

Avian biodiversity assessment studies in a Neotropical wetland – the combination of sampling methods makes the difference

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Abstract. In studies of avian diversity, many different methods have been applied. Since methodological approaches may affect research results, the choice of a given methodology must be consistent with the scientific objectives. The aim of this study was to investigate how different methodologies with their intrinsic limitations help detect and monitor birds to evaluate how they complement each other in the survey of species. Three different assessment methods, mist nets, point counts, and autonomous acoustic recordings were used to serve this purpose in a study of different Pantanal habitats, such as savannas and forests. The point counts detected more species (126 species) than the two other methods autonomous acoustic recordings (113 species) and mist nets (79 species). We observed significant differences in the number of species detected by mist nets and the other two methods. Each survey method identified exclusive species. When comparing habitats, all three methods showed significant differences in bird species composition. Savannas were richer in bird species than forests, and replacement was the main driver responsible for the differences in *beta* diversity between the habitats. The three methodologies, when applied together, proved to be complementary in avian species detection.

Keywords. Point counts; Autonomous acoustic recording; Mist nets, *Beta* diversity.

INTRODUCTION

The management and conservation of bird communities depend on appropriate survey methods. To understand the distribution of species in time and space, extensive data collection is required (Schultz *et al.*, 2013; Brlik *et al.*, 2021). However, many survey-based studies have been restricted to small areas and short time frames (Underwood *et al.*, 2005; Porter *et al.*, 2009). Considering the accelerated degradation of the environment, it is important to select the most efficient and cost-effective method to quickly survey species (Poulsen *et al.*, 1997; Poulsen & Krabbe, 1998; Herzog *et al.*, 2002; Bradfer-Lawrence *et al.*, 2020). In avian surveys, several methods, such

as mist nets (MN), point counts (PC), and autonomous recording units (ARU), have been used. Each of these methods has advantages, limitations, and costs (Sueur *et al.*, 2008) that should be considered together with the data collection effort required and restrictions on species detection capacities (Whitman *et al.*, 1997; Cavarzere *et al.*, 2013; Darras *et al.*, 2018; Smith *et al.*, 2020).

Considering the challenges associated with each method, it is important to consider which of these methods is the most appropriate for the parameters to be studied. MN allows direct contact with captured individuals, which ensures a more accurate identification of bird species. They also enable users to identify the sex of individuals of dimorphic species, verify the juvenile status and

molting stage of individuals, collect body mass information, and estimate population size based on recaptures (MacArthur & MacArthur, 1974; Dunn & Ralph, 2004). Furthermore, nonresident species, such as migratory birds, that do not vocalize in the region can be sampled by this methodology (Pagen *et al.*, 2002). However, this methodology may not be effective in detecting species that exclusively occupy the canopy of the vegetation and aerial species and is affected by the mesh size of the nets, which in certain cases may not capture small species.

The PC method recognizes species visually and acoustically, enabling the identification of species vocalizing both at long distances and hidden in vegetation, in addition to providing estimates of richness and abundance (Volpato *et al.*, 2009). However, this method was initially developed for temperate regions (Blondel *et al.*, 1970), where the avian diversity is relatively small and seasons are well defined, which differ from tropical regions. The limited time of data collection (estimated between 3 and 20 min, Bibby *et al.*, 2000), the difficulties associated with accessing certain areas, the researcher's presence, and the presence of species that do not vocalize during certain periods (*e.g.*, molting) are some of the disadvantages of this methodology (Terborgh *et al.*, 1990). Furthermore, this assessment method requires the involvement of researchers experienced in avian identification through vocalization (Blake & Loiselle, 2001).

Finally, ARU collects audio data in real time over a diel cycle and from places that are difficult to access. Therefore, for rapid species assessment, the use of autonomous acoustic recordings is the most viable method for recording data for long periods of time and sampling species in areas with limited visibility; soundscapes of all sound-emitting organisms can be detected, independent of their activity pattern (*e.g.*, diurnal or nocturnal) (Acevedo & Villanueva-Rivera, 2006; Brandes, 2008; Celis-Murillo *et al.*, 2009; Goyette *et al.*, 2011; Jahn *et al.*, 2017; Darras *et al.*, 2018; Darras *et al.*, 2019; Smith *et al.*, 2020; Metcalf *et al.*, 2021; Pérez-Granados & Schuchmann, 2021a, b; Pérez-Granados *et al.*, 2021a, b). In addition to a greater likelihood of bird detection (Franklin *et al.*, 2020), there is the possibility of automated sound detection of target species when coupled with signal-recognition software, *e.g.*, Kaleidoscope (<https://www.wildlifeacoustics.com>) (Brooker *et al.*, 2020). Although the amount of maintenance and field labor expenses associated with ARU are relatively low, the equipment required is not inexpensive, and specialists are needed to identify the species captured on recordings. Furthermore, the large amount of audio data collected, often in the upper TB level, leads to enormous storage capacity demands (Alquezar & Machado, 2015).

The aim of this study was to observe how different methodologies with their intrinsic limitations detect birds, even if the methods may fail in species detection (MacKenzie *et al.*, 2002), and to evaluate how they could complement each other in the survey of species. We evaluated three different methodologies considering their differences in bird species detection and *beta* diversity in savanna and forest biogeographies.

We expected that ARU would detect a greater number of species than MN and PC because the lower disturbance

of this methodology would lead to a significant reduction in avian vocal activity and behaviors. For PC, we expected the addition of species from different habitats since they are performed over transects, which may include an environmental variation in the vegetation physiognomies and topographies; however, the researcher presence could negatively affect the detection of more species than the ARU. For MN, we expected the inclusion of individuals who do not vocalize, such as young birds, females, and nonbreeding season birds. For *beta* diversity, the replacement and nestedness were expected to decrease in surveys based on ARU, since many more species are expected to be identified by this method based on constant 24 h recordings. On the other hand, higher values of replacement and nestedness are expected for MN since this method is restricted to the immediate locality.

MATERIAL AND METHODS

Study site

This study was carried out in the SESC Pantanal area, Mato Grosso, Brazil (56°25'17.89"W and 16°29'49.46"S). This area includes different types of habitats and comprises savanna and forest formations intersected by the Cuiabá River, one of the major tributaries of the Paraguay River. Data were collected in the dry period between July and September 2014, and eight sampling sites were used: four were characterized as savanna, while the other four were characterized as forest. The regional climate is tropical and humid, with an average annual temperature of approximately 24°C and mean annual rainfall ranging from 1,000 to 1,500 mm (Alvares *et al.*, 2013).

Mist nets

Within each of the eight sampling sites, five MN were installed at two different points, separated from each other by a mean distance of 250 m, for a total of 10 MN (Bibby & Buckland, 1987) per sampling site. The MN were 9 m long and 2.7 m high, had a mesh size of 20 mm × 20 mm and were arranged in a straight line, totaling 45 m in length. The nets were opened at sunrise (approximately 06:00 am) and closed at 11:00 am, when the peak of bird activity was greatly reduced; they were opened again at 03:00 pm and closed at 05:00 pm (beginning of sunset). The mist nets remained in each sampling site for six consecutive days and were installed in another study area thereafter (total 48 days). Together with the species survey, we also collected morphometric data, body mass and sex information with MN, allowing us to verify functional groups.

Point counts

PC was performed in 1,000 m transects located in the vegetation that covered each sampling site. The transect

was divided into four data collection points, each 250 m apart (Bibby & Buckland, 1987). At each of these points, birds were observed and counted, and their vocalizations were recorded for 10 min between each collecting point (standardized interval) using a handheld Zoom H4N recorder. It has been shown that 7 to 20 min of recording time is sufficient for the detection of most bird species (Develey, 2004). Point counts started at 06:00 am and were repeated after seven days. The radius of detection was not considered. A total of 320 min was recorded in the dry period (40 min per area). This methodology was applied for one morning to each of the eight sample areas on different days of the dry season.

Autonomous acoustic recordings

At each of the eight sampling sites, two ARU (model SM2+ with two omnidirectional microphones, Wildlife Acoustics Inc., Firmware Version 3.10) were placed in trees and programmed to record (in stereo and .wav) using a sampling rate of 48 kHz and 16 bits per sample. Recordings were stored on SD memory cards, and the recorders were checked weekly to download data and change batteries. Thereafter, the recorders were moved together with the mist nets to another study site. To compare the species detection of this methodology with that of the MN and PC methods, one hour of sound recordings was collected in each sample area between 06:00 and 07:00 am, the period of highest avian vocal and movement activity (Robbins, 1981; Cavarzere & Moraes, 2010). There were differences in the sampling efforts of each methodology (40 minutes to PC, 1 hour to ARU, and 6 days to MN); nonetheless, it was not the aim of this study to detect the efficiency of bird detection but rather to observe differences in the kind of bird species detected by each methodology.

Statistical analyses

To evaluate the performances of the three methods in determining the variation in bird species between the savanna and forest habitats, we used permutational multivariate analysis of variance (PERMANOVA). PERMANOVA was run with 9,999 permutations using the Bray-Curtis dissimilarity measurement, which shows the dissimilarities between the treatments, to calculate pseudo-F values (Anderson & Walsh, 2013). Next, we applied a similarity percentage (SIMPER) test to examine the contribution of each species to the average similarity within groups (Clarke, 1993). This method consisted of calculating the Bray-Curtis dissimilarity among all pairs of samples and examining the relative dissimilarity contributed by each species. The SIMPER test was applied to each of the methods separately and to the total number of species, considering the whole surveyed community. Each of these analyses was conducted with 9,999 permutations.

Data analysis of the local contribution to *beta* diversity (LCBD) was performed to examine the degree of uniqueness in the species composition of each sampling

site. The LCBD is an index that shows how much each site contributes to the total dissimilarity between sites. It is calculated from the diagonal values in Gower's centered dissimilarity matrix computed using principal coordinate analysis (PCoA). The sites furthest from the graph centroid are the most exceptional or unique (De Cáceres & Legendre, 2013; Legendre, 2014). We tested the significance of the LCBD using random and independent permutations of the species matrix, testing whether species were randomly and independently distributed between sampling sites. The LCBD indices were also extended to replacement and nestedness, indicating underlying ecological processes driving site differences (Legendre, 2014). Next, Spearman correlation was applied to investigate the relation between the LCBD indices and species richness, thus elucidating whether higher values of the LCBD indices represented sites with high or low numbers of species. The significance level was set at $p < 0.05$.

RESULTS

During the dry period of 2014, the data collected through all three methods included 157 bird species from 130 genera and 44 families; the MN method yielded 79 species; the PC method yielded 126 species; and the ARU method yielded 113 species. The most representative families were Tyrannidae (32 species, 20.4%), Thraupidae and Furnariidae (13 species each, 8.3%), and Thamnophilidae and Picidae (10 species each, 6.4%) (Table 1). Of the total number of species (157), 51 species (32.48%) were found by all three methods, and 12 (7.64%), 24 (15.28%), and 12 (7.64%) species were exclusive to the MN, PC, and ARU methods, respectively. MN shared 8 species with the PC and ARU methods, and 42 species were shared by the PC and ARU methods. The total number of species and individuals found in savannas and forests and the number of species in each of the eight sites surveyed by the three methods are summarized in Fig. 1 and Fig. 2. The savanna areas were richer in species and individuals than the forest areas; this finding was confirmed by all three methods. Of all the species identified in this study (157), 21 (13.37%) were exclusive

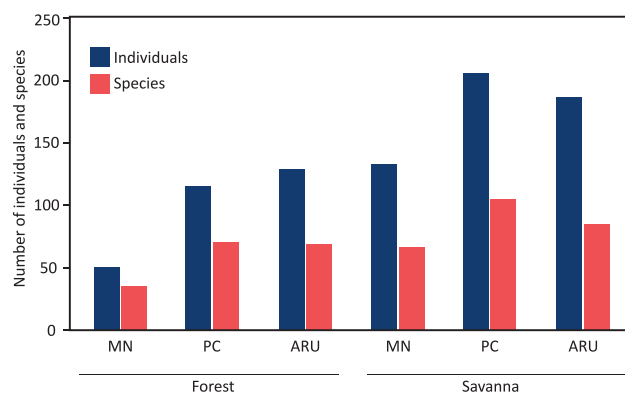


Figure 1. Number of individuals and species detected by three methodologies over the dry period of 2014 in areas of forest and savanna in the north-eastern Pantanal, Mato Grosso, Brazil. MN = mist nets; PC = point counts; ARU = autonomous acoustic recording.

Table 1. Number of bird species of each family detected by three methodologies in one region of the northeastern Pantanal, Mato Grosso, Brazil. MN = mist net; PC = point count; ARU = autonomous acoustic recording.

Family	Number of species		
	MN	PC	ARU
Tinamidae	0	1	1
Cracidae	0	1	2
Columbidae	2	2	3
Cuculidae	1	4	2
Apodidae	0	1	0
Trochilidae	3	1	2
Rallidae	0	2	2
Heliomithidae	0	0	1
Charadriidae	0	1	1
Jacanidae	0	1	1
Rynchopidae	0	0	1
Laridae	0	0	1
Anhingidae	0	1	1
Threskiornithidae	0	3	2
Accipitridae	0	1	1
Trogonidae	0	1	1
Momotidae	0	1	1
Alcedinidae	2	4	4
Galbuliformes	0	0	0
Galbulidae	1	2	1
Bucconidae	1	1	1
Ramphastidae	0	2	0
Picidae	3	9	4
Falconidae	0	2	4
Psittacidae	0	7	6
Thamnophilidae	8	7	4
Furnariidae	12	13	13
Tyrannidae	19	28	21
Pipridae	3	0	0
Tityridae	2	1	2
Vireonidae	2	2	2
Corvidae	0	1	1
Hirundinidae	0	1	2
Troglodytidae	2	3	3
Poliopitilidae	1	1	1
Donacobiidae	0	1	1
Turdidae	1	2	0
Fringilidae	0	1	1
Passerellidae	1	0	1
Icteridae	3	4	4
Parulidae	1	2	1
Thraupidae	10	8	7

to the forest areas, and 60 (38,21%) were exclusive to the savanna areas. The number of species detected by the PC and ARU methods was higher than that detected by the MN method for both forests and savannas (Figs. 1 and 2).

In this study, the PC method yielded the largest number of species in the following categories: canopy (39 species), midstory to canopy (15 species), terrestrial (10 species), terrestrial to canopy (10 species), frugivores (11 species), insectivores (66 species), and omnivores (31 species; confirmed to be the highest number of species in the forest and savanna areas (Table 2)). The ARU detected the largest numbers of species of water birds (4 species), carnivores (4 species), insectivores (6 species),

Table 2. Number of species detected by mist nets (MN), point counts (PC), and autonomous acoustic recordings (ARU) in one region of the northeastern Pantanal, Mato Grosso, Brazil, according to the type of strata, guild, and habitat of the species. Shared = species shared among the three methodologies. PC/ARU = species shared by PC and ARU. Strata: A = aerial; C = canopy; C/A = canopy and aerial; M = midstory; M/C = midstory to canopy; T = terrestrial; T/C = terrestrial to canopy; T/M = terrestrial to midstory; T/U = terrestrial to understory; U = understory; U/C = understory to canopy; U/M = understory to midstory; W = water. Guild: CAR = carnivores; FRU = frugivores; GRA = granivores; INS = insectivores; INV = invertebrates; NEC = nectarivores; OMN = omnivores; OPO = opportunists; PIS = piscivores.

	Group	MN	PC	ARU	Shared	PC/ARU	Total
Strata	A	0	2 (67%)	2 (67%)	0	1 (33%)	3
	C	20 (43%)	39 (85%)	30 (65%)	12 (26%)	15 (33%)	46
	C/A	0	0	1 (100%)	0	0	1
	M	4 (67%)	6 (100%)	6 (100%)	4 (67%)	6 (100%)	6
	M/C	9 (56%)	15 (94%)	12 (75%)	7 (44%)	5 (31%)	16
	T	4 (21%)	15 (79%)	14 (74%)	2 (10%)	8 (42%)	19
	T/C	3 (27%)	10 (90%)	5 (45%)	1 (9%)	3 (27%)	11
	T/M	1 (100%)	0	0	0	0	1
	T/U	5 (83%)	5 (83%)	5 (83%)	4 (67%)	1 (17%)	6
	U	15 (83%)	13 (72%)	13 (72%)	9 (50%)	1 (5%)	18
	U/C	7 (70%)	9 (90%)	9 (90%)	6 (60%)	3 (30%)	10
	U/M	11 (69%)	10 (62%)	12 (75%)	6 (37%)	2 (12%)	16
W	0	1 (25%)	4 (100%)	0	1 (25%)	4	
Guild	CAR	0	2 (50%)	4 (100%)	0	2 (50%)	4
	FRU	4 (29%)	11 (79%)	9 (64%)	1 (7%)	8 (57%)	14
	GRA	4 (67%)	3 (50%)	1 (17%)	0	0	6
	INS	47 (61%)	66 (86%)	59 (77%)	37 (48)	12 (16%)	77
	INV	0	5 (71%)	6 (86%)	0	4 (57%)	7
	NEC	3 (75%)	1 (25%)	2 (50%)	1 (25%)	0	4
	OMN	19 (50%)	31 (81%)	25 (66%)	10 (26%)	10 (26%)	38
OPO	0	1 (100%)	1 (100%)	0	1 (100%)	1	
PIS	2 (33%)	5 (83%)	6 (100%)	2 (23%)	3 (50%)	6	
Habitat	Forest	36 (37%)	71 (73%)	70 (72%)	22 (23%)	28 (29%)	97
	Savanna	67 (49%)	106 (78%)	86 (63%)	38 (28%)	29 (21%)	136

and piscivores (6 species) (Table 2). The MN approach detected a higher number of species of understory birds (15 species) and nectarivores (3 species) (Table 2).

The 20 species most important for the dissimilarity among the habitats in the whole community were also used to verify the differences among the three methods

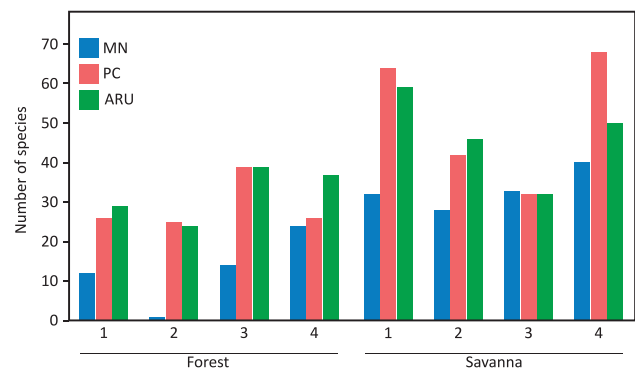


Figure 2. Number of species detected in each of the eight sampling sites using three methodologies over the dry period of 2014 in one region of the northeastern Pantanal, Mato Grosso, Brazil. MN = mist nets; PC = point counts; ARU = autonomous acoustic recording.

Table 3. SIMPER test results. The 20 most common species with the highest average contributions to the total dissimilarity among the habitats (forest and savanna) for each method and overall, considering the species detected by the three methods in one region in the northeastern Pantanal, Mato Grosso, Brazil. The species shared between methods and among all the methods are shown in bold. The values represent the average contributions to dissimilarity, and the values inside the brackets represent the average detection rates in the forest and savanna areas.

Average contribution to overall dissimilarity (%)							
Mist Net	Point Count		Autonomous Acoustic Recording		Total		
<i>Coereba flaveola</i>	2.27 (0.0-1.0)	<i>Thamnophilus doliatus</i>	1.29 (0.0-1.0)	<i>Phacellodomus rufifrons</i>	1.30 (0.0-1.0)	<i>Hemitriccus margaritaceiventer</i>	1.22 (0.0-0.8)
<i>Hemitriccus margaritaceiventer</i>	2.27 (0.0-1.0)	<i>Tyrannus melancholicus</i>	1.03 (0.0-0.7)	<i>Pseudoseisura unirufa</i>	1.30 (0.0-1.0)	<i>Cacicus solitarius</i>	1.16 (0.0-0.7)
<i>Paroaria capitata</i>	2.27 (0.0-1.0)	<i>Cacicus solitarius</i>	1.02 (0.0-0.7)	<i>Tapera naevia</i>	1.30 (0.0-1.0)	<i>Coereba flaveola</i>	1.15 (0.0-0.7)
<i>Phaeomyias murina</i>	2.27 (0.0-1.0)	<i>Hylophilus pectoralis</i>	0.9 (0.2-1.0)	<i>Thamnophilus doliatus</i>	1.30 (0.0-1.0)	<i>Hylophilus pectoralis</i>	1.12 (0.2-0.9)
<i>Cantorchilus leucotis</i>	1.83 (0.2-1.0)	<i>Myiothlypis flaveola</i>	0.9 (0.7-0.0)	<i>Icterus croconotus</i>	1.02 (0.0-0.7)	<i>Phacellodomus rufifrons</i>	1.10 (0.0-0.7)
<i>Cercomacra melanaria</i>	1.83 (0.2-1.0)	<i>Furnarius rufus</i>	0.95 (0.2-1.0)	<i>Saltator coerulescens</i>	0.99 (0.2-1.0)	<i>Thamnophilus doliatus</i>	1.06 (0.0-0.7)
<i>Dysithamnus mentalis</i>	1.83 (0.7-0.0)	<i>Formicivora rufa</i>	0.94 (0.0-0.7)	<i>Cnemotriccus fuscatus</i>	0.99 (1.0-0.2)	<i>Polioptila dumicola</i>	1.01 (0.1-0.7)
<i>Hylophilus pectoralis</i>	1.83 (0.2-1.0)	<i>Phaethornis ruber</i>	0.94 (0.0-0.7)	<i>Pitangus sulphuratus</i>	0.99 (0.0-0.7)	<i>Furnarius rufus</i>	1.00 (0.1-0.7)
<i>Poecilatriccus latirostris</i>	1.83 (0.2-1.0)	<i>Camptostoma obsoletum</i>	0.88 (0.0-0.7)	<i>Furnarius rufus</i>	0.94 (0.2-1.0)	<i>Cercomacra melanaria</i>	1.00 (0.4-1.0)
<i>Synallaxis albilora</i>	1.83 (0.2-1.0)	<i>Coereba flaveola</i>	0.88 (0.0-0.7)	<i>Hypocnemoides maculicauda</i>	0.94 (0.7-0.0)	<i>Saltator coerulescens</i>	0.99 (0.3-0.8)
<i>Phacellodomus rufifrons</i>	1.78 (0.0-0.7)	<i>Eupsittula aurea</i>	0.88 (0.0-0.7)	<i>Cacicus solitarius</i>	0.91 (0.0-0.7)	<i>Myiothlypis flaveola</i>	0.99 (0.6-0.0)
<i>Cacicus solitarius</i>	1.70 (0.0-0.7)	<i>Icterus croconotus</i>	0.87 (0.2-0.7)	<i>Hemitriccus margaritaceiventer</i>	0.91 (0.0-0.7)	<i>Veniliornis passerinus</i>	0.99 (0.0-0.6)
<i>Chionomesa fimbriata</i>	1.69 (0.0-0.7)	<i>Cacicus cela</i>	0.83 (0.7-0.2)	<i>Myiarchus ferox</i>	0.91 (0.0-0.7)	<i>Chionomesa fimbriata</i>	0.92 (0.0-0.5)
<i>Polioptila dumicola</i>	1.69 (0.0-0.7)	<i>Herpsilochmus longirostris</i>	0.83 (0.7-0.2)	<i>Camptostoma obsoletum</i>	0.79 (0.2-0.7)	<i>Camptostoma obsoletum</i>	0.91 (0.0-0.6)
<i>Elaenia flavogaster</i>	1.63 (0.0-0.7)	<i>Hemitriccus margaritaceiventer</i>	0.81 (0.2-0.7)	<i>Hylophilus pectoralis</i>	0.79 (0.2-0.7)	<i>Icterus croconotus</i>	0.90 (0.0-0.5)
<i>Myiothlypis flaveola</i>	1.52 (0.7-0.0)	<i>Polioptila dumicola</i>	0.77 (0.2-0.7)	<i>Polioptila dumicola</i>	0.78 (0.2-0.7)	<i>Poecilatriccus latirostris</i>	0.89 (0.4-0.7)
<i>Picumnus albosquamatus</i>	1.47 (0.2-0.7)	<i>Myiopsitta monachus</i>	0.76 (0.0-0.5)	<i>Veniliornis passerinus</i>	0.78 (0.2-0.7)	<i>Pseudoseisura unirufa</i>	0.87 (0.0-0.5)
<i>Saltator coerulescens</i>	1.43 (0.2-0.7)	<i>Myiozetetes cayanensis</i>	0.76 (0.2-0.7)	<i>Crotophaga ani</i>	0.71 (0.0-0.5)	<i>Taraba major</i>	0.87 (0.4-0.7)
<i>Ramphocelus carbo</i>	1.29 (0.5-1.0)	<i>Rupornis magnirostris</i>	0.70 (0.2-0.5)	<i>Cercomacra melanaria</i>	0.70 (0.5-1.0)	<i>Synallaxis albilora</i>	0.86 (0.5-0.9)
<i>Tachyphonus rufus</i>	1.21 (0.0-0.5)	<i>Chionomesa fimbriata</i>	0.68 (0.0-0.5)	<i>Galbula ruficauda</i>	0.70 (1.0-0.5)	<i>Formicivora rufa</i>	0.86 (0.0-0.5)

(Table 3). The SIMPER results for each of the methodologies showed a similar number of common species (MN, 12 species; PC, 12 species; and ARU, 13 species) when compared with the Simper results considering the three methodologies together (total) (Table 3). However, only 3 species (*Hylophilus pectoralis*, *Procacicus solitarius*, and *Polioptila dumicola*) were found by each methodology SIMPER result (Table 3). PERMANOVA indicated significant differences in bird species composition detected by each methodology when analyzed for the two habitats (forests and savannas). These habitat differences were verified when the three methods were considered separately and together (total) (Table 4).

The dissimilarities in the species compositions were lower when each method was considered independently (MN: $J = 0.89$; PC: $J = 0.87$; and ARU: $J = 0.85$) and higher when all the methodologies were analyzed together ($J = 0.83$) (Fig. 3). The local contributions to β diversity ranged from 0.0 to 0.18 and were negatively correlated with species richness (Fig. 3). This result indicates that, in general, sites with higher uniqueness presented a lower number of species; this pattern was observed in

the forest sites. The total bird community presented high dissimilarity, with 82% of the dissimilarity attributed to replacement and 18% to nestedness. The three methods presented similar replacement and nestedness values (MN: 87% replacement, 13% nestedness; PC: 85% replacement, 15% nestedness; and ARU: 88% replacement, 12% nestedness (Fig. 3). The high overall dissimilarity indicated by the three survey methods reflects the relatively low number of species shared between the savanna and forest habitats. For all three methods, the replacement of species was the main process explaining the patterns of β diversity among the habitats.

DISCUSSION

Different from expectations, PC detected more species than ARU and MN. PC allows the audiovisual detection of birds, as well as the collection of data at different sampling points and in different habitats. ARU allows for species detection 24 hours per day, provides information on life history patterns, e.g., diurnal activities, reproductive and territorial behaviors, and seasonal occurrences (Jahn *et al.*, 2017), and reduces the time and physical demands associated with field work. However, both of these methods fail to detect bird individuals who may not vocalize, such as migrating birds, females, and immatures. MN needed to be in operation for many days to detect the majority of the bird species present in an area. It took 48 days to detect 79 species. However, only 320 min and 480 min for the PC and ARU methods, respectively, were sufficient to exceed the number of species obtained from mist nets (125 species and 113 species).

Table 4. PERMANOVA results showing the significant differences in the bird species composition between the three methodologies and the habitats (forest and savanna).

		F	df	p
All methodologies	Habitat	62.910	1	0.0001
	Method	32.415	2	0.0002
Mist nets	Habitat	3.529	1	0.0279
Point counts	Habitat	17.046	1	0.0302
Autonomous acoustic recordings	Habitat	26.537	1	0.0325

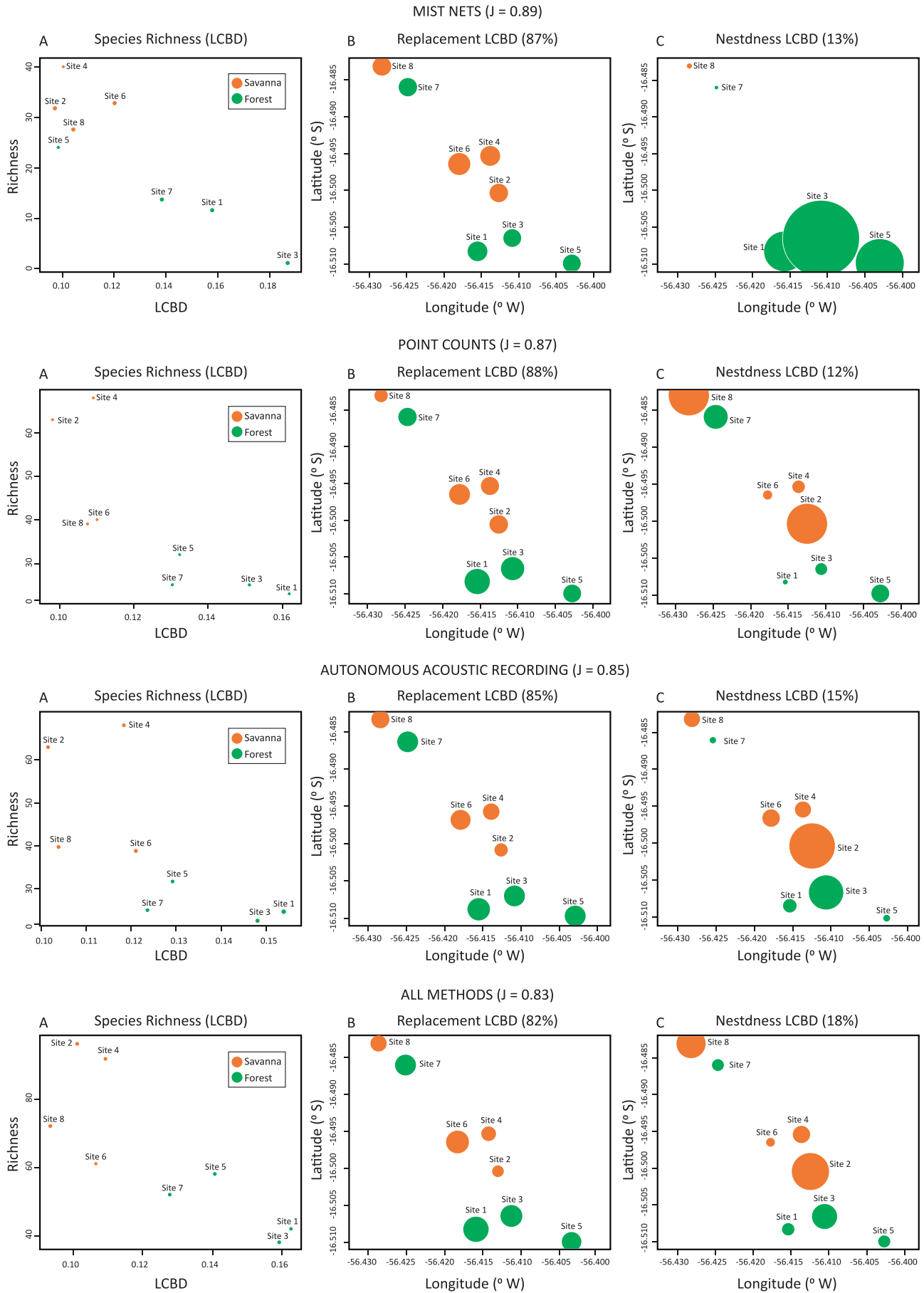


Figure 3. Local contribution to *beta* diversity (LCBD) of avian taxa in the northeastern Pantanal, Mato Grosso, Brazil, in the dry period of 2014. The geographic positions of the savanna sites (orange) and forest sites (green) are shown. The relationship between the LCBD values and species richness is shown in A. The site contributions to *beta* diversity (*i.e.*, the LCBD values) determined by each methodology were divided into two components: replacement B and nestedness C.

Before concluding that MN provides inferior species detection, many advantages are inherent to this methodology. MN allows us to record the sizes and body masses of individuals, which are essential data for defining functional groups and monitoring growth and reproduction (Dunn & Ralph, 2004). It is also essential for surveys in areas with low vegetation, such as the *Cerrado*-impacted wetlands of the Pantanal, with vegetation that reaches 2.7 m tall. MN focus mainly on the understory of vegetation and are expected to restrict species detection (MacArthur & MacArthur, 1974; Karr, 1981; Whitman et al., 1997; Blake & Loiselle, 2001). However, the MN provided valuable information and detected 12 species that the PC and ARU did not.

Since the presence of a researcher or equipment in the field can be a disturbance factor, the three methodologies applied can interfere in different ways with the behaviors of birds, resulting in consequences for their detection. Beyond this interference, these methodologies naturally demand different sampling efforts, which may also influence the detection of species.

It should also be noted that many of the species detected by the PC and ARU are not closely related to certain specific vegetation types, such as savannas or forests. The case of some aerial species such as swallows, aquatic species such as *Anhinga anhinga* and ducks and storks (which we did not detect in the dry period but are very common in receding and wet periods in the Pantanal), species that may only pass through the region, species that prefer open and anthropic regions, and species with wide distributions such as ibises and woodpeckers. All these species are not restricted to savannas or forests since they use the environment as a whole. For this reason, in some studies, only certain groups of species are considered in the analyses, e.g., Cavarzere & Moraes (2010), where only passerines were included in the study to maintain a focus on species with similar feeding characteristics and distributions.

The number of species detected in savannas and forests was similar between PC and ARU in this study. Comparable results were found in other studies comparing the performances of these methodologies, showing no significant differences in the numbers of species detected by PC and ARU (Haselmayer & Quinn, 2000; Celis-Murillo et al., 2012; Venier et al., 2012; Alquezar & Machado, 2015; Stewart et al., 2020). However, depending on the sampling design, ARU can detect nearly all vocalizing avian species when recording 24 hours per day. PC yields extremely time-restricted samples; thus, a much greater field sampling effort is required for an expert in avian bioacoustics to detect all species vocalizing.

We performed PC and ARU occurred because MN focus mainly on the understory of the vegetation and are expected to restrict species detection (MacArthur & MacArthur, 1974; Karr, 1981; Whitman et al., 1997; Blake & Loiselle, 2001). Data collection during the morning, from 06:00 to 08:00 am. This is considered the period of highest activity of birds, with another peak at the end of the day (Blake, 1992). However, it has been suggested that in the early morning hours, the amount of light is

insufficient for birds to become active but adequate for them to communicate with each other, with individuals starting to move by the end of the morning (Berg et al., 2006). As observed for the MN, despite collecting data for 8 h/day, the largest numbers of species and individuals were captured between 09:00 and 11:00 am. In the afternoon, from 04:00 to 05:00 pm, a larger number of species were captured, but in a much smaller proportion than in the morning period. Due to logistical difficulties, the MN and PC methods were not performed by us at night. This highlights one of the benefits of applying parallel ARU, which can be used to detect nocturnal species; however, for this study, we did not use the data collected at night to evaluate only the diurnal detections.

We observed that there were significant differences in the species diversity between the savanna and forest areas when all the methodologies were analyzed together and when they were analyzed independently. The number of bird species was higher in the savanna areas than in the forest areas according to all three methods. The number of species detected by the PC and ARU was higher than that detected by the MN for all the forest and savanna areas, with the exception of a single savanna area. However, the MN detected species that are important for conservation, such as *Antilophia galeata*, an endemic species of the *Cerrado*, and *Sporophila angolensis*, a threatened species in Brazil, that were not detected in either the savanna or forest areas by the PC or ARU. *Antilophia galeata* is a species that occurs mainly in forest regions, whereas *S. angolensis* occurs in savanna areas. As these species were trapped in MN in habitats other than those in which their occurrence was expected, it is evident that the MN also detected species crossing habitats to reach preferred areas. Hummingbird species such as *Phaethornis nattereri* and *Chrysolampis mosquitus*, the latter a migratory species to the Pantanal region, were only verified by MN. PC and ARU detected several species that prefer canopies, such as woodpeckers (9 species), *Ortalis canicollis*, parakeets (5 species), and parrots (2 species); terrestrial species such as *Vanellus chilensis* and ibises (3 species); and others (Appendix 1).

The vegetation structure is an important determinant of the dissimilarity between forest and savanna areas in the Pantanal (De Deus et al., 2020), as verified in this study by the clear differentiation in the bird species composition within habitats. High bird density in savanna habitats increases interspecific competition, resulting in species segregation among different habitats and explaining the role of species turnover as the main component of *beta* diversity (Figueira et al., 2006; Signor & Pinho, 2011). Compositional differences among forest habitats, in contrast, are more affected by species loss, offering evidence of low resource availability (Fjeldså, 1999; Khanaposhtani et al., 2012). Despite the low number of species at these sites, the forest sites were the main contributors to the spatial differences in species composition.

In our experience in the northeastern Pantanal, many species detected only by PC and ARU in the dry period were detected by MN in other seasonal periods (De Deus et al., 2020). Additionally, several canopy species, such

as *Celeus flavus* or midstory species, may occasionally or even explore lower strata at a particular time of day and be captured by mist nets (De Deus et al., 2020). The three methodologies applied together worked complementarily to the understanding of bird community structure, composition, and distribution. The importance of combining different methodologies for bird species assessments have also been suggested in other studies such as Celis-Murillo et al. (2012), Stewart et al. (2020), and Drake et al. (2021).

CONCLUSIONS

Surveys of species diversity are generally performed in a limited manner, either over short time frames or on restricted spatial scales. To identify conservation priorities for ecosystems, sampling all species over seasonal periods and in different habitats, such as complete surveys of species diversity in the Pantanal, is necessary. The use of several methods simultaneously may be impracticable due to logistical or financial issues. In our study, most of the birds in the sampled community were detected by Autonomous Acoustic Recordings and Point Counts. Although some methods have been proven to detect more species, each method provided important data on bird behavior, guild composition, distribution, and unique detections; thus, these methods should be considered complementary (Fig. 4). Furthermore, permanent local field stations in the Pantanal with a long-term biodiversity and conservation research mission could be a solution to reduce the enormous biodiversity knowledge gaps of wetlands and beyond in support of future science-based environmental health protection measures.

OUTLOOK

Technological advances to monitor the occurrence, distribution, and behavior of wildlife have provided, over recent decades, new and noninvasive techniques such as environmental DNA analyses, unmanned aerial vehicles (drones), and camera trapping (Sardà-Palomera et al., 2017; Sebastián-González et al., 2019; Saccò et al., 2022). For avian studies, the latter two, drones and camera traps, have already gained considerable importance, especially in tropical regions and in other areas that are difficult to access logistically. Drones (DS) and camera traps (CT) allow for population density estimation studies and evaluation of species distribution and are useful for occupancy models (MacKenzie et al., 2003; Bouché et al., 2012; Rovero et al., 2013; Radiansyah et al., 2017). Furthermore, the application of these techniques allows for verifying species age, size, and sex. Both methodologies gained importance as tools to study species behavior and occurrence to implement specific conservation strategies. Due to advanced programmable and easy-to-apply software for field studies future widespread applications in avian biodiversity and other fields of research are to be expected (Hodgson et al., 2018; Tanwar et al., 2021).



Figure 4. A Song Meter (acoustic recorder, upper left, marked yellow) and a camera trap (photo and video recorder, lower left, marked green) were jointly applied to study the avian occurrence and behavior of ground-dwelling species, e.g., cracids and tinamous.

AUTHORS' CONTRIBUTIONS: FFD, KLS, MIM: Conceptualization; Methodology; FFD, KLS, WN: Data curation, Formal analysis; FFD, KLS, MIM: Writing, Visualization, Investigation; KLS, MIM: Funding acquisition, Supervision; FFD, KLS, MIM, AST, WN: Writing, reviewing, editing: All authors participated in the discussion of the results and reviewed and approved the final version of the paper.

CONFLICTS OF INTEREST: Authors declare there are no conflicts of interest.

FUNDING INFORMATION: This study is embedded in a long-term research project on biodiversity assessment studies in the Pantanal (<https://cobra.ic.ufmt.br>) run by the Brazilian National Institute of Science and Technology of Wetlands (INAU/UFMT/CNPq/MCTIC). The Brehm Funds for International Bird Conservation, Bonn, Germany, provided technical equipment and field work student support. Logistic support during the fieldwork was kindly provided by the SESC Pantanal Ecological Resort (Polo Socioambiental SESC Pantanal), a private natural heritage reserve in the northern Pantanal. We declare that the study complied with the current national Brazilian laws (Sistema de Autorização e Informação em Biodiversidade, SISBIO, permit nos. 39095, KLS, and 66056, MIM).

ACKNOWLEDGMENTS: We are deeply indebted to Dr. Cristina Cuiabalia Neves, Dr. Waldir Wolfgang Valutky, and MSc. Alexandre Enout for providing the permits and support to work at the SESC Private Reserve.

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SUPPLEMENTARY MATERIAL

Species detected by three different methodologies in forest and savanna sites over the dry period of 2014 in one region of the northeastern Pantanal, Mato Grosso, Brazil. MN = mist net; PC = point count; ARU = autonomous acoustic recording.

	Forest			Savanna				Forest			Savanna		
	MN	PC	ARU	MN	PC	ARU		MN	PC	ARU	MN	PC	ARU
Tinamiforme							Trogoniformes						
Tinamidae							Trogonidae						
<i>Crypturellus undulatus</i>		3	4		4	4	<i>Trogon curucui</i>		2	2			1
Galliformes							Coraciiformes						
Cuculidae							Momotidae						
<i>Ortalis canicollis</i>		3	3		4	4	<i>Momotus momota</i>		1	1			
<i>Crax fasciolata</i>			1			2	Alcedinidae						
Columbiforme							<i>Megaceryle torquata</i>		2	2			2
Columbidae							<i>Chloroceryle amazona</i>		1	1			
<i>Patagioenas cayennensis</i>			1		2	2	<i>Chloroceryle aenea</i>		1	1	1		
<i>Leptotila verreauxi</i>	1	3	4	2	3	4	<i>Chloroceryle inda</i>		1	1	2		1
<i>Columbina talpacoti</i>			1	1		2	Galbuliformes						
<i>Columbina picui</i>					1		Galbulidae						
Cuculiforme							<i>Brachygalba lugubris</i>						1
Cuculidae							<i>Galbula ruficauda</i>	1	3	4	2	2	2
<i>Guira guira</i>					1		Bucconidae						
<i>Crotophaga major</i>		1					<i>Monasa nigrifrons</i>	1	2	2			1
<i>Crotophaga ani</i>				2		2	Piciformes						
<i>Tapera naevia</i>					2	5	Ramphastidae						
<i>Piaya cayana</i>		2		1			<i>Ramphastos toco</i>		1				2
Apodiformes							<i>Pteroglossus castanotis</i>		1				1
Apodidae							Picidae						
<i>Tachornis squamata</i>					1		<i>Picumnus albosquamatus</i>	1	1		3	2	2
Trochilidae							<i>Melanerpes candidus</i>					1	
<i>Phaethornis nattereri</i>	2			3			<i>Veniliornis passerinus</i>			1	2	3	3
<i>Phaethornis ruber</i>			1				<i>Campephilus rubricollis</i>		1	1			
<i>Chrysolampis mosquitus</i>				1			<i>Campephilus melanoleucus</i>		1				1
<i>Chionomesa fimbriata</i>				3	2	2	<i>Celeus flavus</i>		1	2			1
Gruiformes							<i>Celeus lugubris</i>		1				
Rallidae							<i>Piculus chrysochloros</i>					1	
<i>Anurolimnas viridis</i>					1		<i>Colaptes melanochloros</i>						1
<i>Pardirallus nigricans</i>						1	<i>Colaptes campestris</i>						1
<i>Aramides cajaneus</i>					1	1	Falconiformes						
Heliornithidae							Falconidae						
<i>Heliornis fulica</i>			1				<i>Micrastur semitorquatus</i>			1		1	1
Charadriiformes							<i>Caracara plancus</i>					1	2
Charadriidae							<i>Falco rufigularis</i>						1
<i>Vanellus chilensis</i>					2	1	<i>Herpetotheres cachinnans</i>						1
Jacanidae							Psittaciformes						
<i>Jacana jacana</i>					1	1	Psittacidae						
Rynchopidae							<i>Myiopsitta monachus</i>					2	1
<i>Rynchops niger</i>			1				<i>Brotogeris chiriri</i>		4	3		4	4
Laridae							<i>Amazona aestiva</i>		1	2		2	2
<i>Phaetusa simplex</i>			1				<i>Amazona amazonica</i>		2	3		1	2
Suliformes							<i>Eupsittula aurea</i>					3	2
Anhingidae							<i>Diopsittaca nobilis</i>					1	1
<i>Anhinga anhinga</i>		1	2				<i>Psittacara leucophthalmus</i>					1	
Pelecaniformes							Passeriformes						
Threskiornithidae							Thamnophilidae						
<i>Mesembrinibis cayennensis</i>		2	2		1		<i>Taraba major</i>		2	3	2	3	4
<i>Theristicus caerulescens</i>			1		2		<i>Thamnophilus doliatus</i>	1			1	4	4
<i>Theristicus caudatus</i>					2		<i>Thamnophilus pelzelni</i>			1			
Accipitriformes							<i>Dysithamnus mentalis</i>	3	1	1		1	
Accipitridae							<i>Herpsilochmus longirostris</i>		3	2	1	1	
<i>Rupornis magnirostris</i>		1	2		2	2	<i>Formicivora grisea</i>					1	

	Forest			Savanna		
	MN	PC	ARU	MN	PC	ARU
<i>Formicivora rufa</i>				2	3	2
<i>Cercomacra melanaria</i>	1	2	2	4	4	4
<i>Pyriglena leuconota</i>	1		1			
<i>Hypocnemoides maculicauda</i>	2	2	3			
Furnariidae						
<i>Sittasomus griseicapillus</i>	1		1	1	1	
<i>Xiphocolaptes major</i>						1
<i>Xiphorhynchus guttatus</i>	1	1	3	1	1	3
<i>Dendroplex picus</i>		1	3		2	3
<i>Campylorhamphus trochilirostris</i>				1		2
<i>Lepidocolaptes angustirostris</i>		1		2	1	1
<i>Furnarius leucopus</i>	2	4	3	2	3	4
<i>Furnarius rufus</i>		1	1	1	4	4
<i>Phacelodorus rufifrons</i>		1		3	2	4
<i>Phacelodorus ruber</i>					3	2
<i>Cranioleuca vulpina</i>	1	2	3	1	2	3
<i>Pseudoseisura unirufa</i>				2	1	4
<i>Certhiaxis cinnamomeus</i>				1	1	1
<i>Synallaxis albilora</i>	1	2	3	4	4	3
<i>Synallaxis hypospodia</i>				1	1	
Tyrannidae						
<i>Phyllomyias fasciatus</i>		1				
<i>Myiopagis gaimardii</i>		2	2		3	2
<i>Myiopagis viridicata</i>				1	2	
<i>Elaenia flavogaster</i>				3	1	
<i>Elaenia spectabilis</i>					1	
<i>Elaenia parvirostris</i>				2		
<i>Elaenia chiriquensis</i>				1		
<i>Camptostoma obsoletum</i>			1	2	3	3
<i>Phaeomyias murina</i>				4	1	1
<i>Euscarthmus meloryphus</i>			1	1		1
<i>Leptopogon amaurocephalus</i>	1	1				
<i>Inezia inornata</i>			1			1
<i>Hemitriccus striatocollis</i>	2	1	4			2
<i>Hemitriccus margaritaceiventer</i>		1		4	3	3
<i>Poecilatriccus latirostris</i>	1	2	2	4	2	3
<i>Todirostrum cinereum</i>				2	1	1
<i>Tolmomyias sulphureus</i>		1				
<i>Myiophobus fasciatus</i>					1	1
<i>Cnemotriccus fuscatus</i>	2	2	4	2	3	1
<i>Legatus leucophaeus</i>		1		1	2	1
<i>Myiozetetes cayanensis</i>		1	2	1	3	2
<i>Pitangus sulphuratus</i>		1			2	3
<i>Pitangus lictor</i>					2	
<i>Myiodynastes maculatus</i>			1		1	
<i>Megarynchus pitangua</i>		1		2	1	
<i>Empidonomus varius</i>				1		
<i>Tyrannus melancholicus</i>				3	2	
<i>Casiornis rufus</i>	1	1	1	1	2	
<i>Myiarchus swainsoni</i>			1	1	2	
<i>Myiarchus ferax</i>	1	4		2	4	3
<i>Myiarchus tyrannulus</i>		2	1		3	2
<i>Attila bolivianus</i>	1	1				

	Forest			Savanna		
	MN	PC	ARU	MN	PC	ARU
Pipridae						
<i>Neopelma pallescens</i>						1
<i>Antilophia galeata</i>	2					1
<i>Pipra fasciicauda</i>	2					
Tityridae						
<i>Pachyramphus viridis</i>						1
<i>Pachyramphus polychopterus</i>		1		2	1	1
Vireonidae						
<i>Hylophilus pectoralis</i>	1	1	1	4	4	3
<i>Vireo olivaceus</i>		1	1	1	2	
Corvidae						
<i>Cyanocorax cyanomelas</i>		2	1		3	2
Hirundinidae						
<i>Progne chalybea</i>						1
<i>Tachycineta leucorhoa</i>			1		1	
Troglodytidae						
<i>Campylorhynchus turdinus</i>		2	3		2	3
<i>Pheugopedius genibarbis</i>	2	3	4	1	4	4
<i>Cantorchilus leucotis</i>	1	3	3	4	4	4
Poliotilidae						
<i>Poliotilta dumicola</i>		1	1	3	3	3
Donacobiidae						
<i>Donacobius atricapilla</i>					1	1
Turdidae						
<i>Turdus leucomelas</i>						1
<i>Turdus amaurochalinus</i>	2	1		2	1	
Fringilidae						
<i>Euphonia chlorotica</i>		1	1		2	
Passerellidae						
<i>Arremon flavirostris</i>	1				2	2
Icteridae						
<i>Cacicus solitarius</i>					3	3
<i>Cacicus cela</i>		3	1			1
<i>Icterus croconotus</i>		1			1	3
<i>Agelasticus cyanopus</i>					1	1
Parulidae						
<i>Geothlypis aequinoctialis</i>						1
<i>Myiothlypis flaveola</i>	3	3	2			
Thraupidae						
<i>Nemosia pileata</i>						1
<i>Conirostrum speciosum</i>			1	1	1	1
<i>Sicalis citrina</i>						1
<i>Volatinia jacarina</i>				2		
<i>Tachyphonus rufus</i>				2		
<i>Eucometis penicillata</i>	2		1			
<i>Ramphocelus carbo</i>	2	1	2	4	2	2
<i>Sporophila leucoptera</i>				1	1	
<i>Sporophila angolensis</i>	1			2		
<i>Saltator coerulescens</i>	1	2	1	3	3	4
<i>Coereba flaveola</i>				4	3	2
<i>Paroaria capitata</i>				4		
<i>Thraupis sayaca</i>					1	1