



## Original Article

## The sparrow and the hawk: aggressive signaling under risk of predation

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Eavesdropping by predators imposes a major cost on signalers, which in turn have evolved a number of strategies to deal with this cost. These strategies however, have not been well studied in the context of aggressive signaling. Here, we report an experiment on male song sparrows (*Melospiza melodia*) in which we experimentally increased the perceived predation risk by playing Cooper's hawk (*Accipiter cooperi*) calls or control Northern flicker (*Colaptes auratus*) calls in the midst of a simulated conspecific territorial intrusion and assessed the change in signaling strategies. We found that song sparrows clearly discriminated between the hawk call and the flicker call. Specifically, subjects decreased number of songs and wing wave displays (a visual signal of aggressive intent) and increased alarm calling during the hawk playback. However, the change in signaling behaviors did not persist when the simulated intruder resumed his challenge, despite the fact that the subjects were still alarmed as indicated by high rates of alarm calling. Additionally, we found no evidence for the eavesdropping avoidance hypothesis as an explanation for the low amplitude of soft song, the most reliable signal of aggression in this species. These results suggest that male song sparrows flexibly adjust their signaling effort in response to both the predation risk and the need to defend their territory against an intruder.

**Key words:** communication networks, eavesdropping, predation, song sparrows, threat signals.

## INTRODUCTION

Animal communication occurs in a network of signalers and receivers, the latter containing both “intended” and “unintended” receivers, that is, eavesdroppers (McGregor 2005). The presence of multiple receivers often exerts varying and sometimes opposing selective forces that shape signal structure and signaling behaviors. A well-known example is the field cricket song used by males to attract females but which is also eavesdropped on by parasitoid flies: Louder songs attract not only more females but also more parasitoids (Cade 1975), and in highly parasitized areas, males are in the process of losing their advertisement song altogether (Zuk et al. 2006).

One of the best-studied contexts concerns the effects of eavesdropping predators and the cost they exert (Magnhagen 1991). Predators can eavesdrop on both vocal and visual signals and animals have evolved several strategies to deal with predation risk while signaling, such as adjusting their signaling locations (Duncan and Bednekoff 2006; Møller et al. 2008), decreasing signaling rates (Schmidt and Belinsky 2013), and behaving generally more cautiously (Hedrick 2000).

Predation risk is elevated during intense aggressive interactions in which the opponents are likely to attract the attention of predators with aggressive signals while their own attention is trained on their opponent (Jakobsson et al. 1995). One solution would be to refrain from signaling in aggressive interactions but if signals can resolve a dispute without resort to even riskier fights, not signaling could be yet more costly (Logue et al. 2010). Therefore, signals used during aggressive interactions should evolve in a manner to decrease the likelihood of detection by predators. Decreasing the amplitude of acoustic signals when close to the intended receiver for instance would limit the detection of these signals by more distant eavesdropping predators.

“Soft song” in songbirds is a good candidate for a signal that has evolved to function as an aggressive signal while minimizing predation risk. Although most studies of bird song have focused on the loud broadcast songs, many species also have low amplitude songs (Dabelsteen et al. 1998; Reichard and Anderson 2015). Recent studies in several species found that low amplitude song called soft or quiet song is the most reliable signal to predict attack on a taxidermic model of a conspecific (see review in Akçay et al. 2015). This finding presents a puzzle from the perspective of costly signaling theory which predicts that reliable signals are expected to be costly to cheat (Maynard Smith and Harper 2003; Searcy and

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Nowicki 2005). Given that singing in general is energetically cheap and the low amplitude of soft song will make the song marginally less costly to produce (Zollinger and Brumm 2015), soft song does not appear to fit that prediction. Although a few studies have suggested a social cost for soft song in the form of increased risk of retaliation by receivers, which can explain why soft song is reliable (Rek and Osiejuk 2011; Anderson et al. 2012; Templeton et al. 2012), this social cost does not explain why soft song is soft as it could apply equally well to loud song (Akçay et al. 2015).

One hypothesis for why birds sing soft song instead of their normal loud (broadcast) song to reliably signal their aggressive intent is that this reduces the risk of eavesdropping by predators (Dabelsteen et al. 1998; Akçay et al. 2015). There is good evidence that loud broadcast song is costly in terms of predation which is in line with this hypothesis (Mougeot and Bretagnolle 2000; Hale 2004; Lima 2009). There is, however, no direct evidence yet that soft song is adaptive in avoiding eavesdropping and that birds strategically modify the amplitude of their song when predation risk is high (Akçay and Beecher 2012; Akçay et al. 2015). To the best of our knowledge, there has been only a single test of the idea that soft song is adaptive in avoiding eavesdropping by predators (Searcy and Nowicki 2006). In that experiment with song sparrows, Searcy and Nowicki (2006) simulated the presence of a predator by playing song sparrow alarm calls (called “high chips”; Nice 1943) during a simulated intrusion by a conspecific male, but the presence of alarm calls actually led to an increase in the proportion of all songs sung by subjects that were loud sung by the subjects. Thus, the results of this experiment did not support the eavesdropping avoidance hypothesis.

Here, we report an experiment that asks whether males defending their territory against a simulated intruder strategically adjust their signaling behavior in response to a simulated increase in predation risk. We used song sparrows, a North American songbird, with a well-studied signaling system to signal aggressive intent to other conspecifics. This signaling system contains 2 close range signals that have been found to be reliable predictors of attack on a taxidermic mount: soft songs (Searcy et al. 2006) and wing waves (rapid fluttering of the wings without taking off; Akçay et al. 2013). Song sparrows also sing loud broadcast song during aggressive interactions, although these loud songs do not predict attack (Searcy et al. 2014).

In the present experiment, we first staged a brief simulated intrusion by a conspecific male using playback of conspecific song from inside the territory of the subject. This was followed by a short period of heterospecific playback from a nearby tree when we played either Cooper’s hawk (*Accipiter cooperi*) or northern flicker (*Colaptes auratus*) calls to simulate the presence of the respective species in the vicinity. We chose Cooper’s hawks because they are the primary predators of song sparrows in our field site in Washington state (Akçay et al. 2012), and northern flickers as a control because they are common nonpredatory (for song sparrows) birds at our site and their calls are quite similar in cadence, length, and structure to the Cooper’s hawk calls (Figure 1). We reasoned that the simulated presence of a Cooper’s hawk nearby through playback of calls should therefore increase the perceived risk by the sparrow and thus change his signaling behaviors. The heterospecific playback period was followed by a second period of conspecific simulated intrusion at the same location as in the first period. If the sparrows are able to recognize the Cooper’s hawk calls as belonging to a predator and are able to strategically adjust their signaling behaviors, they should decrease the signals that are more risky to

produce. Thus, we expect decreases in the loud songs under predation risk compared with control condition but either an increase or no decrease in soft song if this latter signal is adapted to avoid eavesdropping. These differences should be seen both during the heterospecific playback and should persist afterwards in the second conspecific playback periods. Finally, we also quantified the amount of time birds spent alarm calling (high chipping). Alarm calls in song sparrows are high frequency chips (around 10 kHz, Figure 1c) that are given commonly in response to predators (both aerial and terrestrial) and are likely hard to localize for the predators. The function of alarm calls is not clear at this point, but the most likely function is alarming the mate and/or offspring of the caller. We therefore predicted that alarm calls should increase during and after the hawk playbacks compared with flicker playbacks.

## METHODS

### Study site and subjects

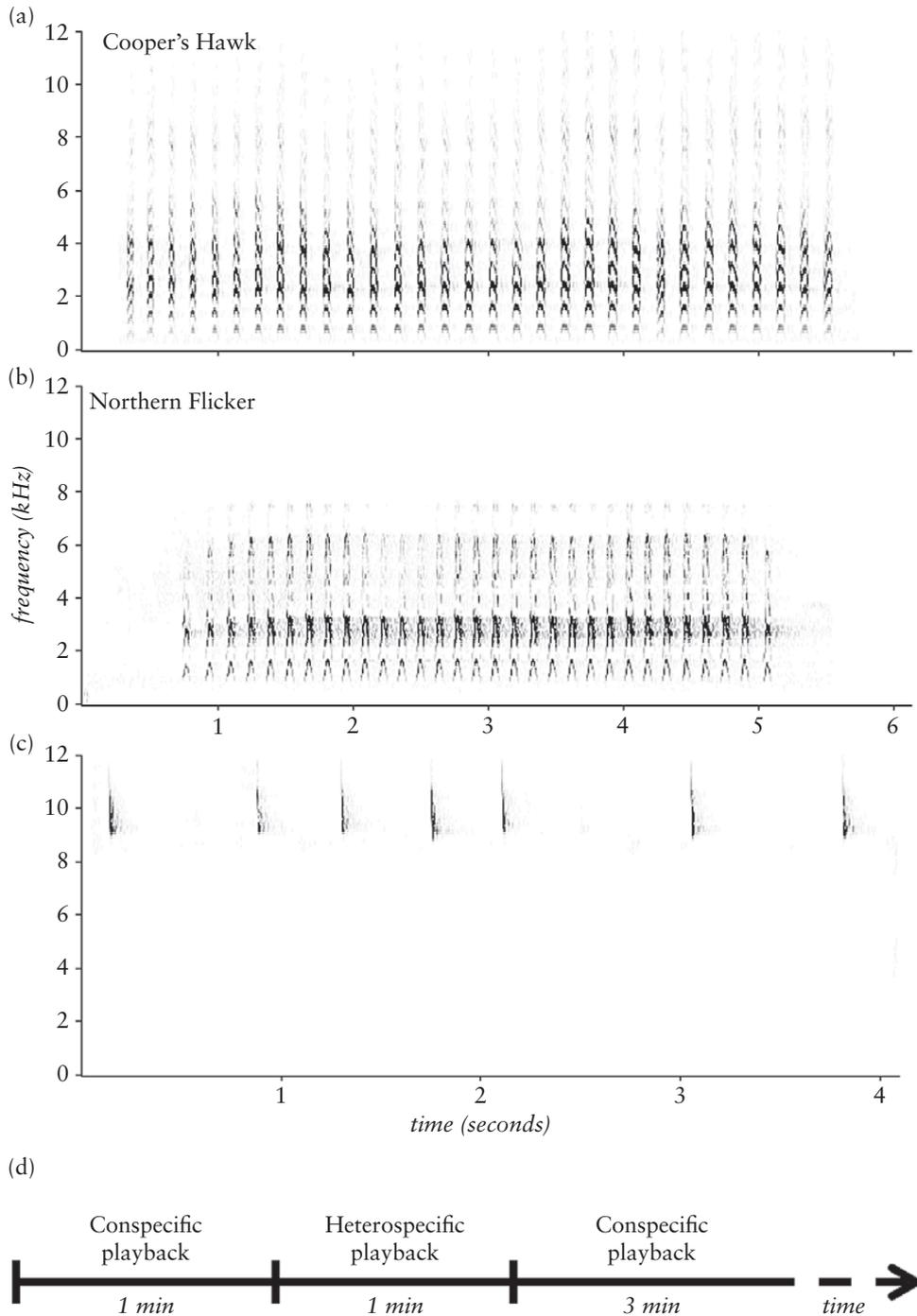
We studied song sparrows in Discovery Park, Seattle, WA. Subjects were 22 males that held territories in Spring 2015. Each male was banded with 3 color bands and a metal US Fish and Wildlife Service band as part of our ongoing long-term field study (Beecher 2008). We recorded the song repertoire of each bird using Marantz PMD 660 Digital solid state recorders and Sennheiser ME-66/K6 directional microphones to make stimulus files.

### Stimuli and procedure

For conspecific playbacks, we used a single song type from each male’s own repertoire (self-song). Extensive evidence suggests that song sparrows respond to self-song in the same way as they respond to a stranger song (e.g., Searcy et al. 1982) and using a song from each male’s own repertoire controls for the familiarity of the stimulus song. We selected a high-quality rendition of a song type at random and created a 10-s stimulus tape by adding silence at the end of the song using the software *Syrinx* (John Burt, Seattle, WA; [www.syrinxpc.com](http://www.syrinxpc.com)). Each subject was tested once with hawk playback and once with flicker playback during the heterospecific playback condition in a within-subject design. The 2 trials were carried out on consecutive days and the order (hawk or flicker) was counter-balanced.

For heterospecific playbacks, we used recordings from Macaulay Library at Cornell Lab of Ornithology, Borror Library at the Ohio State University, and the website *xeno-canto* ([www.xeno-canto.org](http://www.xeno-canto.org)). The recording IDs are given in the [Supplementary Materials](#). We made 13 flicker and 12 hawk tapes from 10 and 12 individual recordings, respectively. We used 9 flicker and 10 hawk tapes twice and the rest of the tapes once. The hawk and flicker stimuli lasted on average (standard deviation) 4.65 (1.11) and 4.72 (1.02) s, respectively; unpaired  $t(23) = 0.27$ ,  $P = 0.79$ . We added silence to these stimulus tapes to create 15-s tapes.

The playback protocol was as follows: 2 or 3 observers set up 2 speakers inside the territory of the focal male, one at approximately the center of the territory and another 15 m away from the first one. The first speaker (xMini) was connected to an mp3 player with a 20-m cable, whereas the second speaker (VicTsing) was a wireless speaker connected to an iPod (Apple Inc.) via Bluetooth and was hung as high as the observer could reach inside a tree. The mp3 player was responsible for the conspecific playback and the iPod was responsible for the heterospecific playback, and each was operated by a different observer. Both speakers played calls at



**Figure 1**

Example sonograms of Cooper's hawk (a), Northern flicker calls (b), and a song sparrow alarm calling bout (i.e., high chipping; c). Panel (d) depicts the timeline of the experiment. Note that the 30-s gaps in between periods are not shown.

approximately 80-db SPL measured at 1 m (Radio Shack 33-2055 sound meter).

Figure 1 shows the timeline of the experiment. We started each trial by playing the self-song of the focal male to lure him in and obtain a baseline response. We continued this first playback period for 1 min after the first response (sighting or song) of the focal male. We then carried out the heterospecific (hawk or flicker) playback. The heterospecific playback was repeated 4 times at a rate of one call per 15s. We reasoned that a calling hawk is not hunting and

therefore not likely to be a direct threat, but a silent hawk whose presence is known may be perceived as a threat. We therefore kept the heterospecific playback short to simulate the presence of the hawk (or flicker) who then may have remained in the area. After the heterospecific playback, we resumed the simulated intrusion by the conspecific for 3 min at the initial location (the conspecific playback was silent during the heterospecific playback period). The conspecific playbacks were presented at a rate of 1 song every 10s. About 30s elapsed between each period.

## Response measures

All trials were recorded using the same equipment as above with 1 observer narrating the entire trial by noting every flight (along with the distance to the speaker), song, wing waves, and bouts of high chipping that are alarm calls given by song sparrows (Nice 1943). One observer (C.A.) also classified each song as soft or loud in the field during the conspecific playback periods. Classification of song as loud or soft by ear, by an experienced observer, has been found to produce a reliable cutoff of the continuous distribution of song amplitude in song sparrow (Anderson et al. 2008); this criterion has been used in experimental work in several different species (e.g., Ballentine et al. 2008; Hof and Hazlett 2010). Because we were interested in the differences in the bird's use of loud versus soft songs, it was crucial that the observer making loud/soft determination be blind with respect to the condition. We achieved this by having this observer put on headphones playing loud music (Cuban Salsa) during the heterospecific playback. The observer kept following the subject and narrating the trial during this period; however, no loud/soft classifications were made for the heterospecific playback period because the blind observer could not hear the bird and the other observers were not blind to the treatment.

From the trial narrations, we extracted the following information for each period separately: rate of flights, proportion of time spent within 5 m of the conspecific playback speaker, rate of soft and loud songs (for conspecific playback periods), rate of all songs (for heterospecific playback period), rate of wing waves, and duration of high chipping bouts (high chipping is an alarm call). High chipping bouts were defined as consecutive high chips that were not more than 5 s apart from each other. We calculated the duration of the high chipping bouts as proportion of the total duration for each period.

## Data analysis

We first assessed whether birds discriminated between the heterospecific calls by comparing the rate of all songs (soft plus loud), wing waves, flights, and proportion of time spent high chipping during the heterospecific playbacks, using Wilcoxon signed-rank tests due to the non-normal distribution of these response variables.

Our main interest then was to ask whether the intervening heterospecific playback lead the changes in signaling behaviors from the first to second conspecific playback periods. We therefore took for each response measure the difference in rates or proportions during the first and last conspecific playback periods (i.e., before and after the heterospecific playback). All difference scores were normally distributed with the exception of change in high chipping. Thus, we used Wilcoxon signed-rank test for change in high chipping and paired *t*-tests for the rest of the comparisons.

## RESULTS

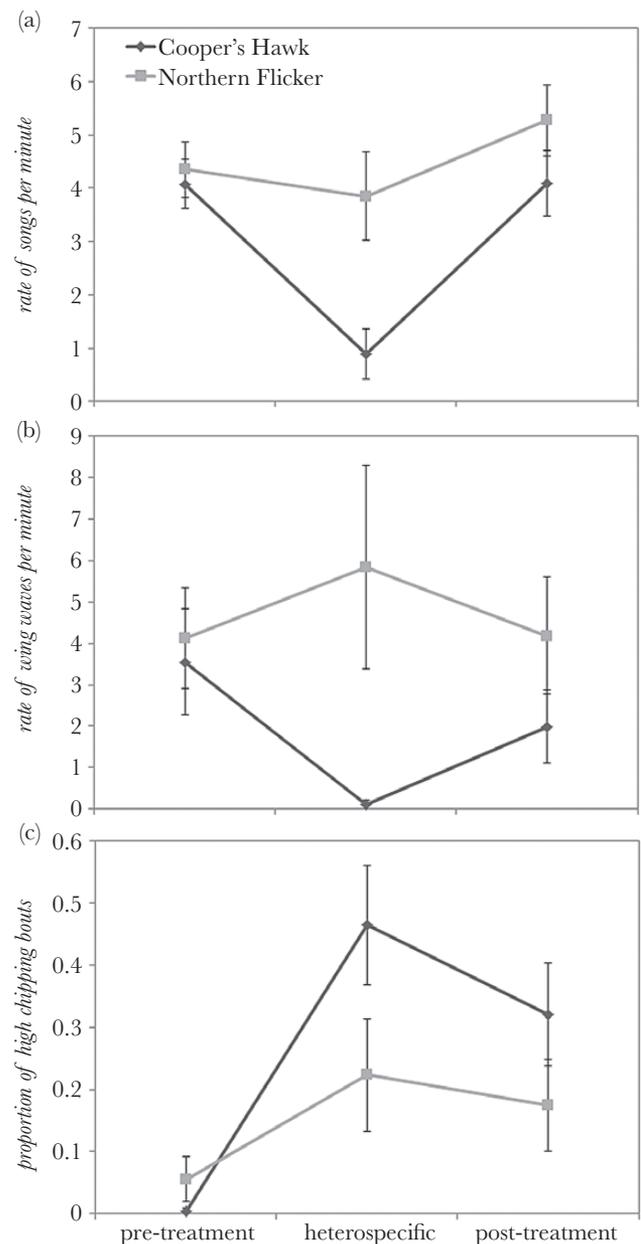
During the heterospecific playback, song sparrows sang significantly fewer songs during hawk playbacks than during flicker playbacks (Wilcoxon signed-rank test,  $Z = 3.045$ ,  $P = 0.002$ ,  $n = 22$ , Figure 2a), gave fewer wing waves ( $Z = 2.20$ ,  $P = 0.028$ ,  $n = 22$ , Figure 2b), and spent more time alarm calling using high chips ( $Z = 2.22$ ,  $P = 0.026$ ,  $n = 22$ , Figure 2c). The rate of flights did not differ between the 2 conditions during the heterospecific playback ( $Z = 0.79$ ,  $P = 0.43$ ,  $n = 22$ ).

Comparing the difference scores in loud songs (between the first and last conspecific playback), we found no significant effect of the

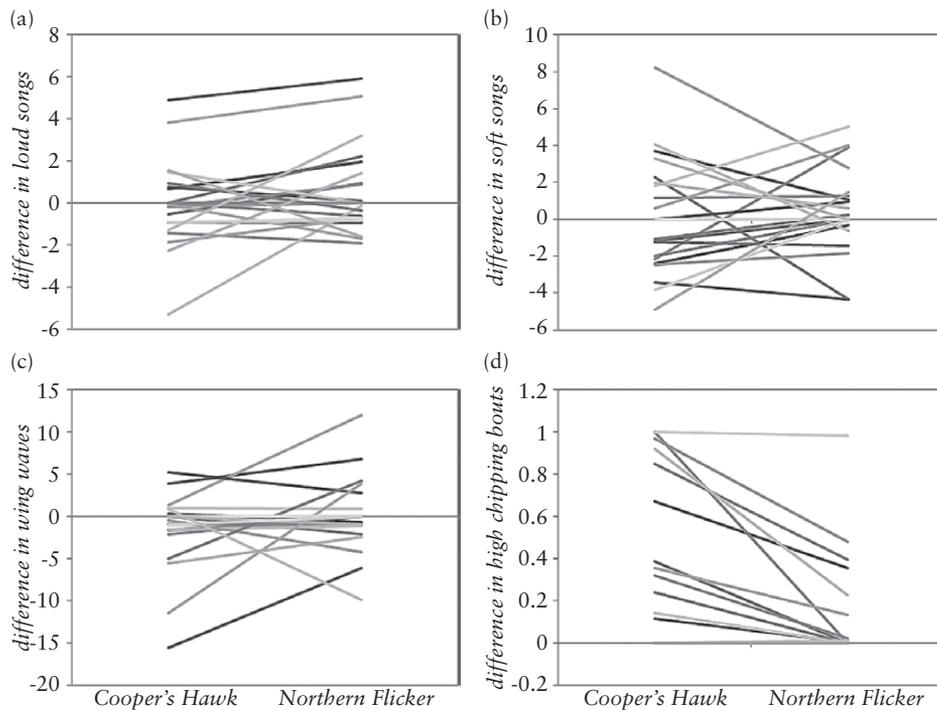
heterospecific playback ( $t_{21} = 1.51$ ,  $P = 0.15$ , Figure 3a). Similarly there was no significant effect in difference scores in soft songs ( $t_{21} = 0.36$ ,  $P = 0.71$ , Figure 3b) or wing waves ( $t_{21} = 1.37$ ,  $P = 0.19$ , Figure 3c). The heterospecific playbacks, however, had a highly significant effect on the change in proportion of time spent high chipping, with more high chipping continuing after hawk playback ( $Z = 3.11$ ,  $P = 0.002$ ,  $n = 22$ , Figure 3d). Finally, treatment did not have an effect on change in rate of flights ( $t_{21} = 0.33$ ,  $P = 0.75$ ) or proportion spent within 5 m, although the latter approached significance ( $t_{21} = 2.01$ ,  $P = 0.058$ ).

## DISCUSSION

In the present study, we found clear evidence that song sparrows are able to recognize one of their main predators, the Cooper's



**Figure 2** Rates of all songs (soft+ loud; a), wing waves (b), and proportion of time spent high chipping (c) across the 3 periods of the experiment. The error bars denote 1 standard error.



**Figure 3**

Change in rates of loud songs (a), soft songs (b), wing waves (c), and proportion of time spent high chipping (d) during the conspecific playback periods before and after the heterospecific playback. Each line represents an individual subject.

hawk from their calls, and strategically adjust their signaling behavior during an aggressive interaction, as evidenced by a reduction of singing and wing waves and an increase in high chipping alarm calls during the heterospecific playback. The changes in behavior would seem to be an adaptive response to the perceived increase in risk of predation brought about by the presence of the Cooper's hawk, as both the song and wing waves (a visual signal) likely makes the signaler more detectable to eavesdroppers (Peake 2005). Interestingly, we found no difference during the heterospecific playbacks in the rate of flights. This is likely due to the fact that flight rates were already low (on average about 1 flight during the heterospecific playback period), and several of the birds flew for cover during the hawk playbacks.

The significant changes in signaling behavior during the heterospecific playbacks add to a growing body of evidence that show that signalers are able to assess the risk of predation and adjust their signaling behaviors accordingly (Mougeot and Bretagnolle 2000; Lima 2009; Schmidt and Belinsky 2013). However, despite the fact that the song sparrows recognized the hawk calls which increased their perception of the risk of predation and were able to adjust their behavior accordingly, these changes did not persist during the second conspecific playback period. Instead, males rapidly resumed singing both loud and soft songs and giving wing waves when the conspecific playback was restarted. This is in contrast to the experiment by Schmidt and Belinsky (2013) who found that the entire dusk chorus of veeries was affected by a rather short owl playback (about 1.5-min playback over 30-min period).

It is unlikely that this failure to find a persistent effect on signaling was due to limited memory, given the fact that one behavior that is most directly indicative of the level of alarm, high chipping, did persist into the second playback following hawk playback as we predicted. Rather, it appears that the renewed challenge from

the simulated intruder is enough to make the signaling behaviors recover even under increased risk of predation. It is also worth noting that the veery experiment was carried out during the dusk chorus when the vocal detection of a nocturnal predator may be perceived as a higher increase in predation risk compared with our manipulation simulating the presence of an unseen daytime predator in broad daylight. Therefore on the whole, the trade-off faced by our song sparrows in the decision to signal or not may have been rather different than the trade-off faced by the veeries in the Schmidt and Belinsky (2013) experiment.

### Soft song as an adaptation to avoid eavesdropping

Our experiment was also designed to test an adaptive hypothesis of soft song, namely that its reduced amplitude has evolved to decrease the risk of being intercepted by predators during an intense interaction with an intruder (Dabelsteen et al. 1998). The hypothesis implies that loud songs are prone to interception, as other studies have found (Mougeot and Bretagnolle 2000; Hale 2004). Thus, under increased risk of predation, soft song use should increase and loud song use should decrease. Our results failed to support this prediction: We found no differences in change in either loud song or soft song between the 2 conspecific playback periods. Given that the strongest effect of heterospecific playback was during the heterospecific playback period itself, it could be argued that perhaps during that period the soft song use increased proportionally. Although we did not classify songs in the field as soft and loud song, it is worth noting that during the heterospecific playback period only 5 subjects sang any songs in Cooper's hawk trials compared with 14 in the northern flicker trials (out of 22 subjects), despite the fact that subjects sang at least 1 song during the first conspecific playback period at every trial except one, a northern flicker trial.

Thus, the main effect of the heterospecific playback period seems to be the cessation of most if not all singing activity.

The current experiment is, to the best of our knowledge, only the second explicit test of the hypothesis that soft song is an adaptation for avoiding being eavesdropped on, and also the second failure to support that hypothesis. In the first attempt, Searcy and Nowicki (2006) simulated increased risk of predation through playback of alarm calls (high chipping) concurrent with conspecific playback to male song sparrows. They found the opposite of what the eavesdropping avoidance hypothesis predicted: In the condition with added alarm calls, the proportion of songs that were soft actually decreased compared with the control condition.

The experiment by Searcy and Nowicki (2006) has been criticized for simulating the presence of a predator only indirectly (Lima 2009). The presence of a second speaker playing song sparrow vocalizations in the form of alarm calls in one condition but not the other also may have influenced the outcome. The present experiment represents an improvement, in that we avoided the concurrent presentation of the conspecific playback with the simulation of the predator (or flicker), and we simulated the predator more directly using hawk vocalizations. It is possible that we may have gotten more persistent effects had we used an actual taxidermic model of a predator that would be visible throughout the trial and further studies with taxidermic mounts would be valuable. Nevertheless, the strong effects during the heterospecific playback period, as well as the persistent effect on alarm calling during the second conspecific playback suggests that simulating the presence of a hawk acoustically is enough to change signaling behaviors significantly.

Therefore, our study again failed to support the eavesdropping avoidance hypothesis to explain the low amplitude of soft song. As we recently argued (Akçay et al. 2015), the hypothesis still has a lot of intuitive appeal and may yet be supported by further evidence, especially given that both tests of the hypothesis have been in song sparrows and tests in other species may yield different patterns. The present study should help researchers in designing future experiments to test this hypothesis in other species as well.

All that said, given 2 explicit tests that failed to support the eavesdropping avoidance hypothesis in song sparrows, we believe that eavesdropping avoidance is unlikely to be main reason why soft song is soft. Instead, aggressive soft song in song sparrows (and other species) may be soft either due to the need to avoid eavesdropping by male or female conspecifics so as to keep the aggressive interaction private or due to the possibility that singing loudly would interfere with visual tracking of the opponent in an aggressive interaction (the readiness hypothesis; Akçay et al. 2011). We believe these alternative (but non-mutually exclusive) hypotheses also need to be tested empirically in the future.

In summary, we found that male song sparrows are able to recognize one of their most common predators by their calls and change their signaling behaviors adaptively. However, signaling behaviors showed no persistent changes as a result of the experimental treatment, despite the fact that subjects gave more alarm calls even after the hawk playback ended. Thus, it appears that the signaling decisions by song sparrows are made flexibly depending on the trade-off between the risk of predation and the need to fend off intruders. How these trade-offs change depending on the circumstance and affect signaling behaviors is an interesting question for future research in this and other species.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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