VEERY SONG CONTAINS FEATURES USED IN AGGRESSION

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Abstract. Vocalizations are an important component of aggressive interactions between male songbirds. Song type matching, song type switching, and song overlapping are all used in passerine aggression. Recent work providing sparrows an opportunity to attack a mount indicates that soft song predicts aggressive behavior in two species. We investigated whether vocalizations of the veery (*Catharus fuscescens*) contain features advertising aggressive intentions. Attracting a territorial male with initial playback, we then presented a robotic veery mount and additional playback to simulate a territorial incursion. We recorded the birds' responses and then measured the vocal features associated with aggression. Male veeries responded to playback but did not physically attack the mount. Faster song rate, squiggle calls, and songs missing the introductory syllable occur more frequently in an aggressive context. Multiple regression models reveal more aggressive birds sing more initially, decrease their song rate at the end of the trial, and continue to delete the introductory syllable of their song. These results suggest that veeries adopt one of two defensive strategies: more aggressive veeries sing while approaching intruders closely but relax shortly afterwards, while less aggressive veeries quietly avoid intruders but sing vigorously afterwards.

INTRODUCTION

Aggressive interactions between organisms involve complex displays of signals. Long before an aggressive situation comes to a physical attack, the individuals involved frequently exchange aggressive or submissive signals, resulting in the escalation or de-escalation of each participant (Hurd and Enquist 2001). These signals span a wide range of taxa and come in many forms, including roaring in red deer (Clutton-Brook and Albon 1979), head-bobs in *Anolis* lizards (DeCourcy and Jessen 1994), specific body postures in mantis shrimp (Dingle and Caldwell 1969), and deep vocalizations in toads (Davies and Halliday 1978). Bird song has also been a classic model for the study of aggressive signaling. Along with mate attraction, territorial defense is one of the major functions of bird song (Searcy and Andersson 1986). These two functions, however, are not entirely separate. In both chickadees and great tits, females listen to male territorial interactions and change their mating choices accordingly (Mennill et al. 2002; Otter et al. 1999). The use of particular vocal signals in aggression has been explored in many different songbird species (Anderson et al. 2005; Ballentine et al. 2007; Beecher et al. 2000; Beecher et al. 1996; Burt et al. 2001; D'Agincourt and Falls 1983; Falls et al. 1982; Mennill and Ratcliffe 2004; Searcy and Nowicki 2008; Searcy et al. 2006; Vehrencamp et al. 2007).

Songbirds use several forms of aggressive signals. Species with vocal repertoires containing multiple song types often utilize these repertoires in aggressive interactions. Singing a song that matches the song type given by an opponent is thought to be an aggressive signal in song sparrows, great tits, western meadowlarks, and banded wrens (Beecher et al. 2000; Beecher et al. 1996; Falls et al. 1982; Vehrencamp et al. 2007). Switching between song types or song type variants within the birds repertoire has also been shown to increase during aggressive encounters in song sparrows and eastern meadowlarks (Searcy et al. 2000; D'Agincourt and Falls 1983). Alternatively, other vocal signals depend on the timing of a bird's song. In black-capped chickadees overlapping a rival's song acts as a threatening signal (Mennill and Ratcliffe 2004). Even simply increasing the rate of singing (Weary et al. 1986b) or changing the amplitude of a song (Searcy et al. 2006; Ballentine et al. 2007) can serve as an aggressive signal. Finally, song quality, a parameter that can affect a males rank (Christie et al. 2004) and reproductive success (Byers 2006; Forstmeier et al. 2002; Nowicki et al. 2002; Ballentine et al. 2004), may be manipulated to serve as an aggressive signal in some species (Dubois et al. 2009).

Classically, the study of vocal aggression has involved measuring vocalizations made in response to playback alone. This approach is problematic, however, because both aggressive and submissive signals are present in an aggressive interaction (Ballentine et al. 2007; Searcy et al. 2009; Searcy et al. 2006). Without providing subjects an opportunity to actually attack, these studies make it difficult to separate aggressive and submissive actions. Recent studies with song sparrows (Searcy et al. 2006) and swamp sparrows (Ballentine et al. 2007) have avoided this problem by first luring territory owners with playback and then providing an opportunity to attack an experimental mount. In both cases, birds who escalated to a physical attack frequently prefaced this action by singing a low amplitude rendition of their species song. Soft song thus acts as a signal of aggressive intentions. Furthermore, territorial male sparrows also respond much more aggressively to playback of soft song (Anderson et al. 2007).

In addition to acoustic signals, such as song, natural aggressive interactions often involve visual along with auditory signals. In fact, the presence of visual signals is sometimes critical to the meaning of the auditory cue (Partan and Marler 1999). Birds are known to use numerous visual signals in aggressive interactions (Hurd and Enquist 2001), and past playback studies have been criticized for ignoring this element (Laidre and Vehrencamp 2008). We used a robotic veery model to provide visual signals of aggression. Robotic models have been used successfully to elicit mating behavior in bowerbirds and aggregating behavior in Australian brush-turkey chicks (Patricelli et al. 2006; Göth and Evans 2004). Underscoring the importance of multimodal signals, túngara frog females respond more strongly to male calls paired with a moving robot than to male calls alone. Robots can also successfully transmit aggressive signals. Robotic sagebrush lizards giving aggressive head-bob displays induce the same behavior in live lizard opponents (Martins et al. 2005). However, robots have not yet been used in songbird studies.

In this study we used the new methodology of the sparrow studies paired with a robot to determine what aggressive signals might be used by a species lacking a large song repertoire but possessing a large call repertoire and acoustically complex songs. We investigated the aggressive vocal behavior of the veery (*Catharus fuscescens*). This thrush species has an average song repertoire of two song patterns (Borror 1964; Samuel 1972), making it unlikely that it engages in song type or repertoire matching. Additionally, song acoustic structure varies considerably between individual males (Borror 1964; Samuel 1972). Composed of frequent, rapid frequency and amplitude modulations, this acoustic structure is complex. Additionally, veeries often sing more than one frequency simultaneously. The independent modulation of these frequencies suggests these birds use two sides of their syrinx to create this complexity (Weary 1986a). Despite this variability in fine structure, each male's song can be divided into 3 basic components (Weary et al. 1986a). The song's first component is a short ascending introductory syllable, the second component is more variable and complex and often includes the highest frequencies, while the third component includes similar syllables with lower frequencies (MacNally et al. 1986; Samuel 1972; Weary et al. 1986a). Veeries have been observed adding or subtracting syllables from their typical pattern during natural singing (MacNally et al. 1986; Samuel 1972; Weary et al. 1986a) and this behavior may have a role in an aggressive context. Veeries also use as many as nine distinct call types that are shared between individuals (Samuel 1972). In an early, largely anecdotal work, Dilger (1956) hypothesized that the ''Veer'' call and an unnamed soft call are used in aggressively charged situations. Additionally, observations of countersinging males gave us reason to believe these calls may play a role in aggression (Ken Schmidt, personal observation). An experimental evaluation of this hypothesis, however, has not yet been undertaken. In fact, few investigations have explored veery vocal behavior during aggression. A playback study by Weary et al. (1986b) did find that veeries respond much more strongly to simulated incursions by strangers than by neighbors, but his vocal measurements were confined to counting the total number of vocalizations.

We used playback and a robotic veery mount to study the vocal response of territorial male veeries to a simulated territorial incursion (see Ballentine et al. 2007 and Searcy et al. 2006). Lured to the area by initial playback, males were then presented with the robotic mount and additional playback. If the veery vocal repertoire contains aggressive signals, we expected those song features to be used more frequently by aggressive individuals in an aggressively charged situation prior to actual physical attack. First, based on earlier work with veeries (Weary

1986b), we believed that elevated song rates and possibly call rates may correlate with aggression. Second, we believed that overlapping songs, which plays a role in chickadee aggression (Mennill and Ratcliffe 2004), may be important with veeries. Third, the large call repertoire of this species led us to believe that a particular call type, most notably the unnamed soft call observed in aggressive contexts (Dilger 1956; Ken Schmidt, personal observation), may function as an aggressive signal. Finally, because of the connection between singing consistency and aggression in other species (Dubois et al. 2009) as well as the tendency of veeries to alter the number of syllables in their song (MacNally et al. 1986; Samuel 1972; Weary et al. 1986a), we believed that syllable consistency may play a role in aggression.

METHODS

This experiment was performed at the Cary Institute of Ecosystem Studies in Dutchess County, New York, U.S.A. between June 5 and June 27, 2009. Trials were conducted between 6:00 and 10:00AM. Subjects were 32 male veeries (*Catharus fuscescens*) from a resident population of territorial birds that could be identified individually by either color bands and/or unique song types, allowing us to test each individual only once. The property's damp deciduous forest provides summer breeding grounds for 50-100 veeries annually.

Playback Stimuli

We constructed three song stimuli exemplars from samples of natural song recorded on the property earlier in 2009. Because veery song can vary considerably between males, three exemplars were chosen to expose our experimental birds to the range of singing they would naturally encounter. One exemplar was a bird who sang a typical song and one exemplar was a bird who sang a very atypical song with the third falling somewhere in the middle. In order to approximate natural conditions as closely as possible, we constructed each set from continuous sections of high quality recordings that we made from a single individual. To ensure each playback recording represented an unfamiliar male, we used exemplars from males holding territories at least 1500m away from the focal male's territory. Recordings were made using a Telinga parabolic reflector, a Sennheiser MKH 62 microphone and a Marantz PMD 660 digital recorder (sampling rate of 44.1kHz, bit rate of 705.5 kbps). Each playback exemplar was composed of three sections of high quality continuous natural singing. The first 1 minute section was composed of mostly songs played back at an average amplitude of 122.2 dB. Following a 1 minute section of silence, an additional minute of songs and calls was played at average amplitude of 116.2 dB. This initial three minute portion was designed to bring the focal male to the area. After three and half minutes of silence, a final two minutes of songs and calls were played at average amplitude of 117.5 dB. We used Raven (Ithaca, NY, USA) to filter out all noise surrounding each vocalization. The amplify command was used on each vocalization to bring it within 11 dB of the average amplitude of the section.

Robotic Veery

A robotic mount covered in an adult male veery skin was used to provide the subjects a focal point for aggression. This mount was constructed using radio-controlled servo motors, typically found in radio-controlled cars, attached to the mount with wire and fishing line. The motor and wires were concealed below the mount in a wooden box. Movement of the motor did produce some noise (1-2dB at 1m away). Directed remotely by radio-control, the mount could move its wings away from its body also well as pivot at the leg-body joint, allowing it approximate the 'upwards display', 'horizontal stretch', and 'wing flicks' noted as aggressive behaviors by Dilger (1956). The wing flicks were remarkably similar to wing flicks we observed in the field, though the upwards display and horizontal stretch were a more rough approximation. In the trials using movement (N=17), upwards, horizontal stretches, and wing flicks were performed sequentially in bouts of approximately 20 seconds separated by approximately 30 seconds. We limited these movements to the time the mount was uncovered but the playback was silent, following the observation by Dilger that vocalizations do not accompany these movements. We also left the mount stationary for 15 of the 32 trials to determine whether it caused a difference in response.

Playback Trials

We modeled our trials after the methods of Ballentine et al. (2007) and Searcy et al. (2006) with slight alterations to account for different levels of overall aggressiveness between veeries and sparrows. While we have frequently heard veeries engaged in territorial countersinging, we have rarely witnessed a physical fight between two veeries (Kara Belinsky, personal observation). We placed our mount and recording set-up well within the territory where the focal male was actively vocalizing, ensuring he was present from the start of the trial. The mount was positioned on top of a 1 meter tripod and covered with cloth to conceal it from view. A playback speaker and recording set-up (Sennheiser MKH 62 microphone with foam windshield and Marantz 670 recorder) were positioned as close to the mount as possible. Two observers sat 15-20m away with a second parabolic recording set-up (Telinga parabolic reflector, a Sennheiser MKH 62 microhpone and a Marantz PMD 660 digital recorder). One observer (CK) recorded all vocalizations from the focal male during the trial while the other (KLB) narrated information about movements, color-bands, and distance from the mount.

In order to minimize the effect of our disturbance on the bird's behavior, we left five minutes of silence between erecting our experimental set-up and the start of the trial. The trial started with 1 minute of songs, followed by 1 minute of silence and then 1 minute of songs and calls (see Figure 1). After three and half minutes of silence we removed the mount cover. If the focal bird was not seen or heard during these first six and a half minutes, the mount was not revealed, the trial was aborted, and the bird was retested on a following day. If the focal bird was present, the final 2 minute playback set was played. Recording continued 10 minutes after this playback ended. Because the playback frequently elicited responses from neighbor birds, we refrained from testing the focal male's neighbors on the same date a trial was attempted on a neighboring territory.

Analysis

After importing each recording into Raven, we identified all songs, calls, and movements made by each bird during the trial. We measured eight different song features in each trial: total songs, song rate, proportion of overlapping songs, total calls excluding squiggle calls, call rate, total squiggle calls, introductory syllable number consistency, and non-introductory syllable number consistency. We calculated song and call rates for each bout where no space longer than 30 seconds occurred between consecutive songs or calls. Rates were then averaged across bouts for each period. We defined overlapping songs as songs that were started while a song from the playback recording was still playing. Our measurements of total calls and call rate included calls defined by Samuel (1972) as "Veer", "Chatter", "Trill", "Low Veer", "Churr", "Low Whistle", and "Purr" calls. Because of the low sample size of many call types, we lumped them together in a single variable. An exception was made for squiggle calls, which occurred with a decent frequency (105 occurrences from 23 birds). We have included a longer description of these calls with our results.

We were also interested in the consistency of the number of syllables contained in the songs (see MacNally et al. 1986 or Weary et al. 1986a for similar definition of syllable). Males show individual variability in the number of syllables typically present in their song and within a single trial individual males also varied their syllable number, sometimes dropping entire portions or abruptly cutting the song short. We used the inverse of the coefficient of variation in the number of syllables as a measure of consistency (see Byers 2006). The ascending introductory syllable was measured separately from the non-introductory portions of the song.

To determine whether certain song features were employed more frequently when engaging with a territorial intruder, we compared the vocal behavior during the 8 minute playback period to the behavior in the post-playback period. We assumed the playback period represented a more aggressive context for several reasons. First, the playback imitated an unfamiliar male in the focal male's territory. Second, the focal male frequently showed signs of agitation during playback such as wingflicks, hopping along a perch, and rapid singing. Finally, males appeared to show little reaction to the mount still present in the post-playback period once the playback had stopped. We compared playback and post-playback values of each vocal response using paired t-tests with

Holm's sequential Bonferroni corrections to correct for multiple comparisons. Log (x+1) transformations were made on variables not satisfying normality assumptions. Wilcoxon tests were run on variables still not sufficiently normal.

To determine whether certain song features were employed by more aggressive individuals, we built three multiple regressions models that explained variation in the time a bird spent within 10m of the mount. Distance from the speaker is classically used as a measure of aggression in playback experiments. Moreover, playback work with swamp sparrows has shown the distance of approach is strongly correlated with actual attacks (Ballentine et al. 2007; Searcy et al. 2006). Birds that chose to spend more time close to the mount both put themselves at higher risk of being attacked and were close enough to engage in physical conflict if they had so chosen. To construct these models, variables were selected using a forward step-wise procedure from a pool of playback (Model 1), post-playback (Model 2), or playback and post-playback variables (Model 3). We then used AIC goodness-of-fit scores to choose the best model among the three. Using AIC goodness-of-fit scores as an independent evaluation of our models' suitability allowed us to avoid some of the weaknesses of the forward step-wise procedure. Lower AIC scores represent a better fit.

RESULTS

We measured the vocal responses of 32 male veeries. 51 trials were attempted but 13 trials were aborted because the focal male did not enter the experimental area. 6 more trials were later determined to be the same individual from a previous trial. The robotic mount was revealed in 38 trials. Of the 32 successful trials, 17 used the robotic movements. Surprisingly, t-tests comparing stationary mount trials to robotic mount trials found no significant differences in any song variable measured. Additionally, in trials where the focal males were clearly visible, they did not appear to be looking at the mount and instead focused their attention on the playback speaker. In four trials the focal male performed what could be classified as a low swoop close to the experimental set-up, but in all these cases the action was directed at the playback speaker and not the mount. No veeries attacked the mount itself. Our focal males were also unaffected by the type of playback stimulus used. 1-way ANOVA's comparing the trials using the three playback exemplars found no significant effects after Holm's sequential Bonferroni corrections.

Vocal Responses to Playback

Three song variables differed significantly between playback and post playback periods. Song rate was significantly faster during the playback period (10.76 ± 0.75 songs per minute) than during the post-playback period (6.81 ± 0.82 songs per minute) (p=0.0009) (Figure 2a). Birds also gave significantly more squiggle calls during the playback period. Out of the 105 squiggle calls that occurred during the experiment, 73 occurred during the playback period. This trend remained significant after controlling for the difference between individual birds (Wilcoxon: p=0.0067) (Figure 2b). Veeries were also significantly less consistent with the number of introductory syllables they sang during the playback period (0.75 ± 0.04) compared to the post-playback period (0.93 ± 0.02) (p =0.0005) (Figure 2c). For all but one bird, this drop of consistency resulted from songs missing the introductory syllable. To maintain a balanced design, trials missing consistency values in either the playback or post playback period were removed from this portion of the analysis, leaving 21 trials in total.

Little record of squiggle calls exists in previous studies. While other call types are given at amplitudes similar to that of songs, squiggle calls have much lower amplitudes, often not noticeable in the field. The specific structure of squiggle calls appears to vary between and within individuals, but all squiggle calls are characterized by fine frequency modulations not present in other call types (see Figure 3). In addition to occurring primarily during the playback period of our experiment, squiggle calls have been heard in singing interactions between neighbors in our study population (Ken Schmidt, personal observation). Dilger (1956) also mentions "faint, high pitched, windy, squealing sounds" given in aggressive situations, which we believe are the same call type.

Vocal Responses Predicting Approach to Speaker

Several song features predicted the time a bird spent close to the mount. We used multiple regressions models to assess which song features best predicted the time spent within 10 meters. We constructed three models first by selecting variables through a forward step-wise procedure from either playback (Table 1a), post-playback (Table 1b), or both playback and post-playback measures (Table 1c) of the same seven song variables as in our previous analysis with the addition of the proportion of songs overlapping the stimulus songs. We then used AIC goodness-of-fit scores to select the model that best explained the time spent within 10m. Table 1 displays the variables selected through a forward stepwise procedure for each model.

A combination of playback and post-playback measures best explained the variability in the time spent within 10m of the mount (Table 1c; p = 0.008; R^2=0.46; AIC=193.53). Birds that sang more songs during playback also spent more time within 10m of the mount (p=0.0077). However, these birds who approached closer also sang at a slower rate during the post-playback period (p=0.0385). In fact, the five birds that never came within 10m of the mount had a higher post-playback song rate (11.75 ± 3.23 songs per minute) than the other birds (5.9 ± 1.41 songs per minute). Birds that spent more time within 10m of the mount less consistently sang their introductory syllable during the post-playback period (p=0.044). Furthermore, the four birds that performed low swoops had a lower consistency score (0.84 ± 0.03) than birds that did not (0.94 ± 0.022). These four birds also spent more time within 10m (213.75 ± 35.69) than the others birds (116.71 ± 18.45).

For all models, multiple input variables were significantly correlated. Given the nature of communication, however, this is not unexpected. Because a bird can only give one vocalization at a time, the occurrence of one type of vocalization will be inversely related to the occurrence of all other types. Table 2 summarizes the significant correlations.

DISCUSSION

Veery song appears to have several features used in aggression. High song rates, squiggle calls, and songs lacking the introductory syllable are utilized in aggressive contexts. Additionally, more aggressive birds sing faster in aggressive encounters but fail to maintain their song rate or introductory syllable consistency.

While playback provoked an adequate response, the veeries in our study failed to respond to our experimental mount, despite numerous attempts as well as the use of a robotic mount. Playback successfully produced aggressive singing behavior and in a handful of cases low swoops towards the speaker, but the mount, which should have been clearly visible to any bird that came within 5m, did not appear to elicit a response. Birds appeared to focus their attention on the playback speaker, never stopping or slowing near the mount. Despite our best efforts to mimic the appearance and movements of a veery, our mount may have been an unconvincing representation. This lack of response may also be due to the time in the breeding season. At the time of our experiment pairing and nesting had already begun, making males less likely to engage in physical disputes (Beecher et al. 2000). In contrast to other species, such as sparrows, physical fights between veeries are also rarely observed in the wild (Kara Belinsky, personal observation). Regardless of its cause, this lack of response to the mount makes us secure in our classification of the post-playback period as a less aggressively charged context.

Several song features occurred with higher frequency in the more aggressive playback context. Constructed from high quality continuous natural singing, the playback recording mimicked an unfamiliar veery singing on a focal male's territory. In many instances these recordings actually elicited singing from multiple neighboring males. Focal males responding to this playback sang faster than they did during the post-playback period. Moreover, our average post-playback song rate of 6.82 songs per minute closely resembles the song rate found in natural singing by Borror (1964) (6-8 songs per minute), lending support to our classification of the post-playback period as less aggressive.

Males also gave significantly more squiggle calls in a playback context. These calls have gone largely undescribed up to this point (but see Dilger 1956). These calls may be the product of the stress of the playback period. Alternatively, they may function as some kind of signal in the aggressive context- either aggressive or submissive. We have also observed these calls during bouts of countersinging between neighboring males. The most noticeable difference between squiggle calls and other veery vocalizations is their low amplitude. These low amplitude calls may have an interesting parallel to the soft song observed in other species (Ballentine et al. 2007; Searcy et al. 2006). It is hypothesized this signal is kept honest because it is an "unambiguous and costly signal of attention" (Ballentine et al. 2007). Birds utilizing this signal sacrifice their ability to communicate to other opponents further away and must be close to an opponent in order for the signal to be received, thus increasing their risk of being attacked (Ballentine et al. 2007; Laidre and Vehrencamp 2008; Searcy and Nowicki 2008). If squiggle calls also function as an aggressive signal, their use likely contains similar costs and benefits.

While all veeries changed their singing behavior between the playback and post-playback periods, birds spending more time close to the mount had vocal patterns distinctly different from their less aggressive counterparts, revealing two defensive strategies. Predicting how much time individuals spent close involved consideration of both playback and post-playback vocal behaviors. Models containing only playback or only post-playback variables did not explain the time spent close to the mount nearly as well as the model that contained both. Overall, veeries appear to adopt one of two defensive strategies. More aggressive birds spending more time near the mount sang many songs in response to the playback recording, however, once the virtual opponent 'disappeared' and the post-playback period began, their singing rate decreased. Conversely, birds that remained far away were more likely to be silent during the playback period yet maintained higher song rates post-playback. In fact, the birds that never came within 10m of the mount had the highest post-playback song rate.

The deletion of the introductory syllable also appears to play a role in aggression. Significantly more songs missing their introductory syllable occurred during the playback period. More aggressive males also used songs missing this phrase more frequently during the post-playback period. Deletion of the introductory phrase has been noted by prior studies on veery song (MacNally et al. 1986; Samuel 1972; Weary et al. 1986a). Though its deletion is noted, the context in which these shortened songs occur was not explored. It is impossible to distinguish with this experiment whether deletion of the introductory syllable conveys significant information. Its absence may be either an aggressive signal or merely a causality of poor performance.

Songs lacking introductory syllables may reflect a poor performance of the species song. High quality songs have been defined in several different ways across species: consistency of pitch and timing in chestnut-sided warblers (Byers 2006), high amplitude in dusky warblers (Forstmeier et al. 2002), properly learned songs in song sparrows (Nowicki et al. 2002), and high frequency/bandwidth ratios in swamp sparrows (Ballentine et al. 2004; Podos et al. 2004). In many of these species females are known to select males singing these higher quality renditions of their species songs (Ballentine et al. 2004; Byers 2006; Forstmeier et al. 2002; Nowicki et al. 2002). Furthermore, song performance can also have an impact on a male's social ranking (Christie et al. 2004). Because the developmental and energetic costs involved in properly learning song early in life, high quality song can be viewed as an honest indicator of male quality (Christie et al. 2004; Nowicki et al. 2002; Searcy and Nowicki 2008). At first glance it may appear contradictory that the birds that continued to produce these "poorly performed" songs were also the males who spent more time within 10m of the mount. However, this relationship between lower quality and increased aggression may also be present in other species. Based on observations of long-term territorial contests, Forstmeier et al. (2002) suggested dusky warblers singing low quality songs partially compensate for decreased success in attracting mates by obtaining better territories. Similarly, Mennill and Ratcliff (2004) found low ranking male chickadees engage more intensely in aggressive disputes. It is possible that male veeries singing lower quality songs were also those that had a stronger motivation to win territorial contests.

If songs lacking an introductory syllable represent poorly performed songs, then this may also reconcile our results with work by MacNally et al. (1986). In investigating which parts of veery song are most important in

eliciting territorial responses, MacNally et al. (1986) found that playback composed of only introductory syllables produced weaker territorial responses. However, playback songs lacking the introductory syllable did not produce the increase in territorial responses that our results might suggest. MacNally's findings would not come as a surprise if deletion of the introductory syllable is not an aggressive signal and instead a product of poor performance.

The possibility that songs missing introductions represent an aggressive signal should not be immediately discounted. A typical song differs notably between individual males, as evident both in our study population and previous work (Borror 1964; Samuel 1972). Despite this overall variability, the introductory syllable is remarkably similar between males (Samuel 1972). While a male may not immediately notice a change in syllable number from an unfamiliar male's typical song, removal of the introductory syllable should be much more conspicuous. Furthermore, the consistency of the number of non-introductory syllables was no different between more aggressive situations and individuals, contrary to what would be expected if syllable consistency reflected quality.

Song rate, squiggle calls, and songs missing introductory syllables play some kind of role in veery aggression. However, the lack of physical attacks observed in our study keeps us from being certain. Further, more targeted investigations are needed to determine whether any of these features advertise a veery's aggressive intentions. Currently, we can identify features that increase in aggressive contexts but cannot determine whether these features play an aggressive or submissive role. Observing the behavior of birds in response to playback with varied song rates and squiggle calls, following similar protocol as Anderson et al. (2007), may shed light on the exact function of these features. Resolving the question of whether introductory syllable consistency represents an aggressive signal is more complicated. MacNally (1986) examined which song syllables are used in species recognition by testing only one syllable type in each playback set. Reversing this method by presenting birds with songs only lacking the introductory phrase would be informative. Investigation of whether the deletion of this phrase indicates poor song performance is also needed. Thus far it is not known whether female veeries use this kind of consistency when selecting a mate or whether consistency in syllable number correlates with reproductive success, dominance status, or male age. Having these details about the individuals studied may help us determine why a particular male adopts a given defensive strategy. In spite of these unresolved questions, it is clear that veery song does indeed play a role in aggressive encounters.

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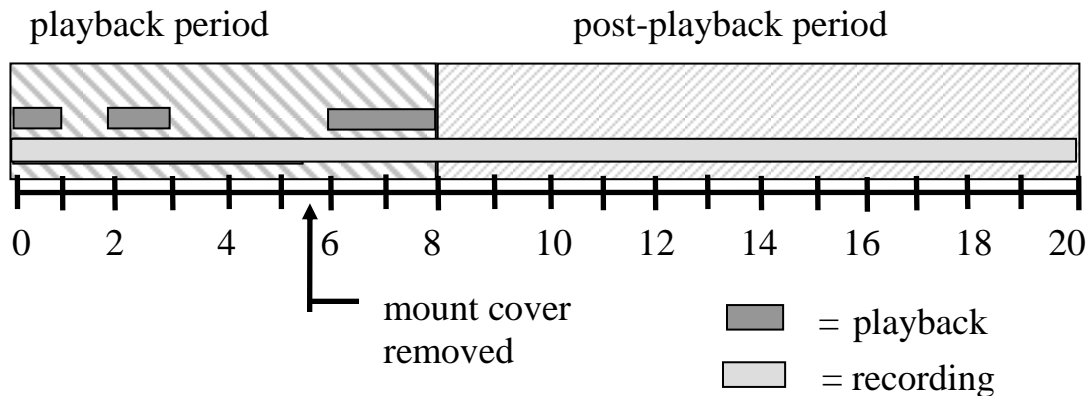
APPENDIX

FIGURE 1. Time-line followed during the playback trials, adapted from Ballentine et al. 2007.

Otter, K., P.K. McGregor, A.M.R. Terry, F.R.L. Burford, T.M. Peake, and T. Dabelsteen. 1999. Do female great tits (Parus major) assess males by eavesdropping? A field study using interactive song playback. Proceedings of the Royal Society of London: B **266**:1305-1309.
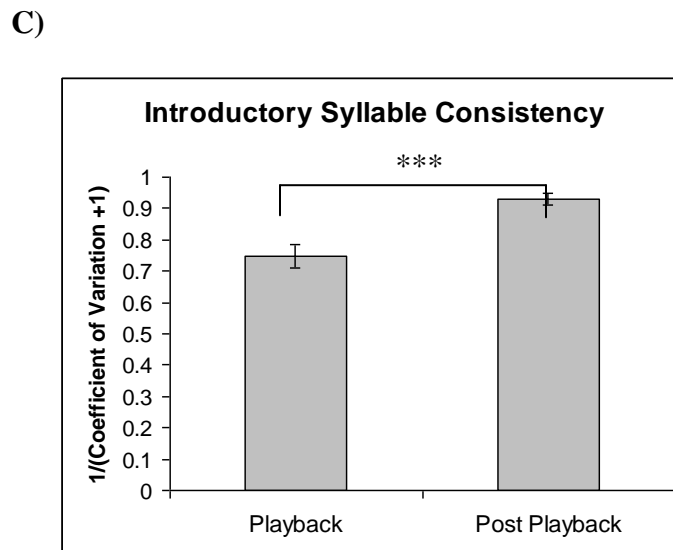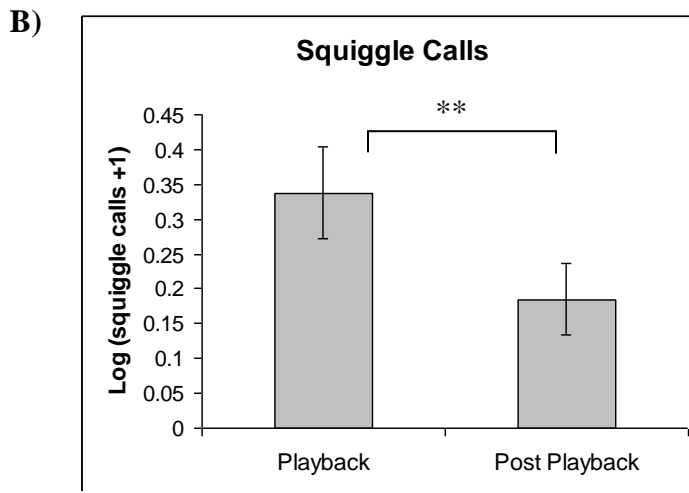
A)

Song Rate

***

Songs per Minute — Playback, Post Playback

B)

Squiggle Calls

**

Log (squiggle calls +1) — Playback, Post Playback

C)

Introductory Syllable Consistency

***

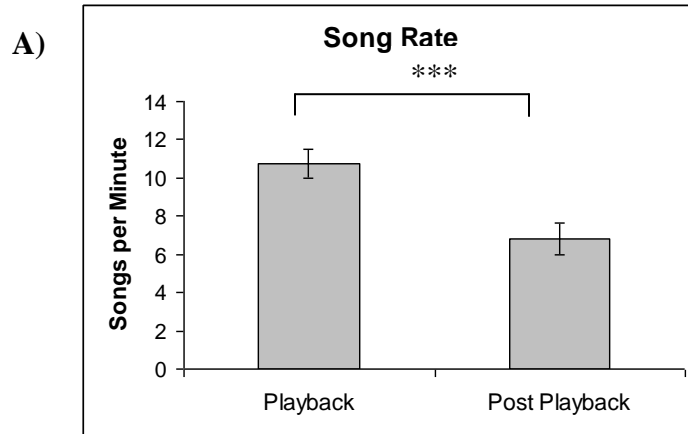*1/(Coefficient of Variation +1)* — Playback, Post Playback

FIGURE 2. Song rate (A), log(squiggle calls +1) (B), and 1/(coefficient of variation in introductory syllable number consistency +1) between playback and post-playback periods. For A and B, N = 32 and for C, N=21 *** = p < 0.001; ** = p < 0.01
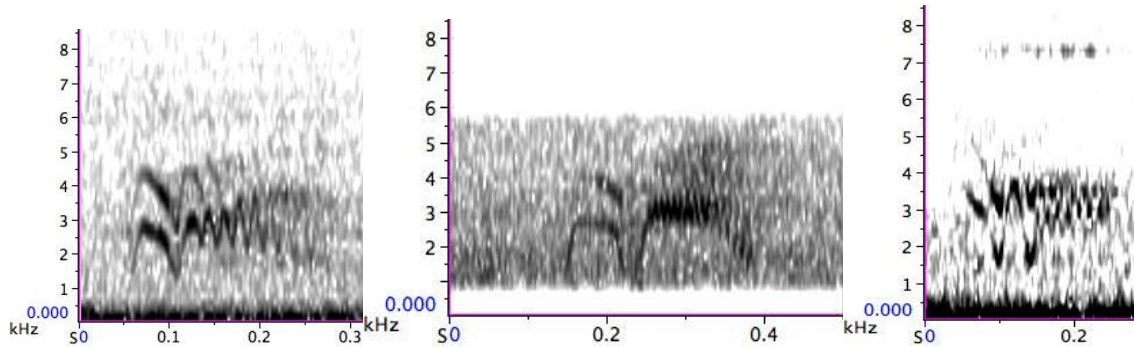

FIGURE 3. Three examples of squiggle calls from different male veeries. Images were taken using Raven.

TABLE 1. Three models constructed through a forward stepwise procedure to explain variation in the time veeries spent within 10m of the mount. AIC goodness-of-fit scores indiciate Model 3 is the best model.

a)

Model 1	Model p-value	Model R^2	AIC
Playback variables only[1]	0.0085	0.28	272.63
Variable	**Coefficient**	**p-value**	
Log (Playback Songs +1)	85.09	0.0115	
Log (Non-squiggle playback calls +1)	-74.09	0.0265	

b)

Model 2	Model p-value	Model R^2	AIC
Post-playback variables only[2]	0.7666	0.003	216.32
Variable	**Coefficient**	**p-value**	
Post-Playback Song Rate	-18.93	0.7666	

c)

Model 3	Model p-value	Model R^2	AIC
Playback and post playback variables[3]	0.008	0.46	193.53
Variable	**Coefficient**	**p-value**	
Log (Playback Songs +1)	102.42	0.0077	
Post-Playback Song Rate	-16.41	0.0385	
Post-Playback Intro Syllable Consistency	-573.25	0.044	

[1]: Log (playback songs +1), playback song rate, Log (playback squiggle calls +1), Log (proportion of overlapping songs), 1/(playback coefficient of variation in introductory syllable number +1), 1/(playback coefficient of variation in non-introductory syllable number +1), playback call rate, Log (playback calls-squiggle calls +1)

[2]: Log (post-playback songs +1), post-playback song rate, Log (post-playback squiggle calls+1), 1/(post-playback coefficient of variation in introductory syllable number +1), 1/(post-playback non-introductory syllable number +1), post-playback call rate, Log (post-playback calls-squiggle calls +1)

[3]: All variables in 1 and 2

TABLE 2. Significant correlations between variables evaluated in AIC goodness of fit models from Table 1.

Variable 1	Variable 2	Correlation Coefficient	p-value
Log (Post-Playback Calls –Squiggle Calls +1)	Post-Playback Call Rate	0.7492	0
Post-Playback Song Rate	Log (Post-Playback Songs +1)	0.7666	0
Log (Proportion of Overlapping Songs +1)	Log (Post-Playback Songs +1)	-0.556	0.001
Post-Playback Song Rate	Log (Proportion of Overlapping Songs +1)	-0.4699	0.0067
1/(Playback Coefficient of Variation in Intro Syllable Number +1)	Log (Playback Squiggle Calls +1)	-0.4584	0.0108
Log (Playback Calls –Squiggle Calls +1)	Post-Playback Call Rate	0.438	0.0122
1/(Post-Playback Coefficient of Variation in Non-Intro Syllable Number +1)	Log (Post-Playback Songs +1)	-0.4688	0.024
Log (Playback Calls –Squiggle Calls +1)	1/(Post-Playback Coefficient of Variation in Intro Syllable Number +1)	0.4391	0.0361
Playback Song Rate	Log (Playback Songs +1)	0.3495	0.0499