Territory size of three Antbirds (Aves, Passeriformes) in an Atlantic Forest fragment in southeastern Brazil

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ABSTRACT. Territory size is an important ecological attribute of populations that has been considered a factor determines population density. Antbirds is a large group of mainly insectivorous Neotropical passerines, usually well represented in bird communities from forested landscapes in Neotropical region. Territory sizes for three Antbirds, *Thamnophilus caerulescens* (Vieillot, 1816) (Variable Antshrike), *Dysithamnus mentalis* (Temmink, 1823) (Plain Antvireo) e *Pyriglena leucoptera* (Vieillot, 1818) (White-shouldered Fire-eye), were mapped and their area estimated by the convex polygon method in a 50 ha forest fragment, in southeastern Brazil. The three species presented small territories of similar sizes ($\leq$ 2 ha) both during the non-reproductive and the reproductive seasons of 2000-2001. Territories overlapped considerably among species but not intraspecifically. Territory sizes increased with body mass of the three species studied (*P. leucoptera* > *T. caerulescens* > *D. mentalis*). We failed to find any effect on territory size for the three species associated with forest edge or distance to the dirt road.
KEY WORDS. *Dysithamnus mentalis*; Thamnophilidae; *Pyriglena leucoptera*; territoriality; *Thamnophilus caerulescens*.

RESUMO. **Tamanho de território de três espécies de Thamnophilidae (Aves, Passeriformes) em um fragmento de Mata Atlântica no sudeste do Brasil.** O tamanho do território é um importante atributo ecológico das populações, sendo considerado um fator que pode determinar densidades populacionais. Os Thamnophilidae formam um grupo diverso de pássaros insetívoros, usualmente representativos nas comunidades de aves em florestas da região Neotropical. Neste estudo estimamos o tamanho de território de três espécies de Thamnophilidae, *Thamnophilus caerulescens* (Vieillot, 1816) (Choca-da-mata), *Dysithamnus mentalis* (Temmink, 1823) (Choquinha-lisa) e *Pyriglena leucoptera* (Vieillot, 1818) (Papa-taoca-do-sul), através do método de polígono convexo, em um fragmento de Mata Atlântica no sudeste do Brasil. Os territórios foram pequenos ($\leq$ 2 ha) para as três espécies e não variaram significativamente entre as estações não reprodutiva e reprodutiva. Os territórios sobrepuseram-se consideravelmente entre as três espécies, mas não em cada espécie. O tamanho dos territórios aumentou com a massa corporal das três espécies (*P. leucoptera* > *T. caerulescens* > *D. mentalis*). Não foi observada nenhuma relação entre o tamanho do território e sua distância à borda da mata e à estrada para as três espécies.
PALAVRAS-CHAVE. *Dysithamnus mentalis*; Thamnophilidae; *Pyriglena leucoptera*, territorialidade; *Thamnophilus caerulescens*.

Territory size is an important ecological attribute of populations because it may determine population density and affect the local distribution and abundance of both intruders and prey (CAPENTER 1987). The adaptive value of territorial behavior has been related to the defense of resources and reproductive success (DAVIES 1978). However, this theme remains a topic for discussion (MØLLER 1990, RODRIGUES 1998), once the factors underlying territoriality are not the same for all species (VERNER 1977).

The benefit of territoriality relies in owners having either more a particular resource or better resources than they would have otherwise. According to PERRINS & BIRKHEAD (1983),

the main resources that birds may defend in territories include food, nesting sites and mates. In a comparative study, SCHOENER (1968), considering birds defending territories where the main resource was food, found that territory size was directly related to the bird's body weight. In the tropics, the predominant territorial system is year-round defense of feeding and nesting territories (STUTCHBURY & MORTON 2001). Year-round territoriality is typical of tropical insectivorous birds (BUSKIRK 1976) and arthropod resources are defensible because they are more or less evenly distributed spatially and temporally (STUTCHBURY & MORTON 2001). However, territory size may change over the season independently of food abundance.

Thamnophilidae is a diverse group in South America and is restricted to the Neotropical region (SICK 1997). Most Thamnophilidae are narrowly associated to the subcanopy or to certain distinct formations in the forest (RIDLEY & TUDOR 1994, STOTZ *et al*. 1996, SICK 1997) and are affected by forest fragmentation (WILLIS 1979, BIERREGAARD *et al*. 1992, SIEVING & KARR 1997). Whereas some species of the family are quite sensitive to forest fragmentation, others apparently derive benefit from it (R. RIBON pers. comm.). Three species, *Thamnophilus caerulescens* (Vieillot, 1816) (Variable antshrike), *Dysithamnus mentalis* (Temmink, 1823) (Plain antvireo) and *Pyriglena leucoptera* (Vieillot, 1818) (White-shouldered fire-eye), were considered in the present study. These species are predominantly insectivorous (DURÃES & MARINI 2005) and react differentially to forest fragmentation (R. RIBON pers. comm.). Our goals were to determine territory size for these three species, evaluating spatial variations in parameters of the territories between the non-reproductive and reproductive seasons. We also evaluated if the distance to the forest edge and a dirt road affect territory size.

MATERIAL AND METHODS

Study area

We conducted this study in a 50 ha forest fragment located at the "Área de Proteção para fins de Preservação do Manancial do Barreiro" (from here on, Barreiro) (20º00'S, 43º59'W), in Belo Horizonte, Minas Gerais state, southeastern Brazil. This forest fragment is at the transition zone between the Cerrado and the Atlantic Forest domains (VELOSO 1966, RIZZINI 1979). The region has a strongly marked climatic regime, with a well defined rainy season between October and March and a dry season lasting from April to September. Barreiro is a 2,000 ha reserve, dominated by open cerrado, but also containing forest fragments of 1, 1.7, 50, and 200 ha. The vegetation of the studied fragment (50 ha) is a seasonal mesophilous forest preserved for about 150 years. There is evidence that the forest has been much more developed in the past at least in part of its extent (CETEC 1993). The fragment is cut by a 5m wide dirt road of restricted use by security and researchers. Trees along the road formed a partial canopy connecting the forest long the two sides of the road, although the road itself was kept open. A 19.3 ha grid was established in the forest fragment with long, narrow trails marked at 50 m intervals, forming 50 m x 50 m squares. This grid included edge and forest interior areas.

Data collection

We captured birds monthly with mist nets at 12 lines in the four forest fragments of the Barreiro. Within the 50 ha fragment, birds were captured from 1995 through 2000 at four mist-net lines being three of them inside the observation grid. Some individuals were attracted to nets with their song playback. Birds were marked with metallic bands provided by CEMAVE (IBAMA) and unique combinations of three plastic color bands.

Observations were conducted with binoculars, mostly between 05:00 and 14:00, from March to August 2000 (non-reproductive season) and from September 2000 to February 2001 (reproductive season). Observations were conducted inside the grid in 5 minutes stops at every 50 m at trail intersections. Singing individuals had their color bands identified, and were followed until disappearing. The area of the grid where each individual was observed was plotted on a map and their territory was recorded until their size ceased to increase. When *P. leucoptera* was observed following ant swarm (*Labidus sp*.), the movement was not considered to demarcation its territory.

Territory was mapped and its area measured by the convex polygon method (ODUM & KUENZLER 1955), which consists in joining the outermost observation points for each bird with a straight line. The largest polygon obtained was taken as the bird territory size. Although this method has been subjected to criticism (WORTON 1987), it was chosen due to its simplicity and wide use in ornithology (*e.g.* JULLIEN & THIOLLAY 1998, WIKTANDER *et al*. 2001, RIBEIRO *et al*. 2002). The smallest perpendicular distances from the center of each territory to the forest edge and to the dirt road were obtained with a 50 m tape.

Statistical analyses

Differences in territory size among species were tested with a one-way analysis of variance (ANOVA) for each season. For *T. caerulescens* and *P. leucoptera*, paired t-tests were used to evaluate the differences in territory sizes and distances of the territory centers to the forest edge and to the road between the non-reproductive and reproductive seasons. For *D. mentalis*, whose number of territory owners in both seasons was very small we used a t-test for independent samples. To evaluate if territory sizes were affected by the distance to forest edge or the road we used multiple regressions, using the data collected for each species in each season. All statistical analyses followed ZAR (1984).

RESULTS

Territory size

The difference in territory size among the three species in the non-reproductive season was just marginally not significant ($F_{2,14} = 3.47$, $p < 0.06$) being, on average, the territory size of *P. leucoptera* > *T. caerulescens* > *D. mentalis* (Tab. I, Figs 1-2). In the reproductive season, the difference was significant ($F_{2,15} = 19.57$, $p < 0.001$). A planned comparison showed significant differences between the territory size of *P. leucoptera* and of the other two species that had smaller territories (both, $F_{1,15} = 37.70$, $p < 0.001$). Differences were marginally significant when compared the territory size of *T. caerulescens* and *D. mentalis* ($F_{1,15} = 4.18$, $p < 0.058$). There were no significant differences in the territory size between seasons for the three species (Tab. II).

Territory stability

A male (3) and two pairs (2 and 8) of *T. caerulescens* that held territories in the non-reproductive season were not observed in the reproductive season. However, another two pairs
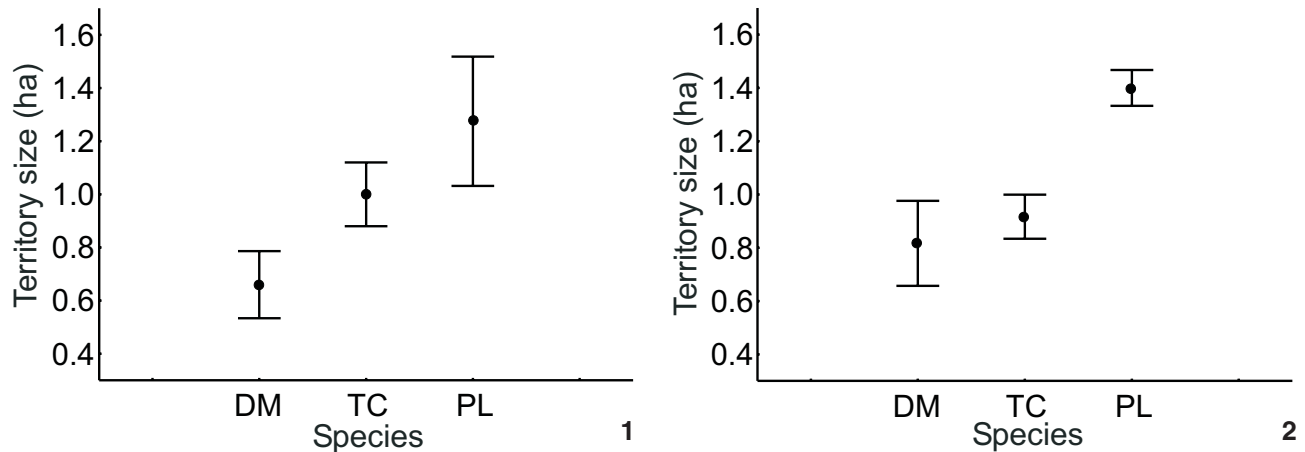
Figures 1-2. Territory sizes in the non-reproductive (1) and reproductive (2) seasons of *Dysithamnus mentalis* (DM), *Thamnophilus caerulescens* (TC), and *Pyriglena leucoptera* (PL) at a forest fragment in southeastern Brazil. Middle points and whiskers represent mean and standard error, respectively.

Table I. Territories spatial parameters in the non-reproductive and reproductive seasons. (N) Number of the territory assess; (D) density of pairs; (PS) pairing success of the territory owners (%); (MAX) maximum value; (M ± ES) mean ± standard error; (MIN) minimum value. * The mean value of the *D. mentalis* territory size was obtained excluding one territory considered outlier in the sample (1.6 ha), being the mean including this territory equal to 0.8 ± 0.2 ha.

Species	N	D	PS	Territory size (ha)			Edge distance (m)			Road distance (m)		
				MAX	M ± SE	MIN	MAX	M ± SE	MIN	MAX	M ± SE	MIN
Non-reproductive season												
Thamnophilus caerulescens	8	0.41	100	1.5	1.0 ± 0.3	0.6	225	118 ± 76	25	142	77 ± 40	37
Dysithamnus mentalis	5	0.26	100	1.0	0.7 ± 0.2	0.3	240	129 ± 69	75	175	80 ± 67	4
Pyriglena leucoptera	4	0.20	100	2.0	1.3 ± 0.6	0.8	117	66 ± 46	27	150	59 ± 64	0
Reproductive season												
Thamnophilus caerulescens	9	0.41	88.9	1.2	0.9 ± 0.2	0.6	325	150 ± 101	40	220	124 ± 65	0
Dysithamnus mentalis *	5	0.31	83.3	0.8	0.7 ± 0.1	0.4	340	147 ± 120	50	220	135 ± 52	90
Pyriglena leucoptera	4	0.20	100	1.6	1.4 ± 0.1	1.3	360	202 ± 46	75	130	101 ± 37	50

Table II. Comparative Student t-test between non-reproductive and reproductive seasons. Significance level: $p \leq 0.05$; * Student t-test for independent samples.

Species	Territory size			Edge distance			Road distance		
	t	df	p	t	df	p	t	df	p
Thamnophilus caerulescens	0.07	5	0.94	- 0.49	5	0.64	-44.5	5	0.07
Dysithamnus mentalis *	0.00	8	1.00	-0.39	8	0.70	-1.68	8	0.13
Pyriglena leucoptera	-0.50	3	0.65	-2.06	3	0.13	-1.91	3	0.15

(10 and 11) and an unpaired male (12) established territories in the area (Fig. 3). The territory of individual-3 was poorly sampled and was not considered in the analyses. Of the five *D. mentalis* pairs monitored during the non-reproductive season, three pairs (1, 2 and 5) maintained their territories. Three new pairs (6, 8 and 9) and an unpaired male (7) established new territories in the reproductive season (Fig. 4). Pairs 3 and 4, observed in the non-reproductive season, were not observed in the reproductive season. The territory of pair 2 was poorly sampled in the reproductive season, and was not considered in the analyses of this period. All *P. leucoptera* pairs maintained their territories in both seasons (Fig. 5).

Population density

In both seasons *T. caerulescens* was the species that presented the highest density, while *P. leucoptera* was the species with lowest density. A small increase in density was observed only for *D. mentalis* in the reproductive season. Interspecific overlapping territories were evident, but intraspecific overlapping territories were not observed for the three species. Analyzing each species separately, territories were spaced and non-overlapping (Figs 3-5).

Pairing success

The four pairs of *P. leucoptera* were paired in both seasons. For *T. caerulescens* and *D. mentalis*, one territory owner of each species did not pair successfully in the reproductive season (individuals 12 and 7, respectively) (Tab. I, Figs 3-4).

Edge and road effect

The distances to the forest edge and the road were very variable and no significant differences were detected between seasons, only a difference marginally significant from the distance of *T. caerulescens* territories to the road (Tab. II). However, territory distances to the forest edge and the road were larger in the reproductive season for the three species (Tab. I). For *P. leucoptera* territories, the minimum distances in relation to the forest edge and the road increased 50-m in the reproductive season. Seemingly, the distance to the forest edge and the road did not affect the territory size (Tab. III).

DISCUSSION

According to Hinde (1956), for species that defend territories within which all activities, such as mating, nesting and foraging occur, the importance of food in such territories is illustrated by the marked relationship between territory size and bird size. Therefore, a positive correlation between territory size and body mass is expected for species with similar diets (Perrins & Birkhead 1983). The average territories size seems to be directly related to the average body mass of the three species studied here, since *D. mentalis* has smaller body mass (12.2 g) and smaller territory (0.7 ha), *P. leucoptera* has larger body mass (26.5 g) and larger territory (1.3 ha) and *T. caerulescens* present intermediate values of body mass (20.6 g) and territory size (1.0 ha). In the Amazon Forest, woodpeckers (Picidae) are larger and defend larger territories, while woodcreepers (Dendrocolaptidae) have smaller body mass and territories (Terborgh *et al.* 1990). These authors reported that the difference between territories of gleaners and snatchers seems best accounted for by their considerably smaller mean size. Therefore, our data and the Terborgh's data for Amazonian Forest confirm the conclusions of the Hinde (1956) and Perrins & Birkhead (1983).

The territory size of *P. leucoptera*, *T. caerulescens* and *D. mentalis* are relatively small in relation to Amazonian birds. In Amazonian Forest the mean territory sizes for all insectivores was 14 ha and only considering Thamnophilidae (body mass ≤ 30 g) the mean territory size was 6.1 ha (Terborgh et al.

1990). Moreover, in the Amazonian Forest Thamnophilidae with smaller body mass than the ones we studied have larger territories (Terborgh *et al.* 1990). The territory size of six species of Thamnophilidae in Atlantic Forest varied from 0.8 to 3.0 ha (Willis & Oniki 2001). These authors found territory sizes for *P. leucoptera* (2-3 ha) relatively larger than the one we found, and *D. mentalis* territory size (0.8 ha) was similar to the one we established. In spite of Oniki's data, our data, Willis & Oniki's and Mendonça & Gonzaga's data indicate that Thamnophilidae territories, in areas of Atlantic Forest, are smaller than the ones of similar species living in the Amazonian forest.

All the avian species for which the size of reproductive territory has been studied in relation to the nesting cycle show temporal changes in territory size (Møller 1990). The methodology used in this study did not allow us to determine changes in the territory size during the reproductive cycle. However, our data indicates that for three species in the study area, the territory size did not vary between non-breeding and breeding seasons. The variation in the territory size can be related to food abundance (Burker & Nol 1998), varying among different forest types and during the breeding season (Stenger & Falls 1959) resulted of the territorial behavior and the trade-off between energy and predation risk (Wiktander *et al.* 2001). In spite of variations in territory size registered for some species, Stutchbury & Morton (2001) consider that in the tropics yearlong territory defense is common and adult survival high, so breeding vacancies may be scarce. Multi-species territoriality of understory birds from Neotropical forest suggests a high yearlong stability of both limits and home ranges areas (Jullien & Thiollay 1998). Despite the strong seasonal variation in food abundance, territory sizes of *Basileuterus flaveolus* (Bair, 1865) (Emberizidae) did not vary between seasons (Duca & Marini 2005). Therefore, our data corroborate the hypothesis that tropical insectivorous birds defend year-round territories.

Although turnover of territory owners have been observed for *T. caerulescens* and *D. mentalis* between seasons, the characteristics of the territories did not present significant differences. Greenberg & Gradwohl (1986), reported that despite a moderate turnover of territory owners, territories of other Thamnophilidae were essentially identical from year to year. The turnover of territory owners also was observed for *T. caerulescens* (Willis & Oniki 2001) and *B. flaveolus* without change in the territories characteristics (Duca & Marini 2005). Several studies have found that territory switching occurs at a low rate in year-round residents (Greenberg & Gradwohl 1986, 1997, Woodworth *et al.* 1999).

The absence of intraspecific overlapping territories and the pattern of territory distribution of *T. caerulescens*, *D. mentalis* and *P. leucoptera* characterize a territorial system for the three species. Territorial intrusions were not common in our study, with just a record of *P. leucoptera* following an ant swarm. According to Willis & Oniki (1988), some Antbirds associated with ant swarm enter in the neighboring territory. In a study con-
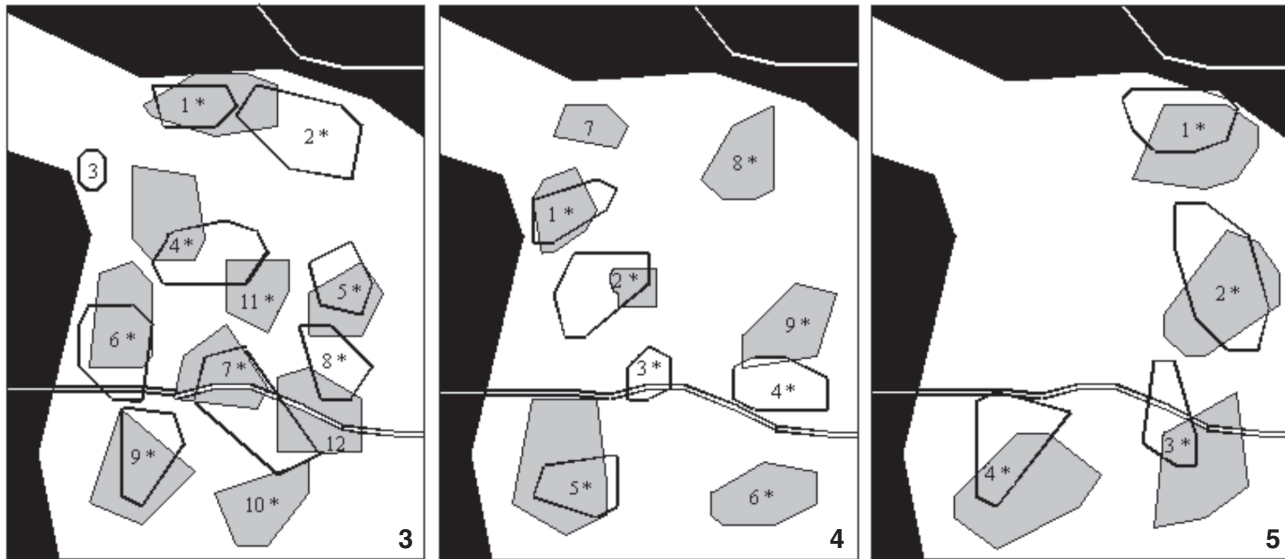
Figures 3-5. Distribution of territories in the non-reproductive (solid line polygons) and reproductive (shaded polygons) seasons of *Thamnophilus caerulescens* (3), *Dysithamnus mentalis* (4) and *Pyriglena leucoptera* (5) at a forest fragment in southeastern Brazil. Numbers indicate territory owner and numbers followed by an asterisk indicate mated individuals. (White) Forest, (Black) Cerrado (Savanna), (═)Dirt road.

Table III. Multiple regressions between territory size and territory distances to the border and road. Significance level: $p \leq 0.05$.

Species	Non-reproductive				Reproductive			
	N	R^2	F	p	N	R^2	F	p
Thamnophilus caerulescens	8	0.14	1.25	0.31	8	0.18	0.67	0.54
Dysithamnus mentalis	5	0.70	2.33	0.29	6	0.19	0.24	0.80
Pyriglena leucoptera	4	0.68	1.10	0.55	4	0.43	0.36	0.75

ducted in the same study area, *B. flaveolus* also had non-overlapping territories (Duca & Marini 2005). Nevertheless, *B. flaveolus* and the three species territories considered here presented great overlapping, indicating that these four species did not have interspecific territoriality in study area. Robinson & Terborgh (1995) documented interspecific territoriality in 10 of 12 species of passerines in Peru Amazon most without overlapping territories. Some of the same species did not have interspecific territoriality elsewhere (Stouffer 1997).

The three species studied here presented stable populations between seasons. The number of pairs of *T. caerulescens* and *P. leucoptera* in the study site showed no seasonal variation and *D. mentalis* showed an insignificant variation. Most insectivorous understory birds do not differ significantly in abundance, despite demonstrating differences in food availability (Wright 1979). Greenberg & Gradwohl (1986) observed no change in the density of other Thamnophilidae between the first year and subsequent years. These authors suggest that these breeding populations are socially regulated at a constant level below the limits directly set by food supply. The pair density of

the three species considered here was similar to the other Atlantic Forest Thamnophilidae of similar size (*e.g.* Willis & Oniki 2001). These authors found *P. leucoptera* pair density of 0.3 pair/ha similar to the one found here (0.2 pair/ha).

Although the factors that determine the territory size are more complex (Parker 1974, Møller 1990), the territoriality can determine the population density, and species with larger territories would tend to present in smaller densities (Carpenter 1987). The inverse relation between territory size and population density has been demonstrated for other passerines (Morse 1976, Yamagishi & Ueda 1986). Considering the territories size of the species that we studied, the expected pair densities would be *D. mentalis*, *T. caerulescens* and *P. leucoptera*, in crescent order. This was somehow observed in our data, since *P. leucoptera* defended larger territories and occurs in lower density (0.20 pair/ha), while *D. mentalis* defended smaller territories and had higher density (0.31 pair/ha). An inversion of that relationship is observed when we compared *D. mentalis* and *T. caerulescens*, which have higher density (0.41 pair/ha) and larger territory size than *D. mentalis*. This can be explained by the

fact that *D. mentalis* is more sensitive to the fragmentation effects than *T. caerulescens*, being significantly affected by the forest size (R. Ribon pers. comm.). Analyzing the distribution maps of the territories, we found that *P. leucoptera* and *D. mentalis* did not occupy the entire available habitat. It might indicate that density could not be the main reason affecting the territory size of these species in the studied forest fragment, which could be affecting the territory size of only *T. caerulescens*. Thus, *D. mentalis* was more sensitive to the fragmentation than *P. leucoptera* (R. Ribon pers. comm.), what could explain the absence of these species on the available habitat in the forest fragment. Willis (1979) suggest that *P. leucoptera* disappears from fragments smaller than 50 ha, but Anjos (2001) recorded this species in forest fragments four times smaller. Even so, the low density of *P. leucoptera* and *D. mentalis* indicate vulnerability to local extinction of these two species. As *T. caerulescens* used the whole available habitat it is likely that the density exerts effect in the regulation of the territory size of this species.

We did not find any relationship between the distances to the forest edge nor the road with the territory sizes and pairing success for the three species observed. Due to our small sample size, however we cannot make safe conclusions. However, it is possible that the edge effect exerts role in the determination of the territories, especially for *D. mentalis*, which is considered a species sensitive to fragmentation (R. Ribon pers. comm.) and less frequently closer to borders and in second-growth woodland (Ridgely & Tudor 1994). The lack of relationship between the distance to the forest edge and the territory sizes for *T. caerulescens* and *P. leucoptera*, agree with the habit of these two species, being common at forest borders (Ridgely & Tudor 1994). *Basileuterus flaveolus* territory sizes were not influenced by the forest border but males defending territories close to edges had higher pairing success (Duca & Marini 2005). In contrast, males of *Seiurus aurocapillus* (Linnaeus, 1766) (Emberizidae) have low pairing success when defending territories close to forest edges (Gibbs & Faaborg 1990). Willis & Oniki (2001) suggest that birds that defend territories in the border need larger areas, because they cannot move in all directions to find food, but it does not seem to be the pattern for *B. flaveolus* (Duca & Marini 2005) and for the three species studied here.

Considering the restricted use of the road in the study area, it was expected that the disturbances from the road would be small. Our results did not present a significant effect of the road in territory sizes and location of the three studied species. However, the marginally significant differences between the distance of *T. caerulescens* territories to the road, and the average increase in the distances from territory centers to the road for the three species in the reproductive season, suggest some adverse effects of the road that were not detected here. In another study of the road effects on understory mixed-species flocks in the Amazon, three of five flocks were restricted to just one side of the road, but two other flocks had territories that spanned the roads (Develey & Stouffer 2001). In the same study,

the authors reported that the roads (without canopy liking the two sides) formed territorial limits for the five flocks living in the area. Thus, our results suggest that road effect in our study area is minimum or, at least, restricted to the cleared area.

ACKNOWLEDGMENTS

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