

## VOCAL DISTINCTIVENESS AND RESPONSE TO CONSPECIFIC PLAYBACK IN THE SPOTTED ANTIBIRD, A NEOTROPICAL SUBOSCINE

SUSANNE C. BARD<sup>1,4</sup>, MICHAELA HAU<sup>2</sup>, MARTIN WIKELSKI<sup>2</sup> AND JOHN C. WINGFIELD<sup>3</sup>

<sup>1</sup>Department of Psychology, University of Washington, Box 351525, Seattle, WA 98195

<sup>2</sup>Department of Ecology and Evolutionary Biology, Princeton University, Guyot Hall 303,  
Princeton, NJ 08544

<sup>3</sup>Department of Zoology, University of Washington, Box 351800, Seattle, WA 98195

**Abstract.** We studied individual variation in song characteristics of the Spotted Antbird (*Hylophylax naevioides*), a Neotropical suboscine, and tested for song discrimination using playback of male neighbors and strangers. Discriminant analysis of four frequency and temporal characteristics of the songs of 25 male and five female Spotted Antbirds revealed significant differences among individuals. Each song was assigned correctly to the individual that produced it with over 70% accuracy. However, during field playback, male Spotted Antbirds did not discriminate between neighbor and stranger song. Our results suggest that selection has not favored the evolution of neighbor-stranger discrimination, perhaps because all conspecific intruders pose a threat. The temporal characteristics of Spotted Antbird songs differed significantly between the sexes, but frequency characteristics did not. Females responded significantly less strongly to male playback than males, suggesting that each sex plays a distinct role in territorial defense.

**Key words:** *Hylophylax naevioides*, neighbor-stranger discrimination, playback experiment, song, Spotted Antbird, tropical suboscine, vocal distinctiveness.

### Variación Individual del Canto y Respuesta al Playback Coespecífico en *Hylophylax naevioides*, un Suboscino Neotropical

**Resumen.** Estudiamos la variación individual de las características del canto de *Hylophylax naevioides*, un suboscino neotropical y evaluamos si esta especie responde de forma diferente al playback de individuos vecinos o desconocidos. Un análisis discriminante de cuatro características temporales y espectrales del canto de 25 machos y cinco hembras de *H. naevioides* reveló que existían diferencias significativas entre individuos. Cada canto fue asignado correctamente al individuo que lo produjo en más del 70% de los casos. Sin embargo, en un experimento de playback en el campo los machos no distinguieron entre el canto de individuos vecinos y desconocidos. Estos resultados sugieren que la selección no ha favorecido la evolución de la discriminación entre vecinos y desconocidos porque todos los intrusos coespecíficos suponen una amenaza. Las características temporales, pero no las espectrales, del canto de los *H. naevioides* difirieron significativamente entre ambos sexos. Las hembras respondieron significativamente menos que los machos al playback con cantos de machos, lo que sugiere que cada sexo desempeña un papel diferente en la defensa del territorio.

### INTRODUCTION

The ability to distinguish between familiar and unfamiliar conspecifics based on vocal cues may help maintain beneficial relationships and minimize costly aggressive interactions between animals (Stoddard 1996). While it has been established that many oscine passerines can discrim-

inate between neighbors and strangers and between other conspecifics (Lambrechts and Dhondt 1995, Stoddard 1996), this issue has not been addressed in suboscine passerines. Furthermore, in Neotropical suboscine species where all individuals of both sexes sing a similar song, it is unclear how individuals of each sex distinguish each other and what role each sex plays in territorial interactions.

Individual vocal discrimination has been demonstrated in a number of vertebrates such as group-living mammals and colonial birds, where complex social relationships require fine percep-

Manuscript received 2 April 2001; accepted 21 January 2002.

<sup>4</sup> Present address: Science and Natural History Film-making, Montana State University, P.O. Box 174120, Bozeman, MT 59717. E-mail: bard@montana.edu

tual abilities (Rendall et al. 1996, Sayigh et al. 1998, Wanker et al. 1998, Holekamp et al. 1999). In several social, nonpasserine birds that do not learn their vocalizations, vocal discrimination has also been demonstrated (Watanabe and Ito 1991, Lengagne et al. 2000). For instance, Speirs and Davis (1991) found that colonial Adélie penguins (*Pygoscelis adeliae*) respond differently to playback of neighbors, strangers, and mates. Some territorial nonpasserine birds exhibit neighbor-stranger discrimination, and the ability to distinguish between familiar neighbors and unfamiliar intruders may be advantageous in territorial maintenance. Examples are the Blue Grouse (*Dendragapus obscurus*; Falls and McNicholl 1979), and the Pukeko (*Porphyrio porphyrio*; Clapperton 1987).

Suboscines are widespread in the Neotropics and many maintain stable territories and long-lasting pair bonds (Greenberg and Gradwohl 1986, Morton 1996, Morton and Derrickson 1996). Discrimination between neighbors and strangers based on vocal cues may also be important to territorial suboscines.

The Spotted Antbird (*Hylophylax naevioides*) is a strongly territorial Neotropical suboscine. Spotted Antbirds are sexually dimorphic, socially monogamous, and stay in pair bonds for many years (Hau et al. 1999, 2000, Wikelski et al. 2000). Males and females codefend large territories of approximately 4.7 ha. (Willis 1972, Robinson et al. 2000). In large and densely vegetated territories, auditory cues may provide more information than visual cues at a distance. Discrimination of the familiar songs of neighbors from the unfamiliar songs of strangers could be favored in this species, to decrease aggressive interactions between neighbors and to aid in territorial defense.

We hypothesized that like many oscines, Spotted Antbirds would respond more aggressively to strangers than to neighbors at the regular territorial boundary. We tested whether Spotted Antbirds can make these distinctions by presenting both sexes with song playback of male neighbors and strangers. We also compared the responses of males and females, to determine whether the sexes defend their territories equally. In species where both sexes sing year round, partitioning of sex roles in territorial defense may be efficient (Willis 1972, Morton and Derrickson 1996, Levin 1996a).

In order for vocal recognition or discrimination to be possible, song characteristics must vary consistently between individuals. In other words, interindividual variation must be high compared with intraindividual variation (Falls 1982). Selection pressure for discrimination of conspecifics could further increase interindividual variability and decrease intraindividual variability (Beecher 1982). We compared the songs of male and female Spotted Antbirds to determine if song varies consistently between individuals. We also assessed what proportion of songs could be classified to the individual that produced them based on a variety of song characteristics, and whether the sexes differed in these characteristics.

## METHODS

### STUDY AREA AND SUBJECTS

Our study area was Limbo Plot, a 100-ha site along Pipeline Road in Soberania National Park, in a lowland moist tropical forest near Gamboa, Panama (9°9'N, 79°45'W). Limbo Plot has a marked grid system, which facilitated the accurate mapping of Spotted Antbird pairs, their territories, and territorial boundaries. North to south, Limbo Plot is marked every 25 m, and east to west every 100 m. This field site is described in detail by Robinson et al. (2000). A map of Spotted Antbird territories on Limbo Plot was kindly provided by J. J. Nesbitt. Each Spotted Antbird at Limbo Plot was color banded for identification.

### RECORDING EQUIPMENT AND PROCEDURES

To obtain recordings for song analysis, we elicited singing behavior by playing male conspecific songs on Spotted Antbird territories. Individuals were recorded in the field using a Sennheiser MZP 816 directional microphone attached to a Sony Professional Walkman tape recorder. We recorded at a distance of 3–4 m until 5–50 songs were collected for each individual. All songs were recorded between 18 June and 20 August 1997.

### SONG VARIATION ANALYSIS

Two hundred fifty-seven song examples from 25 male and five female Spotted Antbirds were digitized and analyzed using SYRINX software (Burt 2001). For each song example we measured center frequency in kHz (the point halfway between the highest and lowest frequency

of the song), frequency range (difference in kHz between the highest and lowest frequency), duration of the song, and song speed (number of song syllables per sec, counting paired short and long elements as a single syllable). Song data were recorded directly into a log file and converted to SPSS 8.0 for Windows (SPSS Inc. 1997) for statistical analysis. We tested whether among-individual song differences exceeded within-individual differences within each sex, using one-way ANOVAs on each of the four characteristics. We also compared male and female song characteristics with ANOVAs on individual means of the four song characteristics.

To determine whether individuals could be correctly classified by their song characteristics we conducted a discriminant function analysis. We used this analysis because if neighbor-stranger discrimination occurs it is probable that birds use a combination of song variables (Clapperton and Hayward 1987, McShane et al. 1995). To test the generality of the classification we estimated classification error rates by cross-validation, which generates a discriminant function by withholding one observation at a time, and then classifies that observation. This controls for the classification bias inherent in constructing discriminant functions with the same observations that they are subsequently used to classify (Johnson and Wichern 1992). To determine which variables were most important in distinguishing individuals, we computed a stepwise discriminant analysis.

#### PLAYBACK PROCEDURES AND CONDITIONS

For the playback experiment, we selected 10 territories held by Spotted Antbird pairs on Limbo Plot. We recorded songs from each male on those territories. All Spotted Antbirds sing only one song type, and stimulus songs were selected randomly from a high-quality subset of a male's total recordings. After recording, the songs were digitized and band-pass filtered to remove insect and other ambient noise using Canary 1.2.1 software (Cornell Bioacoustics Laboratory), with a 44 100 Hz, 16-bit sample rate. Playback tapes were prepared using SOUNDMAKER 1.0.3 software (Micromat Computer Systems, Windsor, California). Playbacks were presented using a Sony TCM-59V tape recorder attached via 15 m of speaker cable to a Sony SRS-A31 6-W speaker.

Each male served both as a subject for playback trials and as a source of a song for trials on his neighbor. Stranger songs were recorded from Spotted Antbird males holding territories at least 5 km from the study site. No individual's song was used on more than one subject, to avoid pseudoreplication (Kroodsma 1989b). Playback trials were conducted between 6 August and 12 September 1997, during the Spotted Antbird breeding season in Panama (May–October, Willis 1972, Wikelski et al. 2000). Playback trials were conducted at the center of each territory and at the border of the territory shared with the neighbor whose song was used as the stimulus. Responses at both locations were recorded because some species reach maximum response levels when they detect intruders at the center of their territory (Stoddard et al. 1990). The response to male playback by both the male subject and his mate was recorded.

Four trials were conducted on each subject's territory: one each with neighbor and stranger stimuli, at both the territorial border and the center of the territory. Territorial boundaries were confirmed by luring each male as far as he would go to the edge of his territory with conspecific male song, one week before the playback trials were initiated.

The playback speaker was mounted on a tripod 0.7 m from the ground at a distance of 4 m from the observer. Trials were conducted between the hours of 06:30 and 11:30 from 6 August 1997 to 12 September 1997. When subjects sang spontaneously before playback, we initiated the trial only after it had stopped singing for 2 min. We broadcast each playback song at 70 dB (at 5 m) every 12 sec, until the subject flew in or vocalized. At this point, the 9-min trial began, consisting of 1 min of silence, 1 min of playback (4 songs spaced at 12-sec intervals), followed by 3 min of silence, 1 min of playback, and 3 more min of silence. Neighbor and stranger treatments were attempted on successive days, weather permitting. If a bird did not appear within 15 min of playback, the trial was aborted for that day and repeated on another day. Trials were also aborted if a male or female from a neighboring territory sang or approached the speaker. The order of neighbor and stranger stimulus presentation was chosen randomly, and neighbor and stranger stimuli were encrypted on the tape box to avoid observer bias. No more

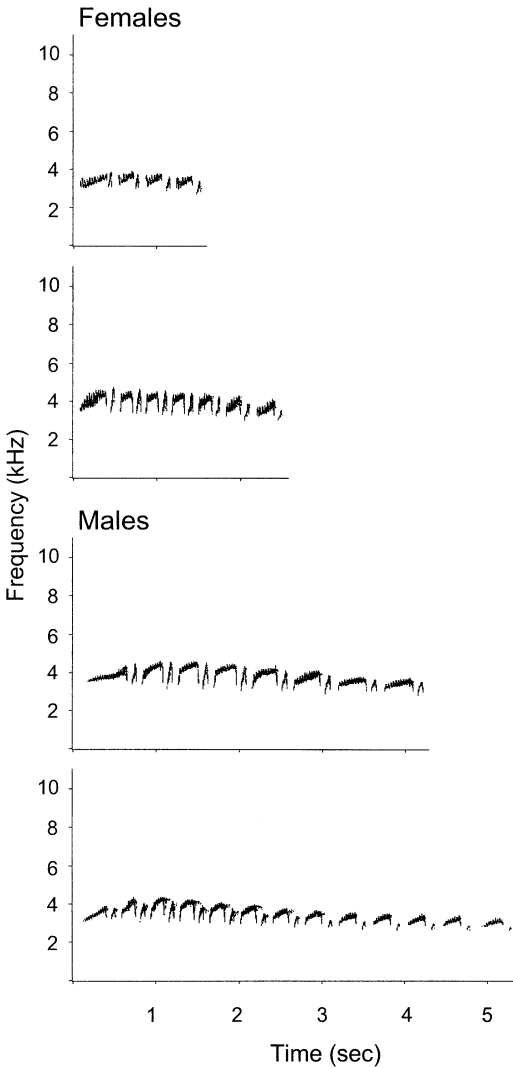


FIGURE 1. Examples of the complete songs of two female and two male Spotted Antbirds recorded near Gamboa, Panama.

than one trial per pair of neighbors was conducted on a given day.

**Response measures.** During each 9-min trial, we recorded the following behaviors of male and female subjects: (1) number of songs, (2) closest approach to speaker (m), (3) number of aggressive calls, (4) number of flights, (5) latency (the time elapsed before first response), and (6) whether the subject made an audible or visible response to playback.

The number of songs, closest approach, number of aggressive calls, and number of flights

TABLE 1. Correlation matrix between four Spotted Antbird song variables in a discriminant function analysis.

Song characteristic	Center frequency (kHz)	Frequency range (kHz)	Duration (sec)	Speed (syllable sec <sup>-1</sup> )
<b>Males <i>n</i> = 25</b>				
Speed	0.15	0.01	-0.23	1.00
Duration	-0.09	0.19	1.00	
Frequency range	-0.03	1.00		
Center frequency	1.00			
<b>Females <i>n</i> = 5</b>				
Speed	-0.14	-0.15	-0.29	1.00
Duration	-0.14	0.34	1.00	
Frequency range	-0.19	1.00		
Center frequency	1.00			

were compared between males in three sets of paired *t*-tests: (1) neighbor vs. stranger at the territorial border, (2) neighbor vs. stranger at the territory center, and (3) mean neighbor and stranger at the border vs. the center.

We compared the response of males to that of their mates for all variables except number of flights. Because male and female responses had unequal variances and were not normally distributed, we used Wilcoxon signed-ranks tests on the mean individual response over all four playback conditions. The proportion of males vs. females responding at all to playback was computed using a chi-square test. SPSS 8.0 was used for these analyses.

**RESULTS**

**SONG VARIATION**

For all song characteristics measured, among-individual song variation exceeded within-individual variation in males ( $F_{24,197} > 13.6, P < 0.001$  for all four characteristics). The result was similar among females ( $F_{4,26} > 8.3, P < 0.001$ ). The songs of two females and two males illustrate the frequency and temporal differences between individuals and between the sexes (Fig. 1). Within each sex, the song variables in the analysis were not strongly correlated (Table 1). Discriminant function analysis with cross-validation revealed that 73% of male Spotted Antbird songs were correctly classified to the individual that produced them based on a linear combination of frequency and temporal characteristics ( $\chi^2_{96} = 1320.3, P < 0.001$ ). The first

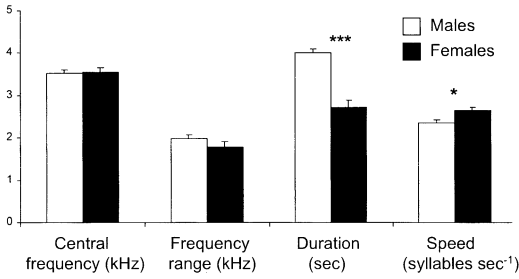


FIGURE 2. Mean  $\pm$  SE song characteristics of male and female Spotted Antbirds recorded near Gamboa, Panama. \* $P < 0.05$ , \*\*\* $P < 0.001$ .

function accounted for 62% of the variance, the second function 25%, the third function 9%, and the fourth function 4%. Each function was independently significant after the functions already entered in the analysis were accounted for. Discriminant function analysis on females revealed that 94% of cross-validated song cases were correctly assigned to the individual that produced them across all functions ( $\chi^2_{12} = 100.8$ ,  $P < 0.001$ ).

A stepwise discriminant analysis revealed that the center frequency was the most important variable in differentiating male songs ( $F_{24,197} = 84.8$ ,  $P < 0.001$ ). After adjusting for center frequency, the remaining variables, song speed, frequency range, and duration of the song, still contributed significantly to individual vocal distinctiveness (song speed  $F_{48,392} = 67.3$ ,  $P < 0.001$ ; frequency range  $F_{72,584} = 44.9$ ,  $P < 0.001$ ; total duration  $F_{96,771} = 32.3$ ,  $P < 0.001$ ).

The sexes differed significantly in the temporal domain of the song (Fig. 2). Females sang shorter songs ( $F_{1,28} = 30.1$ ,  $P < 0.001$ ) at a faster speed than males ( $F_{1,28} = 4.7$ ,  $P < 0.05$ ). In contrast, for the two frequency characteristics (center frequency and frequency range), means for male and female song were not different (center frequency:  $F_{1,28} = 0.05$ ,  $P > 0.8$ ; frequency range  $F_{1,28} = 2.0$ ,  $P > 0.1$ ). The duration of the song was the characteristic most different between the sexes. However, one female did consistently sing songs within the range of males for all characteristics including duration.

RESPONSE TO PLAYBACK

Male subjects did not respond more strongly to stranger playback than to neighbor playback for any response measure (Fig. 3; all  $t_{36} < 1.5$ , all  $P > 0.1$ ). Additionally, there were no differences

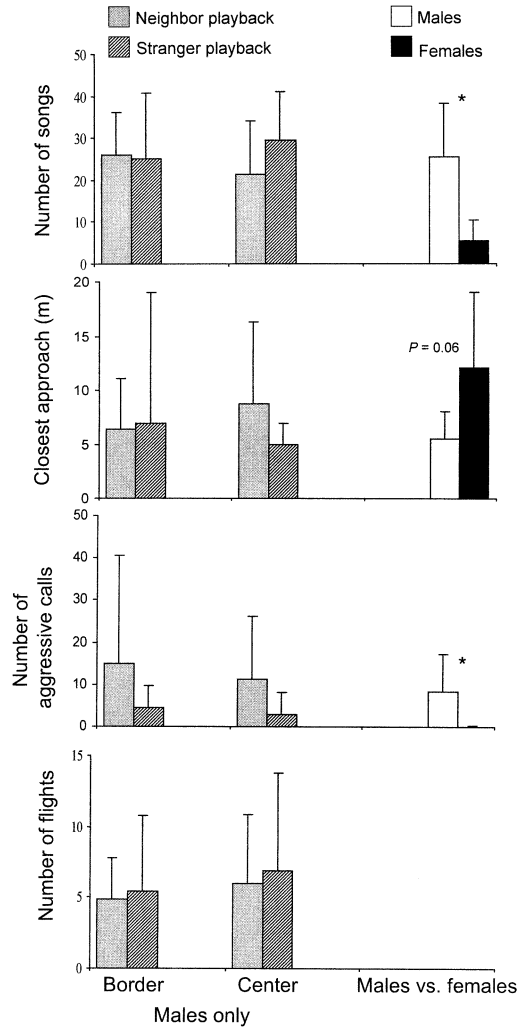


FIGURE 3. Response to neighbor and stranger playback by male Spotted Antbirds at the territorial border and center (left), and a comparison of mean male and female responses across all treatments (right). Female responses to playback were too weak for us to record the number of flights they made. Means  $\pm$  SE are shown. \* $P < 0.05$ .

between neighbor-stranger playback or location treatments on whether a male responded at all (visibly or audibly) to playback during a trial ( $\chi^2_3 = 0.9$ ,  $P > 0.8$ ).

Comparing response by sex, males responded significantly more vigorously than females on all response measures (Fig. 3). Male Spotted Antbirds sang five times more often than females ( $Z = -2.5$ ,  $P < 0.05$ ), females produced almost no aggressive calls compared with a mean male re-



sponse of 7.2 calls per trial ( $Z = -2.5$ ,  $P < 0.05$ ), and males approached an average of 6 m closer than females to the playback speaker, a trend that was nearly significant ( $Z = -1.9$ ,  $P = 0.06$ ). Because these tests do not take into account females that did not respond at all during the trials, they probably underestimate the difference between male and female response. Because female response to playback was so weak, they were too far away for us to record the number of flights they made.

Males were also much more likely to make a visible or audible response to playback than females across all treatments ( $\chi^2_1 = 20.9$ ,  $P < 0.001$ ). Females were equally likely to respond to playback at the border as at the center of the territory ( $\chi^2_1 = 0.004$ ,  $P > 0.9$ ). Females took an average of 4 min longer to respond to playback than their social mate, when they responded at all ( $Z = -2.5$ ,  $P < 0.05$ ).

## DISCUSSION

Vocal discrimination is not possible unless song characteristics vary consistently among individuals (Falls 1982). Our results show that individual Spotted Antbirds sing distinct songs. Center frequency and speed at which the song is produced contribute strongly to these individual differences. However, individual differences are necessary but not sufficient for neighbor-stranger discrimination.

When challenged with playback, male Spotted Antbirds did not distinguish between neighbors and strangers as expected. Subjects were no more aggressive to stranger playback than they were to neighbor playback. While distinguishing between neighbors and strangers could be advantageous to Spotted Antbirds in territorial interactions, this behavior has not been selected.

Song learning for production is considered ubiquitous in the oscine passerines (Nottebohm 1972, Kroodsma 1982). In contrast, suboscine passerines probably do not learn their songs (Kroodsma 1989a, Brenowitz 1991). Suboscine Eastern Phoebes (*Sayornis phoebe*) that were deafened developed normal song in the absence of auditory feedback (Kroodsma and Konishi 1991). No neural regions similar to the song system of oscines have been observed in suboscines (Brenowitz 1997). Oscines exhibit more song variation between individuals than suboscines, a likely result of production learning (Kroodsma 1982). High song variation may facilitate con-

specific discrimination in oscines (Beecher 1982). While there is some evidence of a positive relationship between production learning and perception in oscines (Pytte and Suthers 1999), it has been hypothesized that contextual learning preceded production learning (Janik and Slater 2000) in vertebrates. Janik and Slater (1997) defined contextual learning as the association of a pre-existing signal with a new context. Contextual learning allows animals to use vocal cues to distinguish between conspecifics (Janik and Slater 2000). Spotted Antbirds and other suboscines should be capable of contextual learning in a variety of social interactions, in the absence of production learning.

Ranging, a perceptual process that allows birds to distinguish between signals based on the quality or degradation of the message, may have also preceded production learning (Morton and Derrickson 1996). The Dusky Antbird (*Cercomacra tyrannina*), another Neotropical suboscine, shows perceptual discrimination on the basis of song quality and environmental attenuation (Morton and Derrickson 1996).

If the potential for discrimination of neighbors and strangers exists in Spotted Antbirds through contextual learning or ranging, why has natural selection not favored its evolution? Despite some similarities to the territoriality of temperate species, many aspects of Spotted Antbird territoriality may differ in ways that are not fully understood, making neighbor-stranger discrimination less important. Like many tropical species, Spotted Antbirds must defend their territories constantly against intruders throughout the year (Willis 1972, Wikelski et al. 1999, Hau et al. 2000). They also have larger territories to defend than many temperate species (Willis 1972, Robinson et al. 2000). Tropical birds also tend to sing less often on territory than temperate species (Morton 1996). It is possible, then, that every singing intruder is seen as a potential threat, whether familiar or unfamiliar, and treated with equal aggression.

The differences in song structure and playback responses between males and females in this study have implications for the role each sex plays in territorial interactions. Male Spotted Antbird songs are longer and slower than those of females. These differences may facilitate the recognition of the sex of intruders during territorial defense and help identify potential mates. Willis (1972) observed that male Spotted Ant-

birds are more active in general territorial defense than females. In our study, the lower response to male playback by females in comparison to males suggests that males are more responsible for defense against other intruding males. It is also possible that females in our study did not respond to male playback at all, but rather followed their mates as they became agitated over playback. However, females could play an important role in defense against other intruding females. Recent playback and decoy experiments (MH, pers. obs.) suggest that while female Spotted Antbirds respond less strongly to male playback with a live decoy than males do, females typically respond more aggressively than males to female playback with a decoy. Several empirical studies of other passerine species show similar sex-role differences in territorial interactions. In Bay Wrens (*Thryothorus nigricapillus*), females respond much more aggressively to female playback than to male playback, and vice-versa for males, and females use their songs to deter other females from intruding on their territories (Levin 1996a, 1996b). Wintering female Stonechats (*Saxicola torquata*) are also more aggressive toward other females than to males (Gwinner et al. 1994). Similarly, in Dusky Antbirds, males respond more aggressively to male playback and females respond more aggressively to female playback (Morton and Derrickson 1996).

Additional field and laboratory experiments should be conducted to further test for conspecific discrimination in Spotted Antbirds and other suboscines. In addition to testing for neighbor-stranger discrimination, experiments should be conducted to assess mate recognition and male and female sex roles in territorial defense, to determine the extent of contextual learning in these species and its contribution to social interactions.

#### ACKNOWLEDGMENTS

We thank J. Saucedo, C. Edwards, J. Bosch, J. M. Burt, A. S. Rand, J. J. Nesbitt, J. D. Brawn, D. W. Robinson, T. R. Robinson, and R. Srygley for technical and field assistance in Panama. M. D. Beecher, C. E. Hill, J. M. Burt, S. E. Campbell, N. Hillgarth, J. C. Nordby, K. K. Soma, B. J. Reeves, D. Markiewicz, A. R. Smith, S. O'Donnell, and two anonymous reviewers provided useful comments and suggestions. M. E. Rudd assisted with statistical analyses. We thank the Smithsonian Tropical Research Institute and the Instituto Nacional de Recursos Renovables of the Republic of Panama

for the use of the field site and logistical support. This study was funded by an NSF grant to JCW.

#### LITERATURE CITED

- BEECHER, M. D. 1982. Signature systems and kin recognition. *American Zoologist* 22:477–490.
- BRENEWITZ, E. A. 1991. Evolution of the vocal control system in the avian brain. *Seminars in the Neurosciences* 3:399–407.
- BRENEWITZ, E. A. 1997. Comparative approaches to the avian song system. *Journal of Neurobiology* 33:517–531.
- BURT, J. M. [ONLINE]. 2001. Syrinx-PC, version 2.0., ([www.syrinxpc.com](http://www.syrinxpc.com)) (18 February 2001).
- CLAPPERTON, B. K. 1987. Individual recognition by voice in the Pukeko, *Porphyrio porphyrio melanotus* (Aves: Rallidae). *New Zealand Journal of Zoology* 14:11–18.
- CLAPPERTON, B. K., AND T. L. HAYWARD. 1987. Individuality in contact calls of the Pukeko (Aves: Rallidae). *New Zealand Journal of Zoology* 14:19–28.
- FALLS, J. B. 1982. Individual recognition by sounds in birds, p. 237–278. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Acoustic communication in birds*. Academic Press, New York.
- FALLS, J. B., AND M. K. McNICHOLL. 1979. Neighbor-stranger discrimination by song in male Blue Grouse. *Canadian Journal of Zoology* 57:457–462.
- GREENBERG, R., AND J. GRADWOHL. 1986. Stable territories and constant densities in tropical forest insectivorous birds. *Oecologia* 69:618–625.
- GWINNER, E., T. ROEDL, AND H. SCHWABL. 1994. Pair territoriality of wintering Stonechats: behavior, function, and hormones. *Behavioral Ecology and Sociobiology* 34:321–327.
- HAU, M., M. WIKELSKI, K. K. SOMA, AND J. C. WINGFIELD. 2000. Testosterone and year-round territorial aggression in a tropical bird. *General and Comparative Endocrinology* 117:20–33.
- HAU, M., M. WIKELSKI, AND J. C. WINGFIELD. 1999. Environmental control of reproduction in Neotropical rainforest birds. *Proceedings of the International Ornithological Congress* 22:1720–1739.
- HOLEKAMP, K. E., E. E. BOYDSTON, M. SZYKMAN, I. GRAHAM, K. J. NUTT, S. BIRCH, A. PISKIEL, AND M. SINGH. 1999. Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. *Animal Behaviour* 58:383–395.
- JANIK, V. M., AND P. J. B. SLATER. 1997. Vocal learning in mammals. *Advances in the Study of Behavior* 26:59–99.
- JANIK, V. M., AND P. J. B. SLATER. 2000. The different roles of social learning in vocal communication. *Animal Behaviour* 60:1–11.
- JOHNSON, R. A., AND D. W. WICHERN. 1992. *Applied multivariate statistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.
- KROODSMA, D. E. 1982. Learning and the ontogeny of sound signals in birds, p. 1–23. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Acoustic communication in birds*. Vol. 2. Academic Press, New York.

- KROODSMA, D. E. 1989a. Male Eastern Phoebes (*Sayornis phoebe*; Tyrannidae: Passeriformes) fail to imitate songs. *Journal of Comparative Psychology* 103:227–232.
- KROODSMA, D. E. 1989b. Suggested experimental designs for song playbacks. *Animal Behaviour* 37:600–609.
- KROODSMA, D. E., AND M. KONISHI. 1991. A subsong bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Animal Behaviour* 42:477–487.
- LAMBRECHTS, M. M., AND A. A. DHONDT. 1995. Individual voice discrimination in birds. *Current Ornithology* 12:115–139.
- LENGAGNE, T., T. AUBIN, P. JOUVENTIN, AND J. LAUGA. 2000. Perceptual salience of individually distinctive features in the calls of adult King Penguins. *Journal of the Acoustical Society of America* 107:508–516.
- LEVIN, R. N. 1996a. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiments. *Animal Behaviour* 52:1093–1106.
- LEVIN, R. N. 1996b. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments. *Animal Behaviour* 52:1107–1117.
- MCSHANE, L. J., J. A. ESTES, M. L. RIEDMAN, AND M. M. STAEDLER. 1995. Repertoire, structure, and individual variation of vocalizations in the sea otter. *Journal of Mammalogy* 76:414–427.
- MORTON, E. S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds, p. 258–268. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY.
- MORTON, E. S., AND K. C. DERRICKSON. 1996. Song ranging by the Dusky Antbird, *Cercomacra tyrannina*: ranging without song learning. *Behavioral Ecology and Sociobiology* 39:195–201.
- NOTTEBOHM, F. 1972. The origins of vocal learning. *American Naturalist* 106:116–140.
- PYTTE, C. L., AND R. A. SUTHERS. 1999. A bird's own song contributes to conspecific song perception. *Neuroreport* 10:1773–1778.
- RENDALL, D., P. S. RODMAN, AND R. E. EDMOND. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour* 51:1007–1015.
- ROBINSON, D. W., T. R. ROBINSON, S. K. ROBINSON, AND J. D. BRAWN. 2000. Nesting success of understory forest birds in central Panama. *Journal of Avian Biology* 31:151–164.
- SAYIGH, L. S., P. L. TYACK, R. S. WELLS, A. R. SOLOW, M. D. SCOTT, AND A. B. IRVINE. 1998. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour* 57:41–50.
- SPEIRS, E. A. H., AND L. S. DAVIS. 1991. Discrimination by Adélie Penguins, *Pygoscelis adeliae*, between the loud mutual calls of mates, neighbours, and strangers. *Animal Behaviour* 41:937–944.
- SPSS INC. 1997. SPSS 8.0 for Windows. SPSS Inc., Chicago.
- STODDARD, P. K. 1996. Vocal recognition of neighbors by territorial passerines, p. 356–374. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY.
- STODDARD, P. K., M. D. BEECHER, C. L. HORNING, AND M. WILLIS. 1990. Strong neighbor-stranger discrimination in Song Sparrows. *Condor* 92:1051–1056.
- WANKER, R., J. APCIN, B. JENNERJAHN, AND B. WAIBEL. 1998. Discrimination of different social companions in Spectacled Parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition. *Behavioral Ecology and Sociobiology* 43:197–202.
- WATANABE, S., AND Y. ITO. 1991. Discrimination of individuals in pigeons. *Bird Behavior* 9:20–29.
- WIKELSKI, M., M. HAU, AND J. C. WINGFIELD. 1999. Social instability increases plasma testosterone in a year-round territorial Neotropical bird. *Proceedings of the Royal Society of London Series B* 266:551–556.
- WIKELSKI, M., M. HAU, AND J. C. WINGFIELD. 2000. Seasonality of reproduction in a Neotropical rain-forest bird. *Ecology* 81:2458–2472.
- WILLIS, E. O. 1972. The behavior of Spotted Antbirds. *Ornithological Monographs* 10:1–162.