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Territory defence in tropical birds: are females as aggressive as males?

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Abstract Much of our knowledge concerning the functions of territorial behaviour and how territories are defended by individuals comes from research on birds. The vast majority of this work has focused on temperate zone breeding territoriality in which territories are defended most obviously by males. Our understanding of the female role in territory defence is limited because they are less conspicuous and much harder to observe. We studied sex roles in territory maintenance and defence in a duetting, resident neotropical passerine, the white-bellied antbird (*Myrmeciza longipes*). This species maintains territories and pair bonds year round and both sexes sing and actively participate in territory defence. We performed a series of playback experiments throughout the dry (non-breeding) and wet (breeding) seasons. We exposed territorial pairs to three types of stimuli including: (1) single sex, male only songs, (2) single sex, female only songs, and (3) both sex songs/duets. Contrary to findings for most other tropical species, individuals defended their territories with equal levels of aggression regardless of stimuli. Furthermore, sex roles were very different, with males responding more aggressively than females to all stimuli throughout both seasons. Both males and females consistently responded more aggressively to territorial intrusions during the dry season than during the wet season, likely because food abundance is low in the dry season and territory value is high. Our analysis of duetting behaviour suggests that duets do not serve a significant role in mate guarding, or territory defence.

Key words Sex roles · Territory defence · Tropics · White-bellied antbirds

Introduction

Territory defence in birds has been extensively studied, but primarily in temperate zone species where breeding territories are defended for a short period in spring and summer, and male defence via song and border disputes is conspicuous (Catchpole and Slater 1995). Female territory defence against other females is relatively under-studied in birds because it is more subtle and therefore difficult to observe (Amundsen 2000). Tropical passerines offer a unique opportunity to ask new questions about territorial behaviour because in many species both sexes sing and defend the territory and territory defence takes place all year round (Stutchbury and Morton 2001). Are males and females equally aggressive in territory defence? Do they direct their aggression primarily at same-sexed intruders, or does the pair co-operate and repel all intruders regardless of sex?

The evolution of sex roles is primarily driven by the operational sex ratio (OSR) (Emlen and Oring 1977), which in turn affects the intensity of sexual selection within each sex. Factors that influence OSR include: (1) the relative abundance of each sex (Emlen and Oring 1977), (2) the potential for mating (Clutton-Brock and Vincent 1991), and (3) the stringency of mate choice (Owens and Thompson 1994). These factors appear to be equal for male and female tropical passerines that have a monogamous mating system and yearlong territoriality (Stutchbury and Morton 2001). Furthermore, both males and females require territories and are capable of defending them alone (Levin 1996b; Morton and Derrickson 1996; Fedy and Stutchbury, unpublished data). Greenberg and Gradwohl (1983) concluded that both sexes of dot-winged antwrens (*Microrhopia quixensis*) participate equally in territory defence behaviour. However, this is not the case for all species. In other species of antbirds, males are more aggressive than females (Willis 1973; Morton and Derrickson 1996; Bard et al. 2002).

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In several tropical bird species, individuals of a pair defend their territories primarily against intruders of the same sex (Freed 1987; Levin 1996b; Morton and Derrickson 1996; Appleby et al. 1999; Morton et al. 2000). In playback experiments, both Levin (1996b) and Morton and Derrickson (1996) found that females responded more aggressively to same sex songs than to duets or male songs. Same-sex territory defence by females may deter trespassing, and eviction, by other females (e.g. McElroy and Ritchison 1996). This type of same-sex aggression in females has also evolved in several other taxa with monogamous mating patterns, including several species of monogamous antelope (the dikdik *Madoqua kirkii*, Brotherton and Rhodes 1996; and the klipspringer *Oreotragus oreotragus*, Roberts and Dunbar 2000). Alternatively, year round territory defence by males and females may lead to co-operative territory defence within a pair. Hall (2000) documented apparent co-operative behaviour in a series of playback experiments investigating the function of duetting in magpie-larks (*Grallina cyanoleuca*). In that study, females maintained both territory and pair bond by attempting to exclude intruders of either sex in apparent co-operation with their mates.

We studied sex roles in territory maintenance and defence in the white-bellied antbird (*Myrmeciza longipes*), a resident neotropical passerine which maintains territories and pair bonds year round. Both males and females sing and exhibit aggressive territory defence and pairs routinely duet throughout the year. Like other species of antbirds (Formicariidae), both sexes contribute equally to nest building, incubation and care of the young. We performed a series of playback experiments throughout the dry and wet seasons. We exposed territorial pairs to three types of stimuli including: (1) single sex, male only songs, (2) single sex, female only songs, and (3) both sex songs/duets. Because the threat of eviction from a territory applies only to a same sex competitor we predicted that individuals would defend their territories more aggressively from same sex intruders than opposite sex (Levin 1996b; Morton and Derrickson 1996; Appleby et al. 1999). Territorial intrusions are expected to pose a greater threat to resident birds in the wet season than in the dry season because the majority of breeding occurs during the wet season, mates are likely fertile and thus intruders present an immediate risk of cuckoldry. Furthermore, if an intruder evicts a resident during this period, the evicted bird likely will have difficulty finding a new territory in time to breed that season. Thus, given the importance of territory ownership for breeding, we also predicted that individuals would respond more strongly to playbacks during the wet season than the dry season.

Duets generally have the two key characteristics of a constant lag time between the contributions of the two individuals and a repeated and predictable structure (Langmore 2002). Several non-mutually exclusive hypotheses exist for the function of avian duetting (Hall 2004). One key hypothesis is that duetting may represent a form of co-operative territorial defence between pair members (Wickler 1976; Wickler and Seibt 1980; Hall 2000; Grafe and Bitz 2004; but see Farabaugh 1982). If this hypoth-

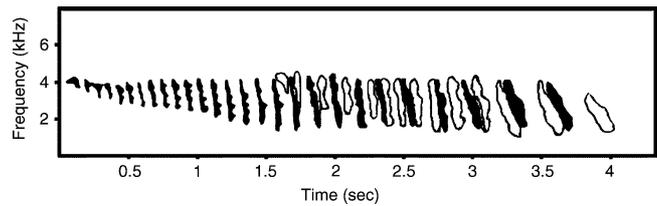


Fig. 1 Tracing of a white-bellied antbird (*Myrmeciza longipes*) duet. *Black* male song, *white* female song. Females join the male song which results in song overlap

esis is correct, then duets should be perceived as more threatening territorial signals than solo songs. If duetting is a more threatening signal, then the proportion of duets sung by the defenders should increase during playbacks compared with natural background rates. Furthermore, duet playbacks should elicit a more aggressive response from the territory owners than single sex playbacks. White-bellied antbirds are unusual because their duetting appears to be almost entirely under female control. A duet is formed when the female begins singing during a male song (Fig. 1). In most other species, either sex can join the song of their mate to create a duet (Farabaugh 1982), and evidence seems to suggest that it may be more common among species for the male to join the female to create the duet (see Langmore 1998). Therefore, we can also predict that duets, as a form of female defence, will be more common in response to female song playbacks than to male song playbacks.

Methods

Study site and study species

White-bellied antbirds inhabit second growth and edge habitat in lowland tropical areas from northern Brazil to central Panama (de Schauensee 1966; Wetmore 1972). They are a medium-sized ($X \text{ bar} + \text{SE} = 29 \text{ g} \pm 0.3$, range = 25–32.5 g), sexually dimorphic, passerine of the Formicariidae family and males are slightly heavier than females (males: $X \text{ bar} + \text{SE} = 28.7 \pm 0.3 \text{ g}$, $n=42$; females: $X \text{ bar} + \text{SE} = 27.5 \pm 0.3 \text{ g}$, $n=29$; t -test $P=0.005$). They are insectivorous birds that associate in pairs throughout the year, forage almost exclusively in the ground leaf litter, and do not follow ant swarms.

Research was conducted from 15 January to 30 July 2000 in Parque Nacional Soberania, Panama ($9^{\circ}7'N$, $79^{\circ}40'W$) at the junction of the Panama Canal and the Chagres River. This area is a tropical lowland forest receiving approximately 2.6 m of rain per year (Karr 1971), almost all of which falls during the wet season. Central Panama has a pronounced dry season from mid-December to late April (Windsor 1990). In general, the non-breeding season for ground foraging, insectivorous birds in this area corresponds with the dry season and lasts approximately from January to April. Breeding can begin in late April, when the wet season begins and litter arthropod populations increase (Levings and Windsor 1982). However, breeding is

highly asynchronous and evidence of breeding can still be found into December for species with similar ecology to white-bellied antbirds (Robinson et al. 2000).

Birds were caught in mist nets by broadcasting a conspecific song on their territory and every individual was banded with a unique colour combination ($n=48$ males and 34 females). Some birds were flushed into the nets when necessary. Territory boundaries were determined by mapping bird locations during song bouts, border disputes and by assessing responses to playback of recorded songs (Falls 1981).

Natural song rates

Data on natural song rates were collected between 0620 and 1230 hours throughout the non-breeding and breeding seasons. Sessions lasted 1 h with a minimum of 24 h between sampling sessions on any one territory (total 140 h, $\bar{X} \pm \text{SE} = 8.8 \text{ h} \pm 0.52$ per territory, $n=16$ territories). Researchers sat quietly on the edge of the territory and recorded all vocalisations of the focal pair. Distance between pairs was recorded every time a pair duetted. Total song rate refers to the number of songs/h for a focal pair and includes solo and duet songs. Natural song rate data were not normally distributed (Shapiro-Wilk $P=0.01$), therefore non-parametric tests were used in all analyses of these data.

Playback experiments

Playback experiments were conducted in the dry season (10 March to 12 April) and the wet season (21 May to 18 June) between 0600 and 1230 hours. Each pair of territorial birds ($n=15$ pairs) was subject to three playback experiments in both seasons. Each experiment involved broadcasting a song stimulus to the focal birds. The three different stimuli were: (1) male song only, (2) female song only, and (3) duets. The order of stimuli presentation was randomised for each pair within each season. Experiments were spaced between 20 and 48 h apart and neighbouring territories were not tested on the same day.

Playback tapes were made from high-quality recordings of territorial individuals located a minimum of 3 km away from the focal pair's territory. This distance is well outside the dispersal range of white-bellied antbirds (Fedy and Stutchbury 2004) and is sufficient to ensure that all individuals were exposed to unfamiliar songs. All recordings were made within 5 m of the subject using a Sony TC-D5 PRO II recorder with a Sennheiser MKH 816 directional microphone. Playback tapes mimicked the typical singing pattern and amplitude of aggressive white-bellied antbirds as determined by observing natural boundary disputes and response to simulated intrusions. Throughout the study we observed 32 boundary disputes (13 territories). During these disputes average male song rate was 2.0 songs/min (SD 0.5), average female song rate was 1.1 songs/min (SD 0.4) and the average number of songs

sung as a duet was 0.7/min (SD 0.3). Each playback tape was made by looping a 1-min segment of a natural recording for 10 min (male song only: 2 songs/min; female song only: 1 song/min; duets: 2 male only songs and one duet/min). Four tapes of different individuals were made for each of the three stimuli (male, female, duets $n=12$ tapes) to avoid the potentially confounding affects of pseudoreplication (Kroodsma 1989). One of the four tapes was chosen randomly for each trial within an experiment.

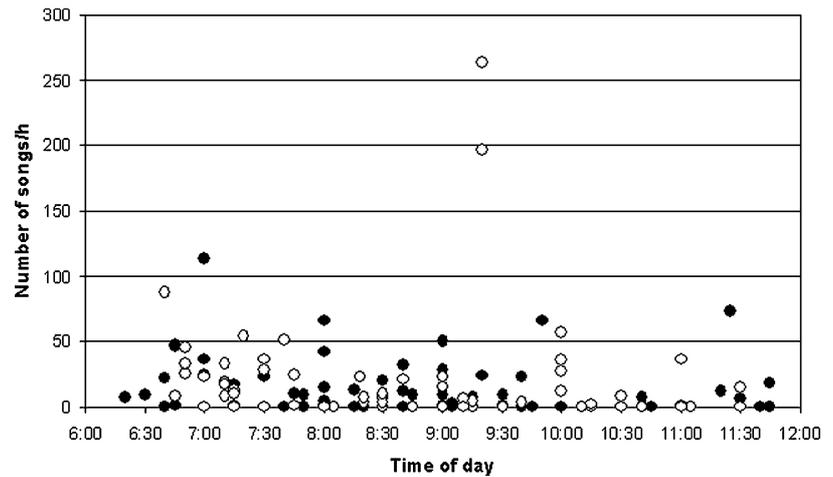
The playback speaker was concealed within a pair's territory a minimum of 15 m from the nearest boundary and observers retired to cover a minimum of 10 m away. Birds showed no response to our presence during the playback experiments. To determine the focal birds' distance to the playback speaker, 5-m intervals around the speaker were marked off with flagging tape. Between each trial the playback speaker was moved 5–10 m within the territory to avoid habituation to any particular location. Focal birds were silent for a minimum of 10 min before each experiment began. This species has low natural song rates and therefore the situation of 10 min of no singing was not uncommon. Songs were broadcast for the first 10 min of the experiments and were followed by a 10-min post-playback silent period. We recorded the behaviour of the resident male and female for the entire duration (20 min). Six variables were collected for all birds during playback experiments: total time responding—time from the first song or movement towards the speaker until the bird moved > 15 m away and stopped singing (TTR; s), the latency to first vocalization of any kind (LFV; s), number of songs (NS), closest approach to speaker (CA; m), time spent between 20 and 5 m to the speaker (T20; s), and time spent < 5 m to the speaker (T5; s). A strong response by territory owners would show high TTR, NS, T20, T5 and low values for LFV and CA. To quantify the intensity of response to the playback experiments a principal components analysis was performed on the variables by the use of the correlation matrix (James and McCullough 1990; McGregor 1992). Principal components analysis does not accommodate missing response values, so it was necessary to insert values for LFV and CA for birds that did not respond. In these cases the individual was assigned an LFV of 1200 s (20 min, the entire duration of the experiment) and a CA of 30 m (the largest recorded in responding birds). All response variables measuring the intensity of an individual's response were entered without transformation, except for CA which was log transformed to achieve a closer approximation of a normal distribution. Means are presented \pm SE throughout and all data were analysed using SPSS v. 10.

Results

Natural song rates

White-bellied antbirds have low natural song rate and although average male song rate was only 12–17 songs/h, in two watches we recorded up to and over 200 songs/h, whereas for 43% of watches no songs were recorded from

Fig. 2 Natural song rates throughout the day. Each circle represents a sampling session. Closed circles dry sessions, open circles wet season sessions. Unlike many other tropical passerines, white-bellied antbirds do not sing a dawn chorus in either the dry or wet season



either the male or female of a pair. The average number of songs/hour for males and females combined did not vary by time of day (0630–1230 hours) throughout the sampling period (Fig. 2, ANOVA: $F_{1,146}=2.4$, $P=0.12$), and there was no dawn chorus. Average total song rate/h in the dry season (12.0 ± 2.9) was not significantly different than in the wet season (17.6 ± 4.1 Wilcoxon signed ranks test: $n=16$, $z=-0.83$, $P=0.41$). When males and females were considered separately the song rate/h of either sex (including solo songs and duets) did not differ between the dry and wet seasons (males: dry 8.3 ± 1.9 , wet 13.5 ± 3.1 , $n=16$, $z=-1.32$, $P=0.19$ females: dry 3.7 ± 1.1 , wet 4.2 ± 1.2 , $z=-0.06$, $n=16$, $P=0.96$). Average male song rate per hour (10.9 ± 1.6) was significantly higher than female song rate per hour (3.9 ± 0.8 , $z=-3.16$, $n=16$, $P<0.001$) across both seasons (Fig. 3). The number of duets given per hour did not differ between the dry (2.7 ± 1.0) and wet seasons (2.6 ± 0.9 , $z=-0.17$, $n=16$, $P=0.87$).

Playback experiments

Song rate for both males and females increased significantly from natural levels during playback experiments. During playback trials individuals averaged 18.6 ± 1.9 songs/20 min. Natural song rates of the same birds were sig-

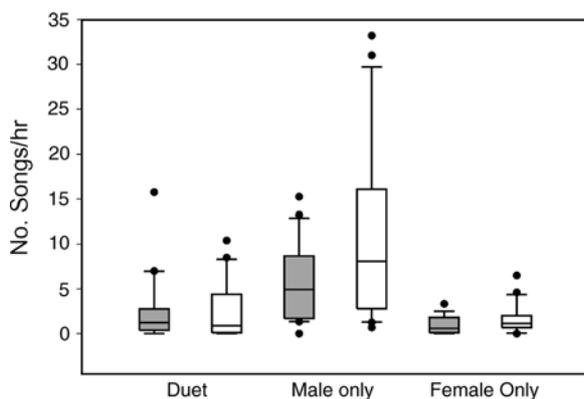


Fig. 3 Box plots showing natural song rates between seasons ($n=16$). Grey boxes dry season, white boxes wet season

nificantly lower 2.6 ± 0.4 songs/20 min ($z=-4.78$, $n=30$, $P<0.001$). In a few cases, territorial individuals did not respond to the playback experiments. In the dry season, males ($n=15$) responded to 100% of the experiments (45/45 trials) and females ($n=15$) responded to 91% of experiments (41/45). Both sexes decreased the number of experiments they responded to in the wet season. Males responded to 88% of the experiments (40/45) and females to 71% of experiments (32/45). Over both seasons combined males responded to 94% of experiments (85/90) and females to 81% (73/90).

The principal components analysis (PCA) showed that PC1 varied positively with TTR, NS, T20 and T5. The range of loadings varied little from T5 (0.78) to T20 (0.95). PC1 varied negatively with the other two variables (LFV, -0.87 ; CA, -0.74). PC1 accounted for 74% of the total variation in the original data set. Data were then analysed using a repeated measures ANOVA (RMA).

There was a significant difference in the intensity of response to playbacks between the dry and wet seasons (MANOVA: $F_{1,15}=6.4$, $P=0.02$) and in the intensity of responses from the different sexes (MANOVA: $F_{1,15}=19.7$, $P<0.001$). Thus, on average, both sexes respond more aggressively to playbacks in the dry season than in the wet season and males consistently respond more aggressively than females throughout both seasons. The different stimuli (male song, female song, duet) did not elicit significantly different responses (MANOVA: $F_{2,15}=0.13$, $P=0.88$). Furthermore, analysis of interaction terms revealed no significant interactions between season, stimuli or sex (season*sex, MANOVA: $F_{2,15}=1.4$, $P=0.27$; stimuli \times sex, MANOVA: $F_{2,15}=1.3$, $P=0.31$, season \times stimuli \times sex, MANOVA: $F_{2,15}=0.8$, $P=0.44$). An RMA was also conducted to see if the presentation order of the tapes had any effect on the intensity of the birds' responses and no significant difference was found within the tape order or the interaction terms (tape order, MANOVA: $F_{2,15}=0.0$, $P=0.99$; season \times tape order, MANOVA: $F_{2,15}=1.2$, $P=0.32$). Figure 4 shows the actual values for three of the key variables (TTR, NS, LFV) which contributed to the calculation of PC1 and reflects the findings of the principal components analysis.

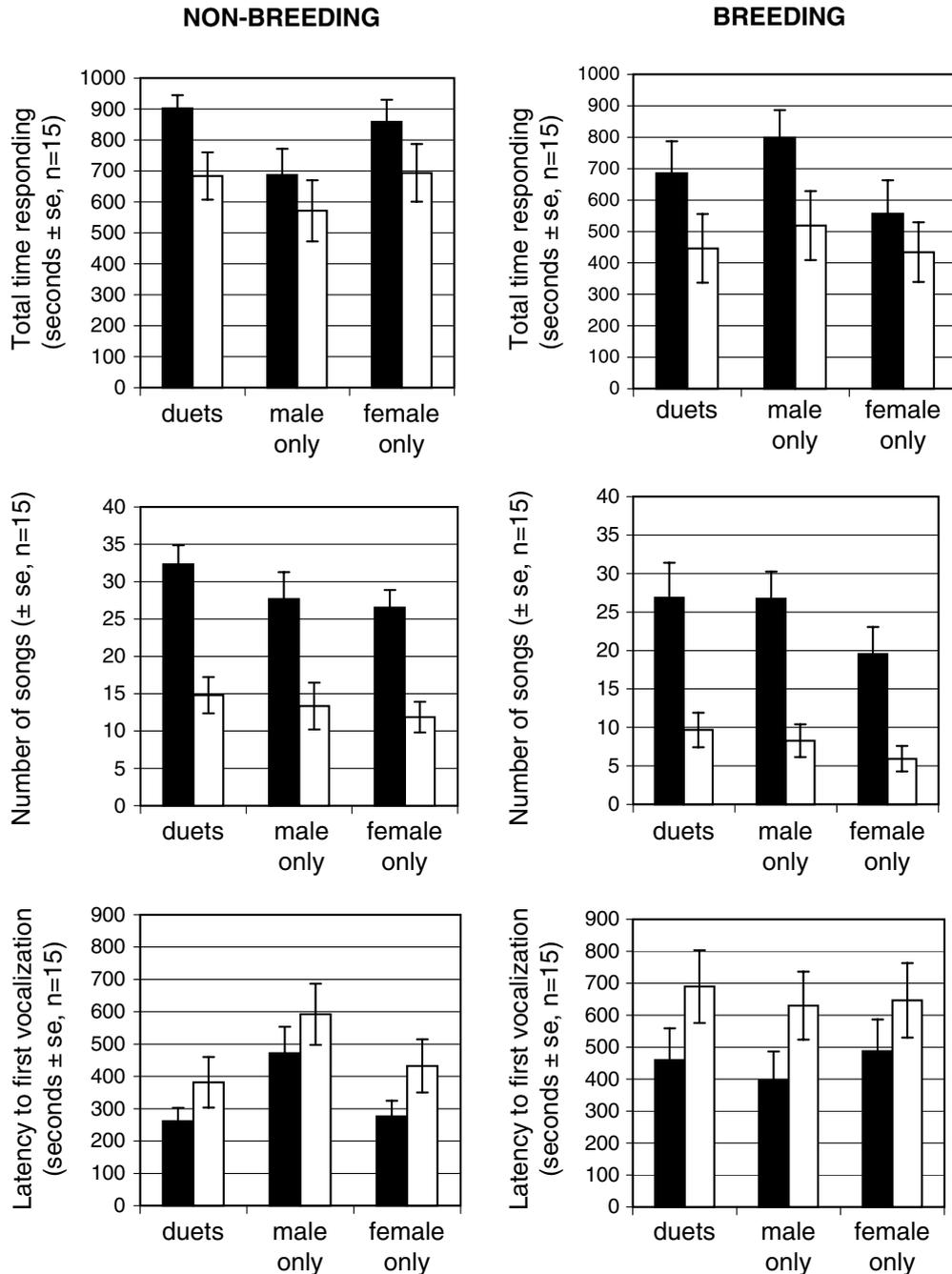


Fig. 4 Male and female responses to the three different playback stimuli. *Black bars* male response, *white bars* female response. Variables reported are: total time responding (s), number of songs, and latency to first vocalisation (s)

Since duetting results from females singing after the male initiates his song, there are two ways to gauge the frequency with which females duet and hence use duetting in territorial aggression. First, what proportion of female songs are given as duets with the male, and second, what proportion of male songs are joined by female song to create a duet? We averaged the proportion of female songs in duets across both seasons in response to male song only and female song only playbacks. Duets occurred in $54\% \pm 8\%$ of female songs in response to female song playback and $56\% \pm 8\%$ in response to male song playbacks. This was

not significantly different ($z = -0.47$, $n = 15$, $P = 0.64$). We conducted a paired analysis of natural duetting behaviour and duets sung during playbacks to determine if a simulated intrusion increases the frequency of duetting by females. An increase in duetting during intrusions may indicate that duets are a more aggressive form of territorial signal than solo songs. We averaged the proportion of songs sung in duets throughout all playback experiments ($n = 6$ experiments per individual) and compared this against the natural duet rate for the same individuals. During the playback experiments females joined 24% of male songs to

create a duet, compared with 27% for natural song observations ($z=-0.97$, $n=14$, $P=0.33$). Similarly, duets comprised 60% of all female songs given during playbacks, and 56% of all female songs during natural observations ($z=-1.16$, $n=14$, $P=0.25$). Summarising, both predictions regarding the possible role of female duetting in territory defence were rejected.

Discussion

The territorial behaviour of white-bellied antbirds is not typical compared with other similar species (Levin 1996b; Morton and Derrickson 1996), demonstrating that our understanding of the prevalent tropical territorial system of year round defence is still quite limited. Sex roles in territory defence were very different, and birds responded with equal aggression to same sex and opposite sex playbacks. Song rates are typically low and there is no conspicuous dawn chorus. This is likely due to low intruder pressure, compared with temperate zone species, and stable territory boundaries with known neighbours (Greenberg and Gradwohl 1986).

Seasons

White-bellied antbirds responded more strongly to playbacks during the dry season. They feed on leaf-litter arthropods which increase dramatically in abundance during the wet season (Levings and Windsor 1982). The stronger responses during the dry season may be the result of a higher territory value, due to a greater competition for rare food resources. This suggests that territory defence may be related to food abundance. Territory defence may be more important when food is limited during the dry season to ensure access to food and avoid competition with intruders over food resources. These findings agree with other theoretical and empirical studies on the role of food resources in territorial behaviour in that an increase in food resources led to a decrease in territorial aggression (Brown 1964; Gill and Wolf 1975; Dubois and Giraldeau 2004). Of course, maintaining territories in the dry season would also secure a breeding position in the wet season, when nesting actually occurs.

Constraints during the breeding (wet) season may account for some of the disparity observed in aggression levels between the two seasons. Attendance at the nest, or young, could constrain participation in territory defence during the breeding season due to time or energy restrictions. If birds were attending to eggs or young it may be too costly in terms of time lost foraging and feeding young to engage in active territory defence. Territory defence may also expose young to predators as territory defence is very conspicuous and young seem to stay close to their parents. We were unable to determine the exact stage of breeding during playbacks in the breeding season, so are unable to directly compare the defence behaviour at different nest stages.

Both sexes also responded to a greater proportion of the playback experiments during the dry season. It is unlikely that focal birds did not hear the playbacks as white-bellied antbird songs are loud and can often be heard across two territories (B. Fedy, personal observation). Territory boundaries were well established and stable and we knew the extent of every marked bird's territory. Furthermore, radio-telemetry has shown it is very rare for a white-bellied antbird to engage in forays that are further than two territories away (Fedy and Stutchbury 2004). Therefore, we can conclude that birds chose to ignore the intrusion when they did not respond to the playback.

Natural song rates were low (males: 11/h, females: 4/h) and similar between both seasons. Although birds are more aggressive during the dry season in response to intrusions, they do not show a higher natural song rate in the absence of intruders. It is unlikely that low song rates were the result of limited food abundance because natural song rates did not increase with higher food abundance in the wet season.

Sex roles

Males are more aggressive in territory defence than females. An inequality in sex roles has been documented in this type of territorial system before, but not to the same degree (Morton and Derrickson 1996). Male white-bellied antbirds consistently responded to more of the playback experiments and were more aggressive than females regardless of stimuli or season. This sex difference in territorial aggression may be connected to the benefits of retaining versus switching mates and territories. Levin (1996a) and Morton et al. (2000) conducted removal experiments on their duetting study species. In both species, it was found that territorial vacancies (both experimentally created and natural) were filled very rapidly (less than 1 day). This rapid replacement rate was observed in another duetting species, the buff-breasted wren (S. Gill and B. J. M. Stutchbury unpubl. data). Furthermore, Levin (1996a) found that bay wrens (*Thryothorus nigricapillus*) would quickly increase their song rate after the loss of a mate and this was interpreted as a means of attracting a new mate. In an even more obvious effort at mate attraction, widowed dusky antbirds (*Cercomacra tyrannina*) begin singing a unique song within minutes of their mate's disappearance (Morton and Derrickson 1996). Such long distance mate attraction efforts do not exist in white-bellied antbirds (Fedy and Stutchbury 2004). Temporary removals of white-bellied antbirds showed no evidence of long-distance song advertisement in widowed males or females (Fedy and Stutchbury 2004). Removed birds were not replaced rapidly, with replacements occurring after 3 days in several cases. Therefore, white-bellied antbirds do not face the same intense/short term threat of replacement which exists in other species. Furthermore, this suggests that in white-bellied antbirds retaining a familiar mate is beneficial as they do not advertise or switch readily. For white-bellied antbirds, sex roles in territory defence may

therefore be tightly linked to the traditional notion of pair bonds. When both sexes readily switch mates and break long-held bonds, territory defence is focussed primarily on same sex individuals (Levin 1996b; Morton and Derrickson 1996). When mate switching is less common, as in white-bellied antbirds, territory defence is equal against all intruders regardless of sex. This implies the pair is co-operating in territory defence, in the sense that each individual benefits by preventing intruders from displacing either themselves or their mate.

White-bellied antbirds are ground foraging birds which likely leads to high predation risk for adults. Therefore, mates may be important for predator vigilance as well as for breeding partners. In a species where life is dangerous, familiar mates may become an important resource for survival. Morton and Stutchbury (2000) found that adult dusky antbirds, which forage in dense vine tangles, had a survival rate of 82%. In our study of white-bellied antbird only 55% of individuals banded in one year survived to the next (Fedy and Stutchbury, unpublished data). Furthermore, using radio telemetry we have found that pair members spend over 60% of their time within 5 m of each other (Fedy and Stutchbury, unpublished data). This reliance on mates for vigilance could partially explain why white-bellied antbirds do not readily switch or advertise for new mates. Each individual within a pair receives benefits from their mates in the form of the non-depreciable 'resource' of predator vigilance which would moderate the conflict between the sexes and allow them to act in a more co-ordinated manner in territory defence. Therefore, predation risk could be playing a significant role in the expression of sex roles in white-bellied antbirds.

The higher levels of aggression shown by males may be the result of a greater threat to their territory position than to females. If males are more likely to be ousted from a territory, males should respond more strongly to male intruders than to female intruders; however, males responded equally to all stimuli. Males would face a greater competition for their territorial position if there were a male-biased sex ratio. However, our data from removal experiments suggests this is not the case. We confirmed the presence of similar numbers of male and female floaters, and male and female vacancies were equally likely to get filled in response to natural and artificially created vacancies (Fedy and Stutchbury 2004).

Breeding activities may also influence sex roles and aggression. Similar male and female mating effort could produce similar levels of aggression by the sexes in both seasons. We observed that males were more aggressive than females during the breeding season. Although males and females likely contribute equally to nest building and care of the young, females still need to invest energy (Walsberg 1983) and/or dietary protein (Ramsay and Houston 1998) into egg production. This may partially influence the unequal sex roles observed during the breeding period. However, this does not explain the differences in aggression levels between the sexes observed during the non-breeding season and is not likely to be a significant factor influencing the disparity in aggression between the sexes.

The ultimate mechanism influencing the difference in aggression levels between males and females is not immediately obvious. However, sexual selection in white-bellied antbirds is likely stronger on males than females, which may explain the sex role differences in territory defence. Males are bigger than females and the species is sexually dimorphic. Furthermore, males sing more than females and are consistently more aggressive to territorial intrusions. Despite the similar threat of replacement between the sexes, competition among males may be high due to control of high quality territories and/or mates. If males are primarily responsible for territory defence then female choice of mates may in turn depend on the male's aggression levels and ability to maintain a high quality territory throughout the entire year.

Duets

Duets represent a more aggressive form of territory defence than solo songs in some species (Hall 2000). Thus, we predicted that males and females would respond more strongly to duet playbacks than to single sex playbacks. This was not the case as individuals responded with equal levels of aggression to single sex and duet playbacks. We also predicted an increase in the proportion of duets in response to the playbacks than observed in natural vocalizations. However, the intense threat posed by the playback experiments did not result in a greater proportion of duets. Female white-bellied antbirds create duets by beginning to sing after the male song begins, but before it ends. Consequently, if birds were more aggressive to intruders of the same sex (Levin 1996b; Morton and Derrickson 1996), more duets should ensue in response to female only playbacks than to male only playbacks. Because white-bellied antbirds do not differentiate their responses between same and opposite sex playbacks, it is not surprising, in retrospect, that they did not differ in the proportion of duets sung in response to female only and male only playbacks. Duets may also function as a form of mate guarding (Hall 2004). If this were the case in white-bellied antbirds we would have observed an increase in duets in response to female only playbacks. No such increase was observed and thus we can conclude that duetting in white-bellied antbirds likely does not function as a form of mate guarding.

Farabaugh (1982) explored the idea that individuals may join in duets to avoid the possibility of mis-directed aggression from their mates. This could be the case in white-bellied antbirds as males respond with equal levels of aggression to male and female songs. It would therefore be beneficial for the female to let her mate know where she is to avoid mis-directed aggression from her mate. This would also allow the male to better focus his efforts on the intruding birds. The use of interactive playback experiments (e.g. Mennill et al. 2002) could be an excellent tool for investigating this possible function of duetting. Temporary removal of a female would allow investigators to playback her song to her mate with two treatments: (1) a trial in which the playback does not duet with the

resident male, and (2) an alternate experiment in which the playback results in duetting with the male. The avoidance of mis-directed aggression hypothesis would predict lower aggression in the male when the female playback overlaps with his songs to form duets.

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