

Small territory sizes and high densities of insectivorous birds in an Atlantic Forest secondary fragment, Brazil

Rômulo Ribon^{1,2,4} and Miguel Â. Marini³

¹ Programa de Pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre, Departamento de Biologia Geral, ICB, Universidade Federal de Minas Gerais, CEP 30161-970, Belo Horizonte, MG, Brazil.

² Museu de Zoologia João Moojen, Departamento de Biologia Animal, Universidade Federal de Viçosa, CEP 36570-000, Viçosa, MG, Brazil.

³ Departamento de Zoologia, IB, Universidade de Brasília, CEP 70910-900, Brasília, DF, Brazil.

⁴ Corresponding author: romulo.ribon@ufv.br

Received on 18 August 2016. Accepted on 27 December 2016.

ABSTRACT: Demographic parameters of birds are essential to understand their ecology and delineate conservation and management plans. This becomes especially important in highly altered biomes such as the Brazilian Atlantic Forest, since the few remaining fragments bear mostly secondary forests where demographic parameters might differ from old-growth forests. Few studies about territory sizes and density have been conducted for entire bird communities or groups of species in the Neotropical region, with a bias towards Central America and the Amazon. In this work we determined territories of Atlantic Forest birds in order to assess their size and density. We conducted spot-mapping in a rectangular 40-ha plot within a 384-ha of secondary semideciduous forest fragment in Viçosa region, state of Minas Gerais, Brazil. We identified 260 territories of 30 species of insectivorous birds. Mean territory size of all species was 2.4 ha, ranging from 0.5 to 7.5 ha. The mean density for all species was 21.7 pairs/100 ha, ranging from 2.5 to 72.5 pairs. The sizes of the territories of many Atlantic Forest birds were by far smaller, and the density higher, than those of conspecific or congeneric species from Amazonian or Central American forests. These geographical differences in territory size and density can be explained by at least two non-exclusive hypotheses: 1) higher primary and secondary productivity in advanced successional secondary forest fragments and; 2) density compensation, given the loss of other competitor species.

KEY-WORDS: density compensation, fragmentation, Minas Gerais, Neotropical, secondary forests, territoriality.

INTRODUCTION

Secondary forests are increasingly replacing pristine forests around the world (ITTO 2002) and are, thus, important for conserving the remaining forest specialist species (Wright 2010). Compared to old-growth forests, secondary forests have lower plant species richness and denser and more homogeneous understory (Guariguata & Ostertag 2001). Compared to secondary forests, Neotropical primary forests have more microhabitats, varying from very open understory under a higher and more closed canopy cover, to open vine tangles and bushes in older treefall gaps, and even to virtually impenetrable, shaded vine tangles in more recent treefall gaps (Robinson & Terborgh 1995, 1997). This mosaic of thicker and more open understory in primary Neotropical forests can result in a strikingly different use and distribution by birds in a given area (Robinson & Terborgh 1995, 1997, Jullien & Thiollay 1998).

These secondary forests are also often isolated and even more disturbed by further human activities, and

the question whether they will hold viable populations depends on several aspects of birds' biology and their knowledge is fundamental for conservation planning and actions. Population viability analyses (Shaffer 1981), for example, require estimates of a number of traits, including population density or territory size (Goldingay & Possingham 1995) which might be important for management strategies (Beissinger & Westphal 1998, Duca *et al.* 2009). In addition, the knowledge of the size and distribution of their territories by habitat types allows a better estimation of their population sizes with respect to vegetation characteristics of forest fragments of a given area, and their use in population-based models (Millsbaugh & Thompson-III 2009).

The Atlantic Forest is among the world's top biodiversity hotspots (Myers *et al.* 2000) with only 1% of the original primary (or old-growth) forest remaining. The current forest cover is estimated at 11–16%, considering forest patches older than 15 years, and comprises thousands of remnants, most of them smaller than 50 ha, highly isolated, and consisting primarily of

forests in secondary succession (Ribeiro *et al.* 2009). Bird species richness, and levels of endemic and threatened species (Stotz *et al.* 1996, Marini & Garcia 2005) are extremely high, but their biological parameters, such as life histories, diets, habitat use, habitat selection and social behavior are largely unknown, as is common for many aspects of Neotropical birds (Heming *et al.* 2013). Furthermore, these Atlantic Forest fragments are already facing local bird extirpations (Ribon *et al.* 2003), and complete extinction of many species in the biome are projected for the future although at a rate lower than expected due to a time-lag response (Metzger *et al.* 2009).

Furthermore, within the Neotropics, there is a bias in the geographical distribution of the studies describing basic characteristics of bird territories, such as density and size. Although there are some species-specific studies from the Cerrado (savannah) Biome (Marini & Cavalcanti 1992, Ribeiro *et al.* 2002, Lopes & Marini 2006, Domingues & Rodrigues 2007, Freitas & Rodrigues 2012, Costa & Rodrigues 2013, Duca & Marini 2014, Marini *et al.* 2014) and the Atlantic Forest (Willis *et al.* 1983, Willis & Oniki 2001, Duca & Marini 2005, Duca *et al.* 2006, Lima & Roper 2009) most of them, including all those more comprehensive (*i.e.* encompassing many species), come from Amazonia and Central America (Terborgh *et al.* 1990, Thiollay 1994, Robinson & Terborgh 1997, Robinson *et al.* 2000, Stouffer 2007, Johnson *et al.* 2011).

Considering that still very little is known about territoriality of Atlantic Forest birds, and that most of the remaining Atlantic Forest is composed by fragments of secondary forests, it is very important to know how bird species that persist in these fragments are distributed in different scales if we want to properly manage and conserve them. In this study we focused on insectivorous birds as they have been reported to be highly vulnerable to forest fragmentation and degradation (Stouffer & Bierregaard-Jr. 1995, Barlow *et al.* 2006, but see Anjos 2006). Thus, we studied bird territories in a secondary Atlantic Forest fragment to verify territory size and bird density. Specifically we wanted to know how large are the territories of Atlantic Forest birds still inhabiting a secondary forest of a highly fragmented area originally covered by pristine forest that has suffered many extinctions (Ribon *et al.* 2003). Furthermore, we wanted to determine the abundance and density of territories of each bird species. Additionally, we also used the few literature accounts on territory sizes of Neotropical birds to compare territory sizes and densities with conspecific or congeneric species from pristine and secondary forests from Amazonian or Central American forests as a way to stimulate further studies comparing pristine and secondary forests across the Neotropic within the same biome.

METHODS

Our study was conducted at Viçosa county, a hilly region in southeastern Minas Gerais, Brazil, that consists of a mix of semideciduous secondary forest fragments, immersed in a matrix of pastures consisting of non-native grasses, non-shaded coffee, *Eucalyptus* plantations, small corn and bean plantations, small vegetable gardens and orchards (≤ 0.5 ha), and narrow linear streams often bordered by cattail (*Typha* spp.). Most native forest have been destroyed along the last 200 years (Brant 2004) and the remaining patches (mostly secondary vegetation) cover mainly hilltops and hillsides. These forest patches are mostly < 50 ha in size and the other matrix components occupy the narrow lowlands and ravines (Pereira 1999, Ribon 2003).

Study area

The observations were made in the largest (384 ha) forest fragment in an area of 10,000 ha surrounding Viçosa county (the *Centro de Pesquisas e Educação Ambiental Mata do Paraíso – MP*, 20°48'07.9"S; 42°51'29.5"W, 690–870 m a.s.l.). The fragment suffered from strong selective logging until the middle 1960's and some parts are regenerating from an unshaded coffee plantation and pastureland. The vegetation is nowadays secondary forest with small patches of initial, intermediate and advanced succession stages. The largest forest fragment (~13,000 ha) near MP is the Serra do Brigadeiro State Park located 37 km in straight line to the east. Our study plot reflected the topography of the region and included lowlands, ravines, hillsides, and hilltops (*sensu* Espartel 1977) within its limits.

Studies in different parts of the MP have shown that areas with vegetation in intermediate and advanced successional stages have almost half of the number of trees and shrubs found in the advanced successional stages (Marangon *et al.* 2003, Pinto *et al.* 2007). At an initial forest stage patch at MP (outside our study plot, but very similar to some of its parts), based on their importance value, the most representative species were *Piptadenia gonoacantha* (Mimosaceae), *Vernonanthura diffusa* (Asteraceae), *Miconia cinnamomifolia* (Melastomataceae), *Piptocarpha macropoda* (Asteraceae) and *Luehea grandiflora* (Malvaceae) (Pinto *et al.* 2007). In the same study, in an advanced successional stage section, inside our study plot, *Euterpe edulis* (Arecaceae), *Piptadenia gonoacantha* (Mimosaceae), *Nectandra lanceolate* (Lauraceae), *Myrcia sphaerocarpa* (Myrtaceae) and *Guapira opposita* (Nyctaginaceae) were the most representative species. Intermediate stage inside our study site is less diverse (Shannon diversity index $H' = 3.31$) and has higher evenness (Pielou's $J' = 0.83$) than advanced forest ($H' = 3.46$; $J' = 0.79$) (Pinto *et al.* 2007).

Historically, 298 bird species (of which 177 forest dependent) have been recorded at MP (Ribon *et al.* 2014), but at least 28 were already extirpated from the Viçosa region, including MP, since 1930's (Ribon *et al.* 2003).

Territory mapping

We mapped the territories of birds in a 40-ha grid, with eleven 400 m trails intersecting five 1000 m trails every 100 m in the central portion of MP. Roughly half of the grid is covered by native forest at late succession stage (studied by Pinto *et al.* 2007) with two patches of native bamboo (*Merostachys* sp. and *Olyra* sp., Poaceae). The other half is dominated by native forest at early or intermediate succession with small patches of shaded *Pteridium* (Dennstaedtiaceae) ferns, a half hectare of *Corymbia citriodora* (Myrtaceae) and one hectare of *Pinus eliottii* (Pinaceae) (Figure 1). All vegetation types have a dense understory.

Because understory and insectivorous birds are often considered as negatively affected by forest fragmentation, destruction, and disturbance (Laurance & Bierregaard-Jr. 1997) we focused our study on the following insectivorous families: Momotidae, Thamnophilidae, Conopophagidae, Dendrocolaptidae, Furnariidae, and Tyrannidae, and in one Cardinalidae, the Red-crowned Ant-tanager (*Habia rubica*) an omnivorous mixed-species flock leader consuming large amount of invertebrates.

To map territories we used territory mapping (or spot-mapping) following guidelines in Bibby *et al.* (1997) at the 40 ha grid plot described above (details in Ribon 2005). The plot had 10-m interval contour lines mapped over a grid that were used to plot bird locations in the field (Ribon 2005). This method by itself suffices to estimate territory sizes and bird densities. Territory mapping only requires that the locations of birds observed and vocalizing, especially simultaneous observations of singing males, to be recorded. We followed this standard method, but used pairs of singing, calling, or observed birds to plot territories of some species (Thamnophilidae, Furnariidae, and Tyrannidae) because both males and females sing (pers. obs.; Sick 1997). Such songs are assumed to be related to territory defense and the limits of their territories are assumed to lie in the space between singing birds.

Even though not required by the territory mapping approach, we also color-banded birds to aid in individual identification. We banded 234 individuals of the focus species (85 recaptures) using 6–12 mist nets opened across our grid (1635 net.h) from August 1999 to October 2000. Nets (12 m × 2.5 m) were placed in different parts of the grid to capture as many individuals as possible. Birds were banded with metallic numbered rings from CEMAVE/

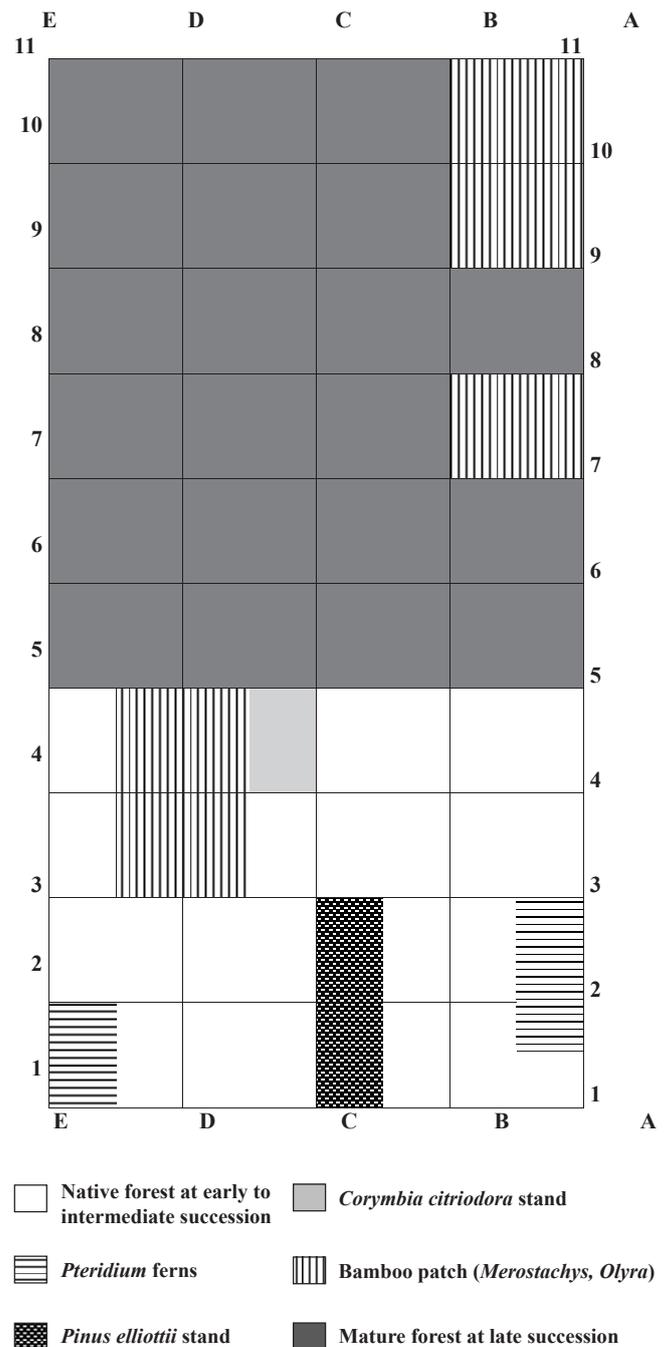


FIGURE 1. Schematic representation of the vegetation at the 40 ha study grid plot established at Mata do Paraíso Research Station, Viçosa, Minas Gerais, Brazil, to map the territories of 30 bird species. Letters and numbers indicate the codes of each of the five 1000 m and eleven 400 m trails opened for the territory mapping.

ICMBio (Permit No. 227) and a combination of two or three color bands.

The entire grid was surveyed 10 times to map bird territories from August to December 2000, each survey occurring at each 10–15 days according to weather conditions. Surveys alternated between 1000 m and 400 m trails. As a morning was not enough to sample all the five 1000 m or all the eleven 400 m trails, two

or three consecutive mornings were spent to survey all the longer or all the shorter trails. All territory mapping was conducted from sunrise to 10:30 h, and birds were observed with a Leica Trinovid 10 × 42 mm binocular. Trails were never left. After 10 visits, we transferred all the locations of each species to a map of the plot, mapped the territories according to Bibby *et al.* (1997), drew each territory contour and further measured them using Autocad 1.4. (by Autodesk). For each territory, we measured its size (in ha). To calculate territory sizes, we used territories entirely inside the plot as well as those that partially overlapped the plot. The exact location of each territory of nine of the species studied along the grid can be found in Ribon (2003).

Among the 76 resident insectivorous bird species at the study site (Ribon *et al.* 2014), we estimated territory sizes of 30 species. Among these, 20 species use the understory and seldom go higher, while 10 species primarily use the mid-story and canopy (Stotz *et al.* 1996, pers. obs.). The sample size for each species varied according to its density and possibility of observation. We used a minimum of three locations (either song, call, visual, or combination of these) to determine the boundaries of bird territories following Bibby *et al.* (1997). However, only one territory each of three different species had three locations, and the general average number of points per territory mapped was 13 (range 3–36). Capture locations and the scarce sightings of banded birds were used to help to solve doubts about territory boundaries obtained after the 10 visits. Recent research suggests that at least 30–40 locations are required for meaningful territory size estimation (Anich *et al.* 2009). Although it is practical to obtain such number of records for species-specific studies (with radio-telemetry or color-banded birds) standard territory mapping still gives accurate estimates and maximize cost-benefit fieldwork effort when a large number of species are studied at the same time (Terborgh *et al.* 1990, Robinson & Terborgh 1995, 1997). Furthermore, the use of territory mapping to estimate bird densities is appropriate if one can distinguish one territory from another. Bird nomenclature and systematic order follow Remsen-Jr. *et al.* (2016).

Comparison with other Neotropical sites

We compared our findings at MP to the few available multispecies territorial studies based on territory mapping in the Neotropics that encompassed several congeneric species found at our study site (Terborgh *et al.* 1990, Thiollay 1994, Robinson & Terborgh 1997, Robinson *et al.* 2000, Johnson *et al.* 2011). All these studies have been conducted in >95–100 ha grids of

primary forest except Robinson *et al.* (2000) that worked on more disturbed forest. To allow a comparison of our densities with those from studies conducted in other Neotropical forests, we estimated the expected number of territories of congeneric species for an area of 100 ha, considering one pair per territory for most species (see above). We did this based in the structural homogeneity of secondary vegetation and in the assumption that birds in these habitats, as at our study plot, are much more evenly distributed than in primary forests (Thiollay 1994, Guariguata & Ostertag 2001, Johnson *et al.* 2011). Although we recognize that territory mapping could lead to less accurate estimates of bird density and smaller territory sizes than radio-telemetry (Streby *et al.* 2012) or detailed following of banded birds (Lima & Roper 2009), we judged it useful for a general comparison to mostly existent data on the Neotropical region (Terborgh *et al.* 1990, Thiollay 1994, Robinson & Terborgh 1997, Robinson *et al.* 2000, Johnson *et al.* 2011) as their data were all based on territory mapping obtained from trail grids. Because of the smaller size of our plot relative to other studies, we considered both birds with territories entirely inside the plot to calculate density, and birds with partial territories inside the plot using a correction factor: densities of birds with partial territories inside the plot were proportional to the part of territory inside it. For example, for a territory that was 50% inside the plot, we assumed a density of 0.5 pairs instead of 1.

RESULTS

We mapped 260 territories of 30 species (Table 1), most of them non-banded. Mean territory size was 2.4 ha (range 0.5–7.5). Mean number of locations to delineate each territory was 12.9, ranging from three to 36 records (Tables 1 and 2). Most territories were smaller than 4 ha (Figure 2). The smallest territory was 0.5 ha (Hangnest Tody-tyrant, *Hemitriccus nidipendulus*; and Greenish Elaenia *Myiopagis viridicata*) and the largest was 7.5 ha (Gray-hooded Attila, *Attila rufus*).

Eleven species were rare and had < 5 territories in our plot. Euler's Flycatcher (*Lathrotriccus euleri*), Rufous Gnateater (*Conopophaga lineata*) and Yellow-olive Flycatcher (*Tolmomyias sulphurescens*) were very abundant, with the largest number of territories demarcated (29, 20 and 19 territories in the 40 ha plot, respectively). General average density for all species was 22 pairs/100 ha, ranging from 2 (Sharp-tailed Streamcreeper, *Lochmias nematura*; and Serra Antwren, *Formicivora serrana*) to 72 pairs/100 ha (Euler's Flycatcher), with 5 species reaching densities of more than 40 pairs/100 ha (Table 3).

TABLE 1. Territory sizes of 30 bird species in a 40 ha Atlantic Forest plot at Viçosa, Minas Gerais, Brazil. N - number of territories of each species; n – mean number of points used to map the territories of each species, followed by the range of points.

Species	N (n; range)	Territory size (ha)	
		Range	Mean ± SE
Rufous-capped Motmot (<i>Baryphthengus ruficapillus</i>)	6 (11.5; 8–14)	1.8–7.8	3.4 ± 0.9
Tufted Antshrike (<i>Mackenziaena severa</i>)	2 (12.5; 7–18)	6.4–6.8	6.6 ± 0.2
Variable Antshrike (<i>Thamnophilus caerulescens</i>)	17 (13.4; 7–22)	0.7–1.7	1.3 ± 0.1
Plain Antwren (<i>Dysithamnus mentalis</i>)	17 (8.4; 5–13)	0.4–1.6	0.9 ± 0.1
Serra Antwren (<i>Formicivora serrana</i>)	1 (8)	--	1.0
Ferruginous Antbird (<i>Drymophila ferruginea</i>)	3 (17.3; 10–29)	0.8–1.3	1.2 ± 0.2
White-shouldered Fire-eye (<i>Pyriglena leucoptera</i>)	16 (15.2; 8–36)	0.3–2.5	1.4 ± 0.1
Rufous Gnateater (<i>Conopophaga lineata</i>)	20 (7.7; 4–12)	0.3–1.2	0.6 ± 0.1
Rufous-capped Spinetail (<i>Synallaxis ruficapilla</i>)	14 (13.9; 6–23)	0.8–2.2	1.6 ± 0.1
Gray-bellied Spinetail (<i>Synallaxis cinerascens</i>)	7 (10.9; 4–19)	1.5–3.5	2.1 ± 0.3
White-collared Foliage-gleaner (<i>Anabazenops fuscus</i>)	9 (18.9; 8–30)	0.7–7.0	3.3 ± 0.6
White-eyed Foliage-gleaner (<i>Automolus leucophthalmus</i>)	3 (21.3; 9–31)	2.1–7.2	5.4 ± 1.6
Streaked Xenops (<i>Xenops rutilans</i>)	4 (15.8; 11–23)	3.7–7.4	6.0 ± 0.8
Sharp-tailed Streamcreeper (<i>Lochmias nematura</i>)	1 (15)	--	2.2
Lesser Woodcreeper (<i>Xiphorhynchus fuscus</i>)	5 (9.6; 5–13)	2.0–4.1	3.3 ± 0.4
Scaled Woodcreeper (<i>Lepidocolaptes squamatus</i>)	8 (9.2; 5–12)	0.7–5.2	2.2 ± 0.5
Black-billed Scythebill (<i>Campylorhamphus falcularius</i>)	5 (9; 3–16)	1.0–4.1	2.8 ± 0.5
Greenish Elaenia (<i>Myiopagis viridicata</i>)	6 (4.6; 3–8)	0.3–1.0	0.5 ± 0.1
Gray Elaenia (<i>Myiopagis caniceps</i>)	3 (7.8; 5–12)	2.0–4.1	3.0 ± 0.6
Sepia-capped Flycatcher (<i>Leptopogon amaurocephalus</i>)	10 (13.5; 9–27)	0.9–3.7	2.3 ± 0.3
Southern Antpipit (<i>Corythopis delalandi</i>)	15 (10.7; 6–19)	0.2–3.0	1.0 ± 0.2
Eared Pygmy-tyrant (<i>Myiornis auricularis</i>)	10 (9.2; 3–16)	0.4–1.9	1.1 ± 0.2
Hangnest Tody-tyrant (<i>Hemitriccus nidipendulus</i>)	3 (7.5; 5–10)	0.3–0.7	0.5 ± 0.1
Yellow-faced Tody-flycatcher (<i>Todirostrum poliocephalum</i>)	8 (19.8; 16–26)	0.3–2.0	1.5 ± 0.2
Ochre-colored Tody-flycatcher (<i>Poecilatriccus plumbeiceps</i>)	2 (12.5; 10–15)	0.9–2.4	1.7 ± 0.8
Yellow-olive Flycatcher (<i>Tolmomyias sulphurescens</i>)	19 (18.3; 8–27)	0.7–2.9	1.6 ± 0.2
White-throated Spadebill (<i>Platyrinchus mystaceus</i>)	12 (15.1; 6–27)	1.2–2.9	2.0 ± 0.2
Euler's Flycatcher (<i>Lathrotriccus euleri</i>)	29 (13.3; 5–31)	0.2–2.0	0.9 ± 0.1
Gray-hooded Attila (<i>Attila rufus</i>)	2 (18.5; 11–26)	3.2–11.7	7.5 ± 4.3
Red-crowned Ant-tanager (<i>Habia rubica</i>)	3 (17.3; 13–21)	2.4–5.7	4.0 ± 1.0

TABLE 2. Territory sizes (ha) of birds at three Neotropical sites. Atlantic Forest birds are aligned at the left.

Species	Viçosa, Brazil ^a	Peru ^b	Panama ^c	Manaus, Brazil ^d
<i>Baryphthengus ruficapillus</i>	3.4			
<i>B. martii</i>			5–8	
<i>Mackenziaena severa</i>	6.6			
<i>Thamnophilus caerulescens</i>	1.3			
<i>T. aethiops</i>		10		
<i>T. schistaceus</i>		8		
<i>T. atrinucha</i>			1	
<i>T. murinus</i>				5.6
<i>Dysithamnus mentalis</i>	0.9			
<i>D. puncticeps</i>			<2	
<i>Formicivora serrana</i>	1.0			
<i>Drymophila ferruginea</i>	1.2			
<i>Pyriglena leucoptera</i>	1.4			
<i>Conopophaga lineata</i>	0.6			
<i>C. aurita</i>				6.3
<i>Synallaxis cinerascens</i>	2.1			
<i>S. ruficapilla</i>	1.6			
<i>Anabazenops fuscus</i>	3.3			
<i>Automolus leucophthalmus</i>	5.4			
<i>A. infuscatus</i>		12		10.6
<i>A. ochrolaemus</i>		11	11	
<i>A. rubiginosus</i>				13.3
<i>Xenops rutilans</i>	6.0			
<i>X. minutus</i>		9	5	13.3

Species	Viçosa, Brazil ^a	Peru ^b	Panama ^c	Manaus, Brazil ^d
<i>Lochmias nematura</i>	2.2			
<i>Xiphorhynchus fuscus</i>	3.3			
<i>X. pardalotus</i>				10.6
<i>Lepidocolaptes squamatus</i>	2.2			
<i>L. albolineatus</i>		14		12
<i>Campyloramphus falcularius</i>	2.8			
<i>C. procurvodes</i>				24
<i>Myiopagis viridicata</i>	0.5			
<i>Myiopagis caniceps</i>	3.0		5–8	6
<i>M. gaimardii</i>		4		5.6
<i>Leptopogon amaurocephalus</i>	2.3	3		
<i>Corythopis delalandi</i>	1.0			
<i>C. torquata</i>		6		5.7
<i>Myiornis auricularis</i>	1.1			
<i>M. ecaudatus</i>		3		
<i>M. atricapillus</i>			3	
<i>Hemitriccus nidipendulus</i>	0.5			
<i>H. zosterops</i>		3		3.9
<i>Todirostrum poliocephalum</i>	1.5			
<i>Todirostrum plumbeiceps</i>	1.7			
<i>T. crysophataphum</i>		7*		
<i>Tolmomyias sulphurescens</i>	1.6			
<i>T. assimilis</i>		6	4	9.1
<i>T. poliocephalus</i>		5		6
<i>Platyrinchus mystaceus</i>	2.0			
<i>P. coronatus</i>		5	6	3.8
<i>P. platyrhynchos</i>		5		5
<i>Lathrotriccus euleri</i>	0.9	5		
<i>Attila rufus</i>	7.5			
<i>A. bolivianus</i>		12		
<i>A. spadiceus</i>		12	8	16
<i>Habia rubica</i>	4	6		
<i>H. fuscicauda</i>			25	
Average	2.4	7.3	7.1	9.2

^a This study. Territory sizes estimated for 100 ha. ^b Terborgh *et al.* (1990). ^c Robinson *et al.* (2000). ^d Johnson *et al.* (2011). ^e Robinson & Terborgh (1997).

TABLE 3. Density of birds (pairs/100 ha) at five Neotropical sites. Atlantic Forest birds are aligned at the left. * – number of individuals.

Species	Atlantic Forest ^a	Peru ^b	Peru ^c	Guyana ^d	Manaus ^e	Panama ^f
<i>Baryphthengus ruficapillus</i>	15					
<i>B. martii</i>						24
<i>Mackenziaena severa</i>	5					
<i>Thamnophilus caerulescens</i>	42.5					
<i>T. aethiops</i>		1				
<i>T. schistaceus</i>		10.5	0.5–21			
<i>T. doliatus</i>			38			
<i>T. murinus</i>				7.75	12.5	
<i>T. amazonicus</i>				4		
<i>T. punctatus</i>				0.25		
<i>T. atrinucha</i>						106
<i>Dysithamnus mentalis</i>	42.5					
<i>D. puncticeps</i>						3.5
<i>Formicivora serrana</i>	2.5					
<i>Drymophila ferruginea</i>	7.5					
<i>Pyriglena leucoptera</i>	40					
<i>Conopophaga lineata</i>	50					
<i>C. peruviana</i>		3				
<i>C. aurita</i>				1	2	
<i>Synallaxis cinerascens</i>	17.5					
<i>S. ruficapilla</i>	35					
<i>S. gujanensis</i>			53			
<i>Anabazenops fuscus</i>	22.5					
<i>Automolus leucophthalmus</i>	7.5					
<i>A. infuscatus</i>		1.5		4.75	7	
<i>A. ochrolaemus</i>		2.5	2–3	1		5
<i>A. rufipileatus</i>			38			
<i>A. rubiginosus</i>					1.5	

Species	Atlantic Forest ^a	Peru ^b	Peru ^c	Guyana ^d	Manaus ^e	Panama ^f
<i>Xenops rutilans</i>	10	4	0.5–4			
<i>X. minutus</i>		6	1.5–7.5	6.5	9	27
<i>X. milleri</i>					4.5	
<i>Lochmias nematura</i>	2.5					
<i>Xiphorhynchus fuscus</i>	12.5					
<i>X. pardalotus</i>					18	
<i>Lepidocolaptes squamatus</i>	20					
<i>L. albolineatus</i>		5			10	
<i>Campyloramphus falcularius</i>	12.5					
<i>C. trochilirostris</i>		0.5				
<i>C. procurvoides</i>			0.5–9	1.25	3	
<i>Myiopagis viridicata</i>	15		5			
<i>Myiopagis caniceps</i>	7.5				5	3
<i>M. gaimardii</i>		4	4–20.5	3.25	12.5	11.5
<i>Leptopogon amaurocephalus</i>	25	2.5	2.5–3	1		
<i>Corythopis delalandi</i>	37.5					
<i>C. torquata</i>		7		3.75	3.5	
<i>Myiornis auricularis</i>	25					
<i>M. ecaudatus</i>		10	10	4	6	
<i>M. atricapillus</i>						3.5
<i>Hemitriccus nidipendulus</i>	7.5					
<i>H. zosterops</i>		5			31	
<i>H. minor</i>				6		
<i>H. josephinae</i>				2		
<i>Todirostrum poliocephalum</i>	20					
<i>Todirostrum plumbeiceps</i>	5					
<i>T. crysophataphum</i>		3.5		3.5–7.5		
<i>T. pictum</i>				3.5	4	
<i>T. nigriceps</i>						0.5
<i>Tolmomyias sulphurescens</i>	47.5					
<i>T. assimilis</i>		4	4–15	2	17.5	15.5
<i>T. poliocephalus</i>		3	3–10		5	
<i>T. flaviventris</i>			4.5–16	0.75		
<i>Platyrinchus mystaceus</i>	30			4		
<i>P. coronatus</i>		7.5	7.5	15	9.5	10
<i>P. platyrhynchos</i>					6	6
<i>P. saturatus</i>					5	3
<i>Latrotriccus euleri</i>	72.5	1.5				
<i>L. virescens</i>						24*
<i>Attila rufus</i>	5					
<i>A. bolivianus</i>		4	4–14			
<i>A. spadiceus</i>		4	2–4	4.5	3	7
<i>Habia rubica</i>	7.5	8.5				
<i>H. fuscicauda</i>						3*
Average	21.7	4.5	12.8	4.3	8.4	15.8

^a This study; density extrapolated for 100 ha from data in Table 1. ^b Terborgh *et al.* (1990). ^c Robinson & Terborgh (1997). ^d Thiollay *et al.* (1994). ^e Johnson *et al.* (2011). ^f Robinson *et al.* (2000).

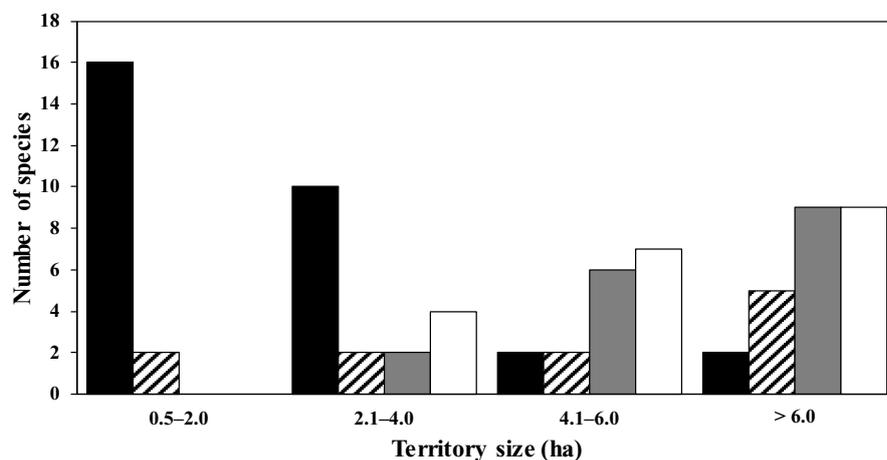


FIGURE 2. Average territory sizes (ha) of birds at the Atlantic Forest (black bars), Panama (Robinson *et al.* 2000) (cross-hatched bars), Manaus (Johnson *et al.* 2011) (grey bars), and Peru (Terborgh *et al.* 1990) (white bars).

DISCUSSION

Small territory sizes (< 5 ha) were common among insectivorous birds in the secondary Atlantic Forest fragment that we studied. Similarly, other species of insectivorous birds found in forested habitats in the Atlantic Forest Biome are known to occupy small territories and occur at high densities, including, Flavescent Warblers (*Basileuterus flaveolus*, 2 ha; Duca & Marini 2005), Variable Antshrikes (*Thamnophilus caerulescens*, 0.9 ha), Plain Antvireos (*Dysithamnus mentalis*, 0.7 ha), White-shouldered Fire-eyes (*Pyriglena leucoptera*, 1.4 ha) (Duca *et al.* 2006), and Black-cheeked Gnateater (*Conopophaga melanops*, 2.94 ha; Lima & Roper 2009). In addition, the territory sizes of six species of Thamnophilidae in São Paulo varied from 0.8 to 3.0 ha (Willis & Oniki 2001). As ours, all the above studies, carried out in the Atlantic Forest, have been conducted in areas that altered by human activities in the past and, thus, had a vegetation structure similar to that of our study area, although the understory of the area studied by Duca *et al.* (2006) was more open because the forest was older (> 150 years) than ours (*c.* 50 years).

When we compare species among other Neotropical biomes, the average territory size at our study site (2.4 ha) was smaller than that of congeneric birds in Panama (average size = 7.1 ha, Robinson *et al.* 2000), Peru (average size = 7.4 ha, Terborgh *et al.* 1990), and Manaus (average size = 9.0 ha, Johnson *et al.* 2011). When comparing congeneric similarly-sized species, 9 of the 11 species in Panama (Robinson *et al.* 2000) and all the 20 species in Peru (Terborgh *et al.* 1990) had larger territories than those from our Atlantic Forest plot. In Manaus, Stouffer (2007) have found the territories of *Conopophaga aurita* and *Corythopis torquatus* were 2 to about 6 times larger than we found for *C. lineata* and *C. delalandi* at MP, respectively.

As territory sizes were small at our grid, bird densities at MP were high. In their study comparing bird densities in 5000 ha tract of Atlantic Forest that suffered selective logging 25 years before their study, in Paraguay, Cockle *et al.* (2005) applied territory mapping “where possible”. They also have found high densities of territories/100 ha for some of the same species that we studied in Viçosa: Eared Pygmy-tyrant, *Myiornis auricularis* (*c.* 68 territories), Rufous-capped Spinetail, *Synallaxis ruficapilla* (*c.* 24 territories), Eared Pygmy-tyrant, *Myiornis auricularis* (*c.* 40 territories), Euler’s Flycatcher, *Lathrotriccus euleri*, Gray-bellied Spinetail, *Synallaxis cinerascens*, White-throated Spadebill, *Platyrinchus mystaceus*, Plain Antvireo, *Dysithamnus mentalis* and Variable Antshrike, *Thamnophilus caerulescens* (all these five species with *c.* 10–20 territories each). These authors have not obtained their data from a grid in the forest area sampled and territory

mapping is not clearly stated by them as the method used for deriving bird densities. However, their estimates are highly suggestive that the pattern we have found in Viçosa can occur also in pristine areas of the Atlantic Forest. It should be noted, though, that although a small number of large territories in an area often demonstrates low bird density, species with small territories that do not occupy most of the available habitat also have low densities, as have been shown for birds with patchy distribution in primary forests in French Guyana (Thiollay 1994).

The average density at our study site (22 pairs/100 ha) was higher than that for congeneric birds in Guiana (average density = 4.1 pairs/100 ha, Thiollay 1994), Manaus (average density = 8.4 pairs/100 ha, Johnson *et al.* 2011), and the two Peruvian sites (average density = 4.5 pairs/100 ha, Terborgh *et al.* 1990; average density = 12.8 pairs/100 ha, Robinson and Terborgh 1997) (Table 3). In Panama the density of 15.7 birds/100 ha was inflated by a very high density of 106 pairs/100 ha of the hyper-abundant Black-crowned Antshrike (*Thamnophilus atrinucha*) which represented almost 50% of all individual birds reported by Robinson *et al.* (2000). It should be noted, however, that when compared to South American forest bird communities, those in Central America have lower species richness, and this could result in higher densities of some populations such as at the more disturbed secondary forest in Panama (Robinson *et al.* 2000), similarly to our results and to those at successional vegetation in Peru (Robinson & Terborgh 1997). Only four of the 16 species compared in Panama (Robinson *et al.* 2000) and four of the 18 species in Peru (Robinson & Terborgh 1997) had higher densities than those in Viçosa. Also, in an additional study conducted near Manaus, Amazonia (Stouffer 2007), territories were larger (average of 13 ha) and densities were lower (average of 3.4 pairs/100 ha) than those of Atlantic Forest birds.

One important difference among the Neotropical studies compared here is the successional stage of the forest. The lowest bird densities and larger territory sizes were found in the sites with old-growth primary forest in Peru (Terborgh *et al.* 1990), Guyana (Thiollay 1994), and Manaus (Johnson *et al.* 2011). The other study site in Peru had an intermediate average density value and was carried out along a primary successional gradient (Robinson & Terborgh 1997). The second highest bird density was observed in Panama (Robinson *et al.* 2000), at a site of primary forest with plenty of gaps created by natural treefalls and storms. All the Atlantic Forest sites have secondary or selectively logged forests, often with dense understory.

Younger successional vegetation stages have higher productivity allowing higher bird density (Robinson & Terborgh 1997, Aleixo 1999). Birds density and territory size in our study site could be a response to a

denser understory and, consequently, a higher abundance of leaves and insects, as indicated by species-specific (Bechard 1982, Hunt 1996) or community (Robinson & Terborgh 1997, Casenave *et al.* 1998) studies. In fact, studies conducted in secondary forests in Amazonia have shown that territory sizes of birds in these habitats are indeed smaller, and bird density higher, than in the primary forests (Kratzer 1997, Robinson & Terborgh 1997, Kattan & Beltran 2002).

Density compensation, a phenomenon originally described for groups of islands (MacArthur *et al.* 1972, Connor *et al.* 2000), could be occurring in the small forest fragments such as MP. Density compensation results in higher density for those bird species able to colonize islands because of the lack of many species that cannot reach them. The lack of many species would thus trigger “competitor release” and “predator release”, allowing wider niches and much higher densities than in the mainland (Stamps & Buechner 1985, Connor *et al.* 2000). Although density compensation does not always happen (Connor *et al.* 2000) it could help to explain the territory patterns of the Viçosa region since we studied territories in a relatively small forest fragment (roughly 380 ha) from where several birds have already gone extinct (Ribon *et al.* 2003). The extirpation of species with niches similar to those that persisted in our area could make it possible for them to expand their use of resources and achieve higher densities and smaller territories.

Even though territory sizes and bird densities are similar among our study and the few other available studies on Atlantic Forest birds, these results should not be generalized to the biome. This is not only because there are many different vegetation subtypes to be studied (*e.g.* lowland *vs.* submontane *vs.* montane forests; southern *vs.* central *vs.* northeastern forests; old growth *vs.* secondary forests), but also because more studies are needed in order to confirm any pattern. In fact, occasional observations and captures with mist-nets by ourselves in the better preserved parts of primary forest at the Sooretama Biological Reserve (22,000 ha), in the nearby state of Espírito Santo, and at the Rio Doce State Park (32,000 ha), in the state Minas Gerais, have shown to us a very low number of birds per unit area. This suggests that at least Lowland Atlantic Forest birds in pristine forests could have a pattern more similar to that found in the Amazon by Terborgh *et al.* (1990), Thiollay (1994), Robinson & Terborgh (1997), Stouffer (2007) and Johnson *et al.* (2011) and opposite to that found in Viçosa and by Cockle *et al.* (2005) in Paraguay.

We showed here that several understory and midstory insectivorous birds have high density and small territory sizes in a secondary forest fragment of the Brazilian Atlantic Forest. This agrees with other studies of bird territories that have been carried out in

the Atlantic Forest to date. Our estimates might be useful to future conservation and management studies in the biome. However, a comprehensive determination and explanation for this proposed pattern in the biome awaits further tests.

ACKNOWLEDGEMENTS

We thank CAPES, CNPq, *Programa de Pós-graduação em Ecologia, Conservação e Manejo de Fauna Silvestre* of the Universidade Federal de Minas Gerais, *Programa Nacional de Biodiversidade/Ministério do Meio Ambiente/Banco Interamericano de Desenvolvimento (PROBIO/MMA/BIRD)*, *Programa Natureza e Sociedade WWF/SUNY* (Project CSR 142-00), *PROBIO-MMA/GEF/BM* (Project *Efeitos Espaciais e Temporais da Fragmentação de Habitats sobre Populações de Insetos e Pássaros*), Departamento de Engenharia Florestal (UFV) for financial support. Serra do Cipó National Park (ICMBio) provided facilities for data analysis. The following helped in several stages of the study: E. R. Luiz, A. B. Andrade, A. C. Ottoni, F. Stanciola, S. L. Ribeiro (*in memoriam*), N. R. Neves, E. C. A. Nieto, H. C. Sari, S. D. Souza, R. F. Fadini. The late C. Bibby helped to solve doubts during territory mapping analysis. We appreciate the improvements in English usage made by Chandler Robbins through the Association of Field Ornithologists' program of editorial assistance. Two anonymous reviewers greatly improved the manuscript.

REFERENCES

- Aleixo, A. 1999. Effects of selective logging on a bird community in the Brazilian Atlantic Forest. *Condor*, 101: 537–548.
- Anich, N. M.; Benson, T. J. & Bednarz, J. C. 2009. Estimating territory and home-range sizes: do singing locations alone provide an accurate estimate of space use? *Auk*, 126: 626–634.
- Anjos, L. 2006. Bird species sensitivity in a fragmented landscape of the Atlantic Forest in southern Brazil. *Biotropica*, 38: 229–234.
- Barlow, J.; Peres, C. A.; Henriques, L. M. P.; Stouffer, P. C. & Wunderle, J. M. 2006. The responses of understory birds to forest fragmentation, logging and wildfires: an Amazonian synthesis. *Biological Conservation*, 128: 182–192.
- Bechard, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. *Condor*, 84: 153–159.
- Beissinger, S. R. & Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, 62: 821–841.
- Bibby, C. J.; Burgess, N. D. & Hill, D. A. 1997. *Bird census techniques*. London: Academic Press.
- Brant, A. 2004. *Desbravamento, caminhos antigos e povoamento dos Sertões do Leste – uma aventura de pioneiros*. Viçosa: Centro de Referência do Professor.
- Casenave, J. L.; Pelotto, J. P.; Caziani, S. M.; Mermoz, M. & Protomastro, J. J. 1998. Responses of avian assemblages to a natural edge in a Chaco Semiarid Forest in Argentina. *Auk*, 115: 425–435.

- Cockle, K. L.; Leonard, M. L. & Bodrati, A. A. 2005. Presence and abundance of birds in an Atlantic Forest reserve and adjacent plantation of shade-grown Yerba Mate, in Paraguay. *Biodiversity and Conservation*, 14: 3265–3288.
- Connor, E. F.; Courtney, A. C. & Yoder, J. M. 2000. Individual-area relationship: the relationship between animal population density and area. *Ecology*, 81: 734–748.
- Costa, L. M. & Rodrigues, M. 2013. Notes on residency, home range, and natural history of the vulnerable Cinereous Warbling-Finch. *Wilson Journal of Ornithology*, 125: 433–438.
- Domingues, L. A. L. & Rodrigues, M. 2007. Área de uso e aspectos da territorialidade de *Schistochlamys ruficapillus* (Thraupidae) em seu período não-reprodutivo. *Aranajuba*, 15: 538–542.
- Duca, C. & Marini, M. Â. 2005. Territory size of the Flavescent Warbler, *Basileuterus flaveolus* (Passeriformes, Emberizidae), in a forest fragment in southeastern Brazil. *Lundiana*, 6: 29–33.
- Duca, C. & Marini, M. Â. 2014. Territorial system and adult dispersal in a cooperative-breeding tanager. *Auk*, 131: 32–40.
- Duca, C.; Guerra, T. J. & Marini, M. Â. 2006. Territory size of three antbirds (Aves, Passeriformes) in an Atlantic Forest fragment in southeastern Brazil. *Revista Brasileira de Zoologia*, 23: 692–698.
- Duca, C.; Yokomizo, H.; Marini, M. Â. & Possingham, H. P. 2009. Cost-efficient conservation for White-banded Tanagers in the Cerrado, central Brazil. *Biological Conservation*, 142: 563–574.
- Espartel, L. 1977. *Curso de topografia*. Porto Alegre: Editora Globo.
- Freitas, G. H. S. & Rodrigues, M. 2012. Territory distribution and habitat selection of the Serra Finch (*Embernagra longicauda*) in Serra do Cipó, Brazil. *Wilson Journal of Ornithology*, 124: 57–65.
- Goldingay, R. & Possingham, H. P. 1995. Area requirements for viable populations of the Australian gliding marsupial *Petaurus australis*. *Biological Conservation*, 73: 161–167.
- Guariguata, M. R. & Ostertag, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, 148: 185–206.
- Heming, N. M.; Greeney, H. F. & Marini, M. Â. 2013. Breeding biology research and data availability for New World flycatchers. *Natureza & Conservação*, 11: 54–58.
- Hunt, P. D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwood forests: evaluation of habitat quality. *Auk*, 113: 875–888.
- ITTO (International Tropical Timber Organization). 2002. Guidelines for the restoration, management, and rehabilitation of degraded and secondary tropical forests. *Policy Development Series*, 13. Yokohama.
- Johnson, E. I.; Stouffer, P. C. & Vargas, C. F. 2011. Diversity, biomass, and trophic structure of a central Amazonian Rainforest bird community. *Revista Brasileira de Ornithologia*, 19: 1–16.
- Jullien, M. & Thiollay, J.-M. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. *Journal of Animal Ecology*, 67: 227–252.
- Kattan, G. H. & Beltran, J. W. 2002. Rarity in antpittas: territory size and population density of five *Gnallaria* spp. in a regenerating habitat mosaic in the Andes of Colombia. *Bird Conservation International*, 12: 231–240.
- Kratter, A. W. 1997. Bamboo specialization by Amazonian birds. *Biotropica*, 29: 100–110.
- Laurance, W. F. & Bierregaard-Jr., R. O. (eds.). 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. Chicago: University of Chicago Press.
- Lima, A. M. X. & Roper, J. J. 2009. Population dynamics of the Black-cheeked Gnatcatcher (*Conopophaga melanops*, Conopophagidae) in southern Brazil. *Journal of Tropical Ecology*, 25: 605–613.
- Lopes, L. E. & Marini, M. Â. 2006. Home range and habitat use by *Suiriri affinis* and *S. islerorum* in central Brazilian Cerrado. *Studies on Neotropical Fauna and Environment*, 41: 87–92.
- MacArthur, R. H.; Diamond, J. M. & Karr, J. R. 1972. Density compensation in island faunas. *Ecology*, 53: 330–342.
- Marangon, L. C.; Soares, J. J. & Feliciano, A. L. P. 2003. Florística arbórea da Mata da Pedreira, município de Viçosa, Minas Gerais. *Revista Árvore*, 27: 207–215.
- Marini, M. Â. & Cavalcanti, R. B. 1992. Mating system of the Helmeted Manakin *Antilophia galeata*. *Auk*, 109: 911–913.
- Marini, M. Â. & Garcia, F. I. 2005. Bird conservation in Brazil. *Conservation Biology*, 19: 665–671.
- Marini, M. Â.; Vasconcellos, M. M. & Lobo, Y. 2014. Territoriality and reproductive biology of the Wedge-tailed Grass-finch (*Emberizoides herbicola*) (Aves: Passeriformes). *Bioscience Journal*, 30: 853–862.
- Metzger, J. P.; Martensen, A. C.; Dixo, M.; Bernacci, L. C.; Ribeiro, M. C.; Teixeira, A. M. G. & Pardini, R. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic Forest region. *Biological Conservation*, 142: 1166–1177.
- Millspaugh, J. J. & Thompson-III, F. R. (eds.). 2009. *Models for planning wildlife conservation in large landscapes*. Burlington: Academic Press.
- Myers, N.; Mittermeier, R. A.; Mittermeier, C. G.; Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853–858.
- Pereira, R. A. 1999. *Mapeamento e caracterização de fragmentos de vegetação arbórea e alocação de áreas preferenciais para sua interligação no município de Viçosa, MG*. Ph.D. Thesis. Viçosa: Universidade Federal de Viçosa.
- Pinto, S. I. C.; Martins, S. V.; da Silva, A. G.; Barros, N. F.; Dias, H. C. T. & Scoss, L. M. 2007. Estrutura do componente arbustivo-arbóreo de dois estádios sucessionais de floresta estacional semidecidual na reserva florestal Mata do Paraíso, Viçosa, MG, Brasil. *Revista Árvore*, 31: 823–833.
- Remsen-Jr., J. V.; Areta, J. I.; Cadena, C. D.; Claramunt, S.; Jaramillo, A.; Nores, M.; Pacheco, J. F.; Pérez-Emán-E, J.; Robbins, M. B.; Stiles, F. G.; Stotz, D. F. & Zimmer, K. J. 2016. A classification of the bird species of South America. American Ornithologists' Union. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm> (access on 10 August 2016).
- Ribeiro, B. A.; Goulart, M. F. & Marini, M. Â. 2002. Aspectos da territorialidade de *Knipolegus lophotes* (Tyrannidae: Fluvicolinae) em seu período reprodutivo. *Aranajuba*, 10: 231–235.
- Ribeiro, M. C.; Metzger, J. P.; Martensen, A. C.; Ponzoni, F. J. & Hirota, M. M. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142: 1141–1153.
- Ribon, R. 2003. *Aves em fragmentos de Mata Atlântica do sudeste de Minas Gerais: incidência, abundância e associação à topografia*. Ph.D. Thesis. Belo Horizonte: Universidade Federal de Minas Gerais.
- Ribon, R. 2005. Demarcação de uma grade de trilhas no Centro de Pesquisas da Mata do Paraíso, Viçosa, Minas Gerais. *Revista Árvore*, 29: 151–158.
- Ribon, R.; Moraes, L. L.; Souza, A. Z. & Mattos, G. T. 2014. Ecologia de avifauna, p. 81–112. In: Lima, G. S.; Ribeiro, G. A.; Gonçalves, W.; Martins, S. V. & Almeida, M. P. (eds.). *Ecologia de Mata Atlântica - Estudos ecológicos na mata do paraíso*. Visconde do Rio Branco: Suprema Gráfica e Editora.
- Ribon, R.; Simon, J. E. & Mattos, G. T. 2003. Bird extinctions in Atlantic Forest fragments of the Viçosa region, southeastern Brazil. *Conservation Biology*, 17: 1827–1839.
- Robinson, S. K. & Terborgh, J. 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology*, 64: 1–11.
- Robinson, S. K. & Terborgh, J. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. *Ornithological Monographs*, 48: 641–672.
- Robinson, W. D.; Brawn, J. D. & Robinson, S. K. 2000. Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecological Monographs*, 70: 209–235.

- Shaffer, M. L. 1981.** Minimum population size for species conservation. *BioScience*, 31: 131–134.
- Sick, H. 1997.** *Ornitologia brasileira*. Rio de Janeiro: Nova Fronteira.
- Stamps, J. A. & Buechner, M. 1985.** The territorial defense hypothesis and the ecology of insular vertebrates. *Quarterly Review of Biology*, 60: 155–181.
- Stotz, D. F.; Fitzpatrick, J. W.; Parker-III, T. A. & Moskovits, D. K. 1996.** *Neotropical birds: ecology and conservation*. Chicago: University of Chicago Press.
- Stouffer, P. C. 2007.** Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. *Auk*, 124: 291–306.
- Stouffer, P. C. & Bierregaard-Jr., R. O. 1995.** Use of Amazonian Forest fragments by understory insectivorous birds. *Ecology*, 76: 2429–2445.
- Streby, H. M.; Loegering, J. P. & Andersen, D. E. 2012.** Spot-mapping underestimates song-territory size and use of mature forest by breeding Golden-winged Warblers in Minnesota, USA. *Wildlife Society Bulletin*, 36: 40–46.
- Terborgh, J.; Robinson, S. K.; Parker-III, T. A.; Munn, C. A. & Pierpoint, N. 1990.** Structure and organization of an Amazonian Forest bird community. *Ecological Monographs*, 60: 213–238.
- Thiollay, J. M. 1994.** Structure, density and rarity in an Amazonian Rainforest bird community. *Journal of Tropical Ecology*, 10: 449–481.
- Willis, E. O. & Oniki, Y. 2001.** Birds of a central São Paulo woodlot: 3. banded species, p. 69–92. *In*: Albuquerque, J. L. B.; Cândido-Jr., J. F. & Roos, A. L. (eds.). *Ornitologia e conservação: da ciência às estratégias*. Tubarão: Unisul.
- Willis, E. O.; Oniki, Y. & Silva, W. R. 1983.** On the behavior of Rufous Gnateaters (*Conopophaga lineata*, Formicariidae). *Naturalia*, 8: 67–83.
- Wright, S. J. 2010.** The future of tropical forests. *Annals of the New York Academy of Sciences*, 1195: 1–27.

Associate Editor: Carla S. Fontana.