ARTIGO

Revista Brasileira de Ornitologia, 17(3-4):163-172
Setembro-Dezembro de 2009

Birds of Pantanal forest patches and their movements among adjacent habitats

Regina de Souza Yabe

Pós-Graduação em Ecologia e Conservação, Universidade Federal de Mato Grosso do Sul, Caixa Postal 549, 79070-900, Campo Grande, MS, Brasil. Universidade do Estado de Mato Grosso – UNEMAT – Campus Universitário de Nova Xavantina, Departamento de Ciências Biológicas, BR-158, KM 148, 78.690-000, Nova Xavantina, MT, Brasil.
E-mail: regyabe@hotmail.com

Recebido em 26/02/2009. Aceito em 11/12/2009.

RESUMO: Aves dos capões do Pantanal e seus movimentos para hábitats adjacentes. Manchas de hábitat estão abertas às influências da matriz circundante e os animais podem se deslocar entre elas de acordo com a permeabilidade da matriz inter-hábitats e da conectividade entre as manchas. Este estudo, conduzido no Pantanal do Abobral, Corumbá, MS, avaliou a composição da comunidade de aves dos capões, quanto a três categorias de espécies com diferentes níveis de associação com o ambiente florestal (espécies florestais, generalistas e de hábitats abertos) e analisou a utilização dos capões (borda e interior) pelas aves de acordo com as três categorias. Também foram avaliados os deslocamentos das aves entre capões e hábitats adjacentes (campo e mata ciliar). Um total de 111 espécies de aves (49 generalistas, 42 de hábitats abertos e 20 florestais) foi registrado por meio de observações e captura. Espécies de áreas abertas foram mais frequentemente capturadas na borda dos capões e espécies florestais, no seu interior. Capões maiores apresentaram maior riqueza e abundância de espécies florestais e maior abundância de aves de hábitats abertos do que capões menores. Um total de 1.286 movimentos foi registrado para 74 espécies (14 florestais, 30 generalistas e 30 de hábitats abertos). O grupo de espécies florestais apresentou o maior percentual de movimentação entre capões e entre a mata ciliar e capões. Espécies generalistas moveram-se mais frequentemente entre capões do que espécies florestais e de ambiente aberto. Já o movimento entre capões e campo foi mais freqüente para as espécies de ambiente aberto. No final do período seco, movimentos para matas ciliares foram mais freqüentes para os três grupos de espécies. Os resultados deste estudo mostraram que a maior parte das espécies registradas nos capões movimentou-se entre os habitats não se restringindo à área dos capões, indicando a importância do mosaico de habitats para assegurar a biodiversidade de aves da região.

PALAVRAS-CHAVE: ambiente em mosaico, aves, hábitat, capões, mata ciliar, movimento, Pantanal, planície inundável.

ABSTRACT: Habitat patches are open to influences from the adjacent matrix and animals can move among them according to the matrix permeability and the connectivity among patches. This study, conducted in *Pantanal do Abobral,* Corumbá, MS, assessed the composition of the bird community of forest patches in relation to three categories of species with different degrees of association with forest environments (forest, generalist, and open-habitat species) and analysed the use of forest patches (edge and interior) according to the three categories. Bird movements between forest patches and adjacents habitats (grasslands and riparian forest) were also assessed. Overall 111 birds species (49 generalist, 42 open-habitat, and 20 forest species) observed or captured were recorded in forest patches. Open-habitat species were more frequent in edges, whereas forest species were more frequent in the interior of forest patches. Larger patches had higher richness and abundance of forest species and higher abundance of open-habitat species than smaller patches. A total of 1.286 movements was recorded for 74 bird species (14 forest, 30 generalist, and 30 open-habitat species). Forest species was the category with higher percentage of species with movements among patches and between patches and riparian forests. Generalist species moved more frequently among forest patches. Open-habitat species moved more frequently from forest patches to grasslands. At the end of dry period, movements to riparian forest were more frequent for the three groups of species. The results of this study indicated that the most of birds observed in forest patches moved among habitats exceeding their area, highlighting the importance of habitat mosaic to assure the bird diversity of *Pantanal.*

KEY-WORDS: birds, habitat, mosaic environment, movement, riparian forest, forest patches, *Pantanal,* wetland.

Unlike real islands, fragments or vegetation patches are rarely surrounded by a neutral or inhospitable environment (Wiens 1995). They are open to influences from the surrounding landscape and animals can move through several habitats, with different frequencies, depending on their propensity to cross the boundary between different vegetation types (Fahrig 2007), on their resistance to move through the inter-habitat matrix (Castellón and Sieving 2006), and on the spatial arrangement and connection of habitats in the landscape (Awade and Metzger 2008, Gillies and St. Clair 2008, Lees and Peres 2008, Yabe *et al.* 2010).

Movements between habitats occur frequently as a response to differences in resource abundance and distribution, causing considerable spatial and temporal variability in bird communities (Blake *et al.* 1990). Whereas populations of some species occur only in patches with one type of vegetation, others need several types of vegetation with varied resources, necessary in different stages of individuals' life cycles (Law and Dickman 1998, Tubelis *et al.* 2004). In patchy landscapes, several species may use multiple habitats (Karr 1990, Nunes 2005, Figueira *et al.* 2006, Tizianel 2008). Thus, the knowledge of animals' movement patterns is essential to establish management strategies for wildlife (Law and Dickman 1998).

The *Pantanal* is a major wetland formed by a mosaic of habitats, wherever vegetation patches produce specialized, sporadic, and abundant resources (Junk 1993). The main characteristic of the region is the large variation of water level, with prolonged and alternating periods of floods and droughts. These conditions of climatic instability are unfavorable to the majority of animal species. Thus, only organisms resistant to climatic variations, generalist and highly vagile species may prosper (Brown Jr. 1986). The structure and dynamics of the *Pantanal* bird community are strongly linked to the environmental heterogeneity and flooding cycles. Resident species try to find necessary resources in different habitats to compensate for availability fluctuations, while seasonal species abandon the area cyclically. The habitat sharing indicates the potential flux of individuals and species between different habitats and, consequently, the complexity, interconnectedness, and flexibility of interactions in a trophic web (Figueira *et al.* 2006).

Even among highly vagile species, the energetic costs of trap-lining multiple patches may reduce the reproductive potential of species occupying small and isolated patches (Hinsley 2000). Thus, species persisting in heavily fragmented landscapes must either tolerate small forest patches or be adept at moving among them (Lees and Peres 2009). Considering the challenges imposed by mosaic environments to animal species, the understanding about which species compose the bird community of forest patches and their movements in a naturally fragmented environment is a relevant question for conservation, having quite a few studies in tropical regions. Therefore, the main objective of this study was to assess the composition of the bird community in forest patches, as well as bird movements between forest patches and adjacent habitats (riparian forests and grasslands) during dry and wet seasons, within the *Pantanal.* More specifically, I tested the hypothesis that bird movement is affected by species type, habitat and seasonality.

METHODS

Study area

The study was conducted in 1999 near the Vermelho River (19°36’S; 56°56’W), in the *Abobral* sub-region of the *Pantanal* (PCBAP 1997), municipality of Corumbá, state of Mato Grosso do Sul, Brazil. The *Abobral* subregion is characterized by forest patches (*capões*), 1-2 m above the seasonally flooded landscape. The vegetation in the study area is a mosaic composed of the Vermelho River riparian forest and forest patches surrounded by natural grasslands. These patches have arboreal-shrubby vegetation and their border contains grassland, flooded

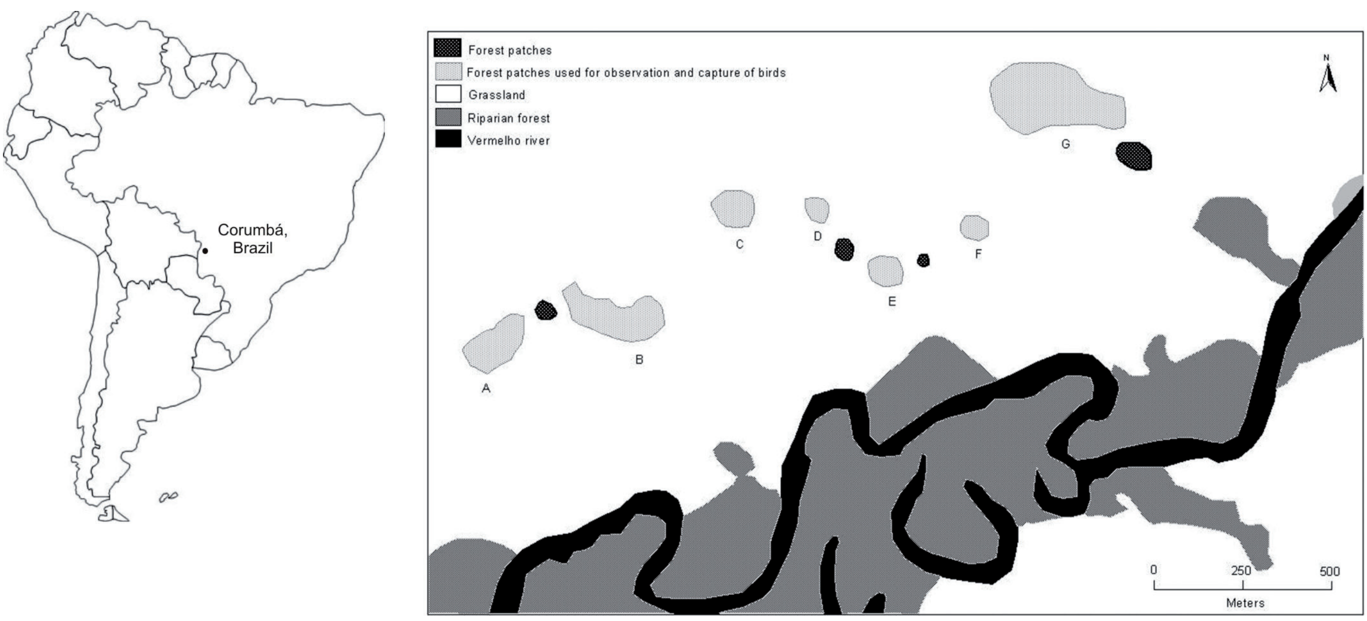

FIGURE 1: Map of South America showing the location of the study area in the *Pantanal* region, state of Mato Grosso do Sul, Brazil, and schematic drawing of survied forest patches (A-G) in the *Abobral* sub-region (modified from Yabe *et al.* 2010).

TABLE 1: Area of the seven patches sampled in the Pantanal, *Abobral* sub-region, and the distances between them.

Variable	Patches						
	A	B	C	D	E	F	G
Area (ha)	1.5	2.3	0.9	0.33	0.6	0.4	4.8
Distance to the two nearest patches (m)	45-462	43-286	135-286	62-135	32-46	119-262	41-262

savanna and riparian forest species, whereas the central portion of patches contains semideciduous species characteristic of non-flooded areas (Damasceno *et al.* 1996). The forest patch-grassland ecotones are steep and characterized by the presence of the palm *Scheelea phalerata* (Mart.) Bur., Arecaceae, and the boundary between the two vegetation types is maintained by a small variation in topography and flood pulsation (Junk 1993).

Mean annual rainfall is around 1,000 mm, most of which occurs from November to March (rainy season). In this period, air temperature averages 27°C, while in the dry season (April-October) the average is 20°C; in the coldest months (June-July) frosts may occur. In this area of the *Pantanal,* flood pulses typically occur from January to March (Ragusa-Netto and Fecchio 2006). The most important economic activities in the region are extensive cattle raising, fisheries and ecotourism. The studied area lies in the center of a cattle farm.

To detect bird movements, I observed and captured birds in the seven largest patches of the study site (Figure 1). Patches varied in size from 0.3 to 4.8 ha, and the distance between adjacent patches varied from 32 to 462 m (164.5 ± 71.5 m) (Table 1).

Data collection

I established two sampling points in the border of each of the seven largest patches, each point facing the two closest adjacent patches. Points were established near the shortest distance between two patches, allowing good observation of bird movements, but far enough to avoid influencing gap-crossing behavior of birds. For patch A, one of the two sampling points was between the patch and the riparian forest of the Vermelho River. Observations were conducted during seven consecutive mornings in March, May, August, September and October 1999. Three hours of observations were spent in each patch (1.5 h for each point), between 06h00 and 09h30, alternating 30 min between the two sampling points, with 5 min intervals for the observer to move between points. This was the period of the day with most bird movements among patches. I used a 2 m high, mobile aluminum platform for a free view of flying birds above the vegetation. For each individual bird I recorded the source and the destination habitat (forest patch, grassland or riparian forest) using 10 x 50 mm Nikon binoculars. Each movement among patches was classified either as movement between known or between unknown patches. Movements between known patches included those between identified source and destination patches, either adjacent or not. Movements between unknown patches are those between non-adjacent patches in which one of the patches, inside or not the study area, was not identified. The movement of monospecific flocks was counted as one observation. All birds were identified to the species level, with the exception of three species of *Myiarchus* flycatchers, two species of *Turdus* thrushes, identified at the genus level, and six species of hummingbirds, identified at the family level. Thus, species from these groups were excluded from analyses at the species level. Nomenclature followed the list of Brazil birds (CBRO 2008).

Movements were classified as follows: M1, among forest patches; M2, between forest patch and grassland; M3, between forest patch and riparian forest (from forest patch A and occasional observations from other forest patches).

I banded birds for 14 days (two days per patch) in January, February, April, and September 1999, in the same patches where I carried out observations. I used 6 m long by 2.6 m high mist-nets, with 36 mm mesh size, opened for 5 h since sunrise. This procedure was repeated in two consecutive mornings. The number of nets used varied with patch size: 20 nets in patches > 1 ha (10 in the interior and 10 at the edge) and 16 nets in patches < 1 ha (eight in the interior and eight at the edge). Only the nets at the edge were fixed in rows. Two rows of 5 nets (in patches > 1 ha) or two rows of 4 nets (in patches < 1 ha) and each row of nets was fixed in the patch border, facing the two closest adjacent patches. All captured birds received a metal band and were immediately released a few meters (< 5 m) of the edge of the patch of capture.

Species were classified in three categories, according to their degree of association with forests, following Silva (1995): (a) species that occur mainly in open vegetation, here called open-habitat species; (b) species that occur in both open vegetation and forests, here called generalist species; and (c) species that live mainly in forest habitats, here called forest species. One species (*Aratinga nenday*) that does not appear on Silva (1995) was classified as generalist, following Tubelis and Tomás (1999). Other three species were classified according to information in Sick (1997): *Phaethornis eurynome* and *Dendrocolaptes picumnus* as forest species and *Jabiru mycteria* as an open-habitat species.

Statistical analyses

To assess if species richness and abundance in each category varied with patch size, I correlated the number of species and the number of individuals in each category against patch area, using Spearman rank correlations. To compare recaptures in the same forest patch where birds were banded with recaptures in others forest patches, I also used a chi-square test. The relationship of categories of species, habitat and season, and their interaction effects in birds movements were established with log-linear analysis of frequency using program Statistica (Statsoft, Inc. 1995). Log-linear analysis provides a way of looking at cross tabulation tables. This method allows testing different factors that are used in the cross-tabulation and their interactions for statistical significance (Ramirez 2002). All analyses except log-linear analysis were conducted with the software BioStat 5.0 (Ayres *et al.* 2007).

RESULTS

The birds of forest patches

Overall, 111 species (14 orders, 31 families) observed or banded (Table 2) were recorded in forest patches, including 49 (44%) generalist, 42 (38%) open-habitat and 20 (18%) forest species. From 69 banded species (367 individuals), 20 (29%) were captured just once, while 12 were the most frequent, corresponding to about 50% of captured individuals. Among these 12 species (in descending order of abundance for category) one was forest species (*Synallaxis albilora*), six were generalist (*Veniliornis passerinus, Hylocharis chrysura, Ramphocelus carbo, Leptotila verreauxi, Campylorhynchus turdinus, Icterus cayanensis*) five were open-habitat (*Furnarius rufus, Turdus rufiventris, Polytmus guainumbi, Eupetomena macroura* and *Pitangus sulphuratus*).

From the total of banded species, 34 were generalist (49%), 22 were open-habitat (32%), and 13 were forest species (19%). These results indicate that generalist and open-habitat species predominated in forest patches.

Open-habitat species used more frequently the edge, whereas forest species used more often the interior of forest patches. The number of captures of generalist species was independent of the environment of captured ($\chi^2 = 25.95$; gl = 2; $p < 0.0001$). However, two open-habitat species were more captured more often at the interior of forest patches: *F. rufus* (57%; n = 21) and *T. rufiventris* (63%; n = 16).

In small forest patches (< 1 ha) the number of forest species varied between 1 to 2, generalist species varied between 4 to 15, and open-habitat species between 5 to 9. In large forest patches (> 1 ha) the number of forest species varied between 5 to 8, generalist species between 13 to 20, and open-habitat species between 9 to 10. There was a positive correlation between the number of forest species and the area of forest patches ($r_s = 0.94$; $p = 0.0013$). This correlation was not significant in the other species categories. Further, the abundance of forest ($r_s = 0.95$; $p = 0.000$) and open-habitat species ($r_s = 0.89$; $p = 0.01$) was significantly correlated with patch area, whereas no such significant correlation was observed for generalist species.

Bird movements

Among the 111 bird species recorded in forest patches, I observed movements in 74 (67%) species (14 forest, 30 generalist and 30 open-habitat species), including 61 species (55%) with M1 (949 movements), 50 (45%) with M2 (237 movements) and 29 (26%) with M3 (100 movements). Forest species was the category with the highest percentage of species with movements among forests patches (14 of 20 forest species), followed by generalist (28 of 49 generalist species) and open-habitat species (19 of 42 open-habitat species). The group formed by open-habitat species had the highest percentage of species with movements between grassland and forest patches (22 species). Forest species was the group with the highest percentage of species (n = 8) with movements to riparian forest, followed by generalist species (n = 14) and open-habitat species (n = 7) (Figure 2).

I recorded 1,286 movements for 74 bird species (105 hours of observation), besides movements recorded for Trochilidae (M1 = 37 and M2 = 25), *Turdus* spp. (M1 = 7), *Myiarchus* spp. (M1 = 8) and by unidentified birds (M1 = 55 and M2 = 7), totalling 1,425 movements.

Log-linear analysis indicated that species category, movement type and month affected the number of bird movement. Marginal association and interaction were statistically significant between species category and month and between species category and movement type (Table 3).

The highest number of movements occured in dry season, mainly in September and October (in the late dry season), for all movement types and for all species categories (Figure 3).

Generalist species moved more frequently among forest patches than forest species and open-habitat species, in all months surveyed, except in August, when the number of movements of forest species surpassed the number of movements of generalist species (Figure 3a). Forest species with the highest frequency of movements among patches were *Amazona aestiva* (n = 87), *Myiozetetes cayanensis* (n = 32) and *Campylorhamphus trochilirostris* (n = 21). Among generalist species, *Thraupis sayaca* (n = 95), *Icterus cayanensis* (n = 78), *V. passerinus* (n = 51) and *Brotogeris chiriri* (n = 45) were the species with highest movement among patches. Open-habitat species that

TABLE 2: Birds registered in the *Pantanal* forests patches in the *Abobral* sub-region, through observations, movement observations and capture (with nets fixed at forest patches edge and interior). Species nomenclature and systematic sequence, of each category of association on forest, follow CBRO (2008).

Species	Movements			Capture local	
	M1	M2	M3	edge	interior
Forest species					
Aburria cumanensis	4	2	1	—	—
Falco rufigularis	1	6	1	—	—
Patagioenas cayennensis	17	1	8	—	—
Amazona aestiva	87	2	18	0	1
Phaethornis eurynome	—	—	—	1	1
Trogon curucui	5	0	0	1	1
Pteroglossus castanotis	2	0	0	1	0
Piculus chrysochloros	10	0	0	1	1
Celeus lugubris	6	0	0	0	3
Campephilus melanoleucos	16	0	1	0	1
Dendrocolaptes picumnus	—	—	—	0	2
Campylorhamphus trochilirostris	21	2	0	2	6
Synallaxis albilora	2	1	0	5	18
Lathrotriccus euleri	—	—	—	1	0
Cnemotriccus fuscatus	—	—	—	0	1
Myiozetetes cayanensis	32	2	2	—	—
Myiodynastes maculatus	—	—	—	—	—
Cyanocorax cyanomelas	12	2	0	0	2
Parula pitiayumi	—	—	—	—	—
Psarocolius decumanus	14	0	2	—	—
Generalist species					
Ortalis canicollis	13	2	2	—	—
Geranospiza caerulescens	1	1	0	—	—
Buteogallus urubitinga	1	0	1	—	—
Herpetotheres cachinnans	1	0	0	—	—
Patagioenas picazuro	1	1	8	—	—
Leptotila verreauxi	22	18	3	9	8
Anodorhynchus hyacinthinus	25	0	75	—	—
Primolius auricollis	1	1	3	—	—
Aratinga acuticaudata	1	0	2	—	—
Aratinga leucophthalma	—	—	—	0	1
Aratinga nenday	—	—	—	—	—
Brotogeris chiriri	45	0	14	6	0
Piaya cayana	—	—	—	—	—
Glaucidium brasilianum	—	—	—	0	3
Anthracothorax nigricollis	—	—	—	1	4
Chlorostilbon lucidus	—	—	—	—	—
Hylocharis chrysura	—	—	—	17	5
Galbula ruficauda	—	—	—	1	4
Ramphastos toco	16	0	6	—	—
Picumnus albosquamatus	0	2	0	1	0
Melanerpes candidus	3	0	0	—	—
Veniliornis passerinus	51	1	0	5	18
Colaptes melanochloros	5	0	0	0	1
Taraba major	4	2	0	2	5
Thamnophilus doliatus	—	—	—	—	—
Xiphocolaptes major	10	0	1	0	1
Phacellodomus ruber	—	—	—	3	0
Pseudoseisura cristata	9	2	0	2	3
Sublegatus modestus	—	—	—	1	0
Megarynchus pitangua	15	1	1	0	1
Empidonomus varius	2	0	0	—	—
Myiarchus ferox	—	—	—	1	1
Myiarchus tyrannulus	—	—	—	—	—
Pachyramphus viridis	—	—	—	0	1
Pachyramphus polychopterus	—	—	—	0	1
Cyclarhis gujanensis	0	2	0	3	0
Cyanocorax chrysops	5	0	0	—	—
Campylorhynchus turdinus	30	2	0	5	8
Turdus leucomelas	—	—	—	0	1
Turdus amaurochalinus	—	—	—	2	3
Coereba flaveola	—	—	—	1	0
Ramphocelus carbo	32	2	0	5	14
Thraupis sayaca	95	4	4	8	0
Thraupis palmarum	5	1	0	1	0
Coryphospingus cucullatus	—	—	—	2	1
Saltator coerulescens	9	3	0	5	2
Procacicus solitarius	26	3	0	2	6
Icterus cayanensis	78	18	1	9	3
Icterus croconotus	15	1	2	4	4
Open-habitat species					
Rhea americana	—	—	—	—	—
Theristicus caerulescens	1	0	0	—	—
Theristicus caudatus	0	1	0	—	—
Jabiru mycteria	—	—	—	—	—
Coragyps atratus	1	5	0	—	—
Cathartes aura	0	2	0	—	—
Cathartes burrovianus	1	1	0	—	—
Gampsonyx swainsonii	1	0	0	—	—
Heterospizias meridionalis	0	1	0	—	—
Rupornis magnirostris	2	2	0	0	1
Buteo albicaudatus	—	—	—	—	—
Buteo melanoleucus	—	—	—	—	—
Caracara plancus	27	6	1	—	—
Milvago chimachima	2	0	1	—	—
Columbina minuta	—	—	—	1	0
Columbina talpacoti	1	1	0	5	0
Columbina picui	3	0	0	5	0
Aratinga aurea	0	0	1	—	—
Crotophaga ani	0	6	0	2	0
Guira guira	0	4	0	—	—
Tapera naevia	—	—	—	—	—
Bubo virginianus	—	—	—	—	—
Eupetomena macroura	—	—	—	8	2
Polytmus guainumbi	—	—	—	11	0
Colaptes campestris	1	0	0	—	—
Formicivora rufa	0	1	0	3	0
Lepidocolaptes angustirostris	—	—	—	—	—
Furnarius rufus	15	19	0	9	13
Schoeniophylax phryganophilus	1	1	0	1	0
Pyrocephalus rubinus	0	1	0	—	—
Machetornis rixosa	6	14	0	4	0
Pitangus sulphuratus	94	33	3	4	6
Tyrannus melancholicus	45	14	4	1	0
Myiarchus swainsoni	—	—	—	1	1
Turdus rufiventris	8	2	0	6	12
Ammodramus hummeralis	0	2	0	1	0
Volatinia jacarina	5	4	0	3	0
Sporophila collaris	—	—	—	7	0
Sporophila angolensis	0	3	0	5	1
Paroaria capitata	1	0	1	1	3
Gnorimopsar chopi	7	28	5	—	—
Agelasticus cyanopus	0	2	0	1	0
Species identified at the family level and at the genus level					
Trochilidae	37	25	0	—	—
Myiarchus spp.	8	0	0	—	—
Turdus spp.	7	0	0	—	—
Sporophila sp.	—	—	—	2	1

TABLE 3: Log-linear analysis of frequency of bird movements among forest patches and between forest patches and adjacents habitats (grassland and riparian forest), in the *Pantanal, Abobral* sub-region.

Effect	Bird movements		
	gl	χ^2	P
Marginal association			
Species and month	8	47,54	0,00
Species and type of movement	4	146,09	0,00
Interactions			
Species X month	8	42,87	0,00
Species X type of movement	4	141,42	0,00

moved more frequently among patches were *P. sulphuratus* (n = 94), *Tyrannus melancholicus* (n = 45) and *Caracara plancus* (n = 27).

Open-habitat species had the highest number of movements from forest patches to grassland in all months surveyed except in September, when generalist species surpassed open-habitat species in this type of movement (Figure 3b). Open-habitat species with the highest number of movement from forest paches to grasslands were *P. sulphuratus* (n = 33), *Gnorimopsar chopi* (n = 28) and *Furnarius rufus* (n = 19). *I. cayanensis, Leptotila verreauxi* and *T. sayaca* were the generalist species with the highest number of movements from patches to grasslands. Among forest species, only *Falco rufigularis* (n = 6) moved to from patches to grassland more than twice.

Movements to riparian forest were more frequent in October in the three groups of species, but mainly in generalist species (Figure 3c). These, represented by *A. hyacinthinus, Primolius auricollis, B. chiriri, Patagioenas picazuro, Megarynchus pitangua, Ortalis canicollis, Ramphastos toco,* and *T. sayaca,* also travelled more frequently to riparian forests in May, when movements of forest species were the lowest – just one observation of *A. aestiva.* From August on, movements of forest species increased, reaching the highest frequency in October. *A. aestiva, F. rufigularis, Psarocolius decumanus* and mainly *P. cayannensis* were the forest species with M3. *A. aestiva* (n = 18) and *P. cayannensis* (n = 8) were the forest species with the highest number of movements from patches to riparian forest. Among generalist species, those with the highest number of M3 were *B. chiririri* (n = 14), *P. picazuro* (n = 8) and *R. toco* (n = 6). The open-habitat species with highest frequency of M3 were *Gnorimopsar chopi* (n = 5) and *T. melancholicus* (n = 4).

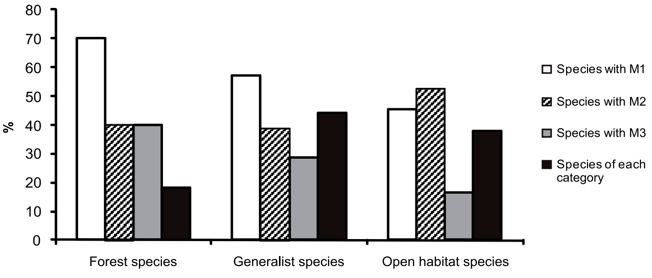

FIGURE 2: Percentage of species observed in the *Pantanal* forest patches, *Abobral* sub-region, according to movement type and category.

In relation to birds captured in forest patches, 42 recaptures occured in the same forest patch where birds were banded and 27 in others patches. The percentage of recaptures in others forest patches varied between 31% (open-habitat species) and 46% (generalist species), with an intermediate value (36%) for forest species. However, there was no association between the place of recapture and the species categories.

DISCUSSION

The forest patches birds

Birds of forest patches are mainly generalist and open-habitat species, with fewer forest species. This dominance of generalist species was also observed in others

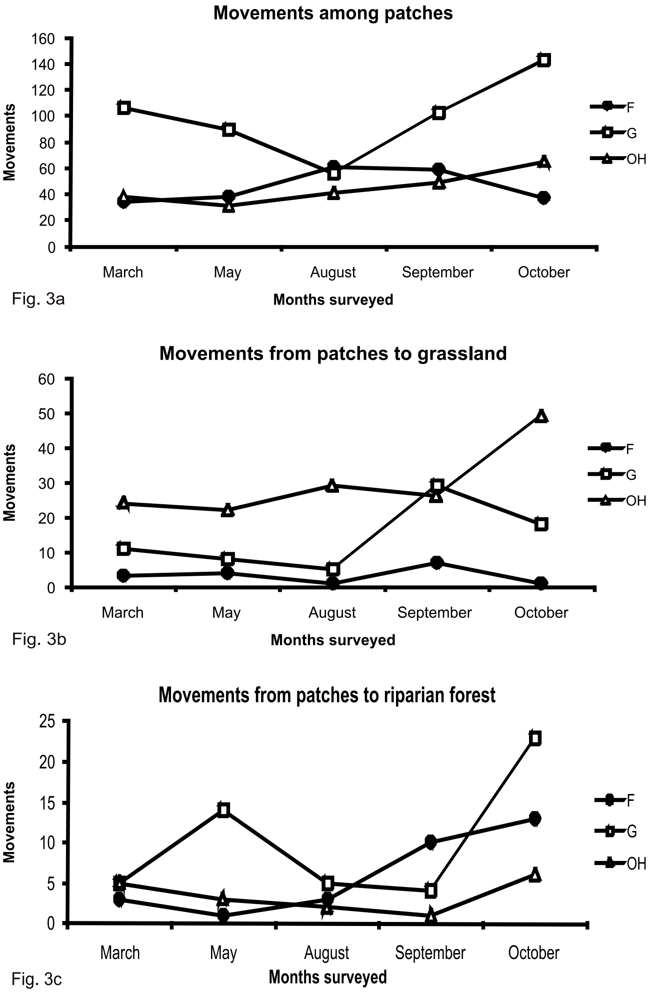

FIGURE 3: Bird movements in the *Pantanal, Abobral* sub-region. (a) M1; (b) M2; (c) M3. F = forest especies; G = generalist species; OH = open-habitat species.

regions of the *Pantanal* (Figueira *et al.* 2006), whereas a greater proportion of non-forest species in relation to forest species was observed in forest patches of *Pantanal de Nhecolândia* (Tubelis and Tomás 1999) and of *Serra da Canastra* National Park, in the Cerrado biome (Andrade and Marini 2001). Open-habitat species were also frequent in forest patches, using mainly the boundary with grasslands. This species composition can be explained both by the small size of forest patches and by the presence of cattle. In *Pantanal,* cattle have considerable effect on the forest understory vegetation, particularly through selective grazing and trampling (Prance and Schaller 1982). Open areas in forest patches may facilitate the settling of open-habitat species, such as *F. rufus.* This suggests that disturbances may result in a higher proportion of edges and semi-open-habitats that favour non-forest species and may also promote the loss of forest interior species and changes in community structure and habitat use, as verified by Thiollay (1999) in tropical rain forests of French Guiana.

In addition to open-habitat species, which use forest patches with considerable frequency, others sometimes use forest patches for roost while flying over the region, resulting in a high percentage of generalist and open-habitat species in forest patches. In the *Pantanal,* aquatic birds such as *Jabiru mycteria* and other Ciconiiformes with colonial breeding also use the forest patches as nest-sites (Marques *et al.* 1996).

Grasslands may be more unstable habitats for birds than forest patches, because of floods during the wet season and burns during the dry season, with higher temperature variation throughout the day and little shelter against the wind and the rain. Because of these conditions, it is probable that non-forest species also seek forest patches for resources and/or protection against the severe weather. Several species, from small seedeaters to open-habitat raptors, need tree trunks and nest-sites that cannot be found in grasslands (Tizianel 2008). Therefore, small forest patches may be habitat of several generalist and open-habitat birds, as also recorded in the Atlantic Forest (Uezu *et al.* 2008).

The high proportion of generalist and open-habitat species in forest patches highlights their importance for these birds. Species such as the trochilids *Polytmus guainumbi* and *E. macroura* are among the most captured birds at the edge of forest patches and were observed several times feeding in these environments. Other authors have also recognized the importance of edges for nectarivores, frugivores and generalists in the *Pantanal* (Figueira *et al.* 2006) and other regions (Willis 1979, Stouffer and Bierregaard Jr. 1995, Thiollay 1999).

While forest species were captured more often inside forest patches, open-habitat species were captured more often at the edges. This pattern of differential habitat use could reduce the competition for resources (Thiollay 1999). On the other hand, the aggressive territorial behaviour of invasive ruderal species could potentially strengthen edge-avoidance in some interior species (Lees and Peres 2009). The species composition in forest edges is variable because of idiosyncratic responses of different species to physical conditions, to interactions with other species or to both (Murcia 1995). Hence, there are forest species that show affinities for the edge, while others prefer to forage in the forest interior, with a clear trend of edge-avoidance (Hansbauer *et al.* 2008).

In large forest patches, the richness and abundance of forest species were higher, probably because the interior of the patch is not as reduced as in small patches. Large forest patches should favour forest species that are more sensitive to edge effects and allow the persistence of larger populations of forest species with low dispersal ability. In the *Serra da Canastra* National Park (Minas Gerais, Brazil), there was higher richness and abundance of forest species in larger forest patches than in smaller ones (Andrade 1999). For generalist and open-habitat species, the increase in patch area was not followed by increased species richness. However, open-habitat species were more abundant in larger forest patches than in smaller ones. This corroborates the hypothesis – originally proposed for reptile species (Rodrigues 2005) – that open-habitat species may have minimum pre-adaptations to use, tolerate and explore forested areas. Accordingly, some open-habitat species may be favoured by open areas within forest patches, formed by cattle grazing and trampling, and by edge habitat, and they can settle in the patches and be favoured by an increase in patch area. The abundance of generalist species did not increase with the increased area of forest patches, probably because these species also use open areas surrounding patches, exceeding the area sampled by nets in this study.

Bird movements

A high percentage of species in the three categories of association with forest environments moved among forest patches. This suggests that the use of a group of forest patches may play a major role in the maintenance of local bird biodiversity (Yabe *et al.* 2010). The semi-linear arrangement of forest patches in clustered sequence must favour species that use more than one patch to reach resources, although they are small in size but large enough to be explored (Yabe e Marques 2001). Studies in forest patches of *Serra da Canastra* National Park (Andrade and Marini 2001) and *Pantanal de Nhecolândia* (Tubelis and Tomás 1999) suggest that a single patch cannot support individuals of most species; thus, the use of several forest patches is necessary to assure enough resources to these species. Plants such as *Ficus* sp., are abundant in forest patches and their fruit production, that occur during dry period, is asynchronous (França *et al.* 2009). Thus, fruit availability in diferent patches at different periods could explain the movement patterns among patches for several bird species. The results of this study indicate that most species recorded during the movement observations, cross open-habitats among forest patches, perhaps due to the high percentage of generalist and open-habitat species. Considering the mosaic environment where forest patches lie, even forest species must be more willing to cross the surrouding matrix.

Several forest and generalist species moved between forest patches and grasslands, although with low frequency. However, these species only moved to grasslands when there were trees or shrubs close to the forest patch, which were used to roost. This enhancing of the connectivity by shrubby vegetation was also observed by Castellón and Sieving (2006) for Chucaos. These observations suggest that, in a very resistant matrix, species are not able to leave the habitat patch (Sieving *et al.* 1996, Uezu *et al.* 2008). Open-habitats with low density of arboreal-shrubby vegetation offer fewer resources to generalist and forest species, thus their movements from forest patches to grasslands must occur less often. Tubelis *et al.* (2004) verified that movements of birds from gallery forests to savannas were higher in areas of denser savanna vegetation, due to their greater suitability as a food source or as shelter. Otherwise, as in the study area, grasslands among forest patches are composed mainly by native grasses and there are few resources to forest and generalist species. Accordingly, grassslands were less attractive, with fewer movements from forest patches to them. In fact, as would be expected, the category with highest species richness and movements to grasslands was the open-habitat species. Only in this category movements between forest patches and grasslands were higher than movements among forest patches. Most species that moved to grasslands comprise a subset of ruderal and/or edge species. According to Lees and Peres (2006), the niche requirements of these species are either met by a small patch or subsidized by the non-forest matrix.

The riparian forest had an important role, especially to several forest species and, to a lesser extent, some generalist species, in agreement with Figueira *et al.* (2006) for the *Pantanal de Poconé.* Tubelis *et al.* (2004) observed a high flow of birds between gallery forests and dense savannas, the latter acting as a landscape supplementation for gallery forest species. The search for abundant and variable resources, especially fruits, justifies higher rates of movements to riparian forest, because about half the species that moved to this habitat include fruits in their diets (Yabe and Marques 2001).

The birds moved more frequently in the late dry season. There was a remarkable increase of bird movements to riparian forest between September (forest species) and October (open-habitat and mainly generalist species). It is possible that the high frequency of movements by some species, such as *A. aestiva, B. chiriri,* and *P. auricollis,* resulted from the pronounced flowering of *Inga vera* that occurs during the transition from dry to wet season (between September and October) (Ragusa-Netto and Fecchio 2006). The nectar of *I. vera* is intensely used by *B. chiriri* during the end of dry season, when parakeets become very abundant in riparian forest (Ragusa-Netto 2007). There was also an increase of movements of generalist species to riparian forests in May, coinciding with the fruiting peak of *Banara arguta, Sapium obovatum, Crataeva tapia, Copernicia alba,* and *I. vera,* during the transition from wet to dry season (March-May, Ragusa-Netto and Fecchio 2006). It is also likely that movements of *R. toco* in October (at the end of the dry period) were associated with higher abundance of fruits of *Cecropia pachystachya* and *Genipa americana* (Ragusa-Netto 2006).

Small forest fragments frequently are not considered important to conservation. However, Loman and Schantz (1991) observed that a group of small fragments clustered in an area can have more species than a corresponding area with fewer larger fragments. Nonetheless, it is important to consider that most of the species found in smaller fragments were not forest species. Uezu *et al.* (2008) noted several forest species in small forest patches and suggested that they use small patches as secondary-habitats and as elements that increase landscape connectivity, facilitating the movements of forest species.

In farming landscapes, even small fragments should be valued and integrate management and conservation plans along with large fragments, due to their contribution to the maintenance of several species (Berstein *et al.* 1994; Traun and Smith 1999; Uezu *et al.* 2008). In these mosaic environments, large forest patches (optimal habitats) and small fragments (sub-otimal habitats) would be related to each other, with individuals moving from optimal to sub-optimal patches and vice-versa (Berstein *et al.* 1994).

Considering that the *Pantanal* is composed by a mosaic of habitats patches and not by a large and continuous forest, it is fundamental that small patches are protected, because several species depend on their integrity as a whole, on a large or small scale. As Figueira *et al.* (2006) pointed out, within the *Pantanal,* although many species may be habitat generalists, those habitats may not be perfectly interchangeable, so that each habitat could provide its own key resources, highlighting the importance of protecting as many different habitat types as possible, to maintain high levels of species diversity. This is especially relevant when the use of these non-floodable areas on a large floodplain is considered. Traditionally, farmhouses were built on forest patches (including *capões* and *cordilheiras*), causing only local and small-scale impacts. Recently, some technologies were introduced in the *Pantanal,* with more severe effects. Large areas of forest patches have been modified by the introduction of exotic grasses, since they are not resistant to floods. Therefore, efforts to assure the conservation of forest patches are warranted, because a significant portion of the *Pantanal* bird fauna depends on them.

ACKNOWLEDGMENTS

I thank Dr. Eliézer José Marques by orientation towards my master dissertation, which led to this manuscript. I am greatful to students of Universidade Federal de Mato Grosso do Sul for field assistance. Financial support was provided by CAPES, CNPq (which also awarded R.S.Y a master fellowship). Logistical support and equipment was provided by Graduate Program in Ecology and Conservation of Universidade Federal de Mato Grosso do Sul. Dr. José Ragusa-Netto and Lucas Aguiar Carrara de Melo provided comments and suggestions on the manuscript. Dr. Guarino R. Colli improved the manuscript by making important suggestions on statistical analysis and English review.

REFERENCES

Andrade, R. D. (1999). *Riqueza de espécies e deslocamento de aves entre ilhas naturais de floresta (capões) do Parque Nacional da Serra da Canastra, Minas Gerais.* Dissertação de mestrado. Belo Horizonte: Universidade Federal de Minas Gerais.

Andrade, R. D. and Marini, M. Â. (2001). Bird movement between natural forest patches in southeast Brazil, p. 125-136. In: J. L. B. Albuquerque; J. F. Cândido Jr.; F. C. Straube and A. Roos (eds.). *Ornitologia e Conservação: da ciência às estratégias.* Tubarão: Editora Unisul.

Ayres, M.; Ayres, M. Jr., Ayres, D. L. and Santos, A. A. S. (2007). *BioStat: aplicações estatísticas nas áreas das ciências bio-médicas.* Belém, Pará, Brazil.

Awade, M. and Metzger, J. P. (2008). Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecology,* 33:863-871.

Bernstein, C.; Krebs, J. R. and Kacelnik, A. (1994). Distribution of birds amongst habitats: theory and relevance to conservation, p. 317-345. In: C. M. Perrins, J. D. Lebreton and G. J. M. Hirons (eds.) *Birds population studies: relevance to conservation and management.* New York: Oxford University Press.

Blake, J. G.; Stiles, F. G. and Loiselle, B. A. (1990). Birds of La Selva Biological Station: habitat use, trophic composition, and migrants, p. 161-182. In: A. Gentry (Org.) *Four neotropical rain forests.* New Haven: Yale University Press.

Brown Jr. K. S. (1986). Zoogeografia da região do Pantanal Mato-grossense, 137-178. In: Anais do 1º Simpósio sobre recursos naturais e sócio-econômicos do Pantanal. Documentos 5 (Corumbá, MS, 1984). EMBRAPA-CPAP e Universidade Federal do Mato Grosso do Sul. EMBRAPA-CPAP.

Castellón, T. D. and Sieving, K. E. (2006). An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology,* 20:135-145.

CBRO – Comitê Brasileiro de Registros Ornitológicos. (2008). Lista das aves do Brasil. www.cbro.org.br (acesso em 07/02/2009).

Damasceno Jr. G. A.; Bezerra, M. A. O., Bortolotto, I. M. and Pott, A. (1996). Aspectos florísticos e fitofisionômicos dos capões do Pantanal do Abobral, p. 74-75. In: Anais do II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal: manejo e conservação. Brasília: EMBRAPA-SPI.

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology,* 21:1003-1015.

Figueira, J. E. C.; Cintra, R.; Viana, L. and Yamashita, C. (2006). Spatial and temporal patterns of bird species diversity in the Pantanal of Mato Grosso, Brazil: implications for conservation. *Brazilian Journal Biology,* 66:393-404.

França, L. F.; Ragusa-Netto, J.; Paiva, L. V. (2009). Consumo de frutos e abundância de Tucano Toco (*Ramphastos toco*) em dois hábitats do Pantanal Sul. *Biota Neotropica,* 9:000-000. www.biotaneotropica.org.br/v9n2/en/abstract?article+bn02109022009 (acesso em 10/09/2009).

Gillies, C. S. and St. Clair, C. C. (2008). Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *PNAS,* 105:19774-19779.

Hansbauera M. M.; Storcha, I.; Leua, S.; Nieto-Holguina, J-P.; Pimentel, R. G.; Knauera, F. and Metzger, J. P. W. (2008). Movements of neotropical understory passerines affected by anthropogenic forest edges in the Brazilian Atlantic rainforest. *Biological Conservation,* 141:782-791.

Hinsley, S. A. (2000). The costs of multiple patch use by birds. *Landscape Ecology,* 15:765-775.

Junk, W. J. (1993). Wetlands of tropical South America, p. 679-739, Vol. I. In: D. Whigham, D. Dykjová and S. Hejný (eds.) *Wetlands of the world: Inventory, ecology and management.* Dordrecht: Kluwer Academic Publishers.

Karr, J. R. (1990). Interactions between forest birds and their habitats: a comparative synthesis, p. 379-393. In: A. Keast (ed.) *Biogeography and ecology of forest bird communities.* The Hague: SBP Academic Publishing.

Law, B. S. and Dickman, C. R. (1998). The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodiversity and Conservation,* 7:323-333.

Lees, A. C and Peres, C. A. (2006). Rapid avifaunal collapse along the Amazonian deforestation frontier. *Biological Conservation,* 133:198-211.

Lees, A. C and Peres, C. A. (2008). Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology,* 22:439-449.

Lees, A. C and Peres, C. A. (2009). Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos,* 118:280-290.

Loman, J. and Schantz, T. V. (1991). Birds in a farmland – more species in small than in large habitat island. *Conservation Biology,* 5(2):176-188.

Marques, E. J.; Nascimento, I. L. S. and Uetanabaro, M. (1996). Pantanal – Aspectos relacionados às aves aquáticas e áreas de reprodução colonial, p. 133-134. In: Anais do II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal: manejo e conservação. Brasília: EMBRAPA-SPI.

Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Tree,* 10:58-62.

Nunes, A. P.; Tomas, W. T. and Ticianeli, F. A. T. (2005) *Aves da fazenda Nhumirim, Pantanal da Nhecolândia, MS.* Embrapa Pantanal – Documentos, 81, 34 pp.

PCBAP – Plano de Conservação da Bacia do Alto Paraguai. (1997). *Diagnóstico dos meios físico e biótico.* Projeto Pantanal, Programa Nacional do Meio Ambiente. Brasília: PNMA.

Prance, G. T. and Schaller, G. B. (1982). Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. *Brittonia,* 34:228-251.

Ragusa-Netto, J. (2007). Nectar, fleshy fruits and the abundance of parrots at a gallery forest in the southern Pantanal (Brazil). *Studies on Neotropical Fauna and Environment,* 42(2):93-99.

Ragusa-Netto, J. and Fecchio, A. (2006). Plant food resources and the diet of a parrot community in a gallery forest of the southern Pantanal (Brazil). *Brazilian Journal of Biology,* 66:1021-1032.

Ramirez, N. (2002). Reproductive phenology, life-forms, and habitats of the Venezuelan Central plain. *American Journal of Botany,* 89:836-842.

Rodrigues, M. T. (2005). A biodiversidade dos Cerrados: conhecimento atual e perspectivas, com uma hipótese sobre o papel das matas de galerias na troca faunística durante os ciclos climáticos, 235-246. In: A. Scariot, J. C. Sousa-Silva, J. M. Felfili (orgs.) *Cerrado: Ecologia, biodiversidade e Conservação.* Brasília: Ministério do Meio Ambiente.

Sieving, K. E.; Willson, M. F. and Santo, T. L. (1996). Habitat barriers to movement of understory birds in fragmented south-temperate rainforest. *Auk,* 113(4):944-949.

Sick, H. (1997). *Ornitologia brasileira.* Rio de Janeiro: Nova Fronteira.

Silva, J. M. C. (1995). Birds of the Cerrado Region, South America. *Steenstrupia,* 21:69-92.

Statsoft, Inc. (1995). Statistica for windows (computer program manual). Tulsa, OK, USA.

Stouffer, P. C. and Bierregaard Jr., R. O. (1995). Use of Amazonian forest fragments by understory insectivorous birds. *Ecology,* 76(8):2429-2445.

Tizianel, F. A. T. (2008). *Efeito da complexidade da vegetação de fitofisionomias naturais e pastagens cultivadas sobre a comunidade de aves em duas fazendas no Pantanal da Nhecolândia, Corumbá, Mato Grosso do Sul.* Dissertação de mestrado. Campo Grande: Universidade Federal de Mato Grosso do Sul.

Thiollay, J. M. (1999). Responses of an avian community to rain forest degradation. *Biodiversity and Conservation,* 8:513-534.

Traun, M. A. and Smith, T. (1999). How small is too small for small animals? Four terrestrial arthropod species in diferent-sized remnant woodlands in agricultural western Australia. *Biodiversity and Conservation,* 8:709-726.

Tubelis, D. P. and Tomás, W. M. (1999). Distribution of birds in a naturally patchy forest environment in the Pantanal wetland, Brazil. *Ararajuba,* 7(2):81-89.

Tubelis, D. P.; Cowling, A. and Donnelly, C. (2004). Landscape supplementation in adjacent savannas and its implication for the design of corridors for forest birds in the central Cerrado, Brazil. *Biological Conservation,* 118:353-364.

Uezu, A.; Beyer, D. D. and Metzger, J. P. (2008). Can agroforest woodlots work as stepping stones for birds in the Atlantic forest region? *Biodiversity and Conservation,* 17:1907-1922.

Wiens, J. A. (1995). Habitat fragmentation: island vs. landscape perspectives on bird conservation. *Ibis,* 137:S97-S104.

Willis, E. O. (1979). The composition of avian communities in remanescent woodlots in Southern Brazil. *Papeis Avulsos de Zoologia,* 33(1):1-25.

Yabe, R. S. and Marques, E. J. (2001). Deslocamento de aves entre capões no Pantanal Mato-grossense e sua relação com a dieta, p. 103-124. In: J. L. B.; Albuquerque, J. F. Cândido Jr., F. C. Straube e A. Roos (eds.) *Ornitologia e Conservação: da ciência às estratégias.* Tubarão: Editora Unisul.

Yabe, R. S.; Marini, M. A. and Marques, E. J. (2010). Movements of birds among natural vegetation patches in the Pantanal, Brazil. *Bird Conservation International,* (in press, doi: 10.1017/S0959270910000067).