

# Population abundance and biomass of large-bodied birds in Amazonian flooded and unflooded forests

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## Summary

Little is known about the contribution of different forest types to the beta-diversity, abundance and biomass of the avifauna in lowland Amazonia. This paper presents data on the large-bodied bird assemblages of adjacent upland (terra firme) and seasonally flooded (várzea and igapó) forests in the lower Rio Purús region of central-western Brazilian Amazonia. We focus our analysis on 23 large-bodied canopy and terrestrial bird species from 10 families, on the basis of 2,044 bird sightings obtained during line-transect censuses conducted over a two-year period. Large toucans comprised the most numerically abundant large birds in terra firme and igapó forests, whereas macaws were the most abundant in nutrient-rich várzea forests that were seasonally inundated by white-water. The aggregate population density of all bird species in terra firme forest was slightly higher than that in várzea forest. Igapó forest, which was seasonally inundated by black-water, sustained the lowest population densities. Terra firme and várzea forests differed considerably in species composition and abundance whereas igapó forest shared many species with both terra firme and várzea. Our results suggest that Amazonian floodplain forests play a major role in the persistence and community dynamics of the large-bodied forest birds.

## Resumo

Pouco se sabe sobre a contribuição de diferentes tipos de florestas aos padrões de beta-diversidade, abundância e biomassa da avifauna na região amazônica. Este artigo apresenta dados à respeito das aves de médio a grande porte em florestas de terra firme e florestas adjacentes sujeitas a inundações sazonais (várzea e igapó) na região do baixo Rio Purús da Amazonia centro-ocidental. Nossa análise, baseada num total de 2,044 observações obtidas durante censos ao longo de transectos, foi direcionada a 23 espécies de aves de médio a grande porte pertencentes a 10 famílias. As aves mais abundantes em florestas de terra firme e igapó foram os tucanos, e as araras as mais abundantes em florestas de várzea. A densidade de população agregada de todas as espécies na terra firme foi ligeiramente mais elevada do que na várzea. A floresta de igapó sustentaram as mais baixas densidades populacionais. Terra firme e várzea diferem consideravelmente na composição e abundância de espécies, visto que a avifauna do igapó é intermediária entre a da terra firme e a da várzea. Os resultados sugerem que as florestas inundáveis tem uma papel muito importante na manutenção das comunidades de aves de grande porte na Amazônia, e principalmente aquelas espécies que usam grandes mosaicos de floresta.

*Keywords:* Brazilian Amazonia, biomass, cracids, floodplain forest, Neotropics

## Introduction

Large-bodied birds comprise an important component of the vertebrate fauna in Amazonian forests. This is underlined by their importance as seed predators (Norconk *et al.* 1997, Trivedi *et al.* 2004) and seed dispersal agents for Neotropical forest trees and shrubs (Théry *et al.* 1992, Silva *et al.* 2002) and their absence would likely affect long-term forest dynamics. These birds are also an important source of animal protein to rural and forest-dwelling peoples in the region. For example, a minimum of 2,590 tons of game birds are harvested each year by the rural population of the Brazilian Amazon alone (Peres 2000) and members of the family Cracidae such as guans, piping guans, chacalacas and curassows were among the most frequently hunted animals at three villages in north-eastern Peru (Begazo and Bodmer 1998). However, despite their ecological and human subsistence role, little information is available on the abundance and vertebrate biomass contribution of large-bodied birds in large-scale Neotropical forest mosaics (but see Terborgh *et al.* 1990).

Amazonia is comprised of a wide range of juxtaposed vegetation types which govern the distribution of the regional biota; while some species exploit a variety of habitats, others are primarily or entirely restricted to a single vegetation type (e.g. Haugaasen and Peres 2005a, b). This high diversity of macro- and micro-habitats is among the many factors that contribute to the high bird species richness in the Neotropics (Orlans 1969, Karr 1976, Terborgh 1980). In lowland Amazonia, unflooded (hereafter, terra firme) and seasonally flooded (várzea and igapó) forests often represent the main differences in macro-habitat types in an otherwise largely continuous closed-canopy forest landscape.

The Lago Uauaçu region of central-western Brazilian Amazonia presents an ideal opportunity to investigate an intact large-bodied bird community in a closed-canopy forest matrix. The region consists of a large mosaic of juxtaposed terra firme, várzea and igapó forests; the forest structure remains almost entirely undisturbed, and subsistence hunting was largely limited to light harvests of large-bodied mammal species such as large rodents and ungulates. As part of a broader investigation of vertebrate assemblage structure and dynamics in Amazonian forests, we here examine the large-bodied bird assemblages of adjacent terra firme, várzea and igapó forests. We report on the population and biomass density estimates, and flock sizes for individual species in the three main forest types and briefly discuss the conservation implications of our findings.

## Methods

### *Study area*

The study took place at Lago Uauaçu in the lower Rio Purús region of central-western Brazilian Amazonia (04° 20' S, 62° 28' W; Figure 1). Lago Uauaçu is a 32-km long crescent-shaped black-water lake which is home to around 30 *caboclo* families who depend on the collection of Brazil nuts (*Bertholletia excelsa* – Lecythidaceae) from the natural *castanhais* (Brazil-nut tree stands) in addition to some small-scale commercial fishing, and highly selective logging and hunting for their annual income or subsistence. However, hunters at Lago Uauaçu were highly selective and only opportunistically killed large birds. Hunting did not take place in our study sites. We are therefore confident that local game harvest at Lago Uauaçu did not affect the population density of large-bodied birds in our census areas. A more detailed description of the study site can be found elsewhere (Haugaasen and Peres 2006)

### *Avian surveys*

All sites were surveyed using a standardised line-transect census protocol described in Peres (1999a) and our results are thus comparable to most sites in the Neotropics where large vertebrate censuses have been carried out (e.g. Peres & Palacios 2007). For our census protocol

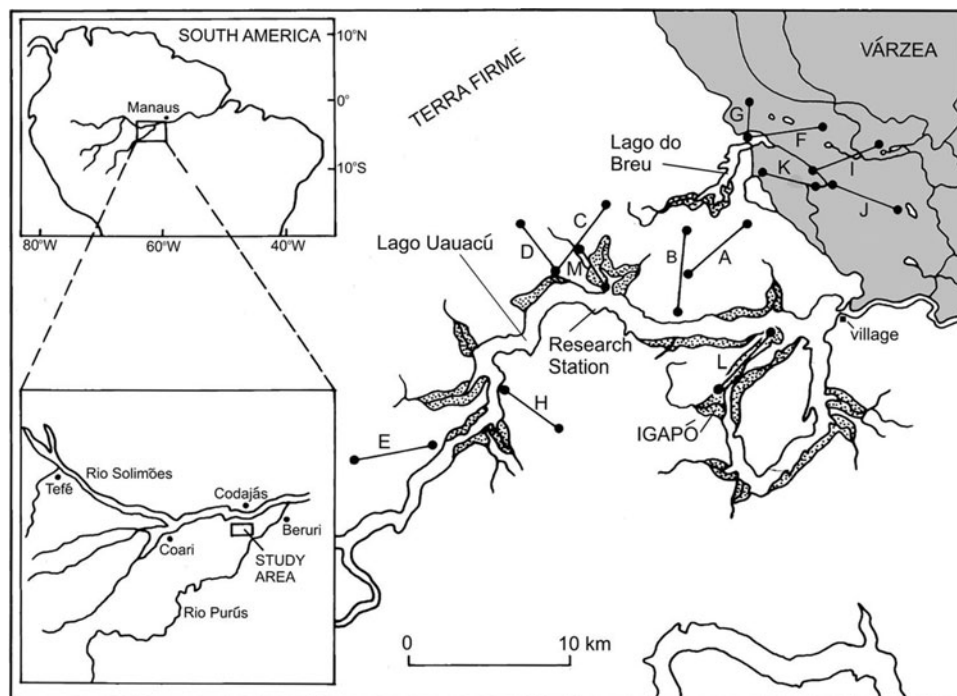


Figure 1. Map of the Lago Uauacú study area in the lower Rio Purús region of central-western Brazilian Amazonia. The main forest types occurring in the region included more extensive tracts of terra firme and várzea forest (open and shaded areas) and smaller patches of igapó forest (dotted areas). Transects A-M (lines) indicate the main focal areas censused in each forest type.

we used a highly reliable field assistant who had been working with our standardised long-term census program for over 10 years and a local hunter who was pre-trained during a pilot study. These highly skilled local field assistants recorded data into a handheld micro-cassette recorder, which could easily be operated in the field. Transects were walked by single observers at average speeds of approximately  $1,250 \text{ m h}^{-1}$  from 07h00 to 11h00 and 13h00 to 17h00, largely coinciding with the peak of vertebrate activity in tropical forests. Observers were rotated on a daily basis between different transects in order to minimise or cancel out potential observer-dependent biases. Censuses were terminated during rainy weather because this affected the intrinsic detectability of different species. Upon a detection event, the time, species identity, group size, perpendicular distance to the group, sighting location along the transect, and detection cue were recorded.

Data on the large-bodied bird population at Lago Uauacú were obtained during surveys conducted in terra firme, várzea and igapó forests in 2002 and 2003. In total, this study is based on a two-way (both outward and return walks) census effort of 2,026 km in terra firme, 2,309 km in várzea, and 277 km in igapó, walked along 13 transects marked with flagging tape every 50 m and ranging from 4,000 to 5,000 m in length (Table 1). This amounted to a total census effort of 4,612 km walked along 62.5 km of transects. The várzea forest trails F to J were separated from terra firme by a  $\sim 50\text{-m}$  wide river channel, whereas trail K intersected a portion of várzea forest that was physically connected to terra firme (Figure 1). Census walks were conducted throughout the annual cycle, but systematically alternated between terra firme and floodplain forests within a season to minimise any potentially confounding effects of seasonality. Censuses

Table 1. List of transects censused in all forest types at Lago Uauaçu.

Transect	Forest type	Sampling effort (km)	Transect length (km)	Map code
Sucurijú	Terra firme	402.95	5.0	A
Breu	Terra firme	382.8	5.0	B
Mirocaia	Terra firme	482.35	5.0	C
Ussicantá	Terra firme	401.3	4.3	D
Aventura	Terra firme	187.4	5.0	E
Patinho	Várzea	624.2	5.0	F
Fortaleza	Várzea	240.0	4.0	G
Palhal	Terra firme	170.0	4.2	H
Trindade	Várzea	418.7	5.0	I
Murí	Várzea	398.45	5.0	J
Jamari	Várzea	627.3	5.0	K
Furo Grande	Igapó	101.0	5.0	L
Igapó Mirocaia	Igapó	176.0	5.0	M
<b>Total</b>		<b>4,612.45</b>	<b>62.5</b>	

along várzea and igapó forest transects were conducted on foot during the low-water season and by using unmotorised dugout canoes during the high-water season. Canoe navigation along flooded forest transects during the inundation period was aided by flags that had to be frequently renewed because of changes in water level. Due to the low sampling effort in igapó forest, the results from this forest type should be seen as preliminary.

### *Species censused*

Data presented here are restricted to diurnal forest-dwelling birds amenable to line-transect censuses. We also include three bird species — Horned Screamer, Muscovy Duck and Hoatzin — that are associated with water, but spend much of their time in the closed-canopy seasonally flooded forest and therefore encountered regularly during censuses. Thus, we focus our analysis on 23 species of mid-sized to large-bodied birds, including cracids, tinamids, trumpeters, wood-quails and ramphastids (for Latin binomials and species authorities, see Table 2). With the exception of Horned Screamer, Muscovy Duck and Hoatzin, all species considered here could be described as either frugivores or granivores, and consumed mature fruit pulp or seeds to a greater or lesser extent (Table 2). These species comprise most of the large-bodied bird species that are targeted by hunters in Amazonian forests. Our species nomenclature follows the BirdLife International online database (BirdLife International 2007).

### *Data analysis*

Census data were analysed using the DISTANCE 4.0 software (Thomas *et al.* 2002). Following the suggestions in Buckland *et al.* (1993) we firstly explored our data by initially including all visual and/or acoustic detection events in the analyses. However, in some cases the detection data included outliers which distorted the model fits. As recommended by Buckland *et al.* (1993), the perpendicular distance data were truncated by 5–10% to provide better fits to the various model estimates in these cases. Models were then selected by evaluating the model robustness, inspection of the shape of the detection curve and the Akaike's Information Criterion (AIC) value following the guidelines in Buckland *et al.* (1993). In this study, group density estimates were derived from Half-Normal models with either cosine or polynomial adjustments which provided the best model fits for our data. Where sample sizes were too small for the DISTANCE

Table 2. Nomenclature, body mass and foraging guild of 23 large-bodied bird species considered in this study.

Species name	Common name	Mean adult body mass (g) <sup>a</sup>	Foraging guild <sup>b</sup>	Forest level <sup>c</sup>
<b>TINAMIDAE</b>				
<i>Tinamus tao</i> (Temminck, 1815)	Gray Tinamou	2000	Sp/Fr	T
<i>Tinamus major</i> (Gmelin, 1789)	Great Tinamou	1170	Sp/Fr	T
<i>Tinamus guttatus</i> (Pelzeln, 1863)	White-throated Tinamou	600	Sp/Fr	T
<i>Crypturellus cinereus</i> (Gmelin, 1789)	Cinereous Tinamou	450	Sp/Fr	T
<i>Crypturellus soui</i> (Hermann, 1783)	Little Tinamou	205	Sp/Fr	T
<i>Crypturellus variegatus</i> (Gmelin, 1789)	Variiegated Tinamou	350	Sp/Fr	T
<i>Crypturellus undulatus</i> (Temmick, 1815)	Undulated Tinamou	540	Sp/Fr	T
<i>Crypturellus bartletti</i> (Sclater & Salvin, 1873)	Bartlett's Tinamou	?	Sp/Fr	T
<b>ANHIMIDAE</b>				
<i>Anhima cornuta</i> (Linnaeus, 1766)	Horned Screamer	3075	Fo	W
<b>ANATIDAE</b>				
<i>Cairina moschata</i> (Linnaeus, 1758)	Muscovy Duck	2550	Fo	W
<b>FALCONIDAE</b>				
<i>Ibtycter americanus</i> (Boddaert, 1783)	Red-throated Caracara	583	Fr/In	A
<b>CRACIDAE</b>				
<i>Ortalis guttata</i> (Spix, 1825)	Speckled Chacalaca	550	Fr/In	A
<i>Penelope jacquacu</i> Spix, 1825	Spix's Guan	1280	Fr/In	A
<i>Mitu tuberosum</i> (Spix, 1825)	Razor-billed Curassow	3060	Fr/Sp	A/T
<i>Crax globulosa</i> (Spix, 1825)	Wattled Curassow	3000	Fr/Sp	A/T
<b>ODONTOPHORIDAE</b>				
<i>Odontophorus stellatus</i> (Gould, 1843)	Starred Wood-quail	310	Fr/In	T
<b>OPISTHOCOMIDAE</b>				
<i>Opisthocomus hoazin</i> (Müller, 1776)	Hoatzin	855	Fo	W/A
<b>PSOPHIIDAE</b>				
<i>Psophia leucoptera</i> (Spix, 1825)	Pale-winged Trumpeter	990	Fr/In	T
<b>PSITTACIDAE</b>				
<i>Ara ararauna</i> (Linnaeus, 1758)	Blue and yellow Macaw	1125	Sp/Fr	A
<i>Ara macao</i> (Linnaeus, 1758)	Scarlet Macaw	1015	Sp/Fr	A
<i>Ara chloropterus</i> (Gray, 1859)	Red-and-green Macaw	1250	Sp/Fr	A
<b>RAMPHASTIDAE</b>				
<i>Ramphastos vitellinus</i> (Lichtenstein, 1823)	Channel-billed Toucan	369	Fr	A
<i>Ramphastos cuvieri</i> (Wagler, 1827)	Cuvier's Toucan	734	Fr	A

<sup>a</sup>Body mass measurements after Terborgh *et al.* (1990) and del Hoyo *et al.* (1992, 1994, 1997, 2002).

<sup>b</sup>Fo = Folivore, Fr = Frugivore, In = Insectivore, Sp = Seed predator

<sup>c</sup>A = arboreal, T = terrestrial, W = aquatic

program (see Table 3), group density estimates were calculated using Kelker's method (Kelker 1945).

Detection data for sympatric congeners of four genera (large tinamous, *Tinamus* spp.; small tinamous, *Crypturellus* spp.; large toucans, *Ramphastos* spp.; red macaws, *Ara macao* and *A. chloropterus*) were pooled because these congeners could not always be unambiguously distinguished in the field. This data pooling procedure also increased sample sizes allowing more robust model fits. Population density estimates were then calculated using mean flock sizes derived from a subset of all visual detection events considered to be reliable flock counts.

Crude biomass estimates were calculated using body mass data derived from Terborgh *et al.* (1990) and del Hoyo *et al.* (1992, 1994, 1997, 2002) and taking the means of the lower and upper

body mass limits presented therein. In the case of the genera *Tinamus*, *Crypturellus*, *Ara* and *Ramphastos* the biomass estimates were calculated using the mean weight of the species present in the region, unless only one species of a genus occurred in a habitat (e.g. *Crypturellus undulatus* and *Tinamus major* in várzea).

A non-metric multidimensional scaling (MDS) ordination based on the Bray-Curtis similarity measure between any two sites was performed to further explore within- and between-habitat differences in community structure at the level of transect (Seaby and Henderson 2004). The abundance measure used in the ordination was the number of individuals (or groups) observed per 10 km walked. Data for some congener species were again pooled together. Forest sites are thus positioned in ordination space according to their bird species composition and abundance. The MDS ordination was performed using the PRIMER v. 5 software (Clarke 1993). An index of multivariate dispersion (Warwick and Clarke 1993) was calculated to investigate the variability among replicate terra firme, várzea and igapó forest samples.

## Results

### *Flock size and abundance*

A total of 2,044 sightings of the 23 bird species from 10 families were recorded during censuses. Most of the birds occurred either in pairs or larger groups. Only the ground-dwelling tinamou (*Tinamus* spp. and *Crypturellus* spp.) were regularly encountered solitarily (Table 3). The largest flocks encountered were formed by the Pale-winged Trumpeters, Red-throated Caracaras, wood-quails and macaws (Table 3).

Large toucans comprised the most abundant birds in terra firme forest (12.6 individuals  $\text{km}^{-2}$ ). Other abundant species in terra firme included Pale-winged Trumpeter, Spix's Guan and Starred Wood-quail. The most abundant species in várzea forest were the red Macaws (8.8 individuals  $\text{km}^{-2}$ ). Despite being primarily solitary, Undulated Tinamou was the second most abundant bird species in várzea (Table 3). Large toucans were clearly the most abundant bird group in igapó forest (Table 3).

### *Spatial organization of the bird assemblage*

Only Starred Wood-quail was restricted to terra firme forest, although other species such as Pale-winged Trumpeter and Spix's Guan were primarily found in this forest type. Horned Screamer, Hoatzin and the regional endemic Wattled Curassow were restricted to várzea forest. None of the species were entirely restricted to igapó forest, which shared different complements of its avifauna with both várzea and terra firme forest. The most marked contrast in species composition was therefore between the bird assemblages of terra firme and várzea forest. This is not surprising given the spatial configuration of the igapó forest, which formed narrow corridors interdigitating the terra firme forest matrix along major perennial streams (Figure 1), but still retained the characteristics of a seasonally flooded environment.

These observations are supported by the MDS ordination (Figure 2). It is clear that terra firme and várzea forest diverged considerably in their bird assemblage composition, distinctly separated at opposite ends of the ordination diagram. The igapó forest sites (L and M) were similarly distinct, appearing to cluster between terra firme and várzea (Figure 2). Várzea transect K also abutted terra firme terraces and therefore had a similar bird assemblage to that of igapó. Várzea site G diverged from the other várzea sites (F, I, J, K) primarily due to higher encounter rates of terrestrial birds such as Great Tinamou and Undulated Tinamou.

The index of multivariate dispersion shows that várzea and igapó forests were more variable in their species composition and abundance (1.489 and 1.333, respectively) than terra firme forests (0.652).

Table 3. Summary of large-bodied bird population and biomass density in terra firme (TF), várzea (VZ) and igapó (IG) forests at Lago Uauacú, Brazil. For a full species list, see Table 2. Dashes signify that a species was not observed in a given forest type.

Species	Group size <sup>(1)</sup> ± SE			N <sup>(2)</sup>			Groups km <sup>-2(3)</sup> ± SE			Individuals km <sup>-2</sup>			Biomass kg/km <sup>-2(4)</sup>		
	TF	VZ	IG	TF	VZ	IG	TF	VZ	IG	TF	VZ	IG	TF	VZ	IG
Tinamidae															
(8 species)															
<i>Tinamus</i> spp. <sup>5</sup>	1.04 ± 0.02	1.11 ± 0.06	1.17 ± 0.17	156	103	6	1.62 ± 0.81	1.48 ± 0.16	0.72*	1.68 ± 0.84	1.64 ± 0.18	0.84	2.11	1.92	0.98
<i>Crypturellus</i> spp.	1.09 ± 0.02	–	1.0	158	–	1	1.28 ± 1.0	–	0.24*	1.4 ± 1.18	–	0.24	0.54	–	–
<i>Crypturellus undulatus</i>	–	1.24 ± 0.04	1.25 ± 0.25	–	203	4	–	3.75 ± 0.33	0.36*	–	4.65 ± 0.41	0.45	–	2.51	0.24
Anhimidae															
<i>Anhima cornuta</i>	–	1.96 ± 0.31	–	–	27	–	–	0.18 ± 0.05	–	–	0.35 ± 0.1	–	–	1.08	–
Anatidae															
<i>Cairina moschata</i>	–	1.6 ± 0.18	1.2 ± 0.13	–	47	10	–	0.72 ± 0.13	0.69 ± 0.29	–	1.15 ± 0.21	0.83 ± 0.35	–	2.93	2.12
Falconidae															
<i>Ibycter americanus</i>	4.39 ± 0.48	3.49 ± 0.4	2.5 ± 0.5	33	38	2	0.34 ± 0.07	0.31 ± 0.07	0.15*	1.49 ± 0.31	1.08 ± 0.24	0.38	0.87	0.63	0.22
Cracidae															
<i>Ortalis guttata</i>	–	3.9 ± 0.47	7.0	–	20	1	–	0.37 ± 0.09	0.15*	–	1.44 ± 0.35	1.05	–	0.79	0.58
<i>Penelope jacquacu</i>	1.75 ± 0.08	1.13 ± 0.09	1.4 ± 0.25	158	16	5	2.54 ± 0.24	0.17 ± 0.05	0.45*	4.45 ± 0.42	0.19 ± 0.06	0.63	5.70	0.24	0.81
<i>Mitu tuberosum</i>	1.36 ± 0.1	1.56 ± 0.09	1.58 ± 0.42	67	203	12	1.22 ± 0.22	2.21 ± 0.19	0.7 ± 0.25	1.63 ± 0.3	3.45 ± 0.3	1.11 ± 0.4	4.99	10.56	3.40
<i>Crax globulosa</i>	–	1.69 ± 0.16	–	–	26	–	–	0.33 ± 0.09	–	–	0.56 ± 0.15	–	–	1.68	–
Phasianidae															
<i>Odontophorus stellatus</i>	4.0 ± 0.34	–	–	34	–	–	1.09 ± 0.22	–	–	4.36 ± 0.88	–	–	1.35	–	–
Opisthocomidae															
<i>Opisthocomus hoazin</i>	–	1.57 ± 0.2	–	–	7	–	–	0.15 ± 0.06	–	–	0.24 ± 0.09	–	–	0.21	–
Psophiidae															
<i>Psophia leucoptera</i>	4.42 ± 0.38	3.75 ± 0.85	8.0	55	4	1	1.57 ± 0.28	0.09*	0.21*	6.94 ± 1.24	0.34	1.68	6.87	0.34	1.66

Table 3. Continued.

Species	Group size <sup>(1)</sup> ± SE			N <sup>(2)</sup>			Groups km <sup>-2(3)</sup> ± SE			Individuals km <sup>-2</sup>			Biomass kg/km <sup>-2(4)</sup>		
	TF	VZ	IG	TF	VZ	IG	TF	VZ	IG	TF	VZ	IG	TF	VZ	IG
Psittacidae (3 species)															
<i>Ara ararauna</i>	3.91 ± 0.83	3.93 ± 0.57	2.17 ± 0.4	11	15	6	0.23 ± 0.08	0.28 ± 0.08	0.54*	0.9 ± 0.31	1.1 ± 0.31	1.17	1.01	1.24	1.32
<i>Ara macao</i> and <i>A. chloropterus</i>	3.84 ± 0.45	3.41 ± 0.18	6.0 ± 0.54	37	180	5	0.47 ± 0.11	2.57 ± 0.27	0.3*	1.8 ± 0.42	8.76 ± 0.92	1.8	2.04	9.92	2.04
Ramphastidae (2 species)															
<i>Ramphastos</i> spp.	2.6 ± 0.17	1.78 ± 0.12	3.07 ± 0.68	239	126	28	4.83 ± 0.4	2.48 ± 0.31	2.77 ± 0.65	12.56 ± 1.04	4.41 ± 0.55	8.5 ± 2.0	11.54	4.05	7.81
<b>Species combined</b>				<b>948</b>	<b>1015</b>	<b>81</b>	<b>15.19</b>	<b>14.74</b>	<b>7.28</b>	<b>37.21</b>	<b>29.4</b>	<b>18.68</b>	<b>37.01</b>	<b>38.09</b>	<b>21.17</b>

<sup>1</sup>Mean group size obtained from all visual detection events.

<sup>2</sup>Number of individual detection events.

<sup>3</sup>All densities derived with DISTANCE (Thomas *et al.* 2002) using the Half-Normal model except \* where Kelker's method (Kelker 1945) was used.

<sup>4</sup>Biomass estimates calculated using data presented in Terborgh *et al.* (1990) and del Hoyo (1992, 1994, 1997, 2002).

<sup>5</sup>All large tinamous (*Tinamus* spp.) in várzea and igapó are great tinamou (*T. major*).



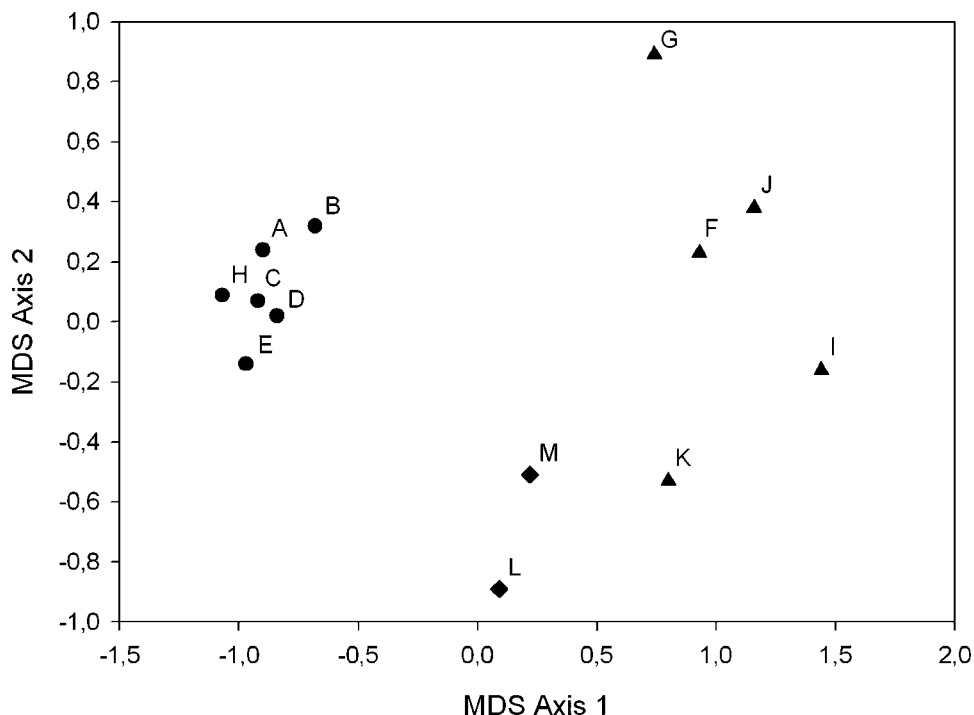


Figure 2. Non-metric multi-dimensional scaling (MDS) ordination of the large-bodied avifauna observed along the 13 transects in terra firme (circles), várzea (triangles) and igapó (diamonds) forest at Lago Uauaçu. Stress=0.05.

### *Patterns of abundance and biomass*

The aggregate population density of all 23 large-bodied bird species in terra firme forest was higher than that in várzea forest, despite the very similar group densities. Igapó forest had the lowest population densities, reflecting the few groups encountered in this forest type (Table 3).

However, despite the lower population density in várzea, the aggregate bird biomass of this forest type ( $38.1 \text{ kg km}^{-2}$ ) exceeded that of both terra firme ( $37.0 \text{ kg km}^{-2}$ ) and igapó forest ( $21.2 \text{ kg km}^{-2}$ ), although the terra firme estimate was only slightly lower than that of várzea. Razor-billed Curassow was the second heaviest bird in the sample (Table 2), and accounted for the highest biomass contribution for any bird in várzea. Despite its relatively small body mass, toucans contributed the highest fraction of the overall biomass in terra firme and igapó forest.

### *Habitat differences at the species level*

Although few large-bodied bird species were unique to any single forest type, there were marked between-habitat differences in population densities (Table 3). Some species were ubiquitous in all three forest types, but were more abundant in one or two than the other(s). For example, Spix's Guan, trumpeters and large toucans were far more common in terra firme than in várzea and igapó forest, whereas Razor-billed Curassows and red macaws were far more common in várzea than in either terra firme or igapó forest (Table 3). In fact, evidence from our censuses and additional observations made throughout the study suggest that there is a clear habitat partitioning between the macaw species. Blue-and-yellow Macaws seem to be more abundant

than the two red macaws in igapó forests around the lake (Table 3) and in the lake headwaters which were distinctive by extensive igapó forests, whereas the two latter species massively outnumbered the former in the várzea floodplains. We also note that although all large tinamous were pooled in the analysis, only the Great Tinamou was observed in both types of flooded forest. Its congeners, the Grey Tinamou and White-throated Tinamou, did not appear to venture into these riparian habitats.

## Discussion

### *Species richness, abundance and biomass*

There are few accurate descriptions of entire avifaunal assemblages in lowland Amazonia (e.g. Cohn-Haft *et al.* 1997), and this is especially the case of seasonally inundated forests. Moreover, most avian studies in poorly known Neotropical forest localities are restricted to species checklists and rarely provide abundance data even for a single forest type. From the inventories that have been published, however, we can surmise that the composition of the large-bodied avifauna at Lago Uauacú is similar to that of other central and western Amazonian sites (Terborgh *et al.* 1984, 1990, Peres and Whittaker 1991). Likewise, it appears that both várzea and igapó forests studied here contained all the species expected to occur in these environments (Remsen and Parker 1983, Rosenberg 1990, Borges and Carvalhaes 2000). The major absentees in our checklist of large-bodied species encountered during census walks are non-forest birds associated with open water (herons, egrets, anhinga, cormorant, ibis) that usually occurred along lake margins and rivers. We also failed to detect piping guans (*Pipile* spp.) during censuses. Piping guans were consistently rare throughout the year at Lago Uauacú, and were observed only three times outside the censuses along the lake edge close to human habitation.

Similarly, a handful of studies from non-hunted sites suggest that the Lago Uauacú region supports an intact population of large-bodied birds (Terborgh *et al.* 1990, Thiollay 1994, Begazo and Bodmer 1998). In fact, some species in these assemblages occurred at higher densities in the forests at Lago Uauacú than at other sites such as Cocha Cashu in southern Peru (Terborgh *et al.* 1990).

On the other hand, the total biomass of bird species censused in a mature floodplain forest at Cocha Cashu was estimated to be  $160 \text{ kg km}^{-2}$  (Terborgh 1986). This is considerably higher than our estimates for the Lago Uauacú terra firme, várzea and igapó forests. A substantially higher biomass estimate is still obtained when we consider only those species included in this study (or their related congeners), by adding up the respective biomass estimates presented in Terborgh *et al.* (1990). Given that hunting pressure is unlikely to have negatively affected the bird populations in both regions, this may be an artefact of different sampling methodologies. However, forest type is an important determinant of Amazonian vertebrate diversity, abundance and biomass (Peres 1997, 1999b, Peres and Janson 1999, Haugaasen and Peres 2005a, b), and even at small spatial scales, changes in topography, soil characteristics and productivity appear to be associated with different species assemblages (Emmons 1984, Terborgh *et al.* 1996). Consequently, any direct comparisons between sites, even with a similar avifauna, may be confounded by environmental variables nested within forest type. It is, however, clear that where detailed observations of the avifauna have been made, tinamids, cracids and ramphastids contribute substantially to the avian biomass (Terborgh *et al.* 1990, Thiollay 1994, Robinson *et al.* 2000) - as was the case at Lago Uauacú.

### *Spatial characteristics of the bird assemblages*

The occurrence of large birds associated with water such as Hoatzin, Horned Screamer and Muscovy Duck (see e.g. Gill *et al.* 1974, Naranjo 1986, Rosenberg 1990, Peres and Whittaker 1991, del Hoyo *et al.* 1994, Domínguez-Bello *et al.* 1994) distinguished seasonally flooded from unflooded forests at Lago Uauacú, with hoatzins and horned screamers being restricted to the

white-water várzeas. In addition, Speckled Chachalacas, which were restricted to sites subjected to high rates of canopy disturbance, were conspicuously absent in terra firme forests. In contrast, terra firme forests were distinctive by the presence of several forest interior ground-dwelling species such as wood-quail and several tinamou species. This is not surprising since várzea and igapó forests are semi-aquatic habitats submerged for as long as six months of the year, and várzea forests were additionally dissected by numerous river channels and leveés which enabled the persistence of birds associated with water even during the dry season.

Seasonal changes in the structure of the large-bodied bird assemblages are not examined here. However, our data show that predominantly terrestrial bird species were absent from várzea forest during the prolonged inundation period (Haugaasen 2004). The assemblage divergence between terra firme and várzea forests is thus primarily attributed to a number of unique bird species and seasonal changes in abundance exhibited by some species in the latter forest type associated with fluctuations in water-level. However, these flooded forest features are less pronounced in igapó forest due to its intimate interdigitation and physical connectivity with the predominant terra firme forest matrix. The importance of between-habitat connectivity is supported by the intermediate placement of várzea transect K in the MDS ordination (Figure 2), which also abutted terra firme forest terraces (Figure 1). Transect G, however, dissected várzea forest which lay on higher ground and therefore exhibited a delayed flood pulse. Its position in the ordination is therefore due to increased encounter rates of terrestrial birds at this location after the low-lying várzea sites (F, I, J and K) had already been flooded.

The spatial characteristics of the bird assemblages thus appeared to be partly a function of physical connectivity and proximity to adjacent terra firme forests, in addition to the strong seasonality of flooded forests. However, these variables are expected to be less important for bird assemblages than for other large vertebrate taxa. Firstly, most large-bodied birds are arboreal and in principle not affected by seasonal floods. Secondly, birds are capable of flight and the relatively narrow ~50 m wide paranã channel, which separated transect F, G, I and J from the others (Figure 1), is therefore not a sufficiently effective fluvial barrier for the dispersal and movements of large birds in the region. This is supported by observations of an Undulated Tinamou, which are considered to have limited flight capability, crossing a 500 m gap of open water (Remsen and Parker 1983). In addition, some ground-foraging species at Lago Uauaçú, such as the Great Tinamou, Undulated Tinamou and Pale-winged Trumpeter, timed their appearances in várzea and igapó forest with the low-water season, and this occurred even in the várzea sites F, G, I and J which were separated from neighbouring forest by terra firme the ~50 m wide paranã channel (Haugaasen 2004). Such seasonal movements may not only be linked to the availability of dry land, but are likely to be intimately related with ephemeral pulses in fruit availability and the deposition of fruits and seeds on the forest floor as the várzea water level receded (Haugaasen and Peres 2007). Indeed, the local abundance of the most wide-ranging of all bird taxa considered here (macaws) at Lago Uauaçú was correlated with monthly estimates of fruit availability in terra firme and várzea forest (Haugaasen and Peres 2007). The importance of igapó in the overall forest matrix is reinforced by the apparently heavy reliance of macaws on immature seeds of rubber trees (*Hevea spruceana*, Euphorbiaceae) during months of fruit scarcity. This tree species was one of the most abundant in both várzea and igapó forest (Haugaasen 2004) and macaws could strip several trees bare within a relatively short period of time (T. Haugaasen, pers. obs.). The ability to range widely across macro-habitats, select ephemeral feeding sites, and include within the home range different habitats exhibiting staggered temporal peaks of food resources (Haugaasen & Peres 2005c) thus seem to be important for several large-bodied bird species at Lago Uauaçú.

### Conservation implications

From a conservation perspective, our results have important implications for the habitat configuration and landscape design of large protected areas. We have shown that a

heterogeneous mosaic of upland and flooded forests is expected to contain a larger number of species, support larger landscape-wide population sizes for species occurring in all forest types and safeguard highly mobile species that appear to depend on different forest types at different times of the year. The importance of such a forest mosaic is even more pronounced if one considers the entire Amazonian avifauna. Remsen and Parker (1983) found that 15% of all bird species in Amazonian forests are restricted to riverine or lake-edge habitats such as igapó and várzea forests, and many species that are largely restricted to terra firme forests are at least seasonally subsidized by riparian or lacustrine habitats.

Additionally, many large-bodied birds such as the cracids, trumpeters and large tinamous are particularly sensitive to hunting (Silva and Strahl 1991, Bodmer 1995, Peres 2000, Peres & Palacios 2007). Of these, cracids seem to be the most vulnerable and are now one of the most threatened bird families in Neotropical forests (Collar *et al.* 1992, Galetti *et al.* 1997, Strahl *et al.* 1997). As these large forest-dwelling birds reach their greatest diversity in the Amazon region (del Hoyo *et al.* 1994, Strahl *et al.* 1997), this translates into a serious conservation concern. Floodplain forests in our region contained the highest population densities of some cracids such as the Razor-billed Curassow and these forests therefore play an important role in the conservation of these species.

Perhaps the most noteworthy species record in this study is the occurrence of Wattled Curassows in our várzea study area. Very little is known about this threatened species (cf. Bennett 2000), which has an extremely patchy distribution across western Amazonia (Collar *et al.* 1992, M. Cohn-Haft, pers. comm.). At Lago Uauaçu, this species was locally abundant within only a small area of várzea forest. This is consistent with reports of *C. globulosa* occurring exclusively in várzea forests and river-islands (Hilty and Brown 1986, Bennett 2000).

In summary, it is clear that the juxtaposed configuration of terra firme and floodplain forests at Lago Uauaçu increased the bird  $\beta$ -diversity of this region, ensuring the persistence of healthy populations of large birds of conservation concern such as cracids. Seasonally inundated Amazonian forests thus form an important complement to terra firme forest in terms of regional-scale biodiversity conservation and should be explicitly considered in large-scale conservation planning.

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