

Migration patterns and seasonal forest use by birds in the Brazilian Pantanal

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Summary

The use of forest habitats and migratory patterns are still unclear for tropical birds. Some are described herein for the Pantanal wetlands of Brazil. Thus, our aim was to describe different patterns of forest habitat use by birds and classify the birds' migration patterns for the northern Pantanal region, Brazil. From September 1999 to December 2003, we sampled four forest types, during which we collected standardised data with mist-net captures and point counts, with additional *ad lib.* observations. We recorded 214 bird species: 113 (52.8%) were total habitat generalists; 41 (19.2%) were forest generalists; 19 (8.9%) were flooded habitat specialists; and 28 (13.1%) were not classified due to the low number of records; three other categories of habitat use divide the remaining 6% of records. About half of the species showed some migratory behaviour, these were classified by us according to the season they spent in the area: 121 species (56.5%) as *residents*, 28 (13.1%) as *run-off and dry migrants*, 11 (5.1%) as *run-off (winter) migrants*, eight (3.7%) as *dry (breeding) migrants*, eight (3.7%) as *dry and flooding (summer) migrants*, eight (3.7%) as *flooding migrants*, three (1.4%) as *flooding and run-off migrants*, and 27 (12.6%) as *uncommon*. We constructed community occupancy models with six of the eight patterns of migration described; flooding migrants and run-off migrants were not modelled since the few species recorded also had very few detections. As expected, the model confirmed that species from all six tested migration patterns arrive and depart from the Pantanal across the seasons. Contrary to most Neotropical forests, there was a high percentage (43.5%) of non-resident species. The results show the need of investing heavily in preserving different landscape units within the Pantanal, but also in the surrounding Cerrado region, in order to conserve resident and short distance intra-tropical migrants.

Introduction

Tropical bird communities are the result of stable and variable habitat components. While some species are resident in an area throughout the year, others may migrate and change the community composition at temporal and spatial scales (Loiselle and Blake 1992). The simultaneous use of different habitats by both migratory and resident birds reflects the complexity, interconnection, flexibility of interactions, and trophic webs that can be established in a mosaic system (Blake and Loiselle 2002, Figueira *et al.* 2006). Thus, each patch of the habitat is important if it is able to supply seasonal needs of a species (Law and Dickman 1998), and this reinforces the well-established importance of preserving extensive areas of habitat mosaic within a landscape.

Many thousands of birds make seasonal movements between North and South America (Sick 1983). The patterns of these migrations are not very well understood, and although there are some studies (Negret and Negret 1981, Marini and Cavalcanti 1990, Stouffer and Bierregaard Jr. 1996, Machado 1997, Vasconcellos and Lombardi 1999, Galetti 2001), most of these have focused on aquatic bird species (Sick 1983, Antas 1994, Azevedo Jr. *et al.* 2001, Olmos and Silva e Silva 2001).

The Brazilian Pantanal is one of the largest wetlands of the world. Due to the flood pulse (Junk *et al.* 1989, Da Silva *et al.* 2001), the strong seasonal cycles of dry and flood periods, and spatio-temporal organisation of habitat patches, the biome's alpha and beta bird diversity changes throughout the year, tracking environmental changes (Signor and Pinho 2011, Pinho and Marini 2012). For the Pantanal bird communities, much attention has been given to aquatic species (Sick 1979, Antas 1994). Although the migratory routes of aquatic bird species in the Pantanal are fairly well documented, with several species known to migrate southward to the wet areas of Rio Grande do Sul State or to Paraná River lowlands (Antas 1994), it has long been recognised that migratory routes of terrestrial birds from the Neotropics are poorly known (Marini and Cavalcanti 1990, Remsen 2001, Stutchbury *et al.* 2009).

Improved knowledge of bird movements and bird migratory patterns in the Pantanal wetland would support and increase the effectiveness of conservation and management policies. Birds have important ecological roles (pollination, insect population control) and migratory species are mobile links that can disperse plant propagules, invertebrates, and diseases over large distances. Therefore, an understanding of migratory patterns and seasonal habitat use by birds can help to evaluate the potential impacts of bird species losses to the economy and human society (Hatchette *et al.* 2004, Liu *et al.* 2005). Consequently, in this study, our aim was to describe different patterns of forest habitat use by birds and classify the birds' migration patterns for the northern Pantanal region, Brazil. In order to make the migration patterns classification reliable we tested if these patterns were biased by detection rates. For uncommon species, we also compared their occurrence within the Pantanal floodplain with records in the surrounding Cerrado plateau, to which many bird species disappear when the Pantanal region is flooded, returning at the beginning of the dry season, when available habitat for nesting and foraging is greater (Nunes da Cunha and Junk 1996, Pinho and Marini 2012).

Methods

Study sites

Bird communities were studied in the Poconé section of the Pantanal (Franco and Pinheiro 1982), at Pirizal (16°15'12"S 56°22'12"W), Poconé municipality, Mato Grosso State, Brazil, from September 1999 to December 2003. The Pantanal's climate is characterised by two well-defined seasons: the dry season, from May to September, and the rainy season, from October to April. From 1999 to 2002, the mean rainfall recorded was 1,159 mm, annual mean minimum temperature was 20.9° C and annual mean maximum temperature was 32.5° C.

In the Pantanal, different types of soils and inundation levels create a mosaic landscape formation (Silva *et al.* 2000, Nunes da Cunha *et al.* 2002, Nunes da Cunha and Junk 2009a,b). According to Nunes da Cunha and Junk (2009a), about 70–80% of the area of the entire Pantanal constitutes an aquatic/terrestrial transition zone, and some 30% of the Pantanal is covered by forest (Nunes da Cunha and Junk 2009b). We studied four forest habitats: two seasonally flooded forests, 'Cambarazal' semi-deciduous forest (SD-F) and 'Landi' evergreen forest (EG-F), which together comprise nearly 12% of the area of the study region and which from now on will be referred as "flooded forests"; and two non-flooded forests, 'Cordilheira' semi-deciduous dry forest (SD-D) and 'Carvoal' deciduous dry forest (D-D), which together comprise nearly 41% of the area of the study region and which will subsequently be referred as "dry forests" (Nascimento and Nunes da Cunha 1989, Nunes da Cunha 1990, Ribeiro 1999, Nunes da Cunha *et al.* 2006, Nunes da Cunha and Junk 2009b). For more details on the area and regarding those aspects of the forests relevant to birds, see Pinho and Marini (2012).

Sampling methods

This study is part of a broader study of the Pantanal birds. To determine habitat use by each species throughout the year we sampled birds using three methods: point counts, mist-netting,

and free observations. For a detailed discussion of sampling methods, and a map of the study sites, see Pinho and Marini (2012).

Data analyses

Habitat use: Climatic and hydrological seasons are distinct in the Pantanal. Since seasonality in the region is governed mostly by fluctuation in water levels (in our study area especially by the Cuiabá River, but also by the Paraguay River), and secondarily by temperature and rainfall (Junk *et al.* 1989, Nunes da Cunha and Junk 2004, Girard 2011), we defined the following three seasons: *flooded*, *run-off* and *dry*, as already described in Pinho and Marini (2012). Presence records made monthly for each species in each forest habitat (by point counts and mist netting) and open areas (by free observations) allowed us to classify bird species according to habitat use using the following categories: *total habitat generalist* (TG), use of two, three or four forest habitats plus open areas; *forest generalist* (FG), use of three or four forest habitats or one dry and one flooded forests; *flooded forest specialist* (FFS), use of both semi-deciduous and evergreen flooded forests; *dry forest specialist* (DFS), use of both semi-deciduous and deciduous dry forests; *forest habitat specialist* (FS), use of only one kind of forest; and *flooded habitat specialist* (FHS), use of one or two flooded forest plus open areas. Species with few records were classified as ‘no status set’.

Patterns of occurrence: Since the literature furnishes no consensus about either how long a species has to be absent from a region to be classified as migratory (Hayes 1995, Cueto *et al.* 2006, Yabe *et al.* 2010), or about the definition of migration (Dingle 2008), we used the following operational definitions: species only recorded for one or two or three non-consecutive months were classified as *uncommon*; species which were recorded in the region for at least 10 months of the year or if it was recorded less than 10 months (nine or eight months) and the absence was not registered continuously for more than two consecutive months were classified as *resident*. If the absence was registered for three consecutive months or more, the species were classified as *migrant*, according to season and length of stay in the area. Those recorded for three or four months in the same season were categorised as either: 1) *flooding migrant*, present between January and April; 2) *run-off* (= winter) *migrant*, present between May and August; or 3) *dry* (= breeding) *migrant*, present between September and December. Those recorded for three to eight months in two seasons were categorised as either: 4) *flooding and run-off migrant*, absent between September and December; 5) *run-off and dry migrant*, absent between January and April; or 6) *dry and flood* (= summer) *migrant*, absent between May and August.

For each season, we calculated birds' frequency of occurrence (FO), following Vielliard and Silva (1990). The Index of Point Abundance (IPA) for each species was calculated for each forest type and season using point count and mist net data (Vielliard and Silva 1990, Aleixo and Vielliard 1995). For bird records made with point counts, we grouped all sampling points from each trail as one event. Similarly, for mist net data we considered each day (10 mist nets times 06h00 to 11h00 period per site) as one event.

To ensure that the variation of detectability over the year did not itself create the migratory patterns found through FO analysis, we constructed community occupancy models that corrected for the detection effect (MacKenzie *et al.* 2006, with PRESENCE 3.1 programme created by Hines 2006). This approach estimates the fraction of species present, defines if the composition of species changed between seasons, and estimates the increase or decrease in species number. Together, it estimates how the variation of detectability affected the above estimators.

Community models were constructed for migratory pattern. For these analyses, we defined each forested habitat as the site, which was surveyed for 90 minutes at nine points per month (with exception of D-D that were surveyed for 80 minutes, at eight points). This is the survey data from 2000 and 2001 of the study, but we randomly excluded some survey points to equalise sampling effort over the sites. Each month was considered a temporal re-sampling. Because the dry season had more re-samplings ($n = 6$), we had to insert some “missed observations” on the data of the other seasons until it reached six samples per season. This gave 24 sample points in each season.

We made six concurrent *a priori* models for the migration patterns determined by FO analyses (see Table 1), modelling the presence of species, probability of a species entering the habitat, probability of a species leaving the habitat, and probability of detection. One group of models was set in PRESENCE as single-season models, which assume that the group of species stays in the Pantanal year-round, and that no new species arrive or depart from it. Another group was set as multi-season models, which assume that the species composition in a given season can be increased or reduced by some species in subsequent seasons. At the same time, the models estimated the effect of detectability over the initial number of species and its changes, one group as with constant effect and another with season-specific or habitat-specific effect. A constant effect means a detection probability less than 1, but the same over the seasons. On the other hand, detection probabilities set as season or habitat-specific means that the detectability varies across these covariates. We chose a model for each migratory pattern when the best ranked model was at least 2 AIC more plausible than the second model. We accepted this model selection approach without any further analyses because, in general, the second ranked model provided a much inferior explanation of the data.

Results

We recorded 214 bird species in the four forest habitats, from 46 families, comprising 113 species of Passeriformes and 101 non-Passeriformes (Appendix S1 in the online supplementary material).

Habitat use

Of the 214 species recorded, 183 occurred in semi-deciduous flooded forest, 157 in evergreen flooded forest, 142 in semi-deciduous dry forest, and 113 in deciduous dry forest. Species tended to be generalists with respect to habitat use and forest types: 52.8% of species were considered total habitat generalists, 19.2% were forest generalists, 8.9% were flooded habitat specialists, 2.8% were flooded forest specialists, 2.8% were forest habitat specialists, 0.5% were dry forest specialists, and 13.1% had 'no status set' due to a small number of records.

Most species were resident in the Pantanal (56.5% of species), and most of them (64.4%) were total habitat generalists, using at least three of the four forest types and open areas; a few residents (12.4%) used two forest types including, at least, one flooded forest; finally, six species (4.1%) were specialists to semi-deciduous flooded forest (e.g. Solitary Black Cacique *Procacicus solitarius*) and only Jabiru (*Jabiru mycteria*) was a resident specialist to evergreen flooded forest, besides open areas.

Among the 37 species that were recorded in two seasons, six occurred in only one forest type, 18 occurred in two forest types, and 13 occurred in three or four forest types (Appendix S1).

Twenty-seven species were present in the region for only one season (flooding, run-off, and dry migrants), of which, five occurred in only one forest type, 17 occurred in two forest types, and five in three or four forest types (Appendix S1).

Some species require some clarification: Red-winged Tinamou *Rhynchotus rufescens* was recorded only in flooded habitats (forests and open areas), but only during the dry season; Hyacinth Macaw *Anodorhynchus hyacinthinus* and Chestnut-bellied Guan *Penelope ochrogaster*, although recorded in only one habitat by standardised methods, were frequently observed using all four forest types and then classified as forest generalist; and Smooth-billed Ani *Crotophaga ani* was classified as resident once the species uses open areas during the whole year, occurring in the dry forest only during the flooding season.

Patterns of Occurrence

The frequency of occurrence (FO) data indicate which forest each species used during the seasons (Appendix S1). Most ($n = 121$, 56.5%) species were considered residents since they were present in the region for at least 10 months, or since they were not absent from the Pantanal for more

Table 1. Records of migrant or uncommon Pantanal species in the surrounding plateau for each month of the year. Numbers indicate the number of records (banded individuals or sightings) of each species in the sites sampled (Appendix S2). Grey bars indicate the months that each species was recorded in the Pantanal.

Species	Type of movement pattern	Month											
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Momotus momota</i>	Dry				1	12	1	5		10	2	1	4
<i>Phaethornis nattereri</i>	Dry						2	2	2	1	7	2	
<i>Ammodramus humeralis</i>	Dry			8	7	3				1			
<i>Nystalus chacuru</i>	Dry					11				4		1	
<i>Cyclarhis gujanensis</i>	Dry		2			25		1	1	14			
<i>Pipra fasciicauda</i>	Flooded		1	11	19	18	14	13	2	7	2	4	1
<i>Thalurania furcata</i>	Flooded		1	6	5	10	7	3	9	11	12	7	1
<i>Glaucis hirsuta</i>	Flooded and Run-off			1		4	3						
<i>Myiarchus swainsoni</i>	Flooded and Run-off							3		12	1		
<i>Chloroceryle inda</i>	Flooded and Run-off				1	5	3	2			1		1
<i>Synallaxis scutata</i>	Run-off				1	3	1		1	1	1	1	2
<i>Tachyphonus rufus</i>	Run-off			2	5	3	2		3	6	6	2	4
<i>Phaethornis pretrei</i>	Run-off and Dry			3		1		3	1	6	1		2
<i>Vireo olivaceus</i>	Run-off and Dry									20	6	4	
<i>Arremon taciturnus</i>	Uncommon		2	3		11	4	4	3	3	3	1	5
<i>Dysithamnus mentalis</i>	Uncommon		2	4	2	26	6	3		8	2	2	3
<i>Leptopogon amaurocephalus</i>	Uncommon			4	3	9	4	3	2	6	4	4	4

than two consecutive months. Passeriformes had more resident species ($n = 75$) than non-Passeriformes ($n = 46$). The number of species in the other migratory classes was: 1) 28 run-off and dry migrants (13.1%); 2) 11 run-off (winter) migrants (5.1%); 3) eight dry and flooding (summer) migrants (3.7%); 4) eight dry (breeding) migrants (3.7%); 5) eight flooding migrants (3.7%); and 6) three flooding and run-off migrants (1.4%). In addition, 27 species (12.6 %) were uncommon in the region (Figure 1).

Among the aquatic species that used forests, 11 had higher IPA values during the flooded season with the lowest values during the dry season, while a further eight species had their highest IPA values during the run-off season.

Most dry migrants occurred in the region during two seasons but left the region during the flooded season.

The year-round IPA for each species varied from 0.0018 to 2.073 (Appendix S1). It was possible to divide the resident species into two groups based on the IPA values from the three seasons. For some species, IPA values were more or less constant throughout the year, while for others the IPA values were higher during the dry season than during the flooded season (Figure 2).

Most of the 27 uncommon species occurred in the region during the dry ($n = 11$) or run-off ($n = 6$) seasons, and only three species visited the region during the flooded season; the other seven uncommon species were recorded in the region in more than one season. Apparently, 35 species do not reproduce in the region since their visit occurred sporadically and only during the winter or the flooded season.

We modelled six of the eight patterns of migration. The flooding migrants and the run-off migrants were not modelled due to the small number of recorded species and the low number of detections. As expected, the models confirmed that species from all six migration patterns colonised and abandoned the Pantanal over the defined seasons.

In five groups, the detectability was found to be much more phytophysiology-specific than season-specific, which means that the seasonal variations encountered by FO were not only variation in detectability, even though, detectability is far from being perfect. For example, dry and flooding migrants were detected more easily in some phytophysionomies than in others. Though this might make it difficult to define where the species is, it does not make it hard to define when the species is in the Pantanal. In fact, the effect of season upon detectability appears to be less than other environmental effects, because even the constant detectability has shown to better explain its variation (Table 2). As a result, the model confirms the tendency that dry and flooding migrant

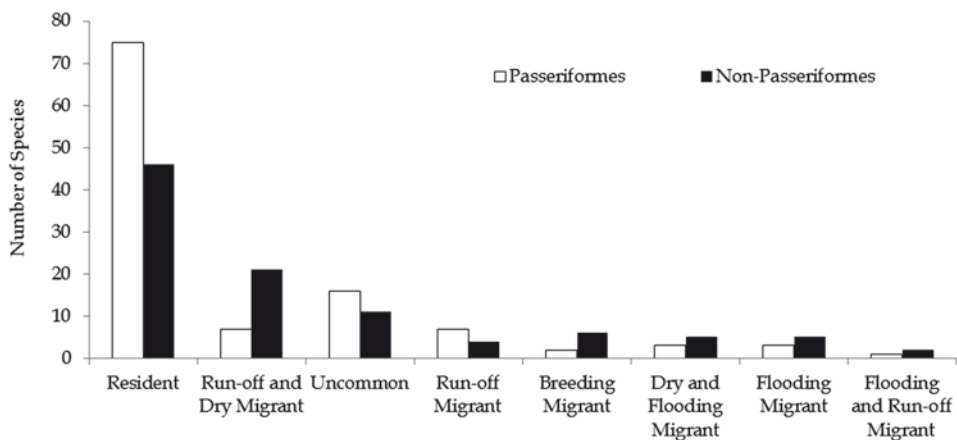


Figure 1. Migratory status of Passeriformes and non-Passeriformes bird species registered at Pirizal, Pantanal of Poconé, Brazil.

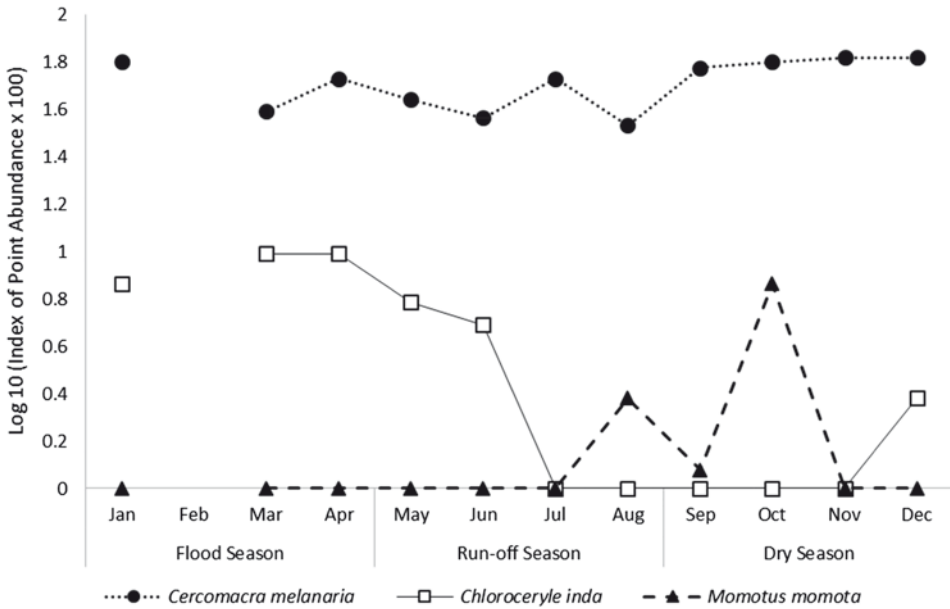


Figure 2. Examples of monthly variation of index of point abundance for resident species (*Cercomacra melanaria*), the flooding (*Chloroceryle inda*) and breeding migrant (*Momotus momota*) recorded at Pirizal, Pantanal of Poconé, Brazil.

species are mostly present in the Pantanal in these seasons, in contrast to the run-off season (Table 2 and Appendix S2).

Resident species were more easily detected than the other groups. As almost all (~85%) of the species from this group were present in all seasons, this suggests that most species stay in the Pantanal throughout the year. Even so, some of these species may undergo local migrations in and out of the Pantanal. The flooded-run-off and the run-off-dry migration patterns had a greater proportion of species than would have been expected in these seasons. Dry migrant was the least-well detected group and the greater proportion of species present in the dry and run-off seasons may be inconclusive, due to increased uncertainty from the low detectability on the estimated parameters.

Table 2. Ranking of the concurrent community models for the patterns of migration. The probability of the species being present on the dry season is set as constant (.) over the habitats in all models, represented as $\psi(.)$. The first three models consider that this probability did not change on the flooding and dry period, because it did not include habitat immigrations, γ , and habitat emigrations, ϵ . The last three models are multi season (s) models, which were best on most of the cases. They defined the immigrations and emigrations as seasonally varied ($\gamma(s)$, $\epsilon(s)$). Five of the migration patterns had the selected models, $\Delta AIC = 0$, that described the phytophysiognomy (phy) effect over detectability stronger than the season effect (p(phy) and p(s)).

Type of migration	ΔAIC to the best model					
	$\psi(.), p(.)$	$\psi(.), p(s)$	$\psi(.), p(\text{phy})$	$\psi(.), \gamma(s), \epsilon(s), p(.)$	$\psi(.), \gamma(s), \epsilon(s), p(s)$	$\psi(.), \gamma(s), \epsilon(s), p(\text{phy})$
Uncommon	31.9	284.5	286.5	10.2	0	9.4
Residents	676.1	680.1	415.8	276.2	279.4	0
Flooding runoff	101.2	353.9	355.9	77.4	69.3	0
Runoff-dry	44.9	611.0	26.3	19.7	23.5	0
Breeding	5.3	547.7	549.7	8.2	10.9	0
Summer	14.4	156.9	158.9	6.3	9.3	0

Uncommon species had highly variable probability of detection over the year (Table 2 and Appendix S2). It was the only group which detectability varied more across the seasons than between habitats. The parameters for the dynamics showed an uncertain change in species composition. For instance, from dry to flooded season, each species was estimated to have 76% probability of emigrating, but this estimate ranges from 0.18% to 0.97% (95% CI). Therefore, we built an *a posteriori* model that better described a random change in the composition of species over the season (setting $\varepsilon = 1 - \gamma$), which was more plausible than the best of the *a priori* set (6.3 Δ AIC; Table 2).

Discussion

Habitat use

Species that are able to use different habitats may vary in abundance within a habitat in response to changes in resources or weather conditions (Loiselle and Blake 1992). Our data indicate that most bird species use flooded and dry forest types, providing evidence that habitat-generalist species are favoured in the Pantanal, probably due to their use of seasonally available resources. This is in agreement with the idea that in mosaic ecosystems, such as the Pantanal, the climatic instability and high abundance of specific and ephemeral resources favour generalist species (Brown Jr. 1986). It has been proposed that resident bird species in the Pantanal could search for additional resources in different habitats in order to compensate for fluctuations in their resource availability (Figueira *et al.* 2006). Moreover, the various landscape units in the Pantanal probably have important ecological roles, such as migration or dispersal corridors, ecological stepping-stones, and refuges or foraging areas (Nunes da Cunha *et al.* 2002). The high number of generalists in the Pantanal supports the idea that habitat generalist species probably live in the edge of habitats, flooding lowlands, gaps or other naturally open areas (Stotz *et al.* 1996). On the other hand, species that cannot adjust their needs to seasonal fluctuations in their resources or predators probably do not persist in such a community (Wolda 1987).

Some aquatic species use, and are even abundant in, evergreen forests, mostly during the flooded season. Likewise, some uncommon species were recorded especially in flooded forests. Several aquatic animals make longitudinal migration during the flooded season in the Pantanal in order to take advantage of the high productivity of flooded areas (Junk 1996). Among the resident birds, however, only the Mato Grosso Antbird *Cercomacra melanaria* and Band-tailed Antbird *Hypocnemoides maculicauda* showed strong association with flooded forests, suggesting that they are adapted to the flooding cycle (Pinho *et al.* 2006). Both species reproduce only in flooded forests (“cambarazais” and “landis”) (Pinho and Marini unpubl. data) and, for the Band-tailed Antbird, also in flooded gallery forests, but only during the flooded season (Pinho *et al.* 2009, Evangelista and Pinho unpubl. data). In addition, the Mato Grosso Antbird and White-lored Spinetail *Synallaxis albilora* make seasonal adjustments in their vertical use of forests (Pinho *et al.* 2006), a similar behaviour to the one described for Leaden Antwren *Myrmotherula assimilis* another antbird in the Amazon (Borges and Carvalhaes 2000).

Migration Patterns

In this study the most problematic detectability variation would be that which varies over the year. This could lead to it being falsely stated that the fraction of species present varies across the year when species are just becoming more or less easy to detect. Although we cannot be certain that the detectability of these species does not change over the year, in the groups, the seasonal effect on detectability is smaller than the phytophysionomy effect. This suggests that here such a tendency as a group does not occur, but cannot exclude the hypothesis that some species could do so. In the Pantanal, phytophysionomy should be considered when designing bird studies (Tizianel 2008). Additionally, detectability also varies among migration patterns. The results of

this study provide important information on how much effort and resources should be invested, and where they should be concentrated, in order to reach effective conservation actions. As a whole, the models that corrected the detection confirmed the pattern of migration found in the primary analyses. However, we cannot be sure that each one of these species really does belong in the class to which we assigned it.

Fewer species of these forests were resident (56.5%) compared to other Neotropical forests (72.0% in Robinson *et al.* 2000; 73.0% in Anjos *et al.* 2007). This high percentage of non-residents (43.5%) might be explained by the strong seasonality of the Pantanal, promoted not only by climatic (temperature and precipitation) fluctuations but mostly by the strong inundation cycles of the region. Many of these Pantanal non-resident birds do not show any migratory behaviour in other parts of their geographical ranges, suggesting that they are exploring favourable times of the year to feed or reproduce in the Pantanal wetland. This also demonstrates that some of these species have flexible migratory behaviour, that adapts to local conditions.

Emigration of these species from the Poconé region of the Pantanal during part of the year raises the question of where they are migrating to. Possible answers to this question include long-distance migration to breeding or wintering grounds, local movement to other Pantanal habitats or local migration to breeding or wintering grounds. Only a few species in the Pantanal avifauna are known long-distance migrants, such as Yellow-billed Cuckoo *Coccyzus americanus*, White-crested Elaenia *Elaenia albiceps* and Vermilion Flycatcher *Pyrocephalus rubinus* (Marini and Cavalcanti 1990, Stotz *et al.* 1996, Sick 1997), which respond to large-scale environmental factors. The second explanation, local movement to other Pantanal habitats during the flooding period, is unlikely for most forest birds because most other alternative habitats (grasslands) are also flooded. Junk (1996) suggested that during flooding, animals would escape to higher habitats, locally named as “cordilheiras”, although this was not observed in the region (Pinho and Marini 2012). It is possible, however, that some species make local movements to gallery forests along watercourses or to elevated patches of Cerrado (tree-dominated savanna) within the Pantanal, habitats we did not sample. Furthermore, since rainfall and flooding coincide in the northern part of the Pantanal where this study was conducted, but do not in the southern part where inundations occur only 2–3 months later (Nunes da Cunha *et al.* 2006), birds from different regions of the Pantanal might show different patterns of residence and migration.

The last explanation for the emigration of these species from the Pantanal during part of the year is that birds make local migration of dozens to hundreds of kilometres to and from the Cerrado plateau surrounding the Pantanal, beyond which is usually considered local habitat shifts. Local migrants are defined as those that reproduce in one type of habitat and stay during the winter in different areas within the same geographical region (Nocedal 1994). This local migration hypothesis, even though counterintuitive for some species, always considered resident elsewhere, if supported, would have several ecological, behavioural and conservation implications. To provide an initial test of this hypothesis, we compiled data from local ornithologists regarding the timing of occurrence of several Pantanal migratory species in five plateau sites surrounding (< 100 km) the Pantanal (Appendix S3). These data consist mostly of banding or observational records of birds made for other purposes, and do not enable us to make quantitative analyses, since sampling efforts varied considerably in time and among sites.

In spite of these constraints, it was possible to collect reasonable evidence for the occurrence in the surrounding plateau of 17 species (Table 1). Among them, seven are residents on the surrounding plateau, probably visiting the Pantanal on a seasonal basis during flooding (Band-tailed Manakin *Pipra fasciicauda* and Fork-tailed Woodnymph *Thalurania furcata*), flooding and run-off (Green-and-rufous Kingfisher *Chloroceryle inda*), run-off (winter) (Ochre-cheeked Spinetail *Synallaxis scutata* and White-lined Tanager *Tachyphonus rufus*), run-off and dry season (Planalto Hermit *Phaethornis pretrei*) and dry (Amazonian Motmot *Momotus momota*) season. Among these seven species, apparently only the last one breeds in the Pantanal.

Another group of three species (Pectoral Sparrow *Arremon taciturnus*, Plain Antvireo *Dysithamnus mentalis* and Sepia-capped Flycatcher *Leptopogon amaurocephalus*) are also resident in the

surrounding plateau, but they are uncommon in the Pantanal. The same will probably hold true for most of the other 17 uncommon species that are not long-distance migrants (Table 1). One species (Cinnamon-throated Hermit *Phaethornis nattereri*) seems to be a long-distance migrant, since it occurs on the surrounding plateau at a similar time of the year, disappearing from the region from December to May, even though it is not considered migratory (Ridgely and Tudor 1994, Sick 1997, del Hoyo et al. 1999). Two species (Red-eyed Vireo *Vireo olivaceus* and Swainson's Flycatcher (*Myiarchus swainsoni*) occur on the surrounding plateau during only three months of the year, which corresponds to the dry season in the Pantanal. Both apparently reproduce in the Pantanal, but migrate from the wetland in the flooded (Red-eyed Vireo) and in the run-off (winter) (Swainson's Flycatcher) seasons.

Lastly, there is a group of four species (Rufous-breasted Hermit *Glauclus hirsutus*, White-eared Puffbird *Nystalus chapcuru*, Rufous-browed Peppershrike *Cyclarhis gujanensis* and Grassland Sparrow *Ammodramus humeralis*) which stay in the Pantanal only during the dry (breeding) season or during the dry and flooded seasons (Rufous-breasted Hermit). All these species have more records on the surrounding plateau exactly during the period when they do not occur in the Pantanal (Table 1), suggesting that they may migrate between the Pantanal and the surrounding plateau on a seasonal basis. However, these species also breed on the surrounding plateau.

Overall, the evidence above indicates that several species of birds might be performing either seasonal or occasional movements between the Pantanal and the surrounding plateau. This implies that several species have year-to-year flexibility in their capacity to develop regional migratory behaviours and to explore resources variable in space and time, year-to-year, depending on water level fluctuation in the floodplain. The conservation implications of these regional movements are threefold: first, it indicates that at least part of the bird community that uses the forests within the Pantanal lowlands might be dependent on the natural habitats of the surrounding plateau through a seasonal use of both of these areas; second, it suggests that the Pantanal may be an area for ingress of several populations from the surrounding plateau; and third, it suggests that several migratory and uncommon species may move from, or travel through, the Pantanal to other regions. A better understanding of all these migratory and movement patterns in the region requires that more studies be done, and may provide new approaches and reasoning to help the establishment of conservation policies for the region (Alves 2007).

Species that migrate only during the breeding season (dry season migrants) arrive at the Pantanal at the end of the run-off season (around April–May) to reproduce, staying in the wetlands until the end of the reproductive season (around early January) when flooding begins. This period between September and December (dry season) had the highest IPA and FO values for the dry season of several migrants. High IPA values are expected during the breeding season as was reported by Aleixo and Vielliard (1995) at Santa Genebra forest, São Paulo State. The flooding season is especially inappropriate for understory species living in flooded forests since the ground and the lower herbaceous strata are flooded for several months.

Most austral migrants do not reproduce in the Pantanal. Six species (Picui Dove *Columbina picui*, White-crested Elaenia, Vermilion Flycatcher, Rufous-tailed Attila *Attila phoenicurus*, Rufous Casiornis *Casiornis rufus* and Swainson's Flycatcher) that are considered austral migrants (Stotz et al. 1996) do not reproduce in the Pantanal, whereas others (Buff-necked Ibis *Theristicus caudatus*, Creamy-bellied Thrush *Turdus amaurochalinus* and Streaked Flycatcher *Myiodynastes maculatus*) reproduce in the study area. However, the former are apparently resident in our study area.

Winter migrants arrive in the Pantanal, probably in response to the reduction of aquatic habitats, in the early run-off season and remain in the region until September, when most start to breed. Yellow-bellied Elaenia *Elaenia flavogaster*, Southern Scrub-flycatcher *Sublegatus modestus*, Vermilion Flycatcher and Black-backed Water-tyrant *Fluvicola albiventer* pass the whole winter in the Pantanal. However, there are no regional breeding records for any of these species.

Greater Ani *Crotophaga major* has a unique occurrence pattern in the region. It was considered a dry and flood migrant, since it arrives in the region at the end of the summer, breeds during the flooding season and leaves the region at the end of the dry season. The species literally disappears

for several months, not only from the Pantanal, but also from all points in its known range, including the Amazon region (Stotz *et al.* 1996). It might move southward following the cyclical flood regime.

In the Pantanal, the migration of aquatic birds is better described than that of other bird guilds (Antas 1994). Aquatic birds reproduce in the Pantanal at the end of the run-off season when food (mostly fish and invertebrates) is more readily available as they become trapped and isolated in small lagoons. These reproductive colonies are considered very important for South American aquatic birds (Antas 1994). These birds leave the Pantanal towards the south at the end of the summer, just before the start of flooding (Antas 1994, Hayes *et al.* 1994).

Several species were considered uncommon in the region, and might be individuals passing through the region or making exploratory movements (e.g. Spot-backed Puffbird *Nystalus maculatus*, Plain-crested Elaenia *Elaenia cristata*).

Conservation applications

The Pantanal, one of the largest freshwater floodplain in the world, is an ecologically highly productive system, dependent on the flood pulse of the tributary rivers from adjacent plateaus (cerrados) of the Pantanal floodplain, which results in an extremely biodiverse and heterogeneous landscape with different degrees of flooding. The flooding is a natural event, which promotes changes in the structure and composition of habitats in this biome (Junk and Silva 1999). Changes in flood pulse in the Pantanal floodplain may cause major transformations in landscape units, especially affecting the forests, which are dependent on the input of energy brought by the rivers (Nunes da Cunha and Junk 2009b).

In the Pantanal, the highest values for richness, abundance and exclusive species of birds have been recorded in forested habitats, with the flooded forests (semi-deciduous forest and evergreen forest) preceding the dry forests (semi-deciduous dry forest and deciduous dry forest). Bird species richness for these forests is affected by the flood pulse within the Pantanal floodplain (Pinho and Marini 2012). Many species of resident and migratory birds make use of these forests, collectively deploying a variety of patterns throughout the year (Appendix S2), to use them as sites for reproduction and foraging. With habitat loss, the community of forest-dependent birds can be negatively affected in its richness, abundance and with possible changes of migratory routes of some species, so that both the migration route, and the suite of species, using it could disappear.

Due to the importance of bird conservation, other habitats should also be evaluated, such as the many types of seasonally flooded savanna parklands (Nunes da Cunha and Junk 2009a). Some of these savanna parkland types are important bird habitats for breeding and foraging. Others, such as termite fields, serve as a resting places for birds during both local movements and longer distance migrations (Yabe *et al.* 2010).

Currently, seasonally flooded savanna parklands are suffering encroachment by shrubs (e.g. *Combretum laxum*) and tree species (e.g. *Vochysia divergens*; Dorado-Rodrigues *et al.* 2015; Nunes da Cunha and Junk 2004) and the replacement of native grasses by the exotic species preferred for cattle grazing, which can resist both flood and drought. Both the encroachment and the replacement result in a lowered biodiversity of herbaceous plants (Rebellato and Nunes da Cunha 2005) and associated insects, and thereby may impact the potential dietary components of insectivorous species of the Pantanal avifauna (Junk and Nunes da Cunha 2012). The pressure for increasing grazing areas also falls on semi-deciduous dry forests which are cut to make way for pastureland; this ill-advised land-management practice reduces the habitats for the wildlife that depend on these areas for refuge during the flood and restrains birds' movements from a habitat to another. Aragona (2008) also calls attention to the fact that areas of semi-deciduous dry forest, which have been traditionally used to build houses and access routes, are now being clear-cut to serve as a dryland refuge for cattle during the flood period (Junk and da Silva 1996), prejudicing the species exclusive to this habitat. Our study found that four species use exclusively semi-deciduous dry forests (Smooth-billed Ani, White-faced Whistling-Duck *Dendrocygna viduata*, Pearl Kite

Gampsonyx swainsonii, and Sulphur-bellied Tyrant-manakin *Neopelma sulphureiventer*). In fact, Harris *et al.* (2005) claim that 40% of forests and native grasslands have been deforested for conversion to pasture for livestock in the floodplain, and this is a cause for extreme concern.

Pinho and Marini (2012) point out that research on other taxa should be taken into account when considering bird conservation planning and management. For example, floristic richness and diversity are higher in semi-deciduous dry forest than in deciduous dry forest (Nunes da Cunha and Arieira 1996, Nunes da Cunha *et al.* 2002). In research with terrestrial small mammals in the same area as the current study, and sampling three of the four forest types presented here (deciduous dry forest excepted), Aragona (2008) pinpointed that, although richness is similar for the three habitats throughout the year, diversity and composition varied between them. Only 21.4% of the species ($n = 3$) are common to all three forest types, while 42.8% ($n = 6$) were exclusive of only one type of forest.

The advance of agribusiness in the adjacent plateau has produced a variety of impacts on the Upper Paraguay River basin and in the Pantanal floodplains, of which only 2.5% is formally protected (Harris *et al.* 2005). For Alho (2008), the biggest problem of the Pantanal floodplain conservation comes from the plateau, where 63% of the natural vegetation cover has been removed. The establishment of farms in those areas has increased deforestation, soil run-off and the consequent silting-up of local rivers, from which materials and agricultural chemicals then leached into the floodplain and contaminate soil and water (Pott and Pott 2004). Moreover, the deforestation in the plateau, by selective habitat destruction on the edges of the Pantanal, also affects the connectivity between the Pantanal with adjacent biomes (plateau-floodplain link), as highlighted by Lourival *et al.* (2009), negatively influencing gene flow of many groups.

Changes in the flood pulse, caused by hydroelectric power plants and commercial canals (hidrovias), also represent risk to the effective continued conservation of birds (Pinho and Marini, 2012; Calheiros *et al.*, 2012), as well as the biota of the Pantanal in general. According to Poff *et al.* (1997), ecological process in river ecosystems are regulated by magnitude, frequency, duration, timing, and rate of change of hydrologic conditions. Calheiros *et al.* (2012) presented a survey of hydroelectric projects to the Pantanal, quantifying the types of hydropower projects: large (7) and small (23) hydroelectric plans and hydroelectricity generating centrals (8) as well as their status: in operation (38), under construction (3), licensed (63) and under consideration (31). If all 135 projects come into operation, they will account for 70% of the water in the entire Pantanal system. In addition, Calheiros *et al.* (2012) call attention to the fact that the majority of the small projects are located/planned for the same river and so the resulting collective impacts will have synergistic effects equal in magnitude to that of a large dam. The negative impacts of dams include fragmentation and modification of aquatic habitats, transforming lotic ecosystem into lentic and semi-lentic ecosystems, altering the flow of matter and energy, and the establishment of barriers to movement for migratory species (Calheiros *et al.*, 2012).

These changes not only mean a reduction of the flood pulse intensity in the floodplain, but may also cause a distortion of the flood cycle, causing a knock-on effect, which can cause the loss, by structural modification, of key habitats for the maintenance of forested birds in the Pantanal. As a consequence, some species may simply vanish from the Pantanal (e.g. Chestnut-bellied Guan, Tropical Pewee *Contopus cinereus*, Red-throated Piping-Guan *Aburria kujubi*).

The loss of natural forests and other habitats in the Pantanal, besides affecting biodiversity in general, also compromises tourist activity, which has generated increasing financial resources for farmers in the region. For Lourival *et al.* (2009), the involvement of local society with an appropriate management of its properties is important for effective preservation of Pantanal biodiversity, since 95% of the land is in private hands.

Several species of birds in the region made shorter or longer movements in response to the flooding regime and to climatic variations. These responses vary considerably among species, including six types of migratory patterns. The existence of these various types of migratory patterns, so different in space and time, indicates the need for complex conservation measures. In order to conserve the greatest possible number of the bird species that use Pantanal forests, habitats must

also be protected in sites to the north and south of the Pantanal, as well as in the neighbouring Cerrado plateau. However, ongoing and planned developmental programmes associated with poor habitat protection may rapidly create a major conservation problem, unless large scale conservation planning is implemented soon.

Supplementary Material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270916000290>

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