ORNITOLOGIA NEOTROPICAL 16: 397–404, 2005

NONBREEDING TERRITORIAL BEHAVIOR OF TWO CONGENERIC ANTBIRDS, CHESTNUT-BACKED ANTBIRD (*MYRMECIZA EXSUL*) AND WHITE-BELLIED ANTBIRD (*M. LONGIPES*)

Bridget J. M. Stutchbury[1], Bonnie E. Woolfenden[1] , Bradley C. Fedy[2], & Eugene S. Morton[3]

[1]Department of Biology, York University, Toronto, Ontario M3J 1P3, Canada.
E-mail: bstutch@yorku.ca

[2]Centre for Applied Conservation Research, Forest Sciences Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada.

[3]Conservation and Research Center, Smithsonian Institution, Front Royal, Virginia 22630, USA.

Resumen. – Comportamiento territorial no-reproductivo en dos hormigueros congenéricos, el Hormiguero Dorsicastaño (*Myrmeciza exsul*) y el Hormiguero Ventriblanco (*M. longipes*). – Utilizamos radiotelemetría durante la época no-reproductiva (seca) para comparar sistemáticamente los movimientos a corto plazo, cantos y comportamiento territorial de dos hormigueros que tienen ecología similar pero ocupan diferentes hábitat. Ambas especies permanecen en parejas y son territoriales a lo largo del año, pero el Hormiguero Dorsicastaño (*Myrmeciza exsul*) es común en hábitat secundarios y de borde, mientras el Hormiguero Ventriblanco (*M. longipes*) es común en bosque maduro. Aunque el Hormiguero Ventriblanco realizó incursiones fuera del territorio durante la época seca, no detectamos ninguna salida en el Hormiguero Dorsicastaño. Los Hormigueros Ventriblancos cantaron más y cubrieron menos área de su territorio por hora (0,01 ha) comparados con los Hormigueros Dorsicastaños (0.16 ha). Las parejas de Hormigueros Ventriblancos forrajearon usualmente a más de 5 m uno del otro y los duetos fueron regulares, aunque de baja frecuencia en la mayoría de las parejas. En las parejas de Hormigueros Dorsicastaños, los individuos forrajearon más separados, frecuentemente a más de 20 m de distancia. Las hembras de Hormigueros Dorsicastaños cantaban ocasionalmente y cuando lo hacían, esto era inmediatamente después del canto de su pareja. Discutimos como estas diferencias en comportamiento territorial y cantos reflejan una mayor estabilidad del alimento, y por lo tanto una mayor estabilidad territorial de la especie de bosque, el Hormiguero Dorsicastaño.

Abstract. – We used radiotelemetry during the nonbreeding (dry) season to systematically compare the short-term movements, singing and territorial behavior of two antbirds that have a similar ecology but occupy different habitats. Both species are paired and territorial year round, but the White-bellied Antbird (*Myrmeciza longipes*) is common in second growth and edge habitat, while the Chestnut-backed Antbird (*M. exsul*) is found in mature forest. Although White-bellied Antbirds made off-territory forays during the dry season, we did not detect any off-territory forays in Chestnut-backed Antbirds. White-bellied Antbirds sang more and covered less area of their territories per hour (0.01 ha) compared with Chestnut-backed Antbirds (0.16 ha). Mated White-bellied antbirds often foraged < 5 m from each other and duetting occurred regularly, though at low frequency for most pairs. In Chestnut-backed Antbirds, pairs foraged farther apart and were often separated by over 20 m. Female Chestnut-backed Antbirds only occasionally sang and, when they did, it was immediately after their mate's song. We discuss whether these differences

in territorial behavior and singing reflect greater food stability, and hence greater territorial stability, in the forest-dwelling Chestnut-backed Antbird. *Accepted 27 April 2005*.

Key words: Territory defense, radiotelemetry, foraging, duetting, song, off-territory forays, Chestnut-backed Antbird, White-bellied Antbird, *Myrmeciza exsul*, *Myrmeciza longipes*.

INTRODUCTION

In tropical passerines, year-round defense of territories by pairs is a common territorial system but relatively little is known about song rates, off-territory forays, and territory defense in these birds (Stutchbury & Morton 2001). We compared the singing behavior and movements of two congeneric antbirds in Panama. The White-bellied Antbird (*Myrmeciza longipes*) is common in second growth and edge habitat (Wetmore 1972) while the Chestnut-backed Antbird (*M. exsul*) occupies forest habitat (Skutch 1969). Their song structures show acoustic adaptation to their different habitats (Morton 1975). A recent molecular phylogeny suggests that the genus *Myrmeciza* is paraphyletic (Irestedt *et al.* 2004); nevertheless, the species' ecology is superficially similar (other than habitat) since they defend territories year-round as pairs, forage on or near the ground, and are insectivorous but do not regularly follow army ant swarms or join mixed-species flocks.

White-bellied Antbirds, a second growth species, have low song rates and unstable territories during the nonbreeding dry season (Fedy & Stutchbury 2004). White-bellied Antbirds make off-territory forays and some individuals abandoned their territory temporarily for several weeks or months, possibly as a response to food shortage (Fedy & Stutchbury 2004). Arthropod abundance in edge and second growth habitat tends to exhibit greater seasonality than in moister habitats like mangrove and forest (Levings & Windsor 1982, Parrish & Sherry 1994, Poulin & Lefebvre 1997). Therefore we expected to find that off-territory forays, and territorial movements in general, would be more restricted in the Chestnut-backed Antbird which occupies mature forest.

We were also interested in determining if song rates differed as a function of habitat. Song rates in year-round territorial passerines are typically low relative to seasonally territorial temperate zone passerines (reviewed in Stutchbury & Morton 2001). Little is known about interspecific variation in singing behavior among tropical passerines, because so few studies have systematically documented song rates. If song rate is driven largely by food availability (e.g., Reid 1987, Cuthill & Macdonald 1990), we would expect to find that during the dry season Chestnut-backed Antbirds (forest habitat) have a higher song rate than White-bellied Antbirds (drier second growth habitat).

METHODS

White-bellied Antbirds were studied during the dry season from January to April of 2000 and 2001 at two sites in Parque Nacional de Soberania, Panama (09º07'N, 79º40'W), one in the town of Gamboa and the other site at the entrance to the Pipeline Road (Fedy & Stutchbury 2004). In these two study sites, the average territory size was 0.7 ha and 2.3 ha, respectively. Most birds were individually color banded, and territory boundaries were determined by mapping bird locations while they sang, noting locations of counter-singing at borders, and by assessing responses to playback of recorded songs. Three types of vocalizations were distinguished: songs, "chips" and "cheers" (Fedy & Stutchbury 2004).

In 2001, eight different pairs of White-

bellied Antbirds (and two other males) were fitted with radio-transmitters early in the dry season (January) and followed for the next 6–8 weeks. BD-2G transmitters (Holohil Systems Ltd., Carp, Ontario) weighing about 2 g each were attached using a figure-eight harness (Rappole & Tipton 1991) made of lightweight cotton embroidery floss. We determined a bird's location using hand-held Yagi antennas and maintained a distance of at least 15 m from the birds. Singing data were collected continuously during 1-h observation periods. The distance separating members of a pair was recorded every 15 min and each time when the pair sang a duet. We tracked each individual for an average of 11.4 h (SD = 4.1, range 4–17) and obtained a total of 205 h of radio-tracking data on individual White-bellied Antbirds. A subset of these data were used for examining the movements of pairs. We had 51 h of radiotracking data where both members of a pair were radio-tagged (average 6.1 h per pair, 4–9 h per pair).

Chestnut-backed Antbirds were studied in February 2003 on Barro Colorado Island, Panama (09°10'N, 79°50'W), which is approximately 10 km from Gamboa. We color banded eight males and two females on eight adjacent focal territories. To determine territory boundaries, we surveyed the trails in an approximately 10-ha area, in the vicinity of the laboratory buildings, by listening for singing birds and conducting regular song playbacks. Three types of vocalizations were distinguished: songs, "snarls" which are often used by the mated pair in answering each other, and "cli-dicks" which are typically used as alarm notes (Skutch 1969).

We radio-tagged five birds on four different territories (one pair and three males but not their mates) using the same methods described above for White-bellied Antbirds. We obtained a total of 24 h of radio-tracking data, with 6 h per territory. Distance between pair members for territories where only the male was radio-tagged were recorded whenever the female vocalized or was seen by the observer.

For analysis of vocalizations, we treated each radio-tracking session as an independent unit, rather than each individual territory, because song rates were highly variable between tracking sessions. For analysis of distances between pair members, we treated the pair distance at 15 min intervals during tracking sessions as independent points. For White-bellied Antbirds, where we had the most observations, we calculated the percentage of observations at critical distances (< 5 m, > 20 m) for each pair.

The rainfall patterns during the dry season were similar for 2001–2003 on Barro Colorado Island, where meteorological records are available (http://striweb.si.edu/esp). Rainfall in February was 14.5, 10.2 and 15.7 mm, respectively, and was 25.6, 46.6, and 2.8 mm in March. The length of the dry season was 136, 123, and 134 d in the three years of the study, all of which are close to the 50 year average of 135 days.

RESULTS

Movements. In White-bellied Antbirds, 6/10 males and 2/8 females made at least one off-territory foray (as reported earlier, Fedy & Stutchbury 2004), and 4 of the 18 White-bellied Antbirds tracked spent > 25% of their time off-territory. Individuals did not sing while off-territory and visited from 1-3 neighboring territories. In Chestnut-backed Antbirds, none of the four males, or the female, ever left their territory during a total of 24 h of tracking. The foray rate off-territory of White-bellied Antbirds (0.12 + 0.20 S.D. trips/h), was significantly higher than for Chestnut-backed Antbirds (Mann-Whitney Test, $Z = 1.75$, N = 22, 1-tailed $P = 0.04$).

It is possible that off-territory forays in Chestnut-backed Antbirds were not detected

TABLE 1. Pair association (% observations) and frequency of duetting (percentage of sessions, and number per hour) and median pair distance when duetting for White-bellied Antbirds (WBAN) and Chestnut-backed Antbirds (CBAN).

Pairs	Pair association		Duetting		
	< 5 m	> 20 m	Sessions	Rate/h	Pair distance (m)
WBAN1	71%	2%	1/9	0.8	< 5
WBAN2	70%	0%	3/6	4.0	< 5
WBAN3	73%	0%	2/8	2.2	< 5
WBAN4	24%	0%	1/5	0.2	5–10
WBAN5	80%	0%	5/7	2.7	< 5
WBAN6	56%	12%	3/5	5.2	5–10
WBAN7	45%	20%	2/4	2.0	5–10
WBAN8	71%	0%	6/7	4.7	< 5
CBAN1	18%	55%	1/6	4.3	5-10
CBAN2[a]	0%	25%	0/5	0.0	–
CBAN3[a]	0%	33%	0/6	0.0	–
CBAN4[a]	0%	33%	1/6	0.3	10–15

[a]Only the male was radio-tagged, so pair association is based on 3–9 observations per pair.

simply because we did not track for a long enough period of time. However, for White-bellied Antbirds the time spent off-territory was not positively correlated with the total time tracked (r = -0.30, n = 18, $P = 0.226$), suggesting that increasing tracking time would not necessarily have increased our detection of forays. Nevertheless, it is possible that the 5 individual Chestnut-backed Antbirds we tracked happened to be individuals that had low (or no) foray behavior, and that a larger sample size would have revealed some individuals that make off-territory forays.

Neither species appeared to patrol territories by ranging over large areas of the territory during tracking sessions. White-belled Antbird pairs covered < 0.025 ha/h in all radio-tracking sessions (n = 19), and averaged 0.01 (± 0.006 SD) ha/h. This corresponds with the pair restricting its movements to an area of 10 m x 10 m during one hour of observation. This area represents an average of only 2% (± 5%, n = 8 territories) of the actual size of the territory. Chestnut-backed Antbirds moved greater distances per hour than White-bellied Antbirds, and covered > 0.025 ha all of the 23 tracking sessions. Chestnut-backed Antbirds moved over an average area of 0.16 ha/h (± 0.17 SD, n = 23), which corresponds with approximately 16% of the territory area.

The two species differed in the closeness of paired individuals during foraging. For White-bellied Antbird pairs, the average proportion of observations < 5 m apart was 61.3% (SD = 18.6, Table 1), compared with only 4.2% (± 7.6, n = 8) that were > 20 m apart. In this species, pairs sometimes sing a duet, with the female's song overlapping with the end of the male song (Fedy & Stutchbury 2004). Duetting was heard in all eight pairs, though at low rate, and most pairs were < 5 m apart at the time of duetting (Table 1). Our information on pair association in Chestnut-backed Antbirds is less complete because we were able to radio-tag only one pair. This pair

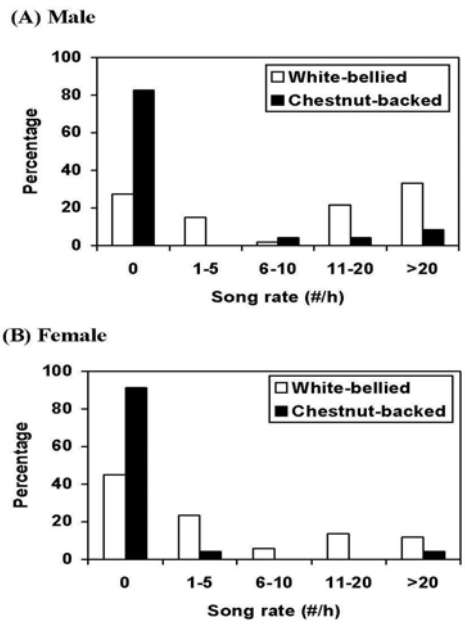

FIG. 1. Song rate (songs/h) of Chestnut-backed and White-bellied Antbirds for (A) males and (B) females during the nonbreeding season. Histogram shows the percentage of observation periods (n = 51 for White-bellied, n = 23 for Chestnut-backed) that had a given song rate.

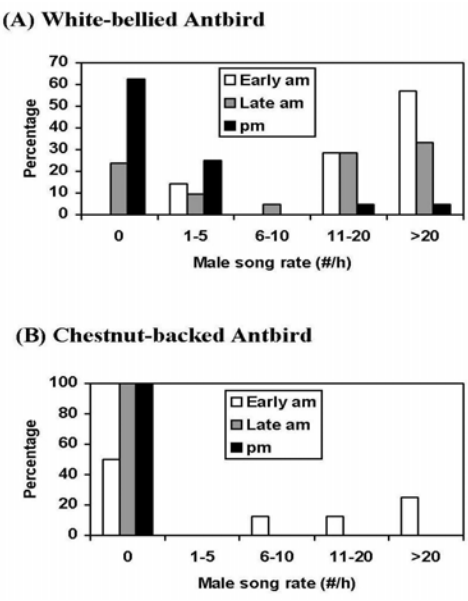

FIG. 2. Male song rate (songs/h) of (A) White-bellied and (B) Chestnut-backed Antbirds at different time periods during the day. Histogram shows the percentage of observation periods (n = 51 for White-bellied, n = 23 for Chestnut-backed) that had a given song rate.

spent only 18.5% of their time within 5 m of each other, and 55.5% of their time > 20 m apart (Table 1). For opportunistic observations on the three other pairs where the male was radio-tagged, the pair members were < 5 m apart for only 1/16 (6.3%) observations and > 20 m apart in 25% (4/16) observations (Table 1). Female Chestnut-backed Antbirds sang infrequently (Fig. 1) and, when they did, it was usually immediately following their mate's song. These "duets" were heard during only two tracking sessions, involving different females. In one case the female sang after her mate 30 times in 60 min, as the pair countersang with a neighboring pair where the female was also singing.

Vocalizations. Between species, Chestnut-backed Antbirds had lower song rates than White-bellied Antbirds, for both males and females (Fig. 1). Within species, female song rates were lower than for males. There was high variation in song rate, even within pairs, which probably reflects responses to challenges by neighbors (e.g., counter-singing with neighbors). Some White-bellied Antbird males sang over 30 times per hour during some tracking sessions, but gave no songs the next. Similarly, the highest song rate recorded for Chestnut-backed Antbird males was 93 songs/h, which occurred while this male (and his mate) were counter-singing with a neighboring pair.

To examine the effect of time of day, we divided our tracking sessions into three periods: early morning (06:30–09:00), late morning (09:00–12:00), and afternoon (12:00–

17:00). During our systematic observation periods, Chestnut-backed Antbirds sang only during the early morning (Fig. 2). However, males will respond to playbacks at all times of day (pers. observ.), and we occasionally heard males singing in late morning or afternoon under natural circumstances. White-bellied Antbirds were also more likely to sing early in the morning (Fig. 2). However, male song was recorded in about 75% of late morning sessions and 38% of afternoon sessions.

Widowed Chestnut-backed Antbird. The male Chestnut-backed Antbird in the radio-tagged pair was killed at night by an ocelot (*Leopardis pardalis*) that was being radio-tracked by another group of researchers, giving us an unexpected opportunity to study the behavior of a widowed female. We radio-tracked the widowed female for 1 h the morning after her mate was killed, 1.5 h that afternoon, and 1 h 2 days afterward. We monitored the territory several times per day, listening for a male replacement. The first day, the female did not elevate her rate of vocalization (no song, no snarls and no cli-dicks were given during tracking sessions). The female covered only a small area per hour (< 0.1 ha) and foraged quietly on or near the ground. Two days later, the female gave multiple snarl calls during tracking, but no song or cli-dick calls. After 4 days, a new male was seen and heard singing on the territory.

DISCUSSION

Territorial movements. White-bellied Antbirds, which occupy second growth and edge habitat, made more off-territory forays than the forest-dwelling Chestnut-backed Antbird. Fedy & Stutchbury (2004) found that in White-bellied Antbirds some individuals even abandoned their territories during the dry season, and suggested that low food supply may explain why White-bellied Antbird territories are so unstable during the dry season. The absence of off-territory forays in the Chestnut-backed Antbird supports this idea, though a longer period of radio-tracking and territory monitoring are needed to confirm the generality of these species differences. In addition, extensive arthropod sampling on the territories of both species, in the same year, would be important for testing whether individual differences in behavior are correlated with food supply on the territory.

We also observed species differences in on-territory movements. Chestnut-backed Antbirds typically covered a larger area (0.16 ha) per hour than White-bellied Antbirds (0.01 ha), despite a similar territory size. Neither species exhibited systematic and frequent patrolling of territory boundaries. Instead, pairs foraged quietly and moved slowly through their territory. This limited patrolling of the territory could reflect a low risk of eviction (Greenberg & Gradwohl 1997, Morton *et al.* 2000, Fedy & Stutchbury 2004). Differences in on-territory movements between species could result from differences in foraging efficiency, food supply and/or eviction risk.

Removal experiments are a highly effective tool for studying territory switching and stability, and the strategies used by widowed birds to gain new mates (Morton *et al.* 2000). In Dusky Antbirds (*Cercomacra tyrannina*), widowed females sing a unique courtship song soon after the disappearance of a mate, and have an elevated song rate until a new mate appears, which typically occurs within one day (Morton *et al.* 2000). In White-bellied Antbirds, widowed females do not have a unique courtship song or elevate their song rate, but instead greatly increase the rate of their "chip" calls within 2 h of their mate's removal (Fedy & Stutchbury 2004). For the one male disappearance in Chestnut-backed Antbirds, the female did not sing in response to her mate's death and did not increase the fre-

quency of her call notes. It took 4 days for a replacement male to arrive, in contrast to White-bellied Antbirds where most male replacements occur within 2 days (Fedy & Stutchbury 2004). Species that superficially appear to have the same "territorial and paired year-round" territorial system may exhibit very different behavioral and vocal responses to territory vacancies.

Song. The differences in song between species were not consistent with the idea that low food supply in second growth and edge habitat would result in low song output. White-bellied Antbirds had a higher song rate than Chestnut-backed Antbirds, and were more likely to sing in late morning and afternoon. We are not aware of any other studies that compare song rate of tropical passerines in different habitat, or relate song output directly to food abundance. Food supplementation experiments during the dry season, in both habitats, would be one way to test if food limitation affects song output. The unstable territories of White-bellied Antbirds could favor a relatively high song rate for territory defense given the documented presence of floaters and intrusions by neighboring birds (Fedy & Stutchbury 2004).

Since the results of this study are based on a comparison of only one species "pair" that differs in habitat type, our conclusions are necessarily cautious. To convincingly show that habitat type (and the seasonality of the food resources) has an effect on territorial movements or singing behavior one would need to replicate this study using many other species. We hope that the interesting differences reported in this study stimulate other researchers to pursue similar questions in other tropical birds.

ACKNOWLEDGMENTS

We thank the Smithsonian Tropical Research Institute for logistical support in Panama. K. Cramer and R. Houlihan assisted with the WBAN field research. B. C. F. was supported by the Natural Sciences and Engineering Research Council (NSERC) Scholarship, York University Faculty of Graduate Studies, and a Sigma Xi Grant-in-aid of Research. Research funding was provided by an NSERC Discovery Grant to BJMS and a Smithsonian Scholarly Studies Grant to ESM. Research was conducted under permits issued by the Autoridad Nacional del Ambiente in Panama.

REFERENCES

Cuthill, I. C., & W. A. Macdonald. 1990. Experimental manipulation of the dawn and dusk chorus in the Blackbird (*Turdus merula*). Behav. Ecol. Sociobiol. 26: 209–216.

Fedy, B. C., & B. J. M. Stutchbury. 2004. Territory switching and floating in the White-bellied Antbird (*Myrmeciza longipes*), a resident tropical passerine in Panama. Auk 121: 486–496.

Greenberg, R., & J. Gradwohl. 1997. Territoriality, adult survival, and dispersal in the Checker-throated Antwren in Panama. J. Avian Biol. 28: 103–110.

Irestedt, M., J. Fjeldså, J. A. A. Nylander, & P. G. P. Ericson. 2004. Phylogenetic relationships of typical antbirds (Thamnophilidae) and test of incongruence based on Bayes factors. BMC Evolutionary Biology 4: 23.

Levings, S. C., & D. M. Windsor. 1982. Seasonal and annual variation in litter arthropod populations. Pp. 355–397 *in* Leigh, E. G., Jr., A. S. Rand, & D. M. Windsor (eds.) The ecology of a tropical forest: Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. Am. Nat. 109: 17–34.

Morton, E. S., K. C. Derrickson, & B. J. M. Stutchbury. 2000. Territory switching behavior in a sedentary tropical passerine, the Dusky Antbird (*Cercomacra tyrannina*). Behav. Ecol. 11: 648–653.

Parrish, J. D., & T. W. Sherry. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: importance of resource seasonality.

Auk 111: 38–49.

Poulin, B., & G. Lefebvre. 1997. Estimation of arthopods available to birds: effect of trapping technique, prey distribution, and bird diet. J. Field Ornithol. 68: 426–442.

Rappole, J. H., & A. P. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. J. Field Ornithol. 62: 335–337.

Reid, M. L. 1987. Costliness and reliability in the singing vigour of Ipswich Sparrow. Anim. Behav. 35: 1735–1743.

Skutch, A. F. 1969. Life histories of Central American birds III. Cooper Ornithological Society, Pacific Coast Avifauna 35, Berkeley, California.

Stutchbury, B. J. M., & E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press, London, UK.

Wetmore, A. 1972. The birds of the republic of Panama, Part 3 – Passeriformes: Dendrocolaptidae (Woodcreepers) to Oxyruncidae (Sharpbills). Smithsonian Institution Press, Washington, D.C.