

Quiet violence: Savannah Sparrows respond to playback-simulated rivals using low-amplitude songs as aggressive signals

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Funding information

Natural Sciences and Engineering Research Council of Canada; University of Windsor

Editor: W. Koenig

Abstract

When animals compete over resources such as breeding territories, they often use signals to communicate their aggressive intentions. By studying which signals are associated with aggressive interactions, we gain a deeper appreciation of animal behaviour. We studied aggressive signalling in male Savannah Sparrows, *Passerculus sandwichensis*, focusing on signals that precede physical attack against territorial intruders. We simulated intruders using song playback and taxidermic models, and we determined which behaviours were associated with physical attack. Previous studies that have used this approach suggest that many species produce songs of dramatically lower amplitude, or “soft songs,” as signals of aggressive intention. Savannah Sparrows, however, are not known to produce soft songs, and therefore, they provided an interesting system for testing signals that predict attack. Of 93 playback subjects, 23 males attacked the simulated intruder and 70 did not. To our surprise, Savannah Sparrows produced soft songs, and the number of soft songs was a significant predictor of attack on the simulated intruder. Birds also showed a nonsignificant tendency to produce more “chip” calls prior to attack on the simulated intruder, whereas three other measured behaviours (aggressive calls, wing waving and passes over the model) did not predict attack. Our study contributes to the growing body of research on aggressive territorial signals and reveals that soft song is an even more widespread signal of aggression in songbirds than previously recognized.

KEYWORDS

aggressive signalling, animal communication, low-amplitude vocalizations, Savannah Sparrows, soft songs

1 | INTRODUCTION

Territorial interactions between rival animals routinely involve the threat of physical aggression. Given that aggressive encounters may result in costly physical attacks, or even death, many animals have evolved signals to facilitate communication during territorial interactions (Laidre & Johnstone, 2013; Vehrencamp, 2000). Some animals use graded signals to convey their intention to escalate or de-escalate

encounters, including high-intensity signals of threat or low-intensity signals of submission (Akçay, Tom, Campbell, & Beecher, 2013; Hof & Podos, 2013; Searcy, DuBois, Rivera-Cáceres, & Nowicki, 2013). Aggressive territorial signals have been documented in diverse animal taxa including mammals (August & Anderson, 1987; Behr, Von Knörschild, & Helversen, 2009; Clutton-Brock & Albon, 1979), birds (Searcy, Anderson, & Nowicki, 2006; Todt & Naguib, 2000), reptiles (Baird, Hardy, & Briffa, 2013), frogs (Bee, Perrill, & Owen,

2000; Reichert & Gerhardt, 2013; Wagner, 1989), fish (Korzan & Fernald, 2007; Triefenbach & Zakon, 2008), molluscs (Schnell, Smith, Hanlon, Hall, & Harcourt, 2016) and arthropods (Jonsson, Kravitz, & Heinrich, 2011; Tibbetts & Sheehan, 2011), yet only recently have animal behaviourists come to understand the function of specific types of signals within a hierarchical signalling system of escalation and de-escalation. One particular experimental protocol helps to reveal the vocal and physical signals that predict attack; it involves the presentation of a simulated territorial rival (a taxidermic model, a painted model, a mirror, or video playback) accompanied by acoustic stimuli (vocal playback; Searcy, et al., 2006). Under this experimental design, animals have the opportunity to attack the simulated rival, and we can gain insight into the function of specific signals by studying the behaviours that precede physical attack.

Animals exhibit tremendous diversity in the signals that communicate aggression (Bortosky & Mathis, 2016; Poole, 1989; Searcy & Beecher, 2009; Triefenbach & Zakon, 2008; Van Dyk & Evans, 2008). For example, cuttlefish, *Sepia apama*, indicate their intention to attack a rival when they produce particular visual displays (specifically, shovel and lateral displays; Schnell et al., 2016), and knifefish, *Apteronotus leptorhynchus*, produce particular electrical signals as predictors of attack against rivals (specifically, chirps and gradual frequency rises; Triefenbach & Zakon, 2008). Birds provide a model system for studying aggressive signals because they produce diverse acoustic signals, including elaborate and variable signals that are commonplace during territorial contests (Todt & Naguib, 2000). Aggressive acoustic signalling behaviours in birds include song matching (King & McGregor, 2016), song overlapping (Helfer & Osiejuk, 2015), variation in song rate (Baker, Wilson, & Mennill, 2012), variation in trill rate and frequency bandwidth (DuBois, Nowicki, & Searcy, 2009), production of

low-amplitude soft songs (Searcy et al., 2006) and production of non-song calls (Ballentine, Searcy, & Nowicki, 2008). The most well-studied system of aggressive contest escalation to date comes from Song Sparrows, *Melospiza melodia* (Akçay et al., 2013; Searcy & Beecher, 2009; Searcy et al., 2006). Male Song Sparrows escalate interactions by matching the songs of their rivals, or de-escalate interactions by switching to nonmatching songs (Akçay et al., 2013). They produce low-amplitude songs, also known as “soft songs,” as their most-threatening signal, which precedes an attack on a rival (Searcy et al., 2006). Subsequent investigations in several bird taxa reveal that low-amplitude signals are often used as high-threat signals (reviewed in Searcy, Akçay, Nowicki, & Beecher, 2014).

Low-amplitude signals are taxonomically widespread vocal behaviours found in birds (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998; Reichard & Welklin, 2015), mammals (Gustison & Townsend, 2015), and invertebrates (Balenger, 2015). Historically overlooked in birds, low-amplitude vocalizations (i.e., soft songs and soft calls) are now known to be used by almost half of North American birds during territorial defence, courtship displays, and alarm, begging or contact signalling (Reichard & Welklin, 2015). Thirty-one bird species are known to produce low-amplitude vocalizations as aggressive signals during displays of territorial defence in North America (Reichard & Welklin, 2015). Furthermore, males and females from six distantly related bird species produce low-amplitude vocalizations as a predictor of attack during territorial contests (Table 1), suggesting that these vocalizations are a taxonomically widespread, and possibly ancestral trait. Low-amplitude vocalizations are interesting from a communication network perspective because they may have evolved to limit the potential for eavesdropping; if low-amplitude vocalizations are associated with

TABLE 1 Summary of studies that experimentally investigated reliable predictors of attack in birds. Measured behavioural responses ranged from low-amplitude vocalizations (soft songs or soft calls), visual displays (e.g., wing waving, throat inflation), aggressive calls (e.g., hoot) to signalling rate. Behavioural responses that were the most reliable predictor of attack are marked with “support.” If behavioural responses were not found to be reliable predictor of attack, they were marked with “no support.” Behavioural responses that were not tested were marked as “not tested”

Species	Behavioural variables				Sample size	Number of attacks
	Soft vocalizations	Visual displays	Aggressive calls	Signalling rate		
Little Blue Penguin (Waas, 1991) ^b	Not tested	Not tested	Support	Not tested	40	NA
Black-capped Chickadee (Baker et al., 2012) ^{a,b}	Not tested	Not tested	Support	Support	38	21
House Wren (Barnett, Sakaluk, & Thompson, 2014) ^b	Not tested	Support	Not tested	Support	37	9
Smooth-billed Ani (Grieves, Logue, & Quinn, 2015) ^{a,b}	No support	Support	No support	Support	14	8
Bachman's Sparrow (Ali & Anderson, 2018) ^a	Support	Not tested	No support	Support	30	8
Song Sparrow (Searcy et al., 2006) ^{a,b}	Support	No support	Not tested	Not tested	95	20
Swamp Sparrow (Ballentine et al., 2008) ^{a,b}	Support	Support	No support	Not tested	31	9
Black-throated Blue Warbler (Hof & Hazlett, 2010) ^{a,b}	Support	Not tested	No support	No support	54	19
Corncrake (Rek & Osiejuk, 2011)	Support	Not tested	Not tested	No support	29	6
Brownish-flanked Bush Warbler (Xia, Liu, Alström, Wu, & Zhang, 2013) ^{a,b}	Support	Not tested	Not tested	Not tested	25	6
Savannah Sparrow (current study) ^{a,b}	Support	No support	No support	Not tested	93	23

^aStudies that followed the playback methods or modified playback methods from Searcy et al. (2006). ^bStudies that used a taxidermic model.

the highest levels of aggression, animals may benefit by minimizing the broadcast of information about their occurrence to nearby animals (Dabelsteen et al., 1998).

Songs are the most conspicuous vocalizations produced by songbirds during aggressive interactions, yet other vocalizations, such as nonsong calls, are also produced by songbirds on their breeding territories and may play a role in communicating aggression. Calls, unlike songs, are simple and short nonlearned vocalizations that serve various functions and can be sex-specific or used by both sexes (Catchpole & Slater, 2008). In past studies that investigated vocal territorial strategies in birds, researchers mainly focused on song rate, song overlapping (a time-specific response to neighbouring songs), song-type matching (a pattern-specific response to neighbouring songs), song switching (a repertoire-related response in birds with large song repertoires) or modulation of fine structural song elements as the primary aggressive signals (Burt, Campbell, & Beecher, 2001; DuBois et al., 2009; Naguib, 2005; Searcy et al., 2006). Surprisingly, few studies have investigated the use of calls as signalling strategies to escalate interactions (Ali & Anderson, 2018; Ballentine et al., 2008), despite their common occurrence during aggressive interactions in birds.

In this study, we explore aggressive signalling during territorial interactions in a temperate songbird, the Savannah Sparrow, *Passerculus sandwichensis*, by applying the experimental protocol developed by Searcy et al. (2006) involving playback and presentation of a taxidermic model to test predictors of physical attack. We chose to study Savannah Sparrows using this approach because this species, in contrast to many other sparrows, is not known to produce low-amplitude soft songs (Ballentine et al., 2008; Reichard & Anderson, 2015; Searcy et al., 2006; Wheelwright & Rising, 2008). Furthermore, despite many previous studies of Savannah Sparrow song (Wheelwright et al., 2008; Williams, Levin, Norris, Newman, & Wheelwright, 2013), we have only rudimentary information about the function of their songs during territorial interactions. Therefore, Savannah Sparrows provide an interesting system for studying predictors of physical attack during territorial song contests. The goal of our study was to explore which signals predict physical attacks during aggressive signalling interactions in Savannah Sparrows. We predicted that Savannah Sparrows would reliably indicate their intention to attack a rival during territorial interactions using singing behaviours, calling behaviours or physical behaviours.

2 | METHODS

2.1 | Study species and study site

Savannah Sparrows are migratory songbirds that live in open grasslands across North America (Wheelwright & Rising, 2008). We conducted our research at Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35'N 66°46'W), a 200-acre island in the Bay of Fundy. This island is home to a strongly philopatric population of Savannah Sparrows (Wheelwright & Mauck, 1998). The birds in this population have been studied for many decades, including

careful annual studies over the last 30 years (Williams et al., 2013; Woodworth, Mitchell, Norris, Francis, & Taylor, 2015). On an annual basis, we captured and banded birds inhabiting the central area of our study site, giving each animal a unique combination of coloured leg bands to facilitate recognition of individuals in the field. Over half of our playback subjects were individually marked animals at the centre of our study site ($n = 52$ individuals). The remaining playback subjects were unbanded males living outside the periphery of the main study area ($n = 41$ individuals). We distinguished between different unbanded individuals on the basis of their territorial position and their individually distinctive song. We mapped each bird's territory boundaries prior to playback by observing their singing behaviour and mapping the area of their song posts relative to nearby landmarks.

Male Savannah Sparrows arrive from migration in mid-April (Woodworth et al., 2016) and begin to establish breeding territories using a variety of vocal signals (Potter, 1972). Males possess a single song type, which they are thought to learn within the first 8 months of life (Wheelwright et al., 2008) and which remains constant throughout an individual's life (Williams et al., 2013). Songs are individually distinctive, with subtle differences in spectro-temporal characteristics that remain consistent through time (Williams et al., 2013). Males produce a variety of calls, including contact calls (the "chip" call), alarm calls and various "aggressive calls" that are associated with aggressive encounters (a.k.a. "buzz calls" and "hostile notes"; Gobeil, 1970; Wheelwright & Rising, 2008). In addition to their songs and calls, males also produce visual displays during territorial establishment including wing waving, flutter flights, tail raising, bill gaping and piloerection of crest feathers, and they also engage in parallel walking and bouts of physical chases (Potter, 1972; Wheelwright & Rising, 2008). The relative importance of Savannah Sparrows' diverse vocalizations and physical displays remains poorly studied.

2.2 | Playback experiment

We conducted our playback trials from mid-April to late-May 2016 between 6:00 a.m. and 12:00 p.m., a time of day when vocal interactions between territorial male Savannah Sparrows are commonplace. Prior to each playback trial, we positioned a taxidermic model of a Savannah Sparrow on top of a FoxPro Scorpion X1A loudspeaker, and we covered the model with a piece of camouflage-patterned cloth. We used four different taxidermic models of similar size and appearance, all mounted in a typical, perched posture. We alternated between these models across trials. We placed small flags on either side of the model, at distances of 1, 2 and 4 m, to help an observer estimate the distance of playback subjects from the model.

A schematic representation of our experimental protocol is provided in Figure 1, showing two phases of playback: the initial period and the experimental period. Our playback experiment followed the general procedure of Searcy et al. (2006) involving the presentation of looped playback of male song and presentation of a taxidermic model. During the initial period, we attracted birds to the playback area by playing songs while the taxidermic model was hidden under a cloth. We played songs for 1 min during the initial period, followed

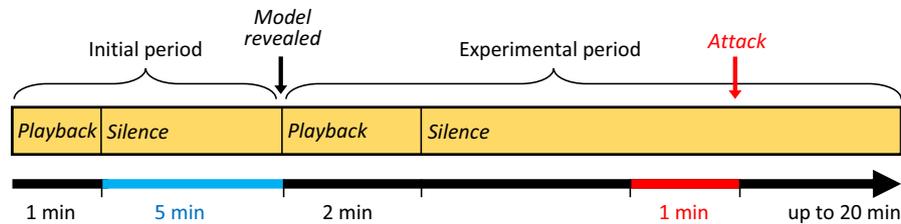


FIGURE 1 Diagram illustrating the timeline of our playback experiment, based on the experimental design of Searcy et al. (2006). There were two playback periods: an initial period and an experimental period. The initial period consisted of a playback phase (1 min) followed by a silent phase (5 min). The experimental period consisted of a playback phase (2 min) followed by a silent phase that lasted up to 20 min or until the subject attacked the taxidermic model. We focused our analysis on two time periods: the initial period and the 1 min prior to attack [Colour figure can be viewed at wileyonlinelibrary.com]

by a 5-min period of silent observation. At 5 min and 45 s, we removed the cloth from the taxidermic model by pulling a string. At 6 min, the experimental period began. During the experimental period, with the taxidermic model exposed, we played songs for 2 min followed by up to 20 min of silent observation, or until the subject attacked the taxidermic model. If the subject attacked the model, we considered the trial complete and we removed the model; this minimized stress to the playback subject and protected the models for later trials. We considered an attack to be any physical contact between the subject and the taxidermic model. Attacks were unambiguous: subjects frequently flew at the taxidermic model, often landing on top of the model and pecking at it. We aborted any trials where males in neighbouring territories also responded, and any trials that did not attract a subject during the initial 5-min period.

During the initial period, we played songs at an amplitude of 87 dB, and during the experimental period, we played songs at a slightly quieter amplitude of 78 dB. We chose these two amplitudes to match those used by Searcy et al. (2006) in their study of Song Sparrows. We confirmed the amplitude of sounds from the loudspeaker in the field with a Casella CEL-240 sound level meter (Casella CEL Inc., Buffalo, NY, USA; C-weighting; fast setting), placed 1.0 m away from the speaker.

To record birds' responses to playback, we used two microphones connected to the two channels of a Marantz PMD661 digital recorder. We placed a Sennheiser ME66/K6 microphone on the ground approximately 45 cm from the speaker and taxidermic model, to capture any low-amplitude sounds produced by the subject while near the model during playback. We mounted a Sennheiser ME66/K6 microphone on a tripod 15–20 m away from the speaker and taxidermic model, to capture broadcast songs produced by the subject. An observer (I.G.M.) narrated the behaviours of the subjects while they responded to the playback, by whispering into the second microphone while seated on the ground next to it.

2.3 | Playback stimuli

We created playback stimuli from recordings we collected from male Savannah Sparrows in 2013–2015. We collected these recordings during spontaneous bouts of singing by territorial birds, using a Marantz PMD661 digital recorder and a Sennheiser ME62/K6 microphone mounted in a Telinga parabola (sampling frequency: 44.1 kHz;

sampling rate: 16 bit; WAVE format). Each playback subject received a different playback stimulus, and we chose stimuli that were recorded from a male at least 10 territories away from the subject (≥ 700 m), ensuring that subjects were unfamiliar with the stimuli. From the original field recordings, we selected a single song with a high signal-to-noise ratio, with little or no overlapping background sound. We then manipulated this song in Audition 3.0 software (Adobe, San Jose, CA, USA): we filtered out background noise with a high-pass filter of 1,000 Hz, and we normalized all sounds to the same amplitude. We then pasted each song into a longer sound file at a rate of six songs per minute, which is a typical song rate for Savannah Sparrows (based on natural song rate from focal recordings).

2.4 | Analysis

We annotated our field recordings of the birds' playback responses in Syrinx-PC sound analysis software (J. Burt, Seattle, WA, USA), creating a second-by-second summary of the playback subjects' behaviour. We measured six aspects of each subject's behaviour: (a) number of broadcast songs, (b) number of soft songs, (c) number of "chip" calls, (d) number of aggressive calls (including both "aggressive flight calls" and "buzz calls" sensu Wheelwright & Rising, 2008), (e) number of times the bird waved its wings and (f) number of passes over the taxidermic model. We included wing waving for comparison purposes with other playback studies of sparrows (Ballentine et al., 2008; Searcy et al., 2006). We note that our ability to maintain visual contact with subjects throughout the trials was constrained by the thick grassy habitat at the study site; our estimates of wing waving are likely underestimates, because subjects sometimes disappeared from our view for brief periods during playback. This also explains why we did not include other physical behaviours like bill gaping or piloerection in our analysis.

Early in our playback trials, we found that subjects often produced low-amplitude "soft songs" (see Results); to differentiate between broadcast songs and soft songs, the field observer indicated whether each song was a "broadcast song" or "soft song." We confirmed whether each song was a broadcast or a soft song by comparing the recording from the two microphones used to record subjects' responses; soft songs were typically visible in the recording from the microphone closest the taxidermic model, but faint or even absent from the microphone positioned next to the

field observer. In several cases, we detected soft songs that were not detected by the recordist in the field, but that were identified during the process of annotation, appearing only in the channel closest to the taxidermic model. These songs could be readily assigned to the subjects because of their overall spectro-temporal properties (see Results).

We focused our analysis on the aforementioned six variables during two time periods: (a) during the first 5 min of the initial period; and (b) during 1 min prior to the time that birds attacked the model during the experimental period. We were interested in comparing birds that attacked the taxidermic model vs. birds that did not attack. To facilitate this comparison, we matched the timing of the 1 min before attack of birds that attacked the model to a corresponding 1-min period from randomly chosen nonattackers, as in previous experiments that used this protocol (Baker et al., 2012; Searcy et al., 2006).

2.5 | Statistical analysis

Our six measurement variables were not normally distributed and could not be normalized through transformation due to a preponderance of zero values. We used nonparametric Mann-Whitney U tests to compare the behaviour of attackers vs. nonattackers for each of the six response variables, and applied Bonferroni correction for multiple comparisons ($\alpha = 0.0083$ for six tests). We also followed the approach used by Ballentine et al. (2008) to analyse similar playback-response data in Swamp Sparrows; we looked at the combinations of variables that predicted attack, comparing attackers and nonattackers using a forward and backward stepwise discriminant analysis. All analyses were conducted in JMP 12.0 (SAS institute, Cary, NC, USA).

3 | RESULTS

Of 93 male Savannah Sparrows that received playback accompanied by a taxidermic model simulating a conspecific rival, 23 males

attacked the model and 70 did not. The playback subjects showed variation in their signalling behaviour, with most subjects producing broadcast songs, chip calls, aggressive calls and some subjects producing wing waving displays and passing over the taxidermic model. To our surprise, a substantial number of birds produced soft songs during the trials ($n = 39$ individuals sang soft songs), a behaviour that had not previously been described in this species (Gobeil, 1970; Reichard & Welklin, 2015; Wheelwright & Rising, 2008). Soft songs were structurally similar to broadcast songs, but included additional notes not present in broadcast songs (Figure 2).

3.1 | Initial period

During the initial period of playback, we found no significant difference between the behaviour of birds that eventually attacked the model and those that did not (Figure 3). Birds that eventually attacked the taxidermic model (hereafter “attackers”) and birds that did not (hereafter “nonattackers”) showed no significant differences in number of broadcast songs ($U = 0.22$, $p = 0.83$), soft songs ($U = 0.84$, $p = 0.40$), chips ($U = 0.87$, $p = 0.38$), aggressive calls ($U = 0.92$, $p = 0.35$), bouts of wing waving ($U = 1.0$, $p = 0.32$) or passes over the speaker ($U = -0.20$, $p = 0.84$). In the forward stepwise discriminant analysis of the six variables, aggressive calls were the only variable that discriminated between attackers and nonattackers (Wilk's $\lambda = 0.93$, $F_{1,90} = 6.92$, $p = 0.01$). A backward stepwise discriminant analysis with the same six variables converged on the same pattern, with aggressive calls as the last variable to exit the model (Wilk's $\lambda = 0.93$, $F_{1,90} = 6.92$, $p = 0.01$).

3.2 | One minute before attack

We compared behaviours between attackers and nonattackers by comparing the minute before Savannah Sparrows attacked the taxidermic model, to a random comparison minute for birds that did not

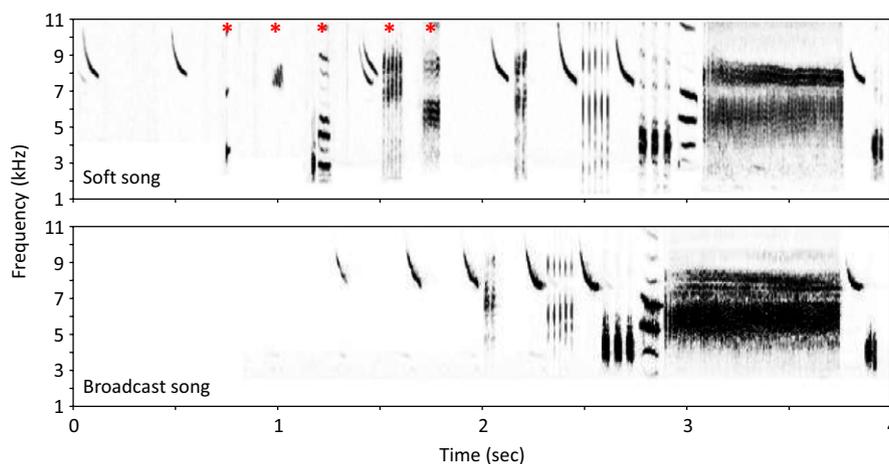
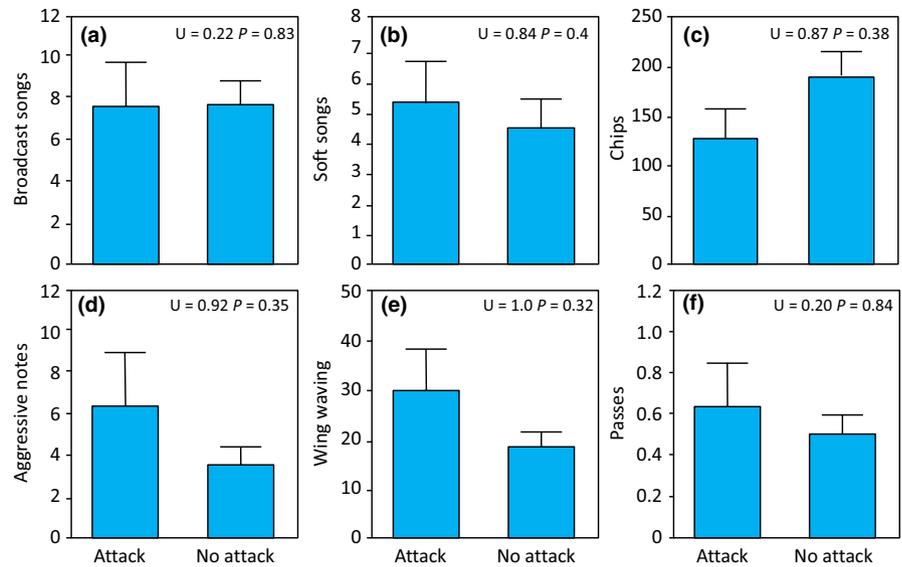


FIGURE 2 Spectrograms of an individual Savannah Sparrow's low-amplitude soft song (top) and broadcast song (bottom). Soft songs and broadcast songs showed a similar structure, but soft songs had a much lower amplitude. Soft songs could also be distinguished from broadcast songs by additional introductory notes that were absent from broadcast songs (indicated by asterisks) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Comparison of the behaviours of Savannah Sparrows that attacked a taxidermic mount vs. those that did not attack, during the 5-min initial period of the playback experiment. The behaviours, shown here as the total number (mean \pm SE), did not differ statistically between attackers and nonattackers during this initial period, for (a) broadcast songs, (b) soft songs, (c) chips, (d) aggressive notes (including both aggressive flight calls and buzzes), (e) wing waving and (f) passes over the taxidermic model [Colour figure can be viewed at wileyonlinelibrary.com]



attack. Attackers sang significantly more soft songs than nonattackers in the minute preceding attack ($U = 3.20$, $p = 0.001$), and they produced more chip calls in the minute preceding attack, although this pattern was not significant after correction for multiple comparisons ($U = 2.26$, $p = 0.02$; Figure 4). Attackers and nonattackers did not differ in the number of broadcast songs ($U = 1.63$, $p = 0.10$), aggressive calls ($U = 0.26$, $p = 0.79$), wing waves ($U = 1.51$, $p = 0.13$) or passes over the model ($U = 1.3$, $p = 0.19$; Figure 4). In the forward stepwise discriminant analysis, amongst the six variables, soft songs entered the model first, followed by number of chip calls; this model discriminated between attackers and nonattackers (Wilk's $\lambda = 0.92$, $F_{2,90} = 3.90$, $p = 0.02$). A backward stepwise discriminant analysis converged on the same pattern, with soft songs and number of

chip calls representing the last variables to exit the model (Wilk's $\lambda = 0.92$, $F_{2,90} = 3.90$, $p = 0.02$).

4 | DISCUSSION

During simulated territorial intrusion, male Savannah Sparrows showed strong aggressive responses to simulated intruders. Twenty-five per cent of males attacked a rival simulated with playback and a taxidermic model. Although soft songs have not previously been described in Savannah Sparrows, we found that territorial males regularly produced soft songs and that males that attacked sang significantly more soft songs prior to attack. In

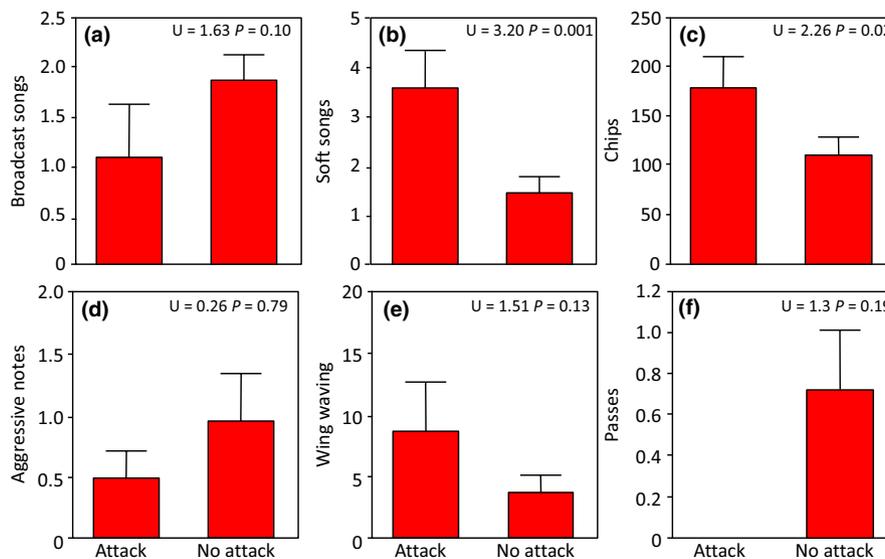


FIGURE 4 Comparison of the behaviours of Savannah Sparrows that attacked a taxidermic mount vs. those that did not attack. For nonattackers, the timing of the 1 min before to attack was matched to a corresponding 1-min period from randomly chosen attackers. Behaviours (mean number \pm SE) differed significantly between attackers and nonattackers with (b) soft songs and showed a nonsignificant tendency to vary with (c) chips, but showed no difference with the other behavioural measures: (a) broadcast songs, (d) aggressive calls (including both aggressive flight calls and buzzes), (e) wing waving and (f) passes over the taxidermic model [Colour figure can be viewed at wileyonlinelibrary.com]

addition, attackers showed a tendency to produce more chip calls compared with nonattackers prior to an attack. We conclude that soft songs, and possibly chip calls, are signals that predict attack in Savannah Sparrows.

Beginning with a study of Song Sparrows just over a decade ago by Searcy et al. (2006), 11 studies have used a playback and model presentation design to explore signals that predict attack during territorial encounters in birds, including both oscine songbirds and nonsongbirds (Table 1). Collectively, this body of work provides growing evidence that soft songs reliably predict attack across diverse species. Deterring rivals with low-amplitude vocalizations, instead of broadcast vocalizations, is an intriguing behaviour. Why do so many different species lower the amplitude of their songs during aggressive territorial interactions? One compelling explanation is the eavesdropping avoidance hypothesis (Dabelsteen et al., 1998), which proposes that individuals sing softly to avoid social eavesdropping by conspecific males or females, or interceptive eavesdropping by predators (McGregor, 1993; Searcy & Yasukawa, 2016). Eavesdroppers can impose high costs on signallers, in the case of both social eavesdropping (Mennill, Boag, & Ratcliffe, 2002) and interceptive eavesdropping (Randall & Matocq, 1997). Two studies have tested the influence of predators on the amplitude of male songs (Akçay, Clay, Campbell, & Beecher, 2016; Searcy & Nowicki, 2006), and both showed that under higher risk of predation, birds do not increase their soft song output. Although more evidence is needed, these results suggest that eavesdropping predators do not pressure birds to sing softly. Similarly, one study tested whether eavesdropping males pressure fighting males to lower their song amplitude during dyadic interactions (Searcy & Nowicki, 2006). In this study, more males intruded on territories when soft songs were sung compared to when songs were broadcast, which contradicts the eavesdropping hypothesis. Males may lower song amplitude to avoid eavesdropping by conspecific females (Dabelsteen, 2005; Vargas-Castro, Sandoval, & Searcy, 2017); to date, no experimental studies have investigated the role of females in the evolution of soft songs.

A second compelling explanation for the production of soft songs by males during aggressive territorial interactions comes from the readiness hypothesis (Akçay, Tom, Holmes, Campbell, & Beecher, 2011). When intruders invade another male's territory, territorial males may benefit by following the intruder at a close distance to visually track them. When singing loudly, however, males often angle their head backward, and this may not allow for visual tracking. Therefore, males may be physically constrained to sing softly in the presence of a rival, to keep track of his whereabouts. Savannah Sparrows are known to have preferred singing perches (Wheelwright & Rising, 2008) on which they have been observed to raise their bill when broadcasting their songs (Clark, 1976; pers. obs.). During our playback experiment, males that sang soft songs seemed to maintain a closed bill and did not tilt their head back while on the ground near the taxidermic model. These observations are consistent with the idea that visual tracking of territorial intruders may constrain males to signal softly.

If soft songs are aggressive signals that predict attack against a rival animal, how do animals maintain an honest signalling system, when a territorial animal could easily "bluff" by producing soft songs even in the absence of their willingness to escalate a territorial interaction? Historically, the honesty of vocal signals was a topic of controversy because aggressive vocal signals were thought to be easy-to-bluff due to their low production cost (Maynard Smith, 1982). In fact, vocal signals can honestly signal aggressive intentions if receivers retaliate against the animals producing aggressive signals (Anderson, Searcy, Hughes, & Nowicki, 2012; Enquist, 1985; Vehrencamp, 2000) or if receivers recognize their bluffing rivals based on past interactions (Laidre, 2005; Van Rhijn & Vodegel, 1980). Under both scenarios, receivers ensure the honesty of aggressive signals by imposing a receiver-retaliation cost on the signallers (Anderson et al., 2012; Enquist, 1985; Vehrencamp, 2000). Future research can develop a deeper understanding of receiver-retaliation costs by adopting a receiver perspective (*sensu* Searcy & Beecher, 2009) using playback simulating a territorial rival producing broadcast song vs. soft song; soft songs should be expected to incite more aggressive reactions.

In addition to songs, calls play a central role during social interactions in birds. Many avian studies that explore acoustic signals during the breeding season focus on songs, but rarely explore calls. Calls were found to be a good predictor of attack in Black-capped Chickadees (Baker et al., 2012) but calls were not good predictor of attack in other studies including Swamp Sparrows (Ballentine et al., 2008), Bachman's Sparrows (Ali & Anderson, 2018) and Black-throated Blue Warblers (Hof & Hazlett, 2010). In our study, chip calls showed a relationship with likelihood of attack, but this relationship was not significant after correction for multiple comparisons. Given that Savannah Sparrows also produce chip calls during nonterritorial interactions and given that they are also produced by females (Wheelwright & Rising, 2008), chip calls may not be a reliable predictor of attack. Future research could investigate whether chip calls differ from soft songs in their functions by focusing on the rate of chip calls during territorial contexts, or through additional playback experiments.

In conclusion, our results show that Savannah Sparrows produce significantly more low-amplitude soft songs before attacking a territorial rival, and tend to produce more chip calls before attacking a rival. Our findings contribute to the growing body of work revealing that many birds rely on low-amplitude aggressive signals to communicate aggression. Future research should focus on testing the hypotheses that attempt to explain the use of low-amplitude vocalizations, as well as elucidating the hierarchical signalling models by investigating low-threat signals that may allow birds to de-escalate interactions. In addition, other signals such as song frequency, song length, song structural elements and even behavioural or visual displays may act as predictors of attack and merit further investigation. Future studies could also target the structural differences between soft songs and broadcast songs, as some key elements of soft songs may indicate aggressiveness. Exploring aggressive signals across a wide array of animals can expand our understanding of animal communication and provide insight into how animals mediate aggressive interactions.

ACKNOWLEDGEMENTS

For logistical support, we are indebted to the Bowdoin Scientific Station; this study represents contribution number 272 from the Bowdoin Scientific Station. For field assistance, we thank K. Hick, K. Lukianchuk and B. Woodworth. For financial support, we thank the Natural Sciences and Engineering Research Council of Canada (NSERC) for their ongoing support to SMD, AEM, DRN and DJM. This research was approved by the University of Windsor Animal Care Committee (AUPP 16-11).

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How to cite this article: Moran IG, Doucet SM, Newman AEM, et al. Quiet violence: Savannah Sparrows respond to playback-simulated rivals using low-amplitude songs as aggressive signals. *Ethology*. 2018;124:724–732. <https://doi.org/10.1111/eth.12805>