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TERRITORY SWITCHING AND FLOATING IN WHITE-BELLIED ANTBIRD (*MYRMECIZA LONGIPES*), A RESIDENT TROPICAL PASSERINE IN PANAMA

BRADLEY C. FEDY[1] AND BRIDGET J. M. STUTCHBURY

Department of Biology, York University, 4700 Keele Street North, Toronto, Ontario M3J 1P3, Canada

ABSTRACT.—We investigated the yearlong territorial behavior of White-bellied Antbirds (*Myrmeciza longipes*) in Panama by conducting 17 experimental removals during the nonbreeding season on both sexes. We also monitored the territorial behavior and occupancy of 48 males and 34 females throughout the nonbreeding and breeding seasons. We tested the importance of territory switching, mate advertisement, foray behavior, and role of floaters. In seven of the removal experiments, both members of a pair were radiotagged and tracked throughout the duration of the experiments. It was predicted that widowed birds would attempt to attract a new mate through increased song rate or unique vocalizations; however, that behavior was not observed in White-bellied Antbirds. We documented a weak response in floaters to territorial vacancies and found that territory switching occurs regularly in response to experimental removals and naturally within populations. We found density of birds in an area influences the probability of replacement and is likely a reflection of territory quality given that birds in high-density areas were in better physical condition, spent less time off-territory, and competed more for those territories. Telemetry revealed that individuals made silent extraterritorial forays during the nonbreeding season. Birds could use those forays to assess the quality and status of neighboring territories and to find food during this period when food abundance is low. Several birds were observed to temporarily abandon territorial behavior for periods from 2 to 13 months, a previously undocumented behavior in this type of territorial system. *Received 7 October 2003, accepted 22 January 2004.*

RESUMEN.—Investigamos el comportamiento territorial de *Myrmeciza longipes* a lo largo del año en Panamá mediante 17 remociones experimentales en ambos sexos durante la estación no reproductiva. También monitoreamos el comportamiento territorial y la permanencia en los territorios de 48 machos y 34 hembras a lo largo de las estaciones reproductiva y no reproductiva. Evaluamos la importancia del cambio de territorios, el despliegue de apareamiento, el comportamiento de incursión y el rol de los individuos flotantes. En siete de los experimentos de remoción, ambos miembros de la pareja fueron marcados con radiotransmisores y seguidos a lo largo de los experimentos. Se predijo que las aves que enviudaron intentarían atraer una nueva pareja mediante incrementos en la tasa de cantos o mediante vocalizaciones únicas; sin embargo, este comportamiento no fue observado en *M. longipes*. Documentamos una respuesta débil en los individuos flotantes hacia los territorios vacantes y encontramos que el cambio de territorios ocurre regularmente como respuesta a las remociones experimentales y de modo natural en las poblaciones. Encontramos que la densidad de aves de un área influencia la probabilidad de reemplazo y probablemente refleja la calidad territorial dado que las aves en áreas de alta densidad estuvieron en mejor condición física, gastaron menos tiempo fuera del territorio y compitieron más por esos territorios. La telemetría reveló que los individuos hicieron incursiones silenciosas fuera del territorio durante la estación no reproductiva. Las aves podrían usar estas incursiones para evaluar la calidad y el estatus de los territorios vecinos y para encontrar alimentos durante este período, cuando la abundancia de alimentos es baja. Se observó que varias aves abandonaron temporalmente el comportamiento territorial por períodos de 2 a 13 meses, lo que representa un comportamiento no documentado previamente en este tipo de sistema territorial.

[1]Present address: Centre for Applied Conservation Research, Forest Sciences Centre, University of British Columbia, 3004-2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada. E-mail: bfedy@interchange.ubc.ca

One of the most predominant territorial systems in the world for passerine species is the yearlong defense of feeding and nesting sites. That type of territorial behavior is common in tropical species (Buskirk 1976) and is exhibited by >65% of all insectivorous passerine species in Panama (Stutchbury and Morton 2001). However, that type of behavior is rare in north temperate passerines where most species defend only seasonal territories. Despite its prominence and the long history of avian territorial research, yearlong territoriality remains one of the least studied and poorly understood systems (Stutchbury and Morton 2001). Those yearlong territories are most often defended by a male and female pair, and that mating and territorial system has been termed "permanent monogamy" (Freed 1987). That form of territorial behavior differs from the temporary territory defence common in nonresident temperate species because it allows individuals to assess territory and mate quality throughout the entire year. Birds that maintain yearlong territories are also capable of attracting new mates or switching territories and mates at any time of the year. Removal experiments have been used extensively in temperate zone systems to address questions of territoriality and have generally found that removed individuals (usually males) are rapidly and repeatedly replaced (Brown 1969, Marra and Holmes 1997). However, removal experiments have been conducted very rarely on tropical passerine species (e.g. Morton 1977, Levin 1996, Morton et al. 2000). Performing those experiments on tropical birds of both sexes can give insights into population dynamics, territory and mate acquisition, sex roles, behavior of floaters, and territorial strategies.

Territory switching is quite common and rapid in response to vacancies (<1 day) in several yearlong territorial tropical birds (Willis 1974, Levin 1996, Greenberg and Gradwohl 1997, Morton et al. 2000). However, its importance as a means of improving territory quality, and thus individual survivorship within relatively stable communities of conspecifics, has just recently been highlighted (Morton et al. 2000). In their study of the Dusky Antbird (*Cercomacra tyrannina*), Morton et al. (2000) suggested that territory switching may be a common strategy used by birds to increase adult survivorship by shifting to territories with high food abundance. However, they were unable to measure food availability directly. In all studies where removal experiments were done on year-round territorial tropical passerines, some vacancies were not filled (Levin 1996, Morton et al. 2000). That suggests that nonterritorial (floater) birds are uncommon in that type of system. Those studies have also found that birds who have lost their mates (widowed birds) increase their song rates (Levin 1996) and use unique, gender-specific, mate advertisement songs (Morton 1996) to attract new mates.

We studied territory acquisition and switching behavior of the White-bellied Antbird (*Myrmeciza longipes*), a resident Neotropical passerine that has yearlong territory defense and pair bonds. White-bellied Antbirds are similar to Dusky Antbirds in that both males and females sing and are capable of defending their territories from conspecifics, even while unmated (B. C. Fedy and B. J. M. Stutchbury unpubl. data). Both species occupy the same habitat type and neither pursue ant swarms. But in contrast to the Dusky Antbird, the White-bellied Antbird has a different foraging niche: ground foraging.

We used removal experiments, radiotelemetry, and monitoring of natural vacancies and movements to test four primary predictions. On the basis of prior studies of tropical passerines, we predicted that (1) territory switching is common (Willis 1974, Greenberg and Gradwohl 1997) and occurs rapidly in response to vacancies (Levin 1996, Morton et al. 2000); (2) widowed birds quickly switch to unique songs and elevate song rates to attract new mates (Levin 1996, Morton et al. 2000). We also predicted that (3) given the absence of extrapair copulation strategies in other year-round territorial species (Dusky Antbird, Fleischer et al. 1997; Buff-breasted Wren [*Thryothorus leucotis*], S. Gill et al. unpubl. data), birds do not make covert forays into neighboring territories (e.g. Stutchbury 1998) to assess mate quality; and (4) floater birds are uncommon and will quickly claim vacant territories (Levin 1996, Morton et al. 2000). Here we document a weak response in floaters to territorial vacancies and observe that territorial adults will temporarily abandon their territories during the nonbreeding season.

Methods

Study site.—Our study was conducted from January to July of 2000 and 2001 in Parque Nacional

de Soberania, Panama (9°7′N, 79°40′W) located at the junction of the Panama Canal and the Chagres River. That area is a tropical lowland forest receiving ~2.6 m of rainfall per year (Karr 1971). We had three study sites within the park. Site one was a low-density experimental area at the beginning of Pipeline Road, slightly fragmented by roads and narrow fields. Site two was an isolated woodlot (~22 ha) in which White-bellied Antbirds were found at higher density. The third site was located 5 km away from the two experimental sites and acted as a control. No removal experiments were conducted at that site, and none of the birds were outfitted with radiotransmitters. All sites consisted of second-growth and edge habitat, which is ideal for White-bellied Antbirds (Ridgely and Gwynne 1989).

Central Panama has a pronounced dry season from mid-December to late April (Windsor 1990). During that period, litter arthropod populations are significantly lower than during the wet season (Levings and Windsor 1982). The nonbreeding season for ground foraging, insectivorous birds in the area corresponds to the dry season and runs approximately from January to April. Breeding can begin in late April, when the wet season begins and litter arthropod populations increase; however, breeding is highly asynchronous and evidence of breeding can still be found into December (Robinson et al. 2000). We used a very conservative definition of the nonbreeding season from mid-January until mid-April. No evidence of breeding was seen during that time.

Study species.—White-bellied Antbirds inhabit second-growth and edge habitat in lowland tropical areas from northern Brazil to central Panama (Meyer de Schauensee 1966, Wetmore 1972). White-bellied Antbirds are a medium-sized (29 ± 0.26 g, range = 25–32.5 g), sexually dimorphic, passerine of the Formicariidae family. They are insectivorous birds that forage almost exclusively in the ground leaf litter. They often maintain territories and associate in pairs throughout the year. Songs are sung individually or in duets, and male and female songs differ significantly in structure (B. C. Fedy and B. J. M. Stutchbury unpubl. data). As in other antbirds (Greenberg and Gradwohl 1997, Morton and Stutchbury 2000), juveniles can be distinguished from adults by iris color that ranges from brown in young birds to a brick-red color in adults (B. C. Fedy pers. obs.).

Removal experiments.—Birds were caught in mist nets by broadcasting a conspecific song on their territory. Every individual was weighed, measured, and color-banded with a unique color combination (n = 48 males, n = 34 females). Some birds were flushed into nets when necessary. Methods were identical between the two years of study, except that in the nonbreeding season of 2001, both members of a pair (n = 22 individuals) were outfitted with radiotransmitters (2 g, BD-2G Holohil Systems Ltd., Carp, Ontario). Birds were not radiotagged in 2000. Transmitters were attached in 2001 using a figure-eight loop harness made of lightweight cotton embroidery floss (Rappole and Tipton 1991). Researchers tracked birds using a hand-held yagi antenna and maintained a minimum distance of 15 m between themselves and the focal birds. Given the dense structure of the birds' habitat, that distance ensured that the researchers' presence did not disturb the birds. Territory boundaries were determined by mapping bird locations while they sang, disputed borders, and by assessing responses to playback of recorded songs (Falls 1981). Telemetry locations also contributed to determination of territory boundaries in 2001.

Removal experiments (n = 17) were conducted during the nonbreeding (dry) seasons of 2000 and 2001. Each experiment involved monitoring focal individuals' movements and vocalization behavior before removal, during removal, and after removal. Pairs were monitored for 1-h sessions with a minimum of 24 h between each session. During each session, we recorded frequency and type of all vocalizations of the focal pair. All sessions took place between 0630 and 1500 hours EST. Singing and movement activity of those birds does not vary significantly between those hours (B. C. Fedy and B. J. M. Stutchbury unpubl. data). In 2001, we used radiotelemetry to accurately locate both members of a pair at 15-min intervals and noted their locations within the territories and their locations relative to each other. All radiotagged birds were spot-checked a minimum of once every two days to monitor their locations and to note any territory shifts or changes. Birds were monitored for a minimum of four 1-h sessions in the two weeks preceding the removal of one pair member.

Birds were then temporarily removed from their territories (four days), kept in small cages under natural lighting conditions, and provided water and meal worms (*Tenebrio* sp.) *ad libitum*. All previous studies of monitoring replacement in response to vacancies suggest that is ample time for replacement to occur (Smith 1978, Levin 1996, Morton et al. 2000). All birds did well in captivity with no individuals losing weight. Singing and movement behavior of the widowed bird remaining on the territory was monitored for 2 h immediately following the removal of their mate and for 1 h each day over the next four days. An individual was considered replaced when another bird of the same sex began to sing, unchallenged, on the focal territory and to duet with the widowed bird. Song rate of newly paired birds is significantly higher than average (B. C. Fedy and B. J. M. Stutchbury unpubl. data), thus making replacements conspicuous and easy to detect. On the fourth day of the removal, a playback experiment was done to measure the level of aggression in unpaired birds and to ensure the removed bird had not been replaced by another. (If a replacement was present, we tried to capture and

color-band it to monitor its behavior after the release of the original territory holder.) The removed bird was released onto its territory on this day. Behavior of all birds on the territory was observed for 2 h immediately following the bird's release. We continued monitoring movement and vocalization behavior of focal birds for 1-h sessions for the following three-to-five days depending on how long it took the removed bird to regain its territory. A minimum of five-days settlement time was allowed after a bird regained its territory (if at all) before removal experiments were done on neighboring territories. All territories on which removal experiments were conducted had at least three neighboring territories.

Vocalization rates of individuals were recorded in both 2000 and 2001, when paired with their mate and when unpaired during the removal experiments, to determine if and how widowed birds advertised for a new mate. Data for paired birds were collected prior to removals or after one week had passed following the release of the removed bird, provided the pair rejoined. Three vocalization types were analyzed. The variables collected were number of songs, "*chips*" and "*cheers*" per hour. The rate of vocalization while paired was determined by averaging the vocalization rate per hour of the focal bird over 4 h of observation. To examine how quickly widowed birds would begin advertising for a new mate, we compared vocalization rates of individuals in the first hour of the removal with the second hour of removal. During each vocalization watch, observers listened for vocalizations that might be unique to unpaired birds.

Natural territory switches.—To monitor natural rates of territory switching or abandonment, all birds were surveyed in all three study sites at the beginning and end of each nonbreeding and breeding season. For surveys, birds on each territory were attracted by playback and identified as either banded or unbanded. Playbacks were done for 10 min (maximum) followed by 10 min of observation. Another study has shown that White-bellied Antbirds respond aggressively to playbacks (B. C. Fedy and B. J. M. Stutchbury unpubl. data); thus, if no birds responded, playbacks were done two more times in the next week. If no response was recorded over those three sessions, the territory was considered unoccupied. Floaters were defined as birds known to be in an area but would not respond with vocalizations to playbacks done near them. These quiet birds were either radiotagged or resighted a minimum of three times. They also did not act territorially in any of the nearby habitats. A previously territorial and banded individual was considered to have abandoned territorial behavior if they no longer sang spontaneously or responded to playbacks for over one month.

To assess the physical condition of the birds, we regressed body mass against tarsus length and used the residuals from that regression as an estimate of physical condition. Therefore, those birds with positive residuals were considered to be in better physical condition than those with negative values (Johnson et al. 1985, Marra and Holmes 2001).

All data were analyzed using SPSS version 10 (SPSS Inc., Chicago, Illinois). We present mean ± SE for all measurements. In all cases, $P < 0.05$ was considered significant. Statistical tests used are presented on a case by case basis. We performed power analyses for statistically nonsignificant results because accepting the null hypothesis carries the probability of Type II experimental error (Steidl et al. 1997). Details of power analyses are presented in conjunction with statistical tests.

Results

Territory Switching–Removal Experiments

Male and female.—Temporary removal of 10 males from pairs resulted in replacement by a new male in six cases. In seven female removals, a new female moved onto the territory in only two cases. There was no significant difference between the sexes in the likelihood of being replaced (Fisher's exact test, two-sided test, $P = 0.34$), although we have low power (power = 0.22 to detect a 50% difference in replacement rate between the sexes) because of modest sample sizes.

High- and low-density areas.—Density of territorial birds differed significantly between the two primary study locations and could affect the likelihood or speed of replacement. In the high-density site, territories were an average of 0.73 ± 0.08 ha; whereas in the low-density site, territories were on average 3× larger (2.38 ± 0.47 ha; Mann-Whitney U, $Z = -3.47$, $P = 0.001$). The physical condition of birds also differed between those two sites. Birds in the high-density site were in better condition than those in the low-density site (high density: 0.285 ± 0.231, $n = 43$; low density: 0.351 ± 0.162, $n = 35$; $t = 2.26$, $P = 0.03$). The likelihood of a removed individual being replaced was related to the density of birds. In the high-density site, 7 of 10 removals resulted in replacement; in the low-density site, only 1 of 7 removed individuals were replaced (Fisher's exact test, two-sided, $P = 0.05$). Both male removals done in the low-density site did not result in replacement.

Replacement individuals.—Of the eight replacement birds of both sexes, three were previously territorial males who switched to a new territory when the vacancy arose, two

were banded individuals who had been floating on and around the territory where the removal was done, and three were unbanded individuals in adult plumage of unknown origin. Replacement individuals were ousted from the territories after the original territory owner was released back onto the territory in six of eight cases. Two cases in which the original territory owner did not regain their territory involved a male that was found dead one day after release and a female who adopted floater behavior after release.

Time to replacement.—The average replacement time for males that were replaced (n = 6) was approximately two days. The range in replacement time varies greatly between different individuals and territories (Fig. 1). The shortest replacement time for a male was 3 h; whereas in two cases, the widowed female remained unmated for three days before a replacement male moved in. Female removals resulted in replacements in only two cases that occurred within 2 and 18 h of the removal. Sample sizes were not large enough to examine differences in time to replacement between the sexes or between the high- and low-density areas.

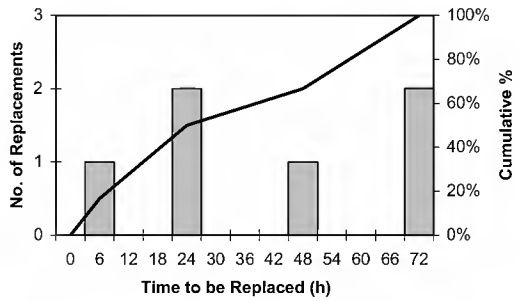

FIG. 1. Time to replacement during male White-bellied Antbird removal experiments (n = 6).

FORAYS AND VOCALIZATIONS

In 2001, we radiotagged and tracked the movements of 18 territorial birds (10 males and 8 females) for a total of 205 h (Table 1). Six of 10 radiotagged males engaged in extraterritorial forays at least once, and two of the six females monitored were also found off-territory. Those movements were all limited to within three territories (20–200 m) of the focal bird's territory. Those birds that left their territories (n = 8) spent an average of 20 ± 5% of the total time tracked off their territory. Birds in the low-density area

TABLE 1. Foray behavior of radiotagged male and female White-bellied Antbirds.

Individual	Total tracked (h)	Time off territory (h)	Time off territory (%)	Number of spot checks	Number of territories visited
			Males		
A	9	–	0	4	–
B	8	0.5	6	4	1
C	13	1	8	7	1
D	10	–	0	2	–
E	8	3	38	6	3
F	8	–	0	1	–
G	5	2	40	1	2
H	12	4	33	–	2
I	15	0.5	3	6	1
J	14	–	0	11	–
			Females		
K	14	–	0	4	–
L	16	–	0	4	–
M	15	–	0	2	–
N	4	–	0	5	–
O	17	–	0	1	–
P	14	1	7	1	1
Q	7	2	29	3	1
R	16	–	0	6	–

(n = 4) spent significantly more time off-territory than those individuals (n = 14) in the high-density area (low density: 27 ± 7%, high density: 6 ± 2%; U = 4.0, P = 0.005). None of the birds vocalized while off-territory. There were a few instances (two birds) in which they foraged onto territories where the owner was also radiotagged. Those intruding birds were often within 5 m of the resident; but given the dense structure of the habitat, we cannot be sure if the intruding male was detected.

Number of songs per hour did not vary significantly between when a female bird was unpaired (1.1 ± 0.4) or paired (2.4 ± 0.8) (Wilcoxon signed-ranks test, Z = –1.10, P = 0.27, n = 7). Using power analysis, we were able to detect a difference between the observed song rate of 2.4 h^{-1} in paired females and 6 h^{-1} in unpaired females, at a power level of 0.95. In unmanipulated situations, we have observed female song rates >15 h^{-1} for elevated song rate; thus, we can confidently conclude that unpaired females do not elevate their singing rate. However, unpaired females chip (20.9 ± 7.0) and cheer (3.8 ± 1.8) at a greater rate per hour than when they are paired (chip 0.9 ± 0.3, cheer 0.6 ± 0.3, chip rate Z = –2.20, P = 0.03; cheer rate: Z = –2.02, P = 0.04, n = 7) (Fig. 2). No such difference seems to exist for males, but data only exist for four individuals (Fig. 3). During removals, Levin (1996) found a 4-fold increase in song rate for unpaired males. We conservatively examined the power of our analysis in detecting a 2.5-fold increase in song rate for solo males (song rate paired: 13.1 ± 6.7, unpaired: 17.8 ± 11.2, Z = –0.73, P = 0.47, power = 0.93). As mentioned we also found no difference in male chip rate between paired and unpaired individuals. We examined the power of our test to detect a difference in chip rate similar to that observed in female White-bellied Antbirds (chip rate paired: 0.5 ± 0.5, unpaired: 3.1 ± 1.9, Z = –1.34, P = 0.03, power > 0.99). We also examined our ability to detect a similar difference in cheer rate for paired and unpaired males based on the 6-fold increase we observed in female White-bellied Antbirds (cheer rate paired: 0.6 ± 0.6, unpaired: 0.2 ± 0.2, Z = –1.00, P = 0.32, power > 0.99). In other removals, the widowed males obtained new mates almost immediately or they abandoned territorial behavior.

Female birds showed a latency of ~1 h before increasing their rate of chip calls (Fig. 4). Song rate did not differ between the first (1.4 ± 0.9) and second (0.8 ± 0.5) hours following removal (Z = –0.45, P = 0.66, n = 7). Using power analysis, we were able to detect a difference between the observed song rate of 1.4 h^{-1} in the first hour following removal and a song rate of 5 h^{-1} in the second hour following the removal of their mate

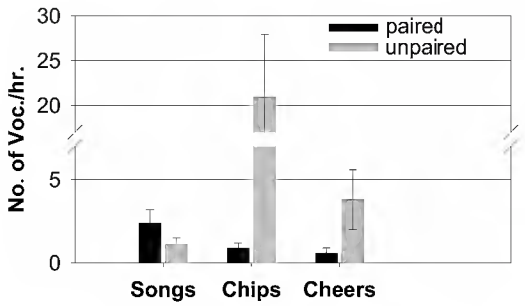

FIG. 2. Female White-bellied Antbird vocalization rates while paired and unpaired (n = 7).

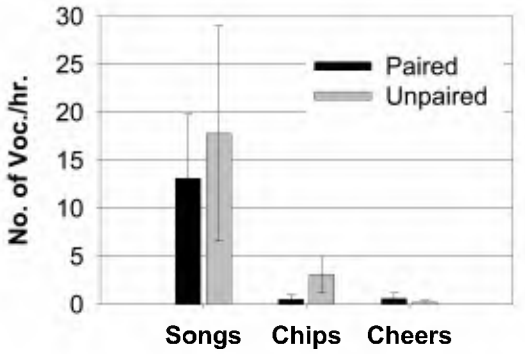

FIG. 3. Male White-bellied Antbird vocalizations while paired and unpaired (n = 4).

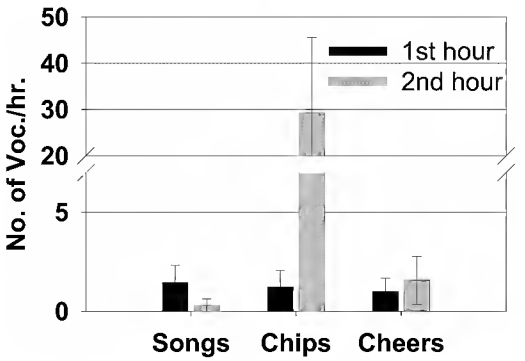

FIG. 4. Vocalization rates of female White-bellied Antbirds in first and second hours following removal of their mate.

at a power of 0.95. Furthermore, the cheer rate of females also did not differ between the first (1.0 ± 0.7) and second (1.2 ± 1.1) hours following the removal ($Z = -0.54$, $P = 0.59$, $n = 7$). Power was calculated as our ability to detect an increase in chip rate equal to that observed in solitary females (power = 0.94). However, the rate of chip calls increased dramatically between the first (1.2 ± 0.8) and second hours (22.8 ± 15.2; $Z = -2.01$, $P = 0.03$, $n = 7$). No unique vocalizations were noted in male or female unpaired birds.

All radiotagged, widowed birds ($n = 7$) stayed within their territory boundaries while unpaired, except one male who switched territories entirely. Furthermore, widowed birds that were not radiotagged ($n = 10$) were also not seen or heard singing off-territory during removal experiments.

Territory Switching–Natural Vacancies

We color-banded and monitored the territory occupancy of 48 male and 34 female birds over 19 months, and within all three study sites, to examine the rate at which vacancies arose naturally and to ensure that switching behavior occurs naturally and not only in response to our experimental manipulations (Table 2). Over that time, 53% (24 of 45) of territorial males moved or died to create a vacancy, which is 24 changes for 66 territory-years (0.36 territory per year). For female birds, we monitored change in 57% (16 of 28) of territorial individuals, making a total of 16 changes over 45 territory-years (0.36 territory per year). Of those birds, six males and three females were resighted elsewhere than on their former territories. As observed during the removal experiments, not all vacancies resulted in replacement. Natural vacancies created by the movement or death of a male resulted in replacement in 67% (16 of 24) of cases. Female replacement occurred in 50% (8 of 16) of cases in which a female moved or died to create a vacancy. In cases of replacement, it is also possible the previous owner was displaced by the "replacement" bird. Similar to experimental removals, there was no difference in the likelihood of males or females being replaced (Fisher's exact test, $P = 0.34$). One of the male replacements was a banded floater known to occupy the territory prior to the original owner's disappearance. The remainder of the replacement birds that filled natural vacancies were unbanded individuals of unknown origin.

Table 2. Causes of natural vacancies.

	Male	Female
Unknown	14	11
Death	2	0
Territory switch	6	2
Nonterritorial behavior	2	3
Total	24	16

Natural territory vacancies arose for one of three reasons. Either the territory owner died, switched to a new territory, or temporarily abandoned territorial behavior. We observed five cases (three female and two male) of previously territorial individuals abandoning territorial behavior. These birds were never sighted farther than two territories from their original territory, and the three that were radiotagged (two male and one female) spent the majority of their time between their original territory and those immediately neighboring them. Three of the five birds were found singing and defending territories again before the end of the study. The two male birds abandoned territorial behavior for 2 and 2.5 months. The three female birds abandoned territorial behavior for 3, 11, and 13 months (almost the entire duration of the study). All birds, except one female, were observed as floaters at least three times. The one female was not observed until she began behaving in a territorial manner again, even though the surrounding area had been intensively surveyed twice.

Floaters

Although vacancies did not always result in replacement, floaters had been banded and resighted consistently in the area. Over the course of the study, we radiotagged and banded seven male and four female adult floaters. We saw unbanded birds moving quietly on territories where both the male and female were banded and vocalizing. Because those floaters were unbanded, it is impossible to know how many there were; but we do know that there were at least one of each sex, in each population, with the exception of one population where male floaters were observed less than three times in the same area. That brings the total number of observed floaters to nine male and seven female floaters over 15 months. Of

those floater individuals, three of the females and one male were radiotagged throughout the 2001 field season. Each of those four floater individuals had a home range less than or equal to four territories, with the male moving farther than any of the females. Floater birds were in similar physical condition as territorial individuals (floaters: 0.117 ± 0.457, $n = 8$; territorial: 0.013 ± 0.160, $n = 70$; $t = -0.271$, $P = 0.80$). We calculated our power to detect a 30% increase in mean body condition in territorial individuals that results in a measure of positive body condition residuals (0.117) approximately equal to the negative measure (–0.117) found in floaters (power = 0.57). All experimental vacancies were filled in cases in which a floater had been observed on a territory ($n = 4$). Floater birds never paired with other nonterritorial birds; however, the opportunity for such behavior existed for at least five of our banded floaters. In those cases, sexually mature individuals of the opposite sex and suitable, vacant, habitat were both available nearby.

Discussion

Territory switching.—Territory switching appears to be an important component of White-bellied Antbird's territorial system for both sexes. Of the eight replacements that occurred in response to removal experiments, three individuals switched from their nearby territories. Switching territories to increase access to food (Bried and Jouventin 1998) and foraging substrate (Morton et al. 2000) has been noted in other species of year-round territorial birds and may help to increase adult survivorship. Food abundance for White-bellied Antbirds is lowest during the nonbreeding season in Panama (Levings and Windsor 1982) and could be a key feature of territory quality for that species. Indeed, in a paired test, we found that individuals were in significantly better physical condition during the breeding (wet) season than the nonbreeding (dry) season (B. C. Fedy and B. J. M. Stutchbury unpubl. data). Thus, switching may be driven by gaining access to territories where adult survival will be enhanced because of better food availability during the dry season. Vacancies created in the high-density study site were filled more frequently and individuals were in better body condition than those in the low-density site. Furthermore, birds in the low-density site spent significantly more time off-territory than those in the high-density site. Territories in the high-density area appear to be higher quality because birds compete more for territory vacancies, birds do not often leave their territories, and birds are able to maintain better body condition through times of low food abundance.

Assessment of territory vacancies and territory quality.—All previous studies that have used removal experiments on passerines of this territorial system have found that replacement birds typically move into vacancies within 24 h of the removal (Levin 1996, Morton et al. 2000). That is not the case for White-bellied Antbirds. The slow replacement rate suggests that territorial status is difficult for floaters and neighbors to assess. That is likely because natural song rates are low (12 songs h^{-1}; B. C. Fedy and B. J. M. Stutchbury unpubl. data), and widowed birds do not advertise loudly for new mates. Furthermore, even though extraterritorial forays could be used for assessment of neighboring territories, movements of territory owners are limited to within one or two territories of their own. So only a long absence by a territory owner would signal to a floater and neighbor a true vacancy. Thus, birds may face some risk of moving onto a territory too soon, usually to be ousted when the original owner returns. Indeed, we found that six of eight replaced birds regained their territories when we released them.

It is expected that widowed birds will try to attract new mates, even in the nonbreeding season, because individuals could benefit from the extra-predator vigilance, resource-finding potential, and territory-defense assistance conferred by having a mate. It may also be more likely an individual will breed in any given year if they maintain a pair-bond throughout the nonbreeding season (Lefebvre et al. 1992). Therefore, we may expect individuals to begin searching for a new mate as quickly as possible after their mate has left. Widowed birds could attract a new mate by ranging farther in their movements to increase the possibility of encountering a new mate or through the use of vocalizations to advertise their unmated status. Long-distance vocal advertisement can take on one of two forms, either an increase in song rate (Levin 1996) or through the use of a unique songs (Morton 1996).

White-bellied Antbirds do not make use of that type of long-distance signal to advertise for a new mate. Instead, females increase their rate of chip and cheer calls that do not transmit far through the habitat. Individuals may use those calls to try and establish contact with their missing mate. Telemetry data also revealed that widowed birds do not range far in search of mates. Despite the absence of long-range advertisement or an increase in the range of widowed birds, replacement still occurred in 60% of male vacancies and 29% of females. Therefore, floaters and neighbors must be assessing the territories. Neighbors may detect vacancies by the absence of duets being sung on the territory. Moreover, because male and female songs differ in structure (B. C. Fedy and B. J. M. Stutchbury unpubl. data), floaters and neighbors can determine from the song which sex is on the territory alone. High song rate may be costly in terms of predation risk and energy consumption for White-bellied Antbirds. Therefore, a widowed bird may opt for less-costly advertisement calls that are nonaggressive toward replacing birds of the opposite sex.

Territorial birds of both sexes left their territories and visited neighboring territories during the dry season. Those movements were not related to mating but could serve as a means of assessing neighboring territory quality in case a vacancy should arise. Birds were observed foraging during their extraterritorial forays, which suggest those forays are also a means of finding food during periods of low food abundance. In their study of three species of antwrens in Panama, Greenberg and Gradwohl (1985) also observed that interloping by neighboring groups and wandering through by dispersing immature birds was more common in the dry season. At a study site in northeastern Colombia with much shorter and less severe dry seasons, Ahumada (2001) found that litter arthropods did not vary significantly throughout the year and observed White-bellied Antbirds breeding in both dry and wet seasons. We predict that extraterritorial forays will be less common during the wet season in Panama and rare throughout the year in northeastern Colombia. In the Dusky Antbird, that type of foray behavior does not exist because abandoned mates will quickly switch to singing a mate attraction song if their mate is gone for more than a few minutes (Morton 1996). Thus, a male or female bird risks losing their mate if they leave the territory. Such a threat does not exist in White-bellied Antbirds. Even though females will increase their chip and cheer rates when a male is removed from the territory, it generally takes them an hour before they increase those rates and even then, as mentioned above, those are not long-distance calls. Therefore, the threat of being replaced while on an extraterritorial excursion is minimal.

Floaters and unoccupied territories.—Removal experiments resulted in replacement eight times, of which two were banded floaters previously sighted on the territories. Three replacements were unbanded individuals of unknown origin and could have been individuals who switched territories or floaters in the area. Birds did not switch far from their original territory, and most territorial birds were banded in the vicinity of the removal experiments. Therefore, it is more likely the unbanded replacements were floaters rather than previously territorial individuals. Furthermore, floaters seem to confine their movements to include a maximum of 3–4 territories that brings them into close proximity of the territorial birds on a regular basis. Confined floating such as this allows the individual to benefit from knowledge of the terrain and potential mates and would also allow them to establish dominance relations with other floaters in the area (Smith 1978). Thus, floaters on a territory would be the first to detect the absence of the territory owner and, therefore, would have the first opportunity to settle into the newly created vacancy. However, many territories remained vacant after an owner left. Given that we found a higher replacement rate in the high-density area where body condition is better and birds spend less time off their own territory, it is possible that floaters and territory owners are less likely to fill vacancies on low-quality territories (Stacey and Ligon 1987, Zack and Rabenold 1989). It may also be more difficult for individuals to detect vacancies in the low-density area given the greater distance between neighbors.

We could not determine the cause of natural vacancies for 62% of individuals. However, we were able to determine that vacancies arise for one of three reasons. Birds either died, switched to new territories, or temporarily abandoned territorial behavior. Territory switching was the cause for vacancy in almost one-quarter

of all naturally occurring vacancies. In their long-term study of Checker-throated Antwrens (*Myrmotherula fulviventris*), Greenberg and Gradwohl (1997) found that one-third of naturally occurring vacancies resulted from territorial switching. It is also possible that birds may have permanently emigrated from the study sites. However, our two primary study sites were structured in such a way that we were able to survey the entire area, and White-bellied Antbirds are not a particularly vagile species. None of our banded individuals were ever found far (maximum 200 m) from their capture site, and none of our radiotagged individuals moved >200 m from their territory (and those were rare occasions). Furthermore, no individuals were ever observed crossing gaps in the forest that were >20 m wide. Permanent emigration from any of the sites would require crossing gaps much larger than 20 m. Thus, permanent emigration from the study sites may have occurred but likely at extremely low rates.

Of particular note in White-bellied Antbirds was the temporary abandonment of territorial behavior. There are no other documented instances of this type of behavior in any other species of tropical, year-round, non-ant following bird. In White-bellied Antbirds, previously territorial birds (outside of removal experiments) abandoned territorial behavior for periods of two months or more during the nonbreeding season. Body condition data and studies on food availability (Levings and Windsor 1982) suggest birds that abandon territorial behavior may be food stressed during that time. Perhaps, when it becomes too costly for some individuals to maintain a territory, they will abandon territorial behavior and adopt the behavior of floater individuals. That likely gives them access to food on neighboring territories because territorial birds were never observed being aggressive to floaters on their territory. We predict that behavior is only temporary, and birds will resume territorial behavior once the breeding season arrives and food is more abundant. That occurred in three of five birds that temporarily abandoned territorial behavior during the nonbreeding season. The remaining two individuals were not observed as territorial again; however, given the timing of our field seasons, we missed the last 3.5 months of each breeding season and they may have began exhibiting territorial behavior again during that time.

Despite similarities in broad habitat associations and in the prevalence of territory switching, territorial behavior in White-bellied Antbirds highlights some interesting contrasts with the Dusky Antbird. White-bellied Antbirds make regular forays off-territory during the nonbreeding season and exhibit longer term, but temporary, abandonment of territorial behavior. Surprisingly, widowed birds do not elevate their song rate or sing distinctive songs to attract new mates. That clearly indicates that more in-depth studies are needed to reveal the subtleties of year-round tropical territorial systems and to understand the differences between species.

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