

Male–male vocal interactions in a territorial neotropical quail: which song characteristics predict a territorial male’s response?

Luis Sandoval¹⁾

(Escuela de Biología, Universidad de Costa Rica, 11501-2060 San José, Costa Rica)

(Accepted: 21 July 2011)

Summary

Males singing within their territories can change their song characteristics in order to interact with conspecifics; males may respond to territorial intrusions by vocalizing, approaching the intruder and/or displaying. I studied male–male interactions by quantifying vocal and behavioural responses of male spot-bellied bobwhites (*Colinus leucopogon*) toward playback of conspecific male songs. Male responses toward playback song depended on the quality of the territorial male’s song relative to the playback stimulus. In this species males who sang songs with higher peak and low frequency, longer song duration, and lower song rate were less responsive to simulated territorial intrusions. Spot-bellied bobwhite males that sang in response to the playback increased the low frequencies of their songs relative to pre-playback song, a vocal behaviour related to dominance in males of other species. Males that approached the speaker sang longer songs, a characteristic associated with increased aggression or motivation to fight in other bird species. The results of this playback experiment suggest that male spot-bellied bobwhite song characteristics according to playback characteristics predict response to territorial intrusions and may, therefore, play an important role in male–male interactions.

Keywords: aggressive signals, *Colinus leucopogon*, playback, song function, territoriality.

1. Introduction

Vocalizations produced during the breeding season by male birds (called songs) are sexual displays used to compete with rival males and/or attract

¹⁾ Corresponding author’s current address: Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, ON, Canada N9B3P4, e-mail: biosandoval@hotmail.com

females (Andersson, 1994; Gil & Gahr, 2002; Catchpole & Slater, 2008). The information encoded in male song evolved in response to pressures imposed by male–female interactions, but the information relayed may differ according to the receiver’s sex (Leitão & Riebel, 2003). For example, in male–male interactions, songs may provide information about male status and dominance (Leonard & Horn, 1995; Rehsteiner et al., 1998), as well as aggressiveness and motivation to fight (Martin, 1984; Arcese, 1987; Studd & Robertson, 1988; Searcy & Beecher, 2009). Conversely, in male–female interactions, songs may relay information related to body size (Kipper et al., 2006), health (Reid, 1987; Garamszegi et al., 2005), age (O’Loughlen & Rothstein, 1995), degree of parental care (Dolby et al., 2005), and/or territory quality (Buchanan & Catchpole, 1997; Brumm, 2004).

Males within a territory occasionally alter their song characteristics and/or behaviour in response to the signals of interacting conspecifics. Vocalizations, approaches and displays are ways that males may respond to a conspecific (Petrie et al., 1991; Brumm & Todt, 2004; Marshall-Ball et al., 2006; Mennill, 2006; Bradley & Mennill, 2009). The role of vocalizations during male–male competition (e.g., song characteristics) have largely been studied in oscine songbirds (Beecher et al., 1996; Dabelsteen et al., 1997; Otter et al., 1999; Burt et al., 2001; Botero & Vehrencamp, 2007; Searcy & Beecher, 2009). In many oscines, song structure allows males to change the arrangement of song elements by including new elements and/or deleting previous ones (Capp, 1992; Beecher et al., 2000; Burt et al., 2001). Males can also alter acoustic characteristics of a song such as frequency, song rate, and duration (Morton & Young, 1986; Dabelsteen et al., 1997; Brumm & Todt, 2004).

Studies of male–male vocal interactions in non-passerine bird species are scarce (Collins, 2004; Searcy & Beecher, 2009). In studies of non-passerine species such as roosters (*Gallus gallus*), and collared doves (*Streptopelia decaocto*), authors report that males produce higher frequency vocalizations and modulate song elements during vocal interactions, respectively (Leonard & Horn, 1995; Ten Cate et al., 2002). In these cases, male–male vocal interactions in non-passerine species involve frequency changes rather than deletion/rearrangement of elements.

Males of the spot-bellied bobwhite (*Colinus leucopogon*), a non-passerine species, are territorial during the breeding season (March to October), and use song to defend their territories against other males and to attract a female

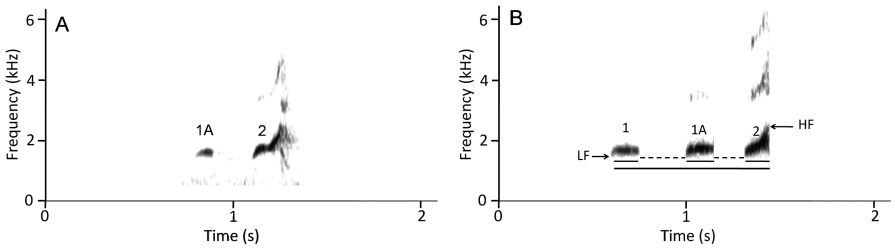


Figure 1. Spectrogram of spotted-bellied bobwhite male songs (A, a song with two elements; B, a song with three elements), showing song elements (1, 1A and 2), the duration of each element (short solid lines), total song duration (long solid line), time between elements (broken lines), the lowest frequency (LF) and the highest frequency (HF).

(Sandoval, 2008, 2011a,b). During this season, unpaired males produce a unique vocalization called song (Figure 1; Sandoval, 2008, 2011a,b), which occurs in other quails including northern bobwhite (*C. virginianus*), California quail (*Callipepla californica*), and scaled quail (*C. squamata*) (Stokes, 1967; Brennan, 1999; Calkins et al., 1999; Dabbert et al., 2009). As in these other quail species, the production of this vocalization ceases once a spotted-bellied bobwhite male pairs with a female, and both leaving the singing territory to find a nesting area (Sandoval, 2008, 2011a). All males sing essentially the same type of song comprised of up to two elements; the first element may be produced once or twice in a given song (Figure 1).

Males only use one singing perch when singing from a bush, but may sing from several closely-spaced perches (less than 2 m apart) close to the ground on exposed rocks or logs (Sandoval, 2008, 2011a,b). Males are likely to hear nearby males singing within 100 m radius, because that is the distance at which humans can hear singing. Therefore, many interactions may begin as vocal interactions, as observed in the northern bobwhite and *Callipepla* species; for example territorial interactions between flocks, male–female interactions within the pair, and between parents and chicks (Stokes, 1967; Goldstein, 1978; Brennan, 1999; Calkins et al., 1999; Dabbert et al., 2009; Sandoval, 2009, 2011a,b).

Due to the difficulty of observing male–male interactions of spot-bellied bobwhites in the field, I simulated territorial intrusions using a song playback. The objective of this research was to determine which song characteristics of territorial males predict aggressive responses (i.e., approaching and singing) to simulated territorial intrusion. If spot-bellied bobwhite songs contain information about male motivation to escalate a conflict, I predict that

aggressive responses will vary among males according to male song characteristics relative to song playback, as proposed by Searcy & Beecher (2009) for passerine birds. More specifically, I expect that males with lower song frequencies relative to song playback, a characteristic related to larger body size in many species (Ryan & Brenowitz, 1985; Bertelli & Tubaro, 2002; Catchpole & Slater, 2008), will respond more aggressively. I also expect that songs produced in response to the song playback will contain more notes of high frequency than in the song produced by the male prior to playback, because increasing frequency signals dominance in galliform species (Leonard & Horn, 1995).

2. Materials and methods

2.1. Field methods

The study was conducted in Getsemaní, Heredia province, Costa Rica (10°01'N, 84°06'W). The 30 ha study area included about 40% coffee plantations and 60% pastures with isolated trees and fences comprised of living trees. I recorded spot-bellied bobwhite males walking along a 3 km transect weekly between 0700 and 1100 h during two consecutive breeding seasons between March and October 2005 and 2006. This transect goes through the whole area without overlap, permitting me to effectively sample the area. I alternated the transect starting point each week. Along this transect, I recorded all 'new' singing males (males singing at sites not previously used by a male), using a tape recorder (Sony TCM-5000EV) and directional microphone (Sennheiser ME 66) for 5 min and from a distance of 5 to 15 m. The initial recording was collected in the absence of artificial stimuli and is considered the 'control song'. To minimize the likelihood of recording the same individual twice, the closest distance between different recording sessions was 100 m when a previously recorded male was not present, and 50 m between recordings in areas when a previously recorded male was present. I checked each territory for males weekly (for a detailed explanation of this method, see Sandoval, 2011a); males reliably sing from the same perches or a nearby one (less than 2 m from the recording perch, especially when they singing on the ground); thus, the probability of recording the same male in a farther perch is very low.

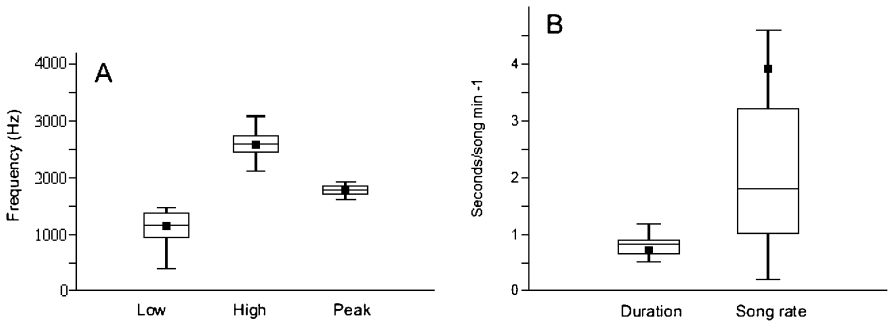


Figure 2. Average values of the stimulus song characteristics (indicated by a black square) relative to song characteristics measured in the spotted-bellied Bobwhite study population in Getsemani, Heredia province, Costa Rica during 2005 and 2006. A is frequency characteristics. B is temporal values. Box represents the upper and lower quartile. Vertical lines are the 95% confidence intervals. Horizontal line is the median value.

Immediately after recording a control song for each male, I played 5 min of songs recorded from a male hatched in captivity, through a speaker in the same spot where the control song was recorded. An observer was located 5–7 m behind the speaker. Using a captive-hatched male's song guaranteed that none of the experimental males would have encountered the stimulus song prior to the playback experiment. The stimulus recording had an average song rate of 4 song min^{-1} , song duration of $0.60 \pm 0.15 \text{ s}$ (mean \pm SD), lowest frequency of $1271.14 \pm 104.27 \text{ Hz}$, highest frequency of $2489.39 \pm 407.54 \text{ Hz}$, and peak frequency of $1845.71 \pm 191.69 \text{ Hz}$. These values fall within the range of the study population (Figure 2; Sandoval, 2011a). See definitions of song measurements below.

I used songs from a single male as the playback stimulus because, according to Hurlbert (1984), when the experimental units, in this case territorial males, have inherent variability, it is necessary to implement a treatment replication (all the sample units need to have the same treatment). Using song stimuli from multiple males to test each individual, as has been previously proposed (e.g., Kroodsmas et al., 2001), is not an effective procedure; each stimulus, even the same type of vocalization (de Kort et al., 2009), may contain different information due to individual variability and the motivational context when it was recorded (Ellis, 2008; Wilson & Mennill, 2010). Therefore, each playback is not a true replicate of the others as it may transmit a different message to the receiver. Thus, differences in the responses observed may be due to differences in the songs used as stimuli and not differences in

the experimental units (de Kort et al., 2009). If we are trying to understand “how the animals themselves perceive the signals” (Kroodsma et al., 2001), the lack of replication from using stimuli with different information obscures our understanding of individuals’ responses (Slabbekoorn et al., 2002).

During playback trials, I annotated the positions of each male using three behavioural categories. I scored a ‘male approach’ if the male moved more than 1 m from his original singing perch towards the direction of the playback speaker. If the male moved more than 1 m from his singing perch in the opposite direction of the playback speaker this movement was scored as ‘male retreat’. If the male remained on the same perch or moved around it within 1 m, it was scored as a ‘static male’. I also noted the time of the first vocalization produced after playback started (‘song response time’), changes in body posture (crest and neck), and the total number of males that I heard singing within 100 m around the focal male 30 min before and after each trial. After the playback finished, I recorded the focal male for 5 min (response song). The playback was broadcast from the internal speaker of an AIWA cassette recorder TP-VS485 at a volume of 70 dB, measured at 2 m from the speaker with a Sper Scientific 840014 mini sound meter (measuring range 32–130 dB). The minimum time lapse for playback between neighbouring males was one week, to minimize any effects that may depend on the prior playback interaction.

2.2. *Sound analyses*

For each focal male, I randomly selected five control songs and five response songs from the recordings made before and after the playback experiments for analysis. I analyzed all songs for males with five or fewer songs. Songs were digitized at a sample rate of 44 100 Hz and a 16 bit resolution using Cool Edit 2000 version 1.0 (Johnston, 1999). Sound analysis was performed using Raven 1.2 (Charif et al., 2004); spectrograms were generated using a Hann window with a time resolution of 5.33 ms, frequency resolution of 93.8 Hz, and transform length of 512 points. I took two different sets of measurements for each song to characterize the fundamental frequencies of the song and its elements. The first set described the total song: song duration, low, high, and peak frequency (the frequency with the highest sound energy; in Raven 1.2 this measurement is called ‘Max Frequency’) (Figure 1); song rate (songs/min) was calculated based on the entire 5-min recording period.

The second set of measurements described each element of male song: duration, time between elements, and low, high, and peak frequency (Figure 1). I included the second set of measurements in the analysis in case there was a trade-off between temporal (e.g., element duration), and acoustical variables (e.g., frequency values) during the interactions, as found in other bird species with vocalizations that are thought to be honest signals (Gil & Gahr, 2002; Dolby et al., 2005).

Song bandwidth was not measured in this study to avoid introducing auto-correlated measures in the statistical analyses. The three frequency variables included in the analyses were uncorrelated ($p > 0.26$, for correlations among them). All recordings have been deposited at the Laboratorio de Bioacústica, Escuela de Biología, Universidad de Costa Rica.

2.3. Statistical analyses

For both sets of song measurements, an average value was calculated for each sampled individual. These values were used in all statistical analyses. I used a Chi-square test of independence to determine if the numbers of males in each behavioural category were different. I used a Multiple Analysis of Variance (MANOVA), to examine whether males in each behavioural category differed according to the five song measurements of the control song, number of singing neighbours, and the song response time. Using another MANOVA, I compared the differences between the control song measurements and the corresponding measurements of the stimulus song, between males that sang and did not sing after the playback. For both MANOVAs, I did an a posteriori analysis to determine which of the song measurements better predicted the approach behaviour or the probability of a male singing after playback. I used paired *t*-tests to compare the song measurements in the control song to the song measurements in the response songs.

3. Results

In total, I obtained control song (pre-playback) recordings for 30 spot-bellied bobwhite males, and recorded response (post-playback) songs for 23 of those males. Males were more likely to stay on the same perch during male playback (static male, $N = 17$), than to approach the speaker (male approach, $N = 9$), or the retreat from the singing perch (male retreat, $N = 4$)

($\chi^2 = 8.60$, $df = 2$, $p = 0.01$). The nine males that approached the speaker lifted their crests and stretch their necks as they began to approach, were static or retreating males did not display any significant body posture change according to the previous posture. These males never walked directly toward the speaker; instead they walked parallel or made a curve to arrive close (2–5 m) to the speaker.

The control songs of males that approached the speaker differed in several song measurements compared to static males and retreating males (MANOVA: $F_{14,26} = 2.79$, $p = 0.01$). The *a posteriori* analysis identified two measurements responsible for the differences. Males that approached the speaker had longer control songs ($F_{2,19} = 5.84$, $p = 0.01$) and took more time to sing the first response song ($F_{2,19} = 4.17$, $p = 0.03$) than males who left or remained on the singing perch (Table 1); approaching males did not sing while they moved toward the speaker. No other song measurements differed significantly ($p > 0.21$ for all posterior comparisons, Table 1).

The control songs of males that sang in response to playback differed from those of males that did not sing in response to playback (MANOVA: $F_{10,48} = 12.93$, $p < 0.001$, Table 2). In *a posteriori* analysis, males that sang had higher peak frequencies and song rate, and longer songs, but lower values of low frequency than males that did not sing. High frequency measurements did not differ between groups (Table 2).

Table 1. Song measurements of control (pre-playback) song, number of singing neighbouring males, and time to first song following playback, as a function of approach behaviours in response to playback.

Measure	Approach	Stay	Retreat
Duration (s)	0.81 ± 0.13*	0.76 ± 0.13*	0.75 ± 0.29*
Low freq. (Hz)	1153.50 ± 199.94	1119.98 ± 277.97	1009.47 ± 442.00
High freq. (Hz)	2513.12 ± 374.00	2659.99 ± 257.64	2930.13 ± 869.65
Peak freq. (Hz)	1748.92 ± 87.13	1777.50 ± 93.25	1766.26 ± 108.43
Song rate (songs/min)	1.84 ± 1.18	2.39 ± 1.44	2.35 ± 1.72
Other males	0.89 ± 0.78	0.82 ± 0.95	1.50 ± 1.29
Response time (s)	106.50 ± 90.31*	33.82 ± 35.71*	15.33 ± 4.72*

Values are average ± standard deviation.

Asterisks indicate that comparisons between approach categories were statistically significant.

Table 2. Song measurements and values of a posteriori comparisons between each control (pre-playback) song measure, according to male vocal response (sing or not) toward playback.

Measure	Not-sing	Sing	$F_{2,28}$	p
Duration (s)	0.65 ± 0.13	0.81 ± 0.14	26.24	<0.001
Low frequency (Hz)	1242.57 ± 169.15	1076.57 ± 292.40	5.98	0.007
High frequency (Hz)	2646.23 ± 282.66	2653.69 ± 449.97	2.25	0.120
Peak frequency (Hz)	1748.85 ± 88.51	1773.08 ± 92.88	11.06	<0.001
Song rate (songs/min)	1.51 ± 1.29	2.43 ± 1.36	44.33	<0.001

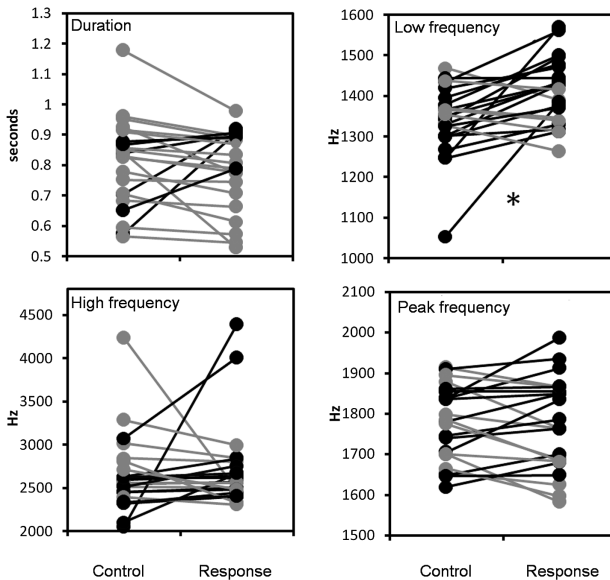


Figure 3. Comparison of a spot-bellied bobwhite male's control (pre-playback) song and his song produced in response to a simulated territorial intrusion ($*p < 0.05$). Grey lines and points represent a decrease in the comparisons, and black colours represent an increase in comparison between control and response songs.

Comparing a male's control song to his own songs given in response to playback showed that males increased the low frequency ($t = -3.15$, $df = 22$, $p = 0.004$, Figure 3) of their songs. They did not significantly alter their song duration ($t = 0.73$, $df = 22$, $p = 0.47$), the high frequency ($t = 1.27$, $df = 22$, $p = 0.22$), or the peak frequency of their songs ($t = -0.007$, $df = 22$, $p = 0.99$, Figure 3). Examining each song element

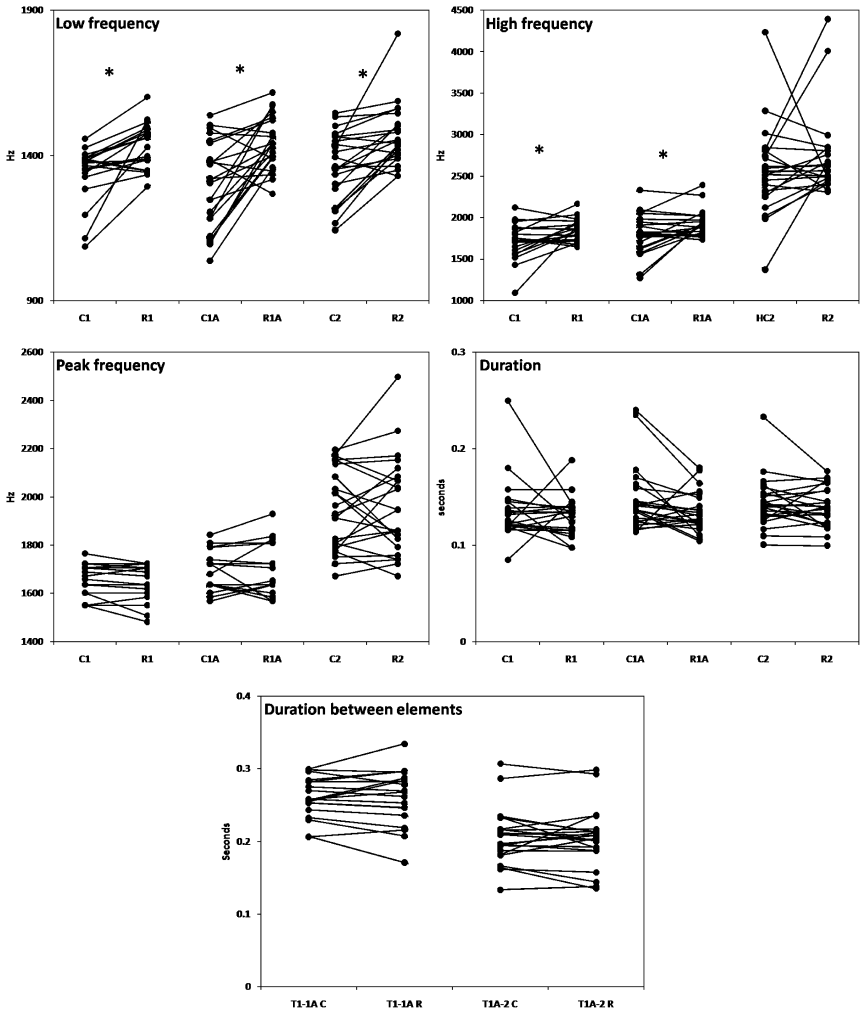


Figure 4. Comparison of control (C, pre-playback) and response (R, after playback) song for each song element measured and the interval between elements (T1-1A and T1A-2) (* $p < 0.05$). For element names, see Figure 1.

separately, males increased the low frequency in all three song elements in response to playback (element 1: $t = -3.73$, $df = 19$, $p = 0.001$; element 1A: $t = -4.36$, $df = 22$, $p < 0.001$; and element 2: $t = -4.22$, $df = 22$, $p < 0.001$, Figure 4), and they increased the high frequency in the two first elements (element 1: $t = -2.74$, $df = 19$, $p = 0.02$; and element 1A: $t = -1.27$, $df = 22$, $p = 0.01$, Figure 4). The values of the other

eight measurements did not differ significantly between control and response songs (paired *t*-test: $p > 0.05$ for all comparisons, Figure 4).

4. Discussion

Responses of spot-bellied bobwhite males toward simulated territorial intrusions depended on the qualities of the territorial male's song relative to the playback stimulus. These results suggest the perception of intruder song characteristics play an important role in the response behaviour and song in this quail species, similar to what has been observed in the California Quail and the Gambel's Quail (Gee, 2005; Gee et al., 2009).

Not all spot-bellied bobwhite males sang in response to simulated male intrusion. Males that responded with song had control songs with higher peak frequency, longer song duration, and lower low frequency than the playback song. Also the presence of eavesdropping females might influence a territorial male's decision of whether or not to sing in response to an intruder (Longue & Forstmeier, 2008), where males have the option of singing only if their song compares well to an intruder's.

Bobwhite males that responded vocally to playback song also consistently changed several song and song element measurements in their response songs compared to their control songs. Unlikely to many passerine species (Collins, 2004; Price et al., 2006; Catchpole & Slater, 2008), the bobwhite males increased the value of the low frequency in the whole song and in each song element. An increase in the low frequency was reported as an aggressive signal in the Collared Dove (Slabbekoorn & ten Cate, 1997), because only large, aggressive males that are more motivated to fight produce this increase (Slabbekoorn & ten Cate, 1997). Similarly in roosters, dominant males produce vocalizations with higher low frequency during male–male interactions, reducing the probability of fights with less dominant males (Leonard & Horn, 1995). Therefore, the tendency of a spot-bellied bobwhite male to increase the low frequency in his response songs to another male song within his territory may be a signal of dominance and/or male quality.

The high frequency in response song as a whole did not change compared to control song. In the analysis of each song element, however, the high frequency of the first two song elements increased. This increase, together with an increase in low frequency, suggests that males are singing these two elements in a higher frequency range. If the higher frequency range of these

song elements is challenging for bobwhite males to produce, it may serve as an indicator of quality, as is the case for song rate and repertoire size in other species (Gil & Gahr, 2002; Collins, 2004). An increase in song frequency requires an increase in energetic investment (Lambrechts, 1996), thus increasing the frequency in the first two elements of the response song may be an indication of male competitive ability (Collins, 2004). In species where song is an honest signal during male–male interactions, changes in frequency and temporal characteristics have also been reported (Lampe, 1991; Smith, 1996; Collins, 2004). Therefore, the changes in song measurements observed in response songs of the spot-bellied bobwhite males suggest that song carries information about male physical characteristics (e.g., body size) and/or behaviour (e.g., motivation to fight).

During playback trials, the majority of focal males remained on their singing perches; approaches toward the speaker were made by only a few males. Approach behaviour is related to fight motivation in other playback experiments (Collins, 2004; Searcy & Beecher, 2009) and, therefore, it is not expected that all males should display this behaviour. Fighting is energetically expensive, and may increase vulnerability to predators and probability of injuries (Andersson, 1994; Collins, 2004). Due to these costs, high quality males may be more likely to fight, because they are better able to afford the costs than low-quality males. This could explain my observation that males that approached the speaker had longer songs. Although song production only requires slightly more energy than other physical activities or vocal behaviours (Horn et al., 1995; Oberweger & Goller, 2001), producing longer songs constantly during the breeding season requires more energy than producing shorter songs (Gil & Gahr, 2002). Thus, male song length may serve as an honest indicator of male quality. Also, longer song elements have been related to higher levels of testosterone in the grey partridge (*Perdix perdix*; Fusani et al., 1994), and more motivation to fight in the barn swallow (*Hirundo rustica*; Galeotti et al., 1997).

Neither pre-playback song rate, nor any of the song frequency measurements in the current study explained the male approach behaviour toward the speaker, but may explain the probability of a male singing in response to a territorial intrusion. Therefore, in this bobwhite, these vocal features may be related to male physical attributes as observed in many other species (Collins, 2004). For example, in northern bobwhite (Goldstein, 1978) and grey partridge (Beani & Dessi-Fulgheri, 1995), two close relatives to the spot-bellied

bobwhite, larger males produce vocalizations with lower frequencies. Additionally, song rate (Galeotti et al., 1997), and song duration (Fusani et al., 1994), are positively correlated with higher levels of testosterone in males in some bird species.

Males that approached took a longer time to sing in response to playback because they did not sing as they were approaching the speaker. Approaching silently may prevent the intruder from locating the resident male during his approach. This behaviour is consistent with the indirect way that males approached the speaker. Although males that approach are probably more motivated to fight, these ‘shy’ approach behaviours may suggest that fighting is a dangerous activity, so males try to avoid it if possible. Alternatively, the territorial male may try to attack the intruder suddenly to avoid injury and a longer fight. The behaviour of lifting the crest during the approach may be an excitation signal, which occurs in other birds (Stokes, 1962; Searcy & Nowicki, 2005) in preparation to closer male interactions. Lifting the neck may be a response to the vegetation height in the study area at ground level (10–30 cm), in an effort to visually locate the intruder, rather than to increase perceived body size.

To summarize the behaviours used in male–male interaction in spot-bellied bobwhite males, I propose the escalated threat behaviours (Figure 5): (1) The intruder enters in the territory and starts to sing. The resident male only responds to the intruder by singing if his songs are ‘better’, as defined above, than the songs of the intruding male. (2) The male approaches the intruder without singing, to avoid being detected and attacked. (3) Once the owner is in close proximity to the intruder, he sings songs that have higher values of low frequency and higher pitch in the first two elements of the song. (4) I did not test whether the third step is the last step and includes the fight, or whether the males use a last cue or cues (e.g., size) to evaluate another male before attacking. To test this last point, it would be necessary to use a stuffed model or a live male in a cage combined with playback. Based on my own observations of male fights in the field ($N = 2$), approach behaviour leads to fights, and the loser male retreats the territory.

In conclusion, song plays an important role in male–male interactions in spot-bellied bobwhites and apparently encodes information about male motivational state and/or quality. Additionally, I found that certain song features in male songs predicted focal male’s responses during singing interactions. The observed responses may be the result of previous experiences

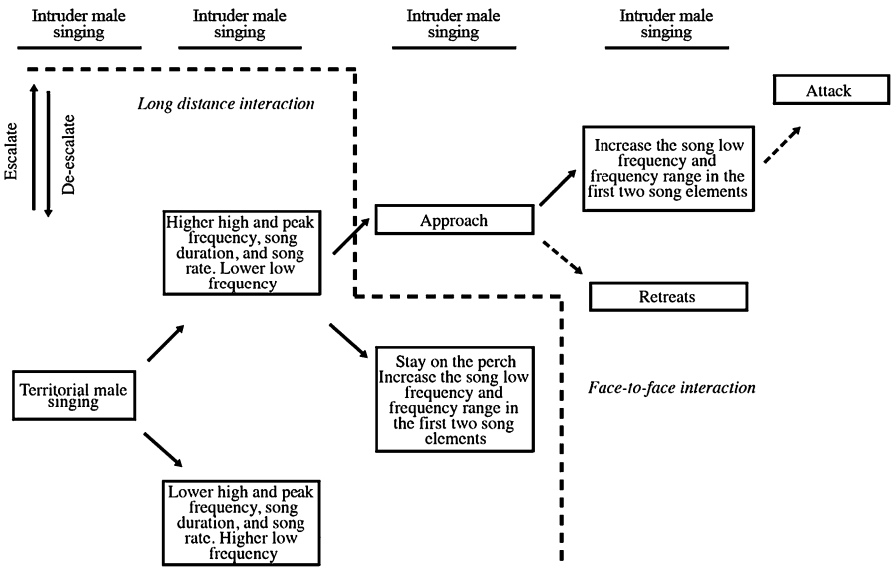


Figure 5. Diagram of interactions between a territorial male spot-bellied bobwhite and an intruder male. The dashed line separates the long distance interactions from the close distance interactions, which both occur inside the territory. Response behaviours (song characteristic and male behaviour) of territorial male are indicated in the boxes: escalation in response is indicated by boxes higher in the diagram and de-escalation by boxes lower in the diagram. The male–male interaction begins inside the territory of the resident male when the intruder starts to sing (upper solid line), likely without visual contact and change the song characteristics. Interaction escalates when the resident male approaches the intruder avoiding be detected (to the right of the dashed line), and sings a few meters from the intruder that continue singing (upper solid lines). The spot-bellied bobwhite signalling system depends on the frequency and time characteristics in the song and how it changes. Solid arrows represent the responses observed during the experiment. Dashed arrows represent hypothetical responses not observed in the experiment due the experimental design.

between bobwhite males, because the perception of song can be learned even in species where song is genetically determined such as sub-oscines and non-passerine birds (Gee, 2005; Gee et al., 2009; Tobias & Seddon, 2009).

Acknowledgements

I wish to thank G. Barrantes, W. Eberhard and Edgardo Arévalo for providing advice on design and analysis of this work. I also wish to thank D. Wilson, J. Chaves-Campos, V. Ruiz-Gutierrez, Julie Koloff, Becky Cramer, Scott MacDougall-Shackleton, and three anonymous reviewers for helpful suggestions on earlier versions of the manuscript. The equipment used in this research was funded by IdeaWild.

References

- Andersson, M. (1994). Sexual selection. — Princeton University Press, Princeton, NJ.
- Arcese, P. (1987). Age, intrusion pressure and defence against floaters by territorial male song sparrows. — *Anim. Behav.* 35: 773-784.
- Beani, L. & Dessi-Fulgheri, F. (1995). Mate choice in the grey partridge, *Perdix perdix*: role of physical and behavioural male traits. — *Anim. Behav.* 49: 347-356.
- Beecher, M.D., Campbell, S.E., Burt, J.M., Hill, C.E. & Nordby, J.C. (2000). Song-type matching between neighbouring song sparrows. — *Anim. Behav.* 59: 21-27.
- Beecher, M.D., Stoddard, P.K., Campbell, S.E. & Horning, C.L. (1996). Repertoire matching between neighbouring song sparrows. — *Anim. Behav.* 51: 917-923.
- Bertelli, S. & Tubaro, P.L. (2002). Body mass and habitat correlates of song structure in a primitive group of birds. — *Biol. J. Linn. Soc.* 77: 423-430.
- Botero, C.A. & Vehrencamp, S.L. (2007). Responses of male tropical mockingbirds (*Mimus gilvus*) to variation in within-song and between-song versatility. — *Auk* 124: 185-196.
- Bradley, D.W. & Mennill, D.J. (2009). Strong ungraded responses to playback of solos, duets and choruses in a cooperatively breeding neotropical songbird. — *Anim. Behav.* 77: 1321-1327.
- Brennan, L.A. (1999). Northern bobwhite (*Colinus virginianus*). — In: The birds of North America online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY. Available online at <http://bna.birds.cornell.edu/bna/species/397>
- Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. — *J. Anim. Ecol.* 73: 434-440.
- Brumm, H. & Todt, D. (2004). Male–male vocal interactions and the adjustment of song amplitude in a territorial bird. — *Anim. Behav.* 67: 281-286.
- Buchanan, K. & Catchpole, C.K. (1997). Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality. — *Proc. Roy. Soc. Lond. B: Biol.* 264: 521-526.
- Burt, J.M., Campbell, S.E. & Beeche, M.D. (2001). Song type matching as threat: a test using interactive playback. — *Anim. Behav.* 62: 1163-1170.
- Calkins, J.D., Hagelin, J.C. & Lott, D.F. (1999). California quail (*Callipepla californica*). — In: The birds of North America online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY. Available online at <http://bna.birds.cornell.edu/bna/species/473>
- Capp, M.S. (1992). Tests of the function of the song repertoire in bobolinks. — *Condor* 94: 468-479.
- Catchpole, C.K. & Slater, P.J.B. (2008). Bird song biological themes and variations. — Cambridge University Press, Cambridge.
- Charif, R., Clark, C. & Fristrup, K. (2004). Raven 1.2 user's manual. — Cornell Laboratory of Ornithology, Ithaca, NY.
- Collins, S. (2004). Vocal fighting and flirting: the functions of birdsong. — In: Nature's music, the science of birdsong (Marler, P. & Slabbekoorn, H., eds). Elsevier Academic Press, San Diego, CA, p. 40-79.
- Dabbert, C.B., Pleasant, G. & Schemnitz, S.D. (2009). Scaled quail (*Callipepla squamata*). — In: The birds of North America online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY. Available online at <http://bna.birds.cornell.edu/bna/species/106>
- Dabelsteen, T., McGregor, P., Holland, J., Tobias J. & Pedersen, S. (1997). The signal functions of overlapping singing in male robins. — *Anim. Behav.* 53: 249-256.

- de Kort, S.R., Eldermire, E.R.B., Valderrama, S., Botero, C.A. & Vehrencamp, S.L. (2009). Trill consistency is an age-related assessment signal in banded wrens. — *Proc. Roy. Soc. Lond. B: Biol.* 276: 2315-2321.
- Dolby, A., Clarkson, C., Haas, E., Miller, J., Havens, L. & Cox, B. (2005). Do song-phrase production rate and song versatility honestly communicate male parental quality in the gray catbird? — *J. Field Ornithol.* 76: 287-292.
- Ellis, J.M.S. (2008). Decay of apparent individual distinctiveness in the begging calls of adult female white-throated magpie-jay. — *Condor* 110: 648-657.
- Fusani, L., Beani, L. & Dessi-Fulgheri, F. (1994). Testosterone affects the acoustic structure of male call in the grey partridge (*Perdix perdix*). — *Behaviour* 128: 301-310.
- Galeotti, P., Saino, N., Sacchi, R. & Møller, A.P. (1997). Song correlates with social context, testosterone and body condition in male barn swallows. — *Anim. Behav.* 53: 687-700.
- Garamszegi, L., Heylen, D., Møller, A.P., Eens, M. & de Lope, F. (2005). Age-dependent health status and song characteristics in the barn swallow. — *Behav. Ecol.* 16: 580-591.
- Gee, J.M. (2005). No species barrier by call in an avian hybrid zone between California and Gambel's quail (*Callipepla californica* and *C. gambelii*). — *Biol. J. Linn. Soc.* 86: 253-264.
- Gee, J.M., Tomaszycki, M.L. & Adkins-Regan, E. (2009). Sex-dependent species discrimination in auditory forebrain of naturally hybridizing birds. — *Brain Behav. Evol.* 74: 258-267.
- Gil, D. & Gahr, M. (2002). The honesty of bird song: multiple constraints for multiple traits. — *Trends Ecol. Evol.* 17: 133-141.
- Goldstein, R.B. (1978). Geographic variation in the "ho-y" call of the bobwhite. — *Auk* 95: 85-94.
- Hurlbert, S.H. (1984). Pseudoreplication and design of ecological field experiments. — *Ecol. Monogr.* 54: 187-211.
- Johnston, D. (1999). Cool Edit 2000. — Syntrillium Software, Phoenix, AZ.
- Kipper, S., Mundry, R., Sommer, C., Hultsch, H. & Todt, D. (2006). Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. — *Anim. Behav.* 71: 211-217.
- Kroodsma, D.E., Byers, B.E., Goodale, E., Johnson, S. & Lui, W.C. (2001). Pseudoreplication in playback experiments, revisited a decade later. — *Anim. Behav.* 61: 1029-1033.
- Lambrechts, M.M. (1996). Organization of birdsong and constraints on performance. — In: Ecology and evolution of acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Cornell University Press, Ithaca, NY, p. 305-320.
- Lampe, H.M. (1991). The response of male redwing *Turdus iliacus* to playback of conspecific songs with or without the terminating twitter. — *Ornis Scand.* 22: 137-142.
- Leitão, A. & Riebel, K. (2003). Are good ornaments bad armaments? Male chaffinch perception of songs with varying flourish length. — *Anim. Behav.* 66: 161-167.
- Leonard, M.L. & Horn, A.G. (1995). Crowing in relation to status roosters. — *Anim. Behav.* 48: 1283-1290.
- Logue, D.M. & Forstmeier, W. (2008). Constrained performance in a communication network: implications for the function of song-type matching and for the evolution of multiple ornaments. — *Am. Nat.* 172: 34-41.
- Marshall-Ball, L., Mann, N. & Slater, P.J.B. (2006). Multiple functions to duet singing: hidden conflicts and apparent cooperation. — *Anim. Behav.* 71: 823-831.

- Martin, K. (1984). Reproductive defense priorities of male willow ptarmigan (*Lagopus lagopus*): enhancing mate survival or extending paternity options? — Behav. Ecol. Sociobiol. 16: 57-63.
- Mennill, D.J. (2006). Aggressive responses of male and female rufous-and-white wrens to stereo duets playback. — Anim. Behav. 71: 219-226.
- Morton, E.S. & Young, K. (1986). A previously undescribed method of song matching in a species with a single song “type”, the Kentucky warbler (*Oporonis formosus*). — Ethology 73: 334-342.
- Oberweger, K. & Goller, F. (2001). The metabolic costs of bird song production. — J. Exp. Biol. 204: 3379-3388.
- O’Loughlen, A. & Rothstein, S. (1995). Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. — Behav. Ecol. Sociobiol. 36: 251-259.
- Otter, K., McGregor, P.K., Terry, A.M.R., Burford, F.R.L., Peake, T.M. & Dabelsteen, T. (1999). Do female great tits *Parus major* assess males by eavesdropping? A field study using interactive song playback. — Proc. Roy. Soc. Lond. B: Biol. 266: 1305-1309.
- Petrie, M., Halliday, T. & Sanders, C. (1991). Peahens prefer peacocks with elaborate trains. — Anim. Behav. 41: 323-331.
- Price, J.J., Earnshaw, S.M. & Webster, M.S. (2006). Montezuma oropendolas modify a component of song constrained by body size during vocal contests. — Anim. Behav. 71: 799-807.
- Rehsteiner, U., Geisser, H. & Reyer, H. (1998). Singing and mating success in water pipits: one specific song element makes all difference. — Anim. Behav. 55: 1471-1481.
- Reid, M.L. (1987). Costliness and reliability in the singing vigour of Ipswich sparrow. — Anim. Behav. 35: 1735-1743.
- Ryan, M.J. & Brenowitz, E.A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. — Am. Nat. 126: 87-100.
- Sandoval, L. (2008). Función del canto y el territorio en machos de la codorniz de monte *Colinus leucopogon* (Odontophoridae: Aves) durante el periodo reproductivo. — MSc thesis, Universidad de Costa Rica, Montes de Oca.
- Sandoval, L. (2009). Descripción del comportamiento de cuidado parental en la Codorniz de Monte (*Colinus leucopogon*). — Int. J. Galliformes Cons. 1: 36-40.
- Sandoval, L. (2011a). Inicio de la época reproductiva y permanencia territorial en machos de *Colinus leucopogon* (Galliformes: Odontophoridae). — Rev. Biol. Trop. 59: 363-372.
- Sandoval, L. (2011b). Crested bobwhite (*Colinus cristatus*). — In: Neotropical birds online (Schulenberg, T.S., ed.). Cornell Lab of Ornithology, Ithaca, NY. Available online at http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=85511
- Searcy, W.A. & Beecher, M.D. (2009). Song as an aggressive signal in songbirds. — Anim. Behav. 78: 1281-1292.
- Searcy, W.A. & Nowicki, S. (2005). The evolution of animal communication: reliability and deception in signaling systems. — Princeton University Press, Princeton, NJ.
- Slabbekoorn, H., Eilers, J. & Smith, T.B. (2002). Birdsong and sound transmission: the benefits of reverberations. — Condor 104: 564-573.
- Slabbekoorn, H. & ten Cate, C. (1997). Stronger territory response to frequency modulated coos in collared doves. — Anim. Behav. 135: 879-895.

- Smith, W.J. (1996). Using interactive playback to study how songs and singing contribute to communication about behavior. — In: Ecology and evolution of acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Comstock Publishing Associates, Ithaca, NY, p. 377-397.
- Stokes, A.W. (1962). Agonistic behaviour among blue tits at a winter feeding station. — Behaviour 19: 118-138.
- Stokes, A.W. (1967). Behavior of the bobwhite, *Colinus virginianus*. — *Auk* 84: 1-33.
- Studd, M.V. & Robertson, R.J. (1988). Differential allocation of reproductive effort to territorial establishment maintenance by male yellow warblers (*Dendroica petechia*). — Behav. Ecol. Sociobiol. 23: 199-210.
- Ten Cate, C., Slabbekoorn, H. & Ballintijn, M.R. (2002). Birdsong and male–male competition: causes and consequences of vocal variability in the collared dove (*Streptopelia decaocto*). — *Adv. Stud. Behav.* 31: 31-75.
- Tobias, J.A. & Seddon, N. (2009). Signal design and perception in *Hypocnemis* antbirds: evidence for convergent evolution via social selection. — *Evolution* 63: 3168-3189.
- Wilson, D.R. & Mennill, D.J. (2010). Black-capped chickadees, *Poecile atricapillus*, can use individually distinctive songs to discriminate among conspecifics. — *Anim. Behav.* 79: 1267-1275.
-