ORIGINAL ARTICLE

Characteristics of male Spot-bellied Bobwhite (*Colinus leucopogon*) song during territory establishment

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Abstract In song-learning birds, male song shows a large inter-individual variation that frequently plays an important role in intra- and inter-sexual selection. In other bird groups, such as Galliformes, song learning is absent, and inter-individual song variation is small and expected to play a minor, if any, role in sexual contexts. In the Spot-bellied Bobwhite (*Colinus leucopogon*) we found that many males have a unique set of song features, and our results suggest that female mate choice in this species is based in part on male song traits. Most paired males in our study had longer songs. In addition, these males established territories in the middle of the breeding season, soon after the onset of the rainy season when increases in herbaceous cover and food resources would likely increase offspring and adult survival.

Keywords Galliformes · Reproductive season · Song variation · Spot-bellied Bobwhite · Territory characteristics

Zusammenfassung

Gesangsmerkmale männlicher Fleckenwachteln (*Colinus leucopogon*) während der Reviergründung

Bei Vogelarten, die Gesangslernen zeigen, weist der Gesang der Männchen eine große individuelle Variation auf, welche häufig eine wichtige Rolle bei der intra- und inter-sexuellen Selektion spielt. Andere Vogelgruppen wie die Hühnervögel (Galliformes) lernen keine Gesänge; die individuelle Variation der Gesänge ist hier gering und spielt zwischen den Geschlechtern vermutlich kaum eine Rolle. Bei der Fleckenwachtel (*Colinus leucopogon*) besitzen dagegen viele Männchen ein individuelles Gesangsrepertoire. Die Ergebnisse dieser Studie weisen darauf hin, dass bei dieser Art die Weibchen ihren Partner zum Teil nach Gesangsmerkmalen wählen. Die meisten verpaarten Männchen hatten längere Gesangsstrophen. Außerdem besetzten diese Männchen ihre Reviere mitten in der Brutsaison, wenn kurz nach dem Beginn der Regenzeit die Zunahme der Krautschicht und der Nahrungsverfügbarkeit die Überlebenswahrscheinlichkeit von Jung- und Altvögeln erhöht.

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Introduction

In song-learning birds, male song is often extremely variable, and in many species males have large repertoires, with each individual often having a unique array of song types (Cicero and Benowitz-Fredericks 2000; Kipper et al. 2006). Male song types may vary in structural (e.g., number and elements arrangement) and acoustic characteristics (e.g., frequency range) among individuals of the same population (Kroosdma et al. 2002; Barrantes et al. 2008). Large repertoires and individual song arrays in song-learning birds apparently evolved through sexual selection by intra-sexual competition and female choice (Peek 1972; Smith 1979; Fedy and Stutchbury 2005; Walcott et al. 2006), and in many species females assess the quality of their potential mates via song (Capp 1992;

Andersson 1994; Goodson and Adkins-Regan 1997; Ballentine et al. 2003; King et al. 2003; Dolby et al. 2005; Garamszegi et al. 2005; Hosoi et al. 2005; Spencer et al. 2005; Tomaszycki and Adkins-Regan 2005; Kipper et al. 2006; Ballentine 2009).

Male song plays an important role in establishing and defending territories in numerous song-learning birds (Krebs et al. 1978; Morse 1980; Beecher et al. 1994; Atkinson 1997; Gil and Gahr 2002). In many of these species, males with higher vocalization rates (Alatalo et al. 1990) and with a higher number of elements in their songs (Kipper et al. 2006) establish their territories and pair with females sooner than males with lower quality songs. By establishing territories early in the breeding season, males are able to increase the probability of selecting a better territory, resulting in higher reproductive success (Catchpole 1980; Eens et al. 1991; Lozano et al. 1995).

In the members of the Phasianidae and Meleagridae families (Galliformes) that have been studied to date, male song plays little or no role in intra- or inter-sexual selection (Vehrencamp et al. 1989; Beani and Dessi-Fulgheri 1995). Instead, body parts (e.g., combs, tail length), body size, and visual displays, all of which vary among males, are more often involved in male–male competition and female choice (Vehrencamp et al. 1989; Zuk et al. 1990; Alatalo et al. 1991; Holder and Montgomerie 1993; Zahavi and Zahavi 1997). There are, however, exceptions within the Galliformes, including a number of tetraonids (grouse family), in which acoustic signals are used in conjunction with visual signals in male–male competition and female choice contexts (Wiley 1974; Gibson and Bradbury 1985; Vehrencamp et al. 1989), and the Grey Partridge, in which females select males with higher pre-choice song rates (Beani and Dessi-Fulgheri 1995).

Among Galliformes, species of the neotropical wood-quail family Odontophoridae have only minor differences in plumage, body size, and crests between sexes (Carroll 1994; Madge and McGowan 2002). Neotropical odontophorid species inhabit either mature forests or dense secondary growth areas where visual contact may be difficult, and acoustic communication becomes relatively more important (Hale 2006a, b; Sandoval 2009, 2011a). In some species of this family, such as the Northern Bobwhite, Crested Bobwhite, California Quail, and Scaled Quail, males sing frequently during the breeding season (Stokes 1967; Brennan 1999; Calkins et al. 1999; Dabbert et al. 2009; Pérez 2000; Sandoval 2008, 2011b), suggesting that male song may play a role in intra-sexual competition and female choice in these birds.

Our study species is the Spot-bellied Bobwhite (*Colinus leucopogon*: Odontophoridae), a terrestrial species that occurs in dense, secondary growth areas and abandoned coffee plantations. During the non-breeding period, individuals of both sexes form coveys of up to 20 individuals (Sandoval 2011b). These coveys disband prior to the breeding season (March–October) and soon after, males begin to sing at ground level or from low perches above the ground. This is an exclusive male behavior that signals the beginning of the breeding season and whose function is possibly to establish territories and attract females (Leber 1975; Sandoval 2008, 2011a). Males cease singing after pairing and then initiate the searching of a nesting site (Sandoval 2008, 2011a). The egg-laying period spans from 10 to 15 days, depending on egg number, followed by a 21- to 23-day incubation period (Sandoval 2011b). Males lack extravagant morphological traits and are socially monogamous during the breeding season (Leber 1975; Madge and McGowan 2002; Sandoval 2011a, b). After breeding, both parents contribute to offspring care (Sandoval 2008, 2009). In our study we addressed two questions: Is there variation in song in the Spot-bellied Bobwhite? And if songs are variable, is this variation associated with territory establishment and female choice? We predicted that: (1) if male song plays an important role in territory establishment and female choice, then songs should vary among males; (2) if male pairing success is correlated with some particular song characteristic, then male song could reflect male quality. We additionally measured characteristics of males' territories and associated these with pairing success.

Methods

Study area

We conducted this study between March and October 2005 and 2006, at Getsemaní, Heredia province, Costa Rica (10°01′N, 84°06′W; 1,300 m a.s.l.). Annual rainfall averages 2,000 mm with a dry season from December to April (Sandoval 2011a). The 30-ha study area comprises pastures with isolated trees (18 ha) and shade coffee plantations (12 ha). We recorded adult male Spot-bellied Bobwhite songs within 50 m of a 3-km transect from 0700 to 1100 hours every week during the study period, alternating the starting point of the transect. Singing males were considered to be territorial if (1) they were observed singing continually for at least 5 min without abandoning an area of a 5-m radius around the main singing perch (the perch most frequently used by a singing male) and (2) the same singing perches were used for 1–9 consecutive weeks. In contrast, singing non-territorial males moved from perch to perch between song bouts and were not observed at the same perches from 1 week to the next. We arbitrarily defined a male's territory as a circle of radius 25 m around the main singing perch. This is the distance

Fig. 1 Spectrograms of two singing Spot-bellied Bobwhite (*Colinus leucopogon*) males. The first male (**a**) has two elements in his song, and the second male (**b**) has three elements due to repetition of the first element. Part of the silent time between two consecutive songs was eliminated to show the two songs of each male. *HF* High frequency, *LF* low frequency, ΔT song duration
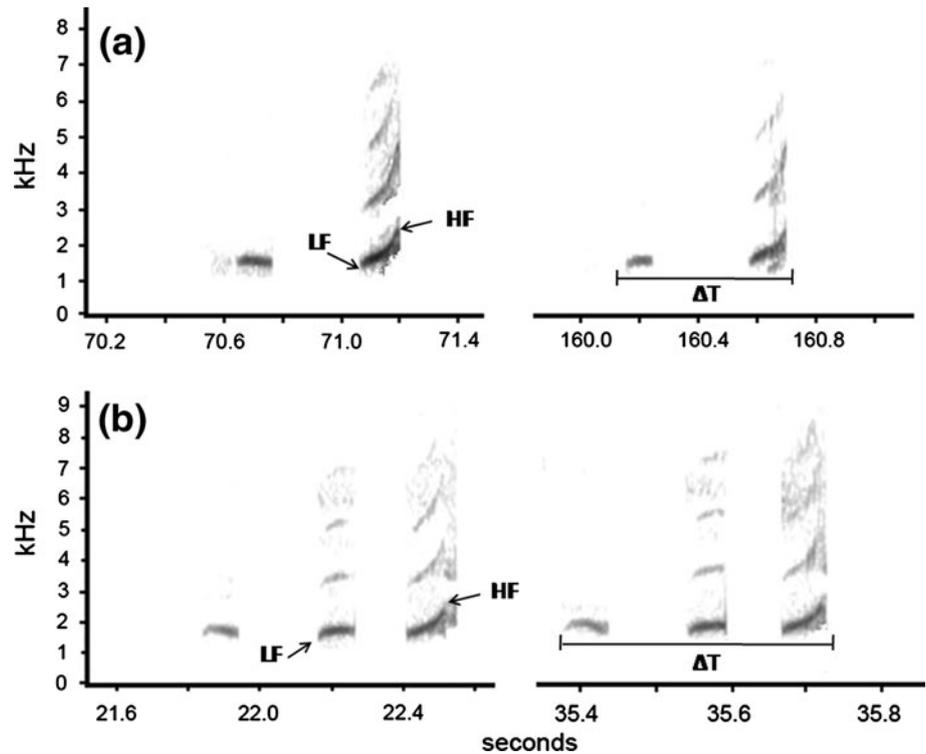
between the two closest main singing perches of two territorial males we observed in this study and is similar to the distance between nearby males reported by Leber (1975).

Males were not banded, but if a male was using the same singing perches during subsequent weeks we considered it as the same individual, based on the high improbability that different males would use exactly the same perch week after week in a single territory (Barrantes et al. 2008; Fitzsimmons et al. 2008). After territory establishment, we searched for a female within each male's territory for 30–40 min each week for up to 4 weeks. A male was considered paired if he was observed with a female in his territory and was no longer singing. If a male was not seen or heard in his territory for three consecutive weeks after initial territory establishment, we assumed that the male had abandoned the territory and therefore placed him in the unpaired group for statistical analyses. This last assumption may have resulted in an overestimation of the number of unpaired males.

Song measurements

We recorded all singing Spot-bellied Bobwhite males in the study area each year. Each male was recorded only the first week that he was heard singing; all recordings were conducted under a clear sky or under partially cloudy conditions. Since males were not individually marked, this sampling procedure reduces the probability of recording the same male more than once in the same breeding season,

although it does not reduce the probability of recording the same male between breeding seasons. To prevent the pseudoreplication of males across years, we analyzed each year independently. The song of males is stereotyped and consists of two or three different elements (Fig. 1). Each singing male was recorded for 5 min from a distance of 5–15 m, using a tape recorder (TCM-5000EV; Sony, Tokyo, Japan) and a ME 66 shotgun microphone (Sennheiser, Hanover, Germany). From each 5-min-long song bout, we randomly selected five high-quality songs (little reverberation) for analysis. For species with innate songs or with little variation in their songs, it has been shown that a small number of randomly selected songs are sufficient to reveal individual patterns of song features (Seddon 2005; Barrantes et al. 2008; Araya-Ajoy et al. 2009). We tested this assumption in a two-sample *t* test in which all song features analyzed in the five songs selected randomly (small sample) were compared against the total songs recorded for those birds with a sufficient sample size (≥ 10 songs recorded; $n = 14$); no significant differences in any of the variables were detected ($P > 0.12$ for all comparisons). For those males with five or fewer recorded songs, all songs were included in the analysis (one male had 4 songs, two had 2 songs, and one had only 1 song). Songs were digitalized at a sampling rate of 44,100 Hz and a resolution of 16 bits with the program Cool Edit 2000 ver. 1.0 (Johnston 1999); subsequent sound analysis was conducted using Raven 1.2 (Charif et al. 2004). From each song spectrogram, we measured the following variables: low frequency

(LF), high frequency (HF), frequency bandwidth (ΔF; difference between HF and LF), maximum frequency (MF; frequency that carry the highest energy), song duration (ΔT), and number of elements (Fig. 1). All recordings were deposited in the Laboratorio de Bioacústica, Escuela de Biología, Universidad de Costa Rica.

Territory features

To compare territory characteristics among males, we counted the number of potential singing perches (e.g., logs, rocks, and branches with a similar height and structural conditions to those used when males sing) and estimated the percentage cover of ramets of tall grass that were at least 25 cm tall and 30 cm in diameter, which represented the potential nesting area within each territory (Leber 1975; Stiles and Skutch 1989). We recorded these data during the first week a male was observed in his territory. Territories were not reused during the same breeding seasons, but in the second study year, six males established territories that overlapped with territories that had been occupied the previous season.

Statistical analyses

The within (CVw) and between (CVb) individual coefficient of variation was calculated each year for the acoustic and temporal variables of male songs ($n = 15$ males per year). Student t tests were used to compare the CVw and CVb means for each variable; $\alpha = 0.008$ was used to reject null hypotheses due to multiple comparisons. We also calculated the CVb/CVw ratio; a ratio >1 indicates that variation is larger between than within individuals, and a ratio >2 indicates that the variable analyzed may possess unique cues for individual recognition, as proposed Vignal et al. (2008) and Seddon and Tobias (2010).

A forward stepwise discriminant function analysis (DFA) was conducted to analyze the variation in acoustic and temporal song variables between males for each year ($n = 15$ males per year). We cross-validated each model to estimate the percentage of correct classifications produced by the DFA at each step using a Jackknife approach (Systat 11; Systat Software). The forward stepwise option excluded from the analysis those highly correlated variables that did not explain the between-individual variance, and cross-validation allowed us to obtain the model that best separated individuals. To analyze the relationship between acoustic and temporal characteristics of male song and time of territory establishment, we grouped males by month (grouping variable) and then conducted a DFA including only the five variables that best separated males based on their song characteristics. In addition, we calculated the centroid for each month using the first two canonical

variables and compared them between years. DFAs were calculated by year, rather than combining both years, to reduce pseudoreplication of males across years. We also compared territory characteristics between paired and unpaired males each year using the Kruskal–Wallis nonparametric analysis of variance (ANOVA).

The Akaike information criterion (AIC) was used to determine which model(s) constructed with ΔT, MF, and LF (the three variables that best separated male songs and contributed to separating males by month) best predict pairing success in males ($n = 6$ paired vs. $n = 9$ non-paired males from each year). We used male pairing success (yes or no) as dependent variable and the song features as independent variables to construct the models. We report the AIC value, and used the change in the small-sample-size corrected version (ΔAIC_c) for model selection (Burnham et al. 2011); models with ΔAIC_c values differing by ≤ 2 were considered to be equally parsimonious with the best supported model ($\Delta AIC_c = 0$). We also calculated the AIC_w, values which represent the model weight and are equivalent to the variance that explains each model (Richards et al. 2011).

Results

Songs from 15 males were recorded in each breeding season. In 2005, males established territories (i.e., began to sing) from March to September, with more males establishing their territories in August ($n = 4$). In 2006, males began to established territories from April through August, with more males establishing their territories in May ($n = 5$). Male song in this species has two or three harmonic elements (Fig. 1a, b). Combining data from both years, we found that five males had only two elements in their songs, 18 males had three elements in all songs, and seven males had three elements in a portion of their songs (3 males in 20% of songs; 2 males in 80% of songs; 1 male in 60% of songs; 1 male in 50% of songs).

The coefficient of variation between males (CVb) was significantly higher than within males (CVw) for two of the six variables (LF and MF) in 2005 and for three variables (ΔT, LF, and MF) in 2006 (Table 1). In 2005, the CVb/CVw ratios were >2 for only LF and MF; in 2006, the CVb/CVw ratios were >2 for ΔT, LF, and MF (Table 1).

In addition, a combination of five variables (number of elements, song duration, and LF, HF, MF) explained a significant proportion of between-male song variation in 2005 and 2006 (2005: Wilks' $\Lambda = 0.002$, $F_{70,237} = 9.26$, $P < 0.001$; 2006: Wilks' $\Lambda = 0.007$, $F_{70,218} = 9.26$, $P < 0.001$). These variables correctly classified 62% of all male songs in 2005 and 50% in 2006. The same acoustic and temporal variables significantly explained a large

Table 1 Coefficient of variation between and within males for six acoustic and temporal variables of the Spot-bellied Bobwhite male song

Variable	CVb	CVw	CVw/CVb ratio	t test[a]	P
2005					
Duration	0.14	0.09	1.56	1.64	0.01
Low frequency	0.23	0.03	8.01*	6.28	0.003*
High frequency	0.05	0.06	0.90	−0.39	0.70
Frequency bandwidth	0.19	0.12	1.65	2.63	0.02
Maximum frequency	0.36	0.02	16.48*	17.14	<0.001*
Elements	0.04	0.04	1.02	0.04	0.97
2006					
Duration	0.19	0.09	2.06*	3.17	0.006*
Low frequency	0.24	0.02	12.7*	16.96	<0.001*
High frequency	0.04	0.10	0.45	−2.74	0.01
Frequency change	0.08	0.23	0.35	−2.92	0.009
Maximum frequency	0.18	0.01	13.52*	2.52	0.006*
Elements	0.03	0.06	0.45	−1.21	0.25

* Song measurements that are significant according to CVb and CVw with an $\alpha = 0.008$ to reject null hypotheses due to multiple comparisons

CVw, CVb, Within and between individual coefficient of variation, respectively

[a] Degrees of freedom for t test are 18 in all cases

proportion of the variance among months in 2005 (Wilks' $\Lambda = 0.11$, $F_{30,230} = 5.67$, $P < 0.001$) and 2006 (Wilks' $\Lambda = 0.23$, $F_{25,205} = 4.02$, $P < 0.001$). Male songs recorded in the middle of the reproductive season were more similar to each other than songs recorded either early or late in the breeding season in both years (Fig. 2). On average, 1.5 paired males [standard deviation (SD) 1.06] and 2.25 unpaired males (SD 1.75) were recorded each month over the course of both breeding seasons. The features of male territories did not vary significantly across months ($P > 0.20$ in all cases): males perched at 1.32 m height (SD 1.40), and the territories had 9.43 bushes (SD 7.78), 8.31 rocks (SD 10.69), 1.62 logs (SD 1.74), and 91.37% of potential nesting area (SD 19.89).

Considering the three variables that have a major effect in separating males (ΔT, MF, LF; based on CVb/CVw ratio), successful males had longer songs (successful: mean 0.83 s, SD 0.03; unsuccessful: mean 0.75 s, SD 0.03; $F_{29,102} = 10.90$, $P < 0.001$), higher MF (successful: mean 1,792.5 Hz, SD 17.2; unsuccessful: mean 1,755.2 Hz, SD 16.2; $F_{29,102} = 21.46$, $P < 0.001$), and lower LF (successful: mean 1,359.1 Hz, SD 7.2; unsuccessful: mean 1,367.8 Hz, SD 12.6; $F_{29,102} = 8.14$, $P < 0.001$) than males that were unsuccessful in pairing with a female. However, from the set of models constructed with these three variables, the model that included only ΔT best predicted male pairing success in each year (Table 2). In contrast, the models constructed with LF, MF, and a combination of the three song features had very little support.

Fig. 2 Mean centroid of the first two canonical functions obtained with the discriminant function analysis (DFA) of male Spot-bellied Bobwhite song characteristics (LF, HF, maximum frequency, ΔT, and number of song elements) by month of the breeding season
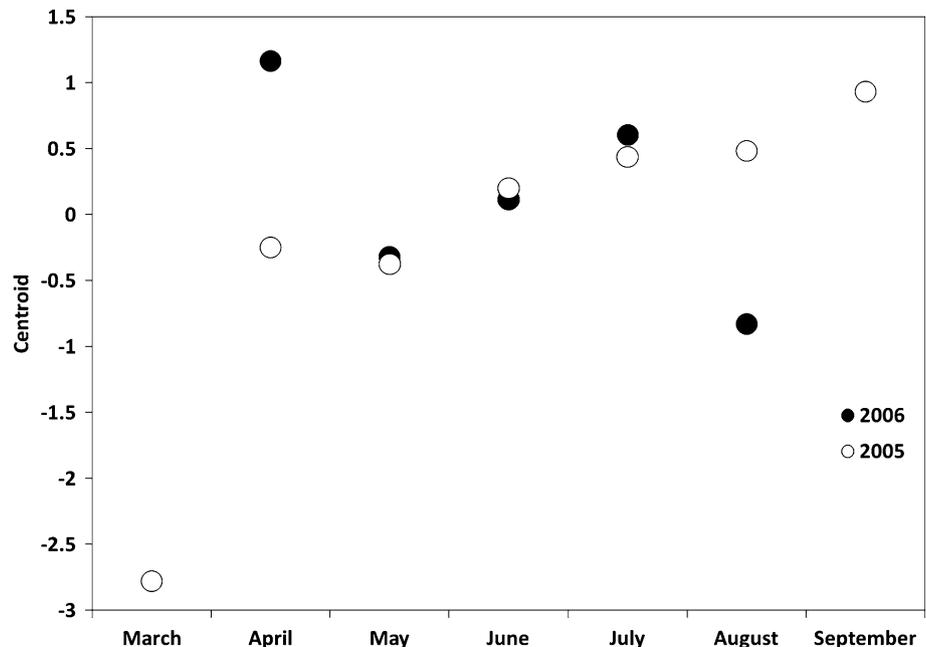
Model	Parameters	n	AIC	ΔAIC_c	AIC_w
2005					
ΔT	**3**	**15**	**−28.69**	**0**	**0.99**
LF	3	15	−6.97	21.72	<0.001
ΔT + LF	4	15	−5.07	25.44	<0.001
MF	3	15	5.73	34.42	<0.001
LF + MF	4	15	6.44	36.95	<0.001
ΔT + MF	4	15	6.63	37.13	<0.001
All	5	15	7.31	40.48	<0.001
2006					
ΔT	**3**	**15**	**−14.8**	**0**	**0.99**
LF	3	15	9.97	24.77	<0.001
ΔT + LF	4	15	11.75	28.37	<0.001
MF	3	15	12.35	27.14	<0.001
LF + MF	4	15	15.42	32.04	<0.001
ΔT + MF	4	15	22.31	38.92	<0.001
All	5	15	25.82	45.11	<0.001

Discussion

In Galliformes, body size, plumage, coloration, spurs, comb size, and coloration of combs have been demonstrated to play an important role in inter- and intra-sexual selection (Zuk et al. 1990; Alatalo et al. 1991; Holder and Montgomerie 1993; Zahavi and Zahavi 1997; Hagelin 2002), while vocalizations have been thought to be relatively unimportant (Vehrencamp et al. 1989; Leonard and Horn 1995; Wilson et al. 2008). Nevertheless, our findings show that temporal and acoustic characteristics of the song did vary among Spot-bellied Bobwhite males and that those males possessing certain variants were more successful in pairing with females than males without those variants. The role of male song in courtship and territorial interactions in this species is possibly associated with the cryptic coloration, limited sexual dimorphism, and often secretive behavior of the species comprising family Odontophoridae. This neotropical group of birds inhabits dense secondary growth vegetation and the understory of mature forests where vocalizations likely play an important role in different communication contexts (Hale 2006b; Sandoval 2009, 2011a).

Sexual selection theory predicts that females should select males based on traits that indicate quality and vary between high- and low-quality males (Zuk et al. 1990; Petrie et al. 1991; Andersson 1994). Male song traits are often used by females of many song-learning birds to evaluate male quality and directly influence female choice (Dolby et al. 2005; Kipper et al. 2006; Mennill et al. 2006). In the Spot-bellied Bobwhite of our study, females paired chiefly with males that had longer songs. The capability to produce longer songs has been demonstrated to increase energetic cost in other birds and seems to play an important role in mating success (Lambrechts 1996; Smith 1996; Oberweger and Goller 2001; Gil and Gahr 2002; Collins 2004). Hence, it is possible that female sexual selection in Spot-bellied Bobwhites may operate on traits that demonstrate variation and, therefore, might be distinctive between males of high and low quality. Our study is the first to suggest that song traits may be used by female odontophorids in mate selection.

Most of the males in our study established territories and paired after the beginning of the breeding season (March), contrary to many other bird species in which the probability of pairing is higher for males that establish territories at the beginning of the breeding season (Howard 1974; Capp 1992; Hoi-Leitner et al. 1995; Kipper et al. 2006). Spot-bellied Bobwhite breeding is likely timed to coincide with the availability of better nesting sites and food resources and maximum offspring protection (Sandoval 2011a), suggesting that female choice is likely based upon a combination of male song traits, time of territory establishment, and territory quality. This species constructs nests at ground level within extremely dense mats of tall grass and other herbaceous vegetation (Leber 1975; Stiles and Skutch 1989; Sandoval 2011b), which also provides offspring and adults with a refuge against predators (Sandoval 2009). The rainy season begins in May, and as tall grasses and other plants grow, there is an increase in the availability of nesting sites, cover for offspring and adults, and food resources, such as arthropods and seeds (Leber 1975; Lusk et al. 2001; Sandoval 2011a). Although we estimated the extent of the potential nesting habitat within each territory, we did not measure the quality or number of nesting places themselves.

One limitation associated with our results is that territory establishment and female choice may not be exclusively based on song features. We did not measure morphological features, such as body size and plumage color, nor visual displays that may either be correlated with acoustical traits or act in concert with acoustical traits and thus influence female choice and male–male competition (Gibson and Bradbury 1985). We also did not measure other territorial features (e.g., fine nesting sites features) that may also be important during female choice. Further experimental studies are necessary to examine the role of different signals on female choice and male–male competition within a multimodal signaling context in this species (Hebets and Papaj 2005).

To summarize, the results of this study demonstrate that temporal and acoustic characteristics of male Spot-bellied Bobwhite song vary within a population. This variation, possibly driven by sexual selection, seems to allow females to select males with a particular set of song and territorial traits. Most males established their territories and paired with females after the beginning of the breeding season. Breeding during this period likely increases the probability of breeding success since it corresponds with the onset of the rainy season when suitable nesting sites, refuge sites, and food availability increase.

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