally tutored songs); these additional birds were not included in the current analysis because they did not learn songs from the interactive or noninteractive tutors.

Interactions Between Birds and Speakers

Although we broadcast the tutor songs in either interactive or noninteractive contexts, the possibility existed that live birds might have interacted differently with the interactive or noninteractive tutors. If live birds interacted more often with the noninteractive tutors than with the interactive tutors, this would have made the difference between the interactive and noninteractive treatments less apparent. To assess whether live birds interacted differently with the interactive and noninteractive tutors, we recorded the vocalizations of birds near the loudspeakers. We collected recordings with automated digital recorders (Wildlife Acoustics Song Meter SM2) placed near a subset of the speaker pairs ($N = 16$ pairs). Recordings were collected in 2015, between 0600 and 1600 hours, between June 19 and June 25 (4–10 days after playback began in that year). For each recording, we chose a 2 h period that included one 1 h block of interactive playback and one 1 h block of noninteractive playback. We chose a 2 h period that showed the lowest level of heterospecific noise or ambient noise from wind or rain. For all analyses we chose a period of daytime singing activity (between the dawn and dusk chorus); for 11 speaker pairs we analysed a period between 0600 and 0800 hours, and for five speaker pairs we analysed a period between 1400 and 1600 hours because of high noise levels during the morning recordings. Savannah sparrow song output is similar at these times of day (Moran et al., 2019). We used Syrinx-PC to annotate all songs produced by the two loudspeakers during the interaction phase and the noninteraction phase, and all songs produced by all live males in the region. We then conducted paired comparisons of each bird's songs during interactive and noninteractive phases of playback ($N = 27$ different males across the $N = 16$ speaker pairs).

To better understand the learning process in Savannah sparrows, such as any interactions that might have occurred between juvenile birds and vocal tutors, we opportunistically collected observations of juvenile birds whenever they were observed near the loudspeakers. One or more field researchers was present on the study site throughout each day during late June and July and early September of each year to collect these observations; in 2013 and 2014 two field researchers were also present throughout August.

Animal Welfare Note

This research was approved by the University of Windsor Animal Care Committee (AUPP 13–15). All bird banding was conducted by experienced bird banders with required permits from the Canadian Wildlife Service. Playback was monitored carefully to ensure it did not cause excessive stress on the subjects; in some cases where territorial animals reacted very aggressively to one loudspeaker at the annual start of the playback in June, we moved the loudspeaker several metres along the boundary with the neighbouring male, and the animals' aggressive responses declined. We ensured that our playback was within the normal level of song output of Savannah sparrows. Long-term observations of the Savannah sparrows that learned experimental tutor songs demonstrated that these animals did not exhibit different survival or different reproductive activities from birds singing population-typical song (details in Mennill et al., 2018).

Table 1
An example of the pattern of broadcast of 12 simulated vocal tutors that engaged in simulated bouts of interactive singing (in bold; tutors A, B, C, D, E, F) or simulated bouts of noninteractive singing (tutors G, H, I, J, K L) when broadcast through the left and right channels of stereo sound files

Hour of day	Speaker pair									
	1	2	3	4	5	6	7	8	9	10
1	**A vs B**	G vs H	**C vs D**	I vs J	**E vs F**	K vs L	**D vs A**	J vs G	**E vs B**	K vs H
2	L vs I	**F vs C**	G vs I	**A vs C**	H vs K	**B vs E**	J vs L	**D vs F**	G vs J	**A vs D**
3	**C vs E**	I vs K	**B vs A**	H vs G	**F vs D**	L vs J	**B vs C**	H vs I	**F vs E**	L vs K
4	H vs J	**B vs D**	K vs J	**E vs D**	L vs G	**F vs A**	K vs I	**E vs C**	I vs H	**C vs B**
5	**D vs C**	J vs I	**F vs B**	L vs H	**C vs A**	I vs G	**A vs E**	G vs K	**B vs F**	H vs L
6	K vs G	**E vs A**	J vs H	**D vs B**	I vs L	**C vs F**	G vs L	**A vs F**	J vs K	**D vs E**
7	**E vs B**	K vs H	**A vs B**	G vs J	**C vs D**	I vs J	**E vs F**	K vs L	**D vs A**	J vs G
8	G vs J	**A vs D**	I vs L	**F vs C**	G vs I	**A vs C**	H vs K	**B vs E**	J vs L	**D vs F**
9	**F vs E**	L vs K	**C vs E**	I vs K	**B vs A**	H vs G	**F vs D**	L vs J	**B vs C**	H vs I
10	I vs H	**C vs B**	H vs J	**B vs D**	K vs J	**E vs D**	L vs G	**F vs A**	K vs I	**E vs C**
11	**B vs F**	H vs L	**D vs C**	J vs I	**F vs B**	L vs H	**C vs A**	I vs G	**A vs E**	G vs K
12	J vs K	**D vs E**	K vs G	**E vs A**	J vs H	**D vs B**	L vs I	**C vs F**	G vs L	**A vs F**
13	**E vs F**	K vs L	**D vs A**	J vs G	**E vs B**	K vs H	**A vs B**	G vs H	**C vs D**	I vs J
14	H vs K	**B vs E**	J vs L	**D vs F**	G vs J	**A vs D**	L vs I	**F vs C**	G vs I	**A vs C**
15	**C vs A**	I vs G	**A vs E**	G vs K	**B vs F**	H vs L	**D vs C**	J vs I	**F vs B**	L vs H
16	L vs G	**F vs A**	K vs I	**E vs C**	I vs H	**C vs B**	H vs J	**B vs D**	K vs J	**E vs D**

The simulated tutors in each speaker pair changed over the course of each day in 1 h blocks. This particular set of stimuli were broadcast in June of 2017.

Statistics

We used a two-tailed binomial test to compare the number of birds that learned songs heard in an interactive versus a noninteractive context, comparing to an equal likelihood of learning songs from an interactive or noninteractive tutor (i.e. 0.5). Given our sample size of 30, at least 21 birds would have had to learn interactive or noninteractive songs in order to indicate a statistically significant effect at $P = 0.05$ with a two-tailed binomial test. All values are presented as means ± SE.

RESULTS

Among 30 male Savannah sparrows that learned their song from a playback-simulated vocal tutor, 13 learned songs from tutors they heard in an interactive context and 17 learned songs from tutors they heard in a noninteractive context (Fig. 3). The likelihood of learning from an interactive or noninteractive tutor was not statistically different (binomial test: $P = 0.58$). Therefore, we found no evidence of preferential learning of songs broadcast in an interactive versus noninteractive context.

Using field recordings of breeding males, we tested whether resident adult birds interacted differently with the interactive or noninteractive experimental tutors, because this could have influenced whether a noninteractive song treatment could have been perceived as interactive. At the outset of each playback period in June of each year, breeding adult male Savannah sparrows clearly responded to the playback-simulated tutors, by approaching the speakers and, in some cases, perching on the speakers and singing. Breeding males had similar levels of song output during interactive broadcasts (37.2 ± 5.8 songs/h) and noninteractive broadcasts (38.3 ± 5.8 songs/h; paired *t* test: $t_{26} = 0.18$, $N = 27$ males sampled during 1 h of paired and unpaired playback, $P = 0.86$; by comparison, daytime vocal output from the loudspeakers was 72 songs/h). Males also showed a similar propensity to overlap the songs from the tutors during interactive 1 h periods (2.3 ± 0.6 overlaps/h) and noninteractive 1 h periods (1.9 ± 0.6 overlaps/h; $t_{26} = 0.6$, $N = 27$, $P = 0.52$) and were similarly likely to be overlapped by the simulated tutors during interactive periods (2.2 ± 0.6 overlaps/h) and noninteractive periods (2.0 ± 0.6 overlaps/h; by comparison, the number of overlaps of each of the simulated tutors was 6 overlaps/h). Therefore, our field recordings show that resident birds behaved in similar fashion during playback, regardless of whether the playback loudspeakers simulated interactive tutors or noninteractive tutors, and that the simulated tutors were the dominant vocal output when compared with nearby singing birds.

We collected field observations of juvenile birds over many weeks of field research in each year of this study; we did not observe juvenile birds interacting with the loudspeakers, whether interactive or noninteractive. Juvenile Savannah sparrows behaved secretively, moving low through grasses, and spent substantial amounts of time in sheltered areas protected by shrubs and trees at the edges of the grassy nesting areas. We never observed a juvenile bird approach a loudspeaker, either during interactive or noninteractive playback, over the 6 years of this investigation.

DISCUSSION

Across five annual cycles, we tutored wild Savannah sparrows with distinctive songs presented either during interactions between two simulated adult tutors, or during stand-alone noninteractive performances. Among 30 birds that learned songs from experimental vocal tutors, less than half learned songs that they had heard in an interactive context. Therefore, contrary to our prediction based on the social eavesdropping hypothesis for vocal learning, our experiment provides evidence that wild sparrows are no more likely to learn songs that they overhear in interactions among adult tutors than they are to learn songs they overhear in a noninteractive context.

Vocal Learning Programmes

With respect to vocal interactions, there are three ways that a vocal-learning animal can learn from tutors: (1) the young animal can interact with tutors directly; (2) the young animal can eavesdrop on tutors as they interact with each other; or (3) the young animal can listen to tutors independently of any interactions. Our experimental design does not allow for meaningful interactions between young birds and tutors given that the simulated tutors were automated playback devices broadcasting looped stimuli. Our analysis of birds' responses to the speakers, and our lack of observed interactions between juvenile birds and loudspeakers in the field, also demonstrates an absence of such interactions. Therefore, direct interactions between young animals and tutors is not essential for vocal learning to take place. Our experimental results do not support the idea that eavesdropping informs tutor choice, given the birds' equivalent likelihood of learning interactive and noninteractive tutor songs. Therefore, we dismiss the second possibility. As a consequence, the third possibility seems most probable and most parsimonious; birds heard sounds produced by vocal tutors, but their learning did not appear to be guided by the interactive or noninteractive context of those tutor songs.

How, then, do wild Savannah sparrows choose which tutor to emulate as they undergo the process of vocal learning? A concurrent experiment involving these same 30 Savannah sparrows focused on the importance of the timing of vocal learning (Mennill et al., 2018). Three subsets of experimental tutor songs were broadcast during a young bird's natal summer, their first breeding spring, or during both periods (Appendix, Fig. A2), and these songs were not equally likely to be learned; no bird ever learned a tutor

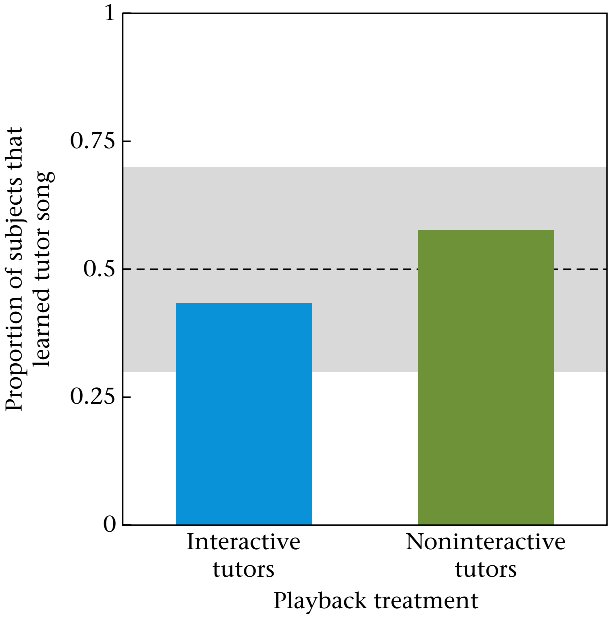

Figure 3. Proportion of Savannah sparrows that learned songs from playback-simulated vocal tutors when the tutor songs were broadcast in an interactive versus a noninteractive context ($N = 30$ birds over a 6-year period). A dashed line is shown for reference at 0.5, which is the expectation if the interactive context of tutors does not play a role in song tutor choice; the grey shaded range shows the threshold for significance at $P = 0.05$ in a two-tailed binomial test with a sample size of 30.

song unless it was heard in their natal summer, and birds overwhelmingly learned songs heard during both their natal summer and first breeding spring (Mennill et al., 2018). Although Savannah sparrows routinely produce just one song type as adults (Williams et al., 2013), early in the spring we have observed many instances of young males producing two or three different song types and then rejecting all but one song, which they retain for the remainder of their lives (Mennill et al., 2018). This process is known as overproduction followed by attrition, and has been documented in other songbirds and in humans (Nelson, 1992, 2000; Peters & Nowicki, 2017). Therefore, we propose that Savannah sparrows have a learning programme that is similar to the programme proposed in other sparrows, including song sparrows (Beecher & Akçay, 2014) and chipping sparrows (Liu & Nottebohm, 2007): young birds retain multiple songs heard during their natal summer and ultimately exclude all but one, based on events during their first breeding spring. Our ongoing research will explore the process of attrition to determine whether the social environment or acoustic environment of a young male's first spring influences the process of attrition. Perhaps eavesdropping is particularly important during that time of year, although the current experiment failed to find support for the idea that birds preferentially retain songs heard in an interactive context in both summer and spring.

The Possibility of Eavesdropping

Given the lack of preference for learning tutor songs heard in an interactive context, our experiment yielded no evidence that eavesdropping on vocal interactions informs vocal learning. An alternative perspective is that eavesdropping does inform vocal learning, but we failed to detect it due to some feature of our experimental design. First, live adult males might have engaged in vocal interactions with the loudspeakers and confounded our attempt to simulate different interactive and noninteractive contexts for eavesdroppers. If live birds interacted with the noninteractive tutors, then all of the broadcast stimuli may have appeared to have been presented in an interactive context to the ears of eavesdropping juveniles. We tested for this possibility by sampling the singing behaviour of birds near the loudspeakers and found no evidence of differences in live birds' singing behaviour in response to the interactive versus noninteractive simulated tutors. Output from the simulated vocal tutors was high compared to live birds (in the 90th percentile of output of birds during the early breeding) and remained at high levels throughout the year, even while output from live birds decreased to low levels later in the breeding season (Moran et al., 2019), so that the playback tutors were the dominant song output that could be heard by juvenile birds. Although we cannot dismiss the possibility that live birds interacted with the interactive simulated tutors, we have no observations to suggest that this was the case.

A second possibility is that our simulated vocal interactions featured no clear ‘winner’ or ‘loser’ that a prospective eavesdropper might preferentially learn from. We designed symmetrical interactions between the simulated vocal tutors, where interactive tutors sang at equal rates with an equal number of alternating exchanges and an equal number of overlapping and overlapped songs. If eavesdropping does inform vocal learning, perhaps young birds would preferentially learn songs that were overheard during an asymmetrical contest, possibly by learning the song of the individual who dominated the contest (i.e. by having higher song output; by overlapping the other tutor more often; or by singing the first or last song). Future experiments could explore this idea by tutoring birds with asymmetrical interactions, where one simulated tutor routinely dominates vocal interactions. Such an experiment might be best performed in a species where the dynamics of vocal exchanges are well resolved, such as song sparrows where repertoire matching and song-type matching are known signals of contest escalation (Searcy & Beecher, 2009). Furthermore, the interactive songs that we broadcast were not associated with a tutor who may or may not have been successful in defending a territory or attracting a mate; instead the songs came from noncorporeal birds that were not associated with a territory or mate. Perhaps eavesdropping is important when it is associated with observable success in terms of territorial rivalry or mate choice. Future experiments could explore this idea by having each particular tutor broadcast from a consistent location.

A third possibility is that our results were influenced by the very high song output of our simulated vocal tutors, or the large number of vocal tutors that we simulated. We designed playback song output to be within the 90th percentile of song output of birds early in the breeding season. With such high output over many months of playback, birds may have habituated to the simulated tutors in terms of their roles in vocal interactions or outside of vocal interactions. We also simulated a large number of vocal tutors, although it is noteworthy that a typical juvenile Savannah sparrow would be exposed to many tens of tutors, at a minimum, during its natal summer and first breeding season (our estimate is based on the territory density of 4.7–9.2 birds per ha, and our observations that young birds range across the study site after fledging, covering many hectares). Previous research that found support for the hypothesis that eavesdropping drives vocal learning of songs in an environment with a small number of vocal tutors (Beecher et al., 2007; Burt et al., 2007). Perhaps the large number of tutors that we simulated meant that birds could not keep track of which tutors were interactive and which tutors were not interactive, or perhaps when juveniles find themselves in an acoustic environment with many potential tutors, eavesdropping is not a dominant mechanism of tutor choice.

The multispeaker playback technique that we used here provides an experimental design that can be used to study other species. Our technique has many advantages, including that the experiment can be conducted with any wild animals that have reasonably high rates of philopatry, and that the experiment takes place amidst the social and environmental complexities of a natural environment. Yet our approach also has challenges: we can only estimate which tutor songs the juvenile birds were exposed to; we cannot quantify the exact length of exposure; and wild tutors may sing in response to the simulated tutors, thereby changing the dynamics of interactive and noninteractive treatments. Our approach would have been more realistic if the simulated tutors had remained fixed in one territorial position, simulating the behaviour of wild Savannah sparrows, instead of moving between loudspeakers. Using a fixed location might increase the frequency with which wild birds learn songs from simulated tutors. Finally, we note that visual cues are known to be important for vocal learning in some birds (for example, in brown-headed cowbirds, *Molothrus ater*, and zebra finches, *Taeniopygia guttata*, both nonterritorial species; Carouso-Peck & Goldstein, 2019; King, West, & Goldstein, 2005), but our experimental manipulation was solely acoustic and included no visual signals; visual eavesdropping could be involved in vocal learning for sparrows, and this idea merits further study.

Conclusion

We found no evidence that young Savannah sparrows eavesdrop on adult song tutors that always engaged in vocal interactions with other simulated tutors versus adult song tutors that never engaged in vocal interactions with other simulated tutors. Our findings stand in contrast to our predictions based on previous investigations in another sparrow species, which suggested that young birds may eavesdrop on interactions between adult tutors (Beecher et al., 2007; Burt et al., 2007; Templeton et al., 2009). Our analysis, with a large number of tutors and tutees, a long time span and a natural context of free-living territorial animals, fails to support the idea that eavesdropping plays a role in tutor choice in Savannah sparrows. Yet given the potential importance of eavesdropping on guiding the development of song, and the evidence supporting the importance of eavesdropping in previous laboratory studies of another sparrow species (Beecher et al., 2007; Burt et al., 2007), further investigations into the importance of social eavesdropping may enhance our understanding of the complex social forces that shape the development of vocal learning.

Acknowledgments

We thank the Natural Sciences and Engineering Research Council of Canada (NSERC) for grants to D.J.M., S.M.D., A.E.M.N. and D.R.N. We also thank Bowdoin Scientific Station for logistical support (this is contribution no. 275 from Bowdoin Scientific Station); S. Dillon of FoxPro Inc. for technical support; the Macaulay and Borror libraries for providing recordings used to create playback stimuli; K. Hick, K. Lukianchuk and K. McGuire for involvement in both field and laboratory components of this study; J. Burant, M. Edmonds, M. Elza, R. Hasson, H. Hess, J. Pakkala and R. Perdigao for field assistance, A. Bailey, H. Begin-Dyck, J. Bodner, K. Cavanaugh, C. Fields, A. Hensel, K. Laroia, Z. Merheb, R. Ouellette, A. Saeed, K. Schoenberger, F. Serhan, A. Rezene, R. Srour, K. Tracey and A. Wilder for assistance with sound analysis; and S. MacDougall-Shackleton, M. Beecher and an anonymous referee for insightful comments that focused our ideas and improved the manuscript.

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Appendix

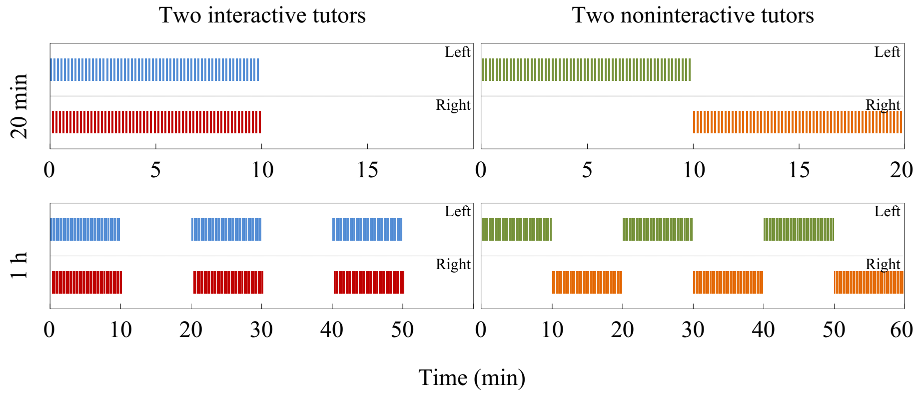

Figure A1. Schematic representation of the playback stimuli used in an experiment designed to study eavesdropping and song learning in Savannah sparrows, here showing the pattern of output at dawn and dusk, in contrast to the pattern of output between dawn and dusk shown in Fig. 2. Schematic representation shows the two-channel stimuli used to simulate two interactive tutors (blue and red) or two noninteractive tutors (green and orange) when broadcast through stereo loudspeakers, shown for 20 min (top) and 1 h (bottom), where each vertical bar represents one song from each simulated tutor. At dawn and dusk each day the simulated tutor song bouts were 10 min long (see Fig. 2 for a schematic representation of the period between dawn and dusk when tutor bouts were 4 min long).

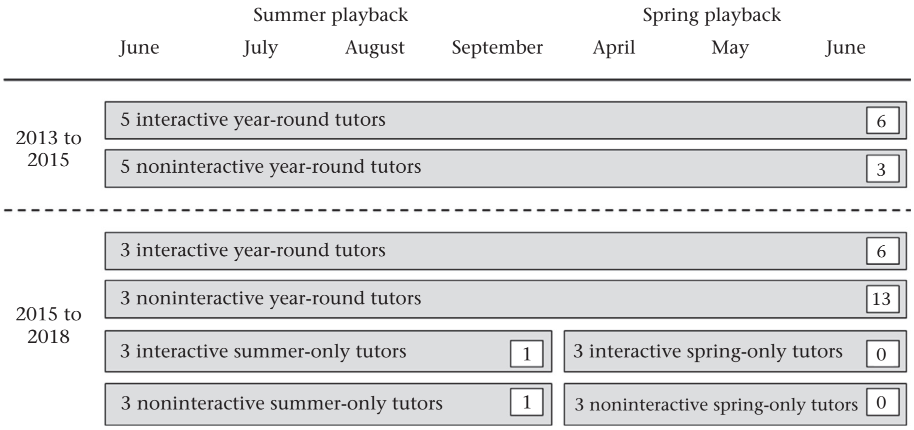

Figure A2. In the first two annual cycles of this experiment (2013 to 2014; 2014 to 2015), 10 simulated tutors were broadcast during both the summer playback period and the spring playback period, five of them in an interactive fashion and five in a noninteractive fashion. In the last three annual cycles of this experiment (2015 to 2016; 2016 to 2017; 2017 to 2018), when we were testing a hypothesis about the seasonal timing of song learning as part of a concurrent study (Mennill et al., 2018), 18 tutors were broadcast at different times of the annual cycle: some stimuli were broadcast year-round, some in summer only and some in spring only. In all years, the interactive and noninteractive stimuli were presented with equal output and amplitude, at equivalent times of day and with similar simulated patterns of movement around the study site; an equal number of interactive tutors and noninteractive tutors were audible at all times in all years. The numbers in the white boxes represent the 30 individuals who learned the stimuli presented in each experimental treatment from Mennill et al. (2018).