Territory size and stability in a sedentary neotropical passerine: is resource partitioning a necessary condition?

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ABSTRACT. Long-term pair bonds and defense of territories year-round are common among tropical passerines. The boundaries of these territories tend to be stable, perhaps reflecting the need to defend an area that, regardless of conditions, provides sufficient food resources. If, however, these stable territories are not, even temporarily, sufficiently large, then intra-pair competition for available food may result, particularly in species with no sexual size dimorphism. With such competition, sex-specific differences in foraging behavior may result. Male and female Dusky Antbirds (*Cercomacra tyrannina*) are not size dimorphic, and pairs jointly defend territories throughout the year. Our objective was to determine if paired Dusky Antbirds exhibited sex-specific differences in foraging behavior. Foraging antbirds were observed in central Panama from February–July 2002 to determine if pairs partitioned food resources. Males and females exhibited no differences in foraging behavior, with individuals of both sexes foraging at similar heights and using the same foraging maneuvers (glean, probe, and sally) and substrates (leaves, rolled leaves, and woody surfaces). These results suggest that Dusky Antbirds do not partition resources and that territory switching, rather than resource partitioning, may be the means by which they gain access to additional food resources.

SINOPSIS. **Tamaño del territorio y estabilidad en un paserino neotropical sedentario: es una condición necesaria la repartición de recursos?**

El mantener la pareja por mucho timepo y la defensa del territoria a través de todo el año es común en los paserinos neotropicales. Los bordes de estos territorios tienden a ser estables, tal vez como un reflejo de la necesidad de defender un área que no empece a su condición, provee de suficientes recursos alimentarios. Sin embargo, si estos territorios estables (aún de forma temporal) no fueran lo suficientemente grandes, entonces pudiera haber como resultado competencia entre parejas por los recursos alimentarios, particularmente en especies en donde no hay dimorfismo sexual en el tamaño. Con esta competencia, pudieran surgir diferencias especificas en la conducta de forrajeo por parte de ambos sexos. El macho y la hembra de *Cercomacra tyrannina*, no son dimórficos y ambos defienden el territoria a través del año. Nuestro objetivo fue determinar si los miembros de esta especie, mostraban diferencias sexuales en su conducta de forrajeo. La conducta alimenticia de estas aves fue estudiada en la parte central de Panamá, de febrero a julio de 2002, para determinar si había repartición de recursos entre la pareja. No se encontró diferencias en los patrones de forrajeo entre los sexos, con ambos individuos forrajeando a alturas similares y utilizando la misma conducta y sustrato para conseguir alimento. Estos resultados sugieren que en la especie no hay repartición de recursos, y que el cambio a otros territorios, al menos en este caso, pudiera ser la forma en donde las aves ganan acceso a otros recursos alimenticios.

Key words: *Cercomacra tyrannina*, Dusky Antbird, foraging, sex-specific, territorial

Long-term associations of males and females, often on year-long territories, are prevalent among passerines in tropical habitats (Willis and Oniki 1972; Buskirk 1976; Freed 1987). Among insectivorous passerine species, 65% in Panama (Morton 1980) and 40% in tropical South Africa (Rowan 1966) have long-term pair bonds and stable territory boundaries. One possible explanation for stability of territory boundaries is that territory size is a response to potential fluctuations in foraging conditions (Holmes 1966), and territories include the minimum area necessary to provide sufficient foraging habitat (Greenberg and Gradwohl 1986, 1997). Energetics (i.e., foraging habitat required to meet metabolic requirements) may prevent territories from becoming smaller, while competition with neighboring conspecifics plus the increased cost of defending larger territories may prevent them from becoming larger (Hixon 1980). While this interaction between energetics and competition may usually

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generate territories with sufficient resources to support a resident pair, the stability of territory boundaries means that, if resource levels decline, pairs cannot gain access to additional resources by expanding their territories. However, under such conditions, pairs may reduce competition for limited resources by intersexual partitioning of foraging habitat.

In temperate areas, intersexual partitioning of foraging habitat through variation in foraging behavior has been documented in a number of woodpeckers (Selander 1966; Ligon 1968; Pasinelli 2000) and songbirds (Williamson 1971; McEllin 1979; Holmes 1986; Sodhi and Paszkowski 1995; Kelly and Wood 1996). Paired males and females partition foraging habitat either by vertical segregation or by differential use of available substrates or foraging techniques (Noske 1986; Kelly and Wood 1996).

Intersexual habitat partitioning has been documented in tropical species, but reported sexual differences in foraging behavior and diet have largely been attributed to differences in either size or morphology. For example, male Montezuma Oropendolas (*Psarocolius montezuma*) are much larger than females, and intersexual differences in foraging behavior are clearly related to differences in size rather than competition for resources (Webster 1997). Similarly, female Frill-necked Flycatchers (*Arses telescopthalmus*) sally from leafy substrates in the upper canopy, while males forage on tree trunks and vine surfaces in the understory (Bell 1982). But this difference is apparently due to morphological differences (Bell 1982). Little is known about the foraging behavior of males and females in species with no size dimorphism or other morphological differences. In one of the few studies of such species, Gradwohl and Greenberg (1984) found no differences between male and female Checker-throated Antwrens (*Myrmotherula fulviventris*) in the types of leaves searched.

Dusky Antbirds (*Cercomacra tyrannina*) are suboscine passerines (family Thamnophilidae) that occupy forest edge and forage for arthropods on vines and brush (Morton and Derrickson 1996). Males and females are similar in size (Ridgely and Gwynne 1989), and pairs jointly defend territories throughout the year (Morton and Stutchbury 2000). Annual reproductive success is low (8%), and adult survival is high (82%), suggesting that Dusky Antbirds occupy territories that enhance adult survival and long-term reproductive success rather than short-term reproductive success (Morton and Stutchbury 2000). In support of this hypothesis, following experimental removals and natural disappearances, most antbirds abandoned territories and mates and paired with other individuals in territories with more foraging substrate (Morton et al. 2000). Such behavior suggests that availability of foraging substrate may be a limiting factor in some territories. If so, pairs of Dusky Antbirds may minimize within-pair competition for food resources by means of sex-specific differences in foraging behavior. The objective of our study was to determine if pairs of Dusky Antbirds partition food resources within their territories and, if so, how.

METHODS

This study was conducted from February–July 2002 in central Panama, 30 km north of Panama City, in the Soberania National Park near Gamboa (9°7'N, 79°40'W) and in forested areas in Gamboa. Both study sites were second growth (70–100 yr) and consisted of mesic forest with abundant edge. The area receives an average of 2.6 m of rain per yr and the climate is strongly seasonal (Levings and Windsor 1985). In 2002, the dry season in Panama began on 18 January and ended on 21 May (Smithsonian Tropical Research Institute's Terrestrial Environmental Sciences Program).

Between 3 February and 11 March 2002, Dusky Antbirds ($N = 34$; 17 males, 17 females) were captured in mist nets using playback of conspecific songs, and individuals were banded with unique combinations of colored plastic bands to permit individual identification. Three females and one male had been color-banded previously (Morton and Stutchbury 2000). Four additional birds (three males and one female) were captured and banded on 6 and 7 June 2002 as replacements for birds that had disappeared. For each captured bird, we measured bill length (from the tip of the upper mandible to the gape), bill depth and width (measured at the anterior of the nares), and culmen length (the distance from the front edge of the nares to the tip of the upper mandible). In addition, to increase our sample size, we measured the bills of 21 male and 16 female

Dusky Antbirds in the ornithology collection at the Museum of Natural Science at Louisiana State University in June 2003. Mean mass of male and female Dusky Antbirds is 16.0 g and 15.2 g, respectively (Morton and Stutchbury 2000).

For each focal pair, a territory map was created by establishing a grid (consisting of a series of 5 m × 5 m sections), then noting locations of the pair within the grid. Territory boundaries were determined during the dry season (February–April) by monitoring the movements of focal pairs ($N = 17$), noting the location of interactions between adjacent pairs, and using playback of conspecific songs to initiate territorial disputes. Boundaries were not determined for four territories because resident pairs exhibited little response to playback. Each focal territory was visited at least every four days. During observation periods of 20–60 min, the location of all observed foraging attempts and movements by both pair members were noted on maps of their territory. Daily, monthly, and seasonal (wet vs. dry) maps were generated to permit examination of possible differences in space use by paired birds.

During each visit to a focal territory, the first five foraging attempts by each member of the resident pair were quantified. A foraging attempt was defined as "a discreet action by a bird to obtain food in a particular place regardless of its duration or success" (Werner and Sherry 1987). For each foraging attempt, we noted the bird's height above ground, with height categorized as on the ground, lower than 0.5 m, 0.5–1.0 m, 1–2 m, 2–4 m, 4–6 m, or higher than 6 m. We also noted the perch substrate (branch, vine, or palm) and the diameter of the substrate on which the bird was perched.

Foraging maneuvers of Dusky Antbirds were categorized as glean, probe, sally, bite, or peck. Picking food items from nearby substrates, including reaching by extension of the legs or neck, was categorized as gleaning. A sally was defined as a flight from a perch specifically to attack a food item on a substrate while the bird was still in the air. Probing was defined as inserting the bill into a substrate to capture hidden arthropods, while pecking involved driving the bill against a substrate to dislodge a prey item. Finally, biting was defined as grasping a substrate with the bill and pulling or tearing with the intent of dislodging a prey item. During some foraging attempts, multiple maneuvers were used.

Foraging substrates used by Dusky Antbirds were categorized as vine surface, woody surface, or leaf. Leaf condition (live or dead) and leaf surface from which the prey was taken (upper or lower) was also noted. The location of a foraging antbird's mate was recorded, if possible, as both the horizontal distance of the mate from the focal foraging individual and the mate's height above the ground (same height categories as used in foraging observations). The outcome of each foraging attempt, if determined, was recorded, and, if successful, the size of captured prey items was categorized relative to the length of the antbird's bill (smaller than bill length, 1–2× bill length, or >2× bill length). If possible, the identity of the prey was determined to the lowest taxonomic category possible.

Characteristics of the bills of males and females were compared using *t*-tests. Multivariate analysis of variance was used to examine possible differences in the foraging behavior of male and female Dusky Antbirds. For comparisons of distances between mates during the wet and dry seasons, we used repeated measures analysis of variance. Values are presented as mean ± 1 SE.

RESULTS

Morphology. There were no significant differences between male and female Dusky Antbirds in our study population in bill length, depth, or width (Table 1). However, culmen length was significantly longer in males than females (Table 1). Analysis of study skins revealed a significant difference between male and female Dusky Antbirds in bill length ($t_{35} = 2.63$, $P = 0.013$), culmen length ($t_{35} = 3.75$, $P = 0.001$), and bill width ($t_{35} = 2.05$, $P = 0.048$) but not in bill depth (Table 1).

Foraging behavior. We observed 607 foraging attempts by 43 individuals between 5 February and 30 July 2002. Dusky Antbirds visually search upper and lower surfaces of leaves, as well as the surfaces of vines, branches, and trunks. Birds foraged at a mean height of 2.8 ± 0.09 m ($N = 588$) primarily on small vines (61% of 581 attempts) and branches (30%) with a mean diameter of 0.7 ± 0.03 cm ($N = 460$). While foraging, the mean distance

Table 1. Bill measurements of male and female Dusky Antbirds captured during this study and of males and females in the collection at Louisiana State University Museum of Natural History.

Bill character[c]	Males[a] Mean ± SE	Females[b] Mean ± SE	t	P
This study				
Culmen	1.10 ± 0.17	1.05 ± 0.09	2.35	0.04
Length	2.07 ± 0.37	2.01 ± 0.19	1.65	0.18
Depth	0.46 ± 0.04	0.47 ± 0.06	0.14	0.78
Width	0.51 ± 0.03	0.50 ± 0.07	0.48	0.87
LSU collection[d]				
Culmen	1.05 ± 0.01	1.01 ± 0.01	3.75	0.001
Length	2.07 ± 0.09	1.98 ± 0.02	2.63	0.013
Depth	0.45 ± 0.01	0.44 ± 0.01	1.05	0.301
Width	0.48 ± 0.02	0.47 ± 0.02	2.12	0.048

[a] Sample sizes for males in this study were $N = 11$ for culmen and length and $N = 10$ for depth and width. Sample size for males in the LSU collection was $N = 21$.

[b] Sample sizes for females in this study were $N = 12$ for culmen and length and $N = 6$ for depth and width. Sample size for females in the LSU collection was $N = 16$.

[c] All measurements are in millimeters.

[d] Birds in the LSU collection were collected in Panama (5 females, 3 males), Honduras (8 females, 14 males), Costa Rica (1 female, 3 males), and Ecuador (1 female, 1 male), and the source of one female was unknown.

between members of a pair was 5.6 ± 0.28 m ($N = 449$). From perch substrates ($N = 581$), predominantly vines (61%) and small branches (30%), antbirds searched leaves (80%) and surfaces of small vines (14%) and branches (6%) for insect prey ($N = 593$). Dusky Antbirds also occasionally perched on palm fronds (*Attalea butyracea*; 6.4%) and searched accumulated leaf litter for prey. This occurred infrequently (two attempts by males and five attempts by females) and was not included in the analysis of substrate use. Most leaves on which birds foraged were alive (58%), and most foraging attempts ($N = 293$) were directed at the lower surface, or underside, of leaves, vines, and branches (65.9%).

The most frequently used Dusky Antbird foraging maneuver ($N = 607$) was gleaning (59%), followed by probing (15%), sallying (11%), and biting (5%). We were able to identify 38 prey items captured by Dusky Antbirds, and most were larvae (Lepidoptera and Diptera, 55.2%), spiders (Arachnida, 10.5%), and roaches (Blattaria, 10.5%). For observations where the outcome was known ($N = 306$), antbirds successfully captured a prey item 91.5% of the time, and 89% of prey items ($N = 254$) were smaller than bill size.

Multivariate analysis revealed no difference in the foraging behavior of male and female Dusky Antbirds (Table 2; Wilk's lambda = 0.004, $F_{1,14} = 16.7$, $P = 0.19$). Males and females foraged at similar mean heights, foraged from similar perches on similar substrates, and used the same foraging maneuvers (Table 2). Although not statistically significant, females probed more than males (Table 2) and used dead leaves as foraging substrate (46.8%) more often than males (29.5%). Males and females captured prey of similar sizes (0.60 times bill length for both).

Paired birds foraged closer to each other during the wet season ($F_{1,24} = 4.65$, $P = 0.04$), with a mean distance between mates of 6.2 ± 0.4 m during the dry season and 4.9 ± 0.4 m during the wet season. However, for all other variables (perch height, perch diameter, prey size, perch type, foraging maneuvers, substrate type, and where foraging attempts were directed), we found no seasonal (wet vs. dry) differences ($P > 0.26$) in the foraging behavior of Dusky Antbirds.

Territory size and stability. Dusky Antbird territories ($N = 13$) averaged 0.49 ± 0.11 ha, but three territories were larger than the others and averaged 1.2 ± 0.13 ha. Excluding

Table 2.   Perches, maneuvers, and substrates used by foraging male and female Dusky Antbirds in central Panama.

Variable	Males Mean ± SE	Females Mean ± SE	F	P
Perch				
Height (m)	2.9 ± 0.2	3.0 ± 0.2	0.06	0.80
Diameter (cm)	0.78 ± 0.10	0.74 ± 0.08	0.01	0.99
Perch type				
Branch (%)	28.1 ± 2.8	25.6 ± 6.3	0.23	0.64
Vine (%)	58.7 ± 6.4	59.8 ± 7.1	0.01	0.93
Palm (%)	7.8 ± 3.5	8.1 ± 3.2	0.6	0.45
Maneuver				
Glean (%)	64.2 ± 6.3	62.0 ± 4.2	0.03	0.87
Probe (%)	9.5 ± 3.2	16.8 ± 3.3	1.93	0.19
Sally (%)	9.7 ± 3.3	9.1 ± 3.0	0.01	0.93
Substrate				
Leaf (%)	69.8 ± 5.5	59.0 ± 5.6	0.59	0.45
Rolled leaf (%)	12.9 ± 4.0	18.4 ± 4.8	1.66	0.22
Woody (%)	13.5 ± 3.7	12.8 ± 4.6	2.09	0.17
Dead substrate (%)	29.5 ± 5.0	46.8 ± 3.2	4.06	0.064
Upper surface (%)	30.8 ± 6.3	35.4 ± 8.8	0.01	0.94

those outliers, territories ($N = 10$) averaged 0.30 ± 0.10 ha in size. Territory defense consisted largely of both males and females singing at territorial boundaries, and territorial intrusions that led to a chase or fighting were infrequent (three in 259 observation hr). Territory boundaries remained stable throughout the study. In two cases, focal individuals (one male and one female) moved to different territories, were replaced by new individuals, and territory boundaries remained unchanged. Also, two adult males disappeared and were replaced by two juvenile males, while on another territory, both members of the resident pair were replaced. In none of these cases did boundaries change.

DISCUSSION

We found no differences in the foraging behavior of male and female Dusky Antbirds. Similarly, Gradwohl and Greenberg (1984) reported no differences in the foraging behavior of another member of the family Thamnophilidae, the Checker-throated Antwren. Behavioral differences between males and females may result from sexual size dimorphism in bill structure (Webster 1997), and such dimorphism oc-

curs in Dusky Antbirds (Table 1). However, sexual differences in culmen length, bill length, and bill width were small (less than a millimeter), and any impact on foraging behavior seems unlikely (see Holmes 1986).

Gleaning was the most common foraging maneuver used by Dusky Antbirds, and frequent use of this maneuver has also been reported in *Drymophila* antbirds (Leme 2001). Gleaning is an energetically inexpensive maneuver because acrobatic movements are not used (Remsen and Robinson 1990). Most foraging attempts by Dusky Antbirds were directed at the lower surface, or underside, of substrates. Greenberg and Gradwohl (1980) estimated that more than 90% of the avian understory insectivory in Panamanian forests is directed towards the lower surfaces of leaves and found that five of seven antbirds studied showed a preference for foraging on lower leaf surfaces. In the same study, Greenberg and Gradwohl (1980) found that most diurnal arthropods were located on lower rather than upper leaf surfaces, and also suggested that insectivorous birds forage on lower surfaces because of better visibility.

Dusky Antbirds in our study, particularly females, often foraged for insects on dead leaves. Dead leaves have a higher relative abundance of

large insect prey (>5 mm) than live leaves (Gradwohl and Greenberg 1982; Greenberg 1987; Rosenberg 1993). In Jamaica, the Dominican Republic, and Belize, the average ratio of estimated insect biomass (grams) in dead versus live leaves was 153:1 (Greenberg 1987). While patchily distributed (Rosenberg 1990), dead leaves are among the least seasonal of tropical forest resources (Remsen and Parker 1984; Boinski and Fowler 1989) and provide a relatively stable prey base for *Myrmotherula* antwrens (Gradwohl and Greenberg 1984; Remsen and Parker 1984; Rosenberg 1993) and possibly other species.

Among passerines in temperate areas, differences in the foraging behavior of males and females may occur when dominant males displace subordinate females and cause them to forage on different substrates (Peters and Grubb 1983; Hogstad 1991; Matthysen et al. 1991). Greenberg and Gradwohl (1983) found no evidence that Dot-winged Antwren relationships were structured by dominance. Similarly, our observations of foraging behavior revealed no such dominance relationships in Dusky Antbirds, with paired males and females typically foraging near each other and using similar foraging techniques.

Differences in the foraging behavior of males and females may represent a means of minimizing competition when resources are limited (Bell 1982; Smith and Nol 2000). In areas with seasonal variation in rainfall, insect abundance is lower during the dry season than the wet season (Fogden 1972; Wolda 1980). As a result, sexual differences in foraging behavior, if they occur, would likely be more apparent during the dry season (Chesser 1995). However, we found no seasonal differences in the foraging behavior of Dusky Antbirds. Male and female antbirds in our study did forage closer together during the wet season than during the dry season, but this may simply have been an artifact of courtship behavior.

In summary, male and female Dusky Antbirds in our study foraged at similar heights, used similar foraging maneuvers and substrates, and paired males and females exhibited no differences in space use within territories. Thus, our results suggest that pairs of Dusky Antbirds in Panama do not partition food resources on territories. Our results, and those of other investigators (Greenberg and Gradwohl 1986;

Morton and Stutchbury 2000), also indicate that Dusky Antbird territories are stable and boundaries do not change with changes in prey density. Therefore, territory switching, rather than resource partitioning, may be a means to gain access to more resources, with Dusky Antbirds switching to territories with more foraging substrate when the opportunity arises (Morton et al. 2000).

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