Rarity of birds in the Jaú National Park, Brazilian Amazon

S. H. Borges

Borges, S. H., 2006. Rarity of birds in the Jaú National Park, Brazilian Amazon. *Animal Biodiversity and Conservation*, 29.2: 179–189.

Abstract

Rarity of birds in the Jaú National Park, Brazilian Amazon.— The rarity patterns of 368 bird species recorded in the Jaú National Park (JNP), Brazilian Amazon, were analysed using the method of seven forms of rarity based on the interaction of geographical distribution, habitat specificity, and local population size. Rare species were identified in a wide taxonomic, ecologic and body size spectrum, indicating the complexity of distinguishing rare and common species. Birds with large populations tended to occupy several habitats in a highly significant relationship. General rarity was not correlated with body size. Birds foraging in ground, understory and antbirds (Thamnophilidae and Formicariidae), were identified as especially rare in JNP. The method of seven forms of rarity is useful as a first step in identifying rare species for conservation purposes since it considers several biological features at once.

Key words: Amazonian birds, Extinction, Rarity, Neotropical birds.

Resumen

Rareza de aves en el Parque Nacional de Jaú, Amazonia Brasileña.— Los patrones de rareza de 368 especies de aves en el Parque Nacional de Jaú (PNJ), Amazonia Brasileña, fueron analizados usando el método de las siete formas de rareza basado en la interacción de distribución geográfica, especificidad de hábitat y tamaño de la población local. Las especies raras fueron identificadas según un amplio espectro taxonómico, ecológico y de tamaño del cuerpo lo que explica la complejidad de distinguir especies raras y comunes. Las aves con poblaciones grandes tienden a ocupar varios hábitats en una relación altamente significativa. No fue encontrada ninguna correlación entre rareza y tamaño del cuerpo. Las aves que forrajean en el suelo, sotobosque y hormigueros (Thamnophilidae y Formicariidae) fueron consideradas como especialmente raras en el PNJ. El método de las siete formas de rareza es útil como primer paso en la identificación de especies raras en proyectos de conservación ya que considera varias características biológicas al mismo tiempo.

Palabras clave: Aves amazónicas, Extinción, Rareza, Aves neotropicales.

(Received: 23 VI 06; Conditional acceptance: 29 XI 06; Final acceptance: 27 XII 06)

Sérgio Henrique Borges, Museu Paraense Emílio Goeldi, Depto. de Zoologia, Av. Perimetral 1901/1907, 66077–530, Belém, PA, Brazil.

Current address: Fundação Vitória Amazônica, R. Estrela D'Alva, casa 07, Conjunto Morada do Sol, Aleixo, 69060–510, Manaus, AM, Brazil. E-mail: sergio@fva.org.br

Introduction

Protection of ecosystems or individual species threatened by extinction are common strategies to conserve biodiversity. Protection of individual species in tropical regions is limited by the relative scarcity of natural history information. To deal with this limitation, conservation biologists identify features that make species susceptible to extinction (Terborgh, 1974; Terborgh & Winter, 1980; Arita et al., 1990). Since rare species tend to be more susceptible to extinction (Terborgh & Winter, 1980; Dobson et al., 1995; but see Karr, 1982 for exceptions) determining the relative rarity of a particular species can be useful in defining its conservation status.

At least two complementary approaches have been adopted by researchers in the study of rarity: temporal and static (Dobson et al., 1997). The temporal approach implies monitoring populations and updating natural history information of species identified as threatened by extinction. This approach is used by conservation institutions such as IUCN and Birdlife International. The static approach uses general biological parameters to classify species into rarity categories (Dobson et al., 1997; Yu & Dobson, 2000). The static approach deals with qualitative and less-detailed biological information to identify species that require further study of their conservation status (Roma, 1996; Dobson et al., 1997).

The most popular method for the static analysis of rarity is the seven forms of rarity proposed by Rabinowitz et al. (1986), based on geographical distribution, habitat specificity and local population size. In this method, species with reduced geographic distributions, low abundance, and restricted habitat use show the highest level of rarity. In contrast, species with wide geographical distributions that use several habitats and have large populations are considered common. Researchers have considered the method of Rabinowitz et al. (1986) simple and useful and have applied it to investigate patterns of rarity in plants (Rabinowitz et al., 1986; Pitman et al., 1999), butterflies (Thomas & Mallorie, 1985), birds (Kattan, 1992; Goerk, 1995; Roma, 1996), and mammals (Yu & Dobson, 2000).

The rarity of Neotropical birds has been investigated in regions severely impacted by human activities in Colombia and Brazil (Kattan, 1992; Goerk, 1995; Roma, 1996). In this study the method of Rabinowitz et al. (1986) is applied to investigate patterns of rarity in the resident avifauna of the Jaú National Park (JNP), a region dominated by relatively undisturbed habitats. The avifauna of the region has been studied over the last 10 years (Borges et al., 2001; Borges, 2004a), providing an opportunity to investigate natural patterns of rarity. The principal aim of this study was to investigate the rarity of birds in a specific region of the Amazon and compare the results with other studies to evaluate the generality of rarity patterns obtained in distinct ecological and geographic context in the Neotropics. The paper also analyses the importance of ecological traits of birds such as body size and diet to determine the rarity in JNP avifauna. These traits were chosen since they have been found to correlate with rarity and susceptibility to extinction in several studies (Terborgh, 1974; Willis, 1979; Kattan, 1992). Specifically, the following questions were asked: (1) what proportion of JNP avifauna fall into each of the rarity categories proposed by Rabinowitz et al. (1986)? (2) are rarity patterns associated with different guilds and taxonomic affiliations or are they random, or at least independent of, ecological and taxonomic groupings? (3) is there a relationship between rarity categories and the body size of birds? (4) are the patterns of rarity in JNP avifauna similar to other Neotropical sites?

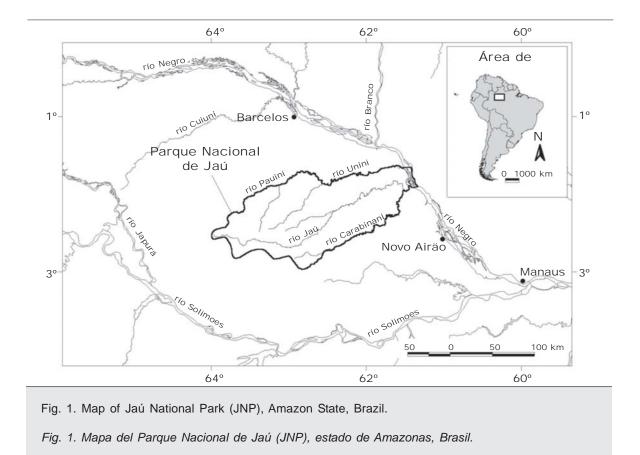
Material and methods

Study area

Jaú National Park (JNP) covers 2,272,000 ha and is located in the central region of the Brazilian Amazon on the west bank of the lower portion of the Rio Negro (fig. 1). Several forest and nonforest vegetation types compose the complex landscape of the region which is dominated by natural or near-undisturbed vegetation (Borges et al., 2001). Terra firme forest is the dominant vegetation in the region, covering approximately 70% of JNP (Ferreira & Prance, 1998). The next most common habitat type at JNP is igapó forest, occupying approximately 12% of the JNP area. Igapó forests are forests that are seasonally inundated by blackwater rivers and streams and the floristic composition is very distinct from terra firme forests (Ferreira, 1997). JNP also has small areas of vegetation associated with sandy soils generally categorized as campinaranas, low-canopy woods and campinas; open fields with sparse cover of small trees (Anderson, 1981; Vicentini, 2004). Other vegetation types found at JNP include palm forests (buritizais) and a mosaic of disturbed vegetation resulting from human activities, mainly traditional agriculture. These vegetation types occupy only a very small proportion of the JNP area.

Parameters of rarity

The JNP Bird Checklist, updated with recent fieldwork, was used to examine rarity patterns (Borges et al., 2001; Borges, S. H., unpublished data). Aquatic (e.g. herons) and migrant species were omitted from the analyses. Birds were identified to subspecies by examining geographical distributions of subspecies and comparing birds collected in the region with voucher specimens deposited in the Museu Paraense Emílio Goeldi bird collection (Borges, 2004a). The catalogues of Pinto (1944, 1978) and more recent taxonomic revisions of selected species (e.g. Isler et al., 1999; Zimmer & Whittaker, 2000; also see Borges, 2004a for a more extensive list of references) were used to classify



specimens to subspecies. The taxonomic rank of subspecies was chosen because it more accurately depicts the geographical distributions of the taxons. For example, the Great Tinamou (*Tinamus major*), a bird widely distributed in the Amazon basin, has 12 different subspecies with a much more restricted geographical distribution (Del Hoyo et al., 1992). A potential problem in using subspecies in the analysis is that future taxonomic revisions could demonstrate that some taxa considered here are not valid taxonomic entities. However, recent taxonomic studies on Neotropical birds, including some taxons analysed here, resulted in recognition of several subspecies as good species (e.g. Isler et al., 1999).

The method of seven forms of rarity requires information on geographical distribution, with species classified as either widespread or restricted; habitat specificity, with species categorized as specialists or generalists; and population size, with populations considered either large or small. For each of these parameters, the following procedure was adopted:

Geographical distributions

Bird species or subspecies distributed along the northwestern edge of the Amazon basin, mainly north of the Rio Amazonas and west of the Rio Negro, were classified as having a restricted geographical distribution. The range of some of these

species extends into more eastern regions of the Amazon (e.g. Roraima state in Brazil), but they are likely not found in the Guyana. Birds distributed in more than one sector of the Amazon Basin (e.g. both west and east of the Rio Negro) were considered to have a wide distribution. This classification included a few exceptions. The antwren Myrmotherula klagesi, for example, is found along the upper Rio Tapajós and lower Rio Negro and may be categorized as a widely distributed species. However, the known range of *M. klagesi* is very small and associated with fluvial islands (Ridgely & Tudor, 1994). The catalogues of Pinto (1944, 1978), Ridgely & Tudor (1989, 1994) and Del Hoyo et al. (1992, 1993, 1996, 1997, 1999, 2001, 2002, 2003, 2004) were used to determine the geographical distributions of bird species and subpecies.

Habitat specificity

Bird species were classified by habitat according to information in the JNP Checklist (Borges et al., 2001). This classification was modified in some cases, according to more recent field observations. A bird species was considered a habitat specialist if it was recorded in only one habitat type; those recorded in more than one habitat type were considered generalist species. Only natural or near–undisturbed habitats were considered in this classification.

Population size

This is the hardest information to obtain due to the difficulty of quantitatively evaluating bird populations in tropical ecosystems. General classifications such as rare, infrequent, or common have been adopted in bird rarity studies (Kattan, 1992; Goerck, 1997). The populations of bird species in JNP were categorized as large or small in a qualitative way based on a previous ten-year field study complemented with quantitative studies (Borges & Carvalhaes, 2000; Borges et al., 2004; Borges, 2004a). The absolute population size was considered. The hummingbird Polytmus theresiae, for example, is a common bird in campinas, but the population was considered small since campinas make up a very small proportion of the region, making this species rare when considering JNP as a whole.

Statistical analyses

The parameters described above make-up an eight-cell matrix (table 1) into which each bird species is incorporated. Each cell in the matrix was numbered one through four indicating the vulnerability index (VI) of a species (Goerk, 1995). The values one through three indicate whether a species is considered rare in one, two, or three of the rarity parameters. Species that are not rare in any of the three parameters received the number four, and are assumed to have low vulnerability to extinction. Rarity was analyzed considering all three parameters (global rarity), as well as considering only population size and habitat specificity (local rarity). On a local scale, a species was rare if it had a small population and used only one habitat. A G-test was used to test for dependence among the rarity parameters and separate γ^2 tests for pairwise comparisons among parameters (2 x 2 contingency tables). In order to examine relationships among vulnerability index and body size, bird species were classified as small (below median weight) or large (above median weight). The body size data (weight in grams) was taken from previous JNP field work or the literature (Borges, unpubl. data; Karr et al., 1990; Del Hoyo et al., 1992, 1993, 1996, 1997, 1999, 2001, 2002, 2003, 2004). Guild membership was determined by diet (e.g. frugivores, insectivores etc.) and foraging strata (ground, understory and canopy), and was based on literature (Karr et al., 1990) and personal field experience. Homogeneity tests (χ^2) were used to see if birds from different guilds and families were homogeneously distributed across vulnerability categories.

Results

Forms of rarity

Rarity patterns of 368 bird species distributed across 40 families or subfamilies were considered in this

study (annex 1). Most species (77%) have a wide geographical distribution throughout the Amazon Basin. Approximately 83 species (23%) are restricted to the northwestern part of the Amazon basin, mostly north of the Rio Amazonas and west of the Rio Negro. Almost half (46%) the birds are restricted to only one habitat and approximately 106 (29%) were classified as having small populations. The majority of species (58%) were classified as rare in one (124 species) or two (89 species) of the three rareness measures (table 1). One hundred and thirty–six species (37%) were classified as not rare in any of the three parameters (table 1). In contrast, only 19 species were considered rare in all three parameters.

The parameters defining rarity were not independent of each other (G = 68.11, df = 3, p < 0.01). The geographical distribution of species was not significantly associated with population size or habitat specificity (table 2). In contrast, birds with large populations tended to occupy several habitats in a highly significant relationship (table 2).

Population size and habitat specificity determined the rarity of birds at a local scale. Accordingly, 170 species were restricted to one habitat, while 198 were habitat generalists. In terms of population size, 262 bird species had large populations and 106 small. Eighty-four species were both habitat specialists and had small populations, these being the rarest birds in JNP. The majority of the locally rare species were restricted to either *igapó* flooded forest (n = 37) or *terra firme* forest (n = 34). Few rare species were specialists of *campinas* (n = 8) and *campinaranas* (n = 5).

There was no difference in the mean weight of habitat specialists $(148 \pm 29 \text{ g}, \text{ n} = 170)$ and generalists $(150 \pm 28 \text{ g}, \text{ n} = 198; T \text{ value} = -0.042, \text{df} = 366, P = 0.48)$. In contrast, birds with small populations at JNP were heavier $(231 \pm 59 \text{ g}, \text{ n} = 106)$ than species with large populations $(116 \pm 15 \text{ g}, \text{ n} = 262)$ (T value = 2.62, df = 366, P = 0.005).

Guilds and rarity patterns

No significant association was found between the vulnerability index and diet of bird species in either global ($\chi^2 = 12.75$, df = 12, P = 0.387) or local analyses ($\chi^2 = 0.96$, df = 34, P = 0.91). In contrast, the vulnerability index was significantly associated with foraging strata ($\chi^2 = 14.87$, df = 6, p = 0.02), with more ground– and understory–foraging birds falling into the highly vulnerable category (IV1) than expected by chance.

Body size was not related to vulnerability within diet categories. The mean weights of rare and common species at a local scale were not different from each other when compared within diet groups (T test, P < 0.10 for all comparisons).

Significant associations were found between population size and habitat specificity in canopy insectivores ($\chi^2 = 8.77$, df = 1, P = 0.003), understory

Table 1. Number and proportions of bird species in Jaú National Park distributed across the seven forms of rarity of Rabinovitz et al. (1986). The numbers in parenthesis are vulnerability index.

Tabla 1. Número y porcentaje de especies de aves en el Parque Nacional de Jaú distribuidas entre las siete formas de rareza de Rabinovitz et al. (1986). Los números entre paréntesis son los índices de vulnerabilidad.

	Geographic distribution				
	Wide		Restricted		
	Several	One	Several	One	
Large	Large population				
	136–37% (4)	67–18% (3)	40–11% (3)	19–5% (2)	
Sma	II populatio	n			
	17–5% (3)	65–18% (2)	5–1% (2)	19–5% (1)	

insectivores (χ^2 = 63.574, df = 1, *P* = 0.0000), and canopy omnivores (χ^2 = 8.20, df = 1, *P* = 0.004). In all cases, species with large populations occupied several habitats and species restricted to one habitat were near–equally distributed in both large and small populations.

Taxonomic affiliation and rarity patterns

Comparisons within bird families with large sample sizes (more than 20 species) showed that antbirds (Thamnophilidae and Formicariidae) had a greater number of species in the high vulnerability categories (VI 1 and 2) than expected by the general distribution (χ^2 = 8.51, df = 3, *P* = 0.03). In contrast, the flycatchers (family Tyrannidae) had more species in the low vulnerability categories (IV 3 and 4) than expected (χ^2 = 8.53, df = 3, *P* = 0.03).

Analysis at a more refined taxonomic level is constrained by the reduced sample sizes. However, the genus *Myrmotherula* is illustrative, as there are 10 species in the JNP region. One species (*M. klagesi*) was considered rare in all three parameters, four species (*M. ambiqua, M. haematonota, M. multostriata*, and *M. assimilis*) were rare in two parameters, and one species (*M. cherriel*) was rare in one parameter (geographical distribution). Four species (*M. brachyura, M. axillaris, M. longipennis*, and *M. menetriesii*) were classified as common in all three parameters.

No relationship was detected between body size and rarity at global or local scales in within-family analyses. Neither was there any difference in the Table 2. Number of bird species of Jaú National Park distributed across rarity-defining parameters. *P* -values were obtained from χ^2 tests of independence.

Tabla 2. Número de especies de aves del Parque Nacional de Jaú distribuidas según los parámetros que definen rareza. Los valores P fueron obtenidos a través de pruebas χ^2 de independencia.

Rarity defining parameters

Geographic distrib ($P = 0.93$; df = 1)	ution x habi	tat
(/ = 0.00, 01 = 1)	One	Several
Wide	132	153
Restricted	38	45
Geographic distrib ($P = 0.91$; df = 1)	ution x popu	lation
	Large	Small
Wide	203	82
Restricted	59	24
Habitat x population $(P = 0.000; df = 1)$		
	Large	Small
One	86	84
Several	176	22

mean weight of rare and common species at the local scale (T test, P < 0,10 for all comparisons).

There was a strong dependence of population size on habitat specificity among the antbirds ($\chi^2 = 17$, df = 1, P < 0.001), with species restricted to one habitat tending to have small populations. The same pattern was observed in ovenbirds and woodcreepers (Furnariidae and Dendrocolaptidae) ($\chi^2 = 6.74$, df = 1, P = 0.009). In this case, however, birds with high habitat specialization were near–equally distributed in large and small populations.

Discussion

Rarity in Neotropical avifaunas

The seven forms of rarity methodology has been applied to other Neotropical regions, including the Andean region of Colombia (Kattan, 1992), Brazilian Atlantic forest (Goerck, 1997), and eastern Amazon (Roma, 1996). Several modifications to the original methodology were made in these studies. For example, birds were identified to subspecies only in the JNP and eastern Amazon studies (Roma, 1996). Although these differences may influence comparability among studies, these four studies allow us to search for general patterns of rarity in Neotropical birds.

Geographical distribution, population size and habitat specificity were found to be inter-dependent in all studies. However, only in JNP was geographical distribution independent of population size and habitat specificity, suggesting that the importance of geographical distribution to define patterns of rarity in birds vary among the regions. Indeed, the proportion of species with restricted distributions was higher in the Andes (61%) and Atlantic Forest (30%) compared with JNP (23%). This pattern likely results from the fact that the geographic range of birds in the Andean region and, perhaps in Atlantic forests, tends to be narrower and defined by a highly fragmented (naturally and anthropogenic) montane landscape (Peterson & Watson, 1998). In contrast, the distribution of Amazonian birds is broadly delimited by large expanses of lowland forest subdivided by the major rivers (Peterson & Watson, 1998; Haffer, 1992).

The proportion of species with a small population is similar in the Andes (34%), the Atlantic forest (31%) and the JNP (29%). In contrast, habitat specialists are responsible for a larger proportion of species in Andes (62%) and Atlantic forest (63%) than in JNP (46%). Habitat specialists in Colombia, Atlantic Forest and eastern Amazon were birds found only in primary forests and generalists were also found in edges and secondary habitats. In the current study, all non-anthropogenic vegetation types (forest and non-forests) found in JNP were considered in habitat categorization. The differences in proportion of habitat specialists could result from distinct criteria used for setting the habitat specialization in the studies compared.

Species of the families Dendrocolaptidae, Thamnophilidae, Formicariidae and Furnariidae have been identified as especially rare in Colombia and eastern Amazon (Kattan, 1992; Roma, 1996). In JNP, only the antbirds show a tendency towards intrinsic rarity. The flycatchers (Tyrannidae), in contrast, tend to have large populations and occupy several habitats. Bird families traditionally recognized as rare and threatened by extinction, such as Accipitridae (hawks) and Psittacidae (parrots), were not identified as especially rare in JNP, but were so in the Andes and eastern Amazon. The antwrens (genus Myrmotherula) and the tyrant flycatchers (genus Hemmitricus) are prone to rarity and highly threatened by extinction in the Atlantic forest (Goerck, 1997). In contrast, members of these genera exhibit variable levels of rarity in JNP (annex 1).

Insectivorous and frugivorous birds were disproportionately rare in the eastern Amazon, Colombia, and Atlantic Forest (Kattan, 1992; Goerck, 1997; Roma, 1996). In contrast, no relationship was found among rarity categories and feeding guilds in the JNP avifauna. Canopy omnivores had an excess of species in the less–vulnerable categories in eastern Amazon (Roma, 1996). This relationship was not found in the JNP avifauna, but a high number of flycatcher species, most of them canopy omnivores, also fell into less vulnerable categories of rarity (IV3 and IV4).

Body size has been identified as a good indicator of rarity in mammals (Arita et al., 1990; Dobson & Yu, 1993; Yu & Dobson, 2000). In birds, however, the relationship between body size and rarity is highly variable among taxons, guilds and scales of analyses. In this study, no correlation was found between general rarity and body size, although large birds tended to have small populations. In the eastern Amazon a significant, yet weak, correlation between body size and both global (rs = 0.127) and local (rs = 0.174) vulnerability (Roma, 1996) was found. In Colombia, rare frugivorous birds and tanagers (Thraupinae) tended to be larger than common species (Kattan, 1992).

The studies compared herein were conducted in distinct ecological zones (e.g. Andes region, Amazon lowland) with different levels of habitat degradation in a widespread Neotropical region. Although some coincident results emerge, no largely consistent patterns of bird rarity were found. Uncertainly remains whether these inconsistencies result from modifications in Rabinowitz et al.'s (1986) method or are due to inherent characteristics of different Neotropical avifaunas.

Conservation

Results of this study call attention to several factors that, if focused on, may strengthen future studies of rarity in Neotropical birds. Population size is strongly associated with habitat specificity. Some of the rarest birds of JNP are found in very restricted habitats such as campinas (e.g. Polytmus theresiae, Formicivora grisea, and Schistochlamys melanopis), igapó flooded forests (e.g. Nonnula amaurocephala), or fluvial islands (e.g. Thamnophilus nigrocinereus and Myrmotherula klagesi). This finding reinforces the importance of habitat heterogeneity to regional bird distribution in the Amazon basin (Remsem & Parker, 1983; Rosenberg, 1990; Kratter, 1997; Whitney & Alvarez, 1998; Borges & Carvalhaes, 2000; Borges, 2004b). The inclusion of local vegetation heterogeneity in the sampling design for biological inventories is crucial in rarity analyses.

The taxonomic categories adopted also affect the results of rarity studies (Goerck, 1997). This is particularly relevant in the Amazon basin, where a high number of polytypical species is found and the application of Biologal Species Concept underestimates the bird species diversity (Bates et al., 1998; Bates & Demos, 2001). In these cases, geographical distributions of species can only be accurately delimited by analyzing the distributions of subspecies involved. Moreover, subspecies ranking is suggested to be useful in conservation analysis, especially in the Neotropics (Bates & Demos, 2001; Phillimore & Owens, 2005). Rare species were singled out of a large pool of species, across a wide taxonomic, ecologic and body size spectrum. Even species in the same genus with similar diet and body size varied greatly in rarity. Such variability complicates the process of distinguishing between rare and common species. Because it considers several biological features in conjunction, the methodology of seven forms of rarity is especially useful as a first approximation to identifying rare species for conservation purposes (Roma, 1996).

Acknowledgments

Financial and logistical support for this study came from WWF–Brazil, Fundação Vitória Amazônica, and CAPES. Technicians at Fundação Vitória Amazônica, especially S. Iwanaga, C. Durigan, R. von Lira and Marcelo Moreira, provided much help throughout the study. My Ph. D. committee, A. Aleixo, M. Luiza, T. Cristina, M. A. dos S. Alves, L. P. Gonzaga, and J. M. Cardoso da Silva (adviser) reviewed an early version of the manuscript and made helpful contributions. Catherine Bechtoldt did the English proofreading.

References

- Anderson, A., 1981. White–sand vegetation of Brazilian Amazonia. *Biotropica*, 13: 199–210.
- Arita, H., Robinson, J. G. & Redford K. H., 1990. Rarity in neotropical forest mammals and its ecological correlates. *Conservation Biology*, 4: 181–192.
- Bates, J. M. & Demos, T., 2001. Do we need to devalue Amazonia and other large tropical forests? *Diversity and Distributions*, 7: 249–255.
- Bates, J. M., Hackett, S. & Cracraft, J., 1998. Arearelationships in the Neotropical lowlands: an hypothesis based on raw distributions of Passerine birds. *Journal of Biogeography*, 25: 783–793.
- Borges, S. H., 2004a. Avifauna do Parque Nacional do Jaú: um estudo integrado em ecologia de paisagens, biogeografia e conservação. Ph. D. Thesis, Univ. Federal do Pará/Museu Paraense Emílio Goeldi, Bélem, Pará.
- 2004b. Species poor but distinct: bird assemblage in white sand vegetation in Jaú National Park, Brazilian Amazon. *Ibis*, 146: 114–124.
- Borges, S. H. & Carvalhaes, A., 2000. Bird species of black water inundation forests in the Jaú National Park (Amazonas State, Brazil): Their contribution to regional species richness. *Biodiversity and Conservation*, 9: 201–214.
- Borges, S. H., Cohn–Haft, M., Carvalhaes, A. M. P., Henriques, L. M., Pacheco, J. F. & Whittaker, A., 2001. Birds of Jaú National Park, Brazilian Amazon: species check–list, biogeography and conservation. *Ornitologia Neotropical*, 12: 109–140.
- Borges, S. H., Henriques, L. M. & Carvalhaes, A., 2004. Density and habitat use by owls in two

Amazonian forest types. Journal of Field Ornithology, 75: 176–192.

- Del Hoyo, J., Elliot, A. & Sargatal, J. (Eds.), 1992. Handbook of the Birds of the World. Vol. 1, Ostrich to Ducks. Linx Edicions, Barcelona.
- 1993. Handbook of the Birds of the World. Vol. 2, New World Vultures to Guineafowl. Linx Edicions, Barcelona.
- 1996. Handbook of the Birds of the World. Vol. 3, Hoatzin to Auks. Linx Edicions, Barcelona.
- 1997. Handbook of the Birds of the World. Vol. 4, Sandgrouse to Cuckoos. Linx Edicions, Barcelona.
- 1999. Handbook of the Birds of the World.
 Vol. 5, Barn–Owls to Hummingbirds. Linx
 Edicions, Barcelona.
- 2001. Handbook of the Birds of the World. Vol. 6, Mousebirds to Hornbills. Linx Edicions, Barcelona.
- 2002. Handbook of the Birds of the World. Vol. 7, Jacamars to Woodpeckers. Linx Edicions, Barcelona.
- 2003. Handbook of the Birds of the World. Vol. 8, Broadbills to Tapaculos. Linx Edicions, Barcelona.
- 2004. Handbook of the Birds of the World. Vol. 9, Cotingas to Wagtails. Linx Edicions, Barcelona.
- Dobson, F. S., Smith, A. T. & Yu, J., 1997. Static and temporal studies of rarity. *Conservation Biology*, 11: 306–307.
- Dobson, F. S. & Yu, J., 1993. Rarity in Neotropical forest mammals revisited. *Conservation Biology*, 7: 586–591.
- Dobson, F. S., Yu, J. & Smith A. T., 1995. The importance of evaluating rarity. *Conservation Biology*, 9: 1648–1651.
- Ferreira, L. V., 1997. Effects of the duration of flooding on species richness and floristics composition in three hectares in Jaú National Park in floodplain forest in Central Amazonia. *Biodiversity* and Conservation, 6: 1353–1363.
- Ferreira, L. V. & Prance, G. T., 1998. Species richness and floristic composition in four hectares in the Jaú National Park in upland forests in Central Amazonia. *Biodiversity and Conservation*, 7: 1349–1364.
- Goerck, J., 1997. Patterns of rarity in the birds of the Atlantic forest of Brazil. *Conservation Biology*, 11: 112–118.
- Haffer, J., 1992. On the "river effect" in some forest birds of southern Amazonia. *Boletim do Museu Paraense Emílio Goeldi (série Zoologia)*, 8: 217–245.
- Isler, M. L., Isler, P. R. & Whitney, B., 1999. Species limits in antbirds (Passeriformes; Thamnophilidae): the *Myrmotherula surinamensis* complex. *Auk*, 116: 83–96.
- Karr, J. R., 1982. Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology*, 63: 1975–1978.
- Karr, J. R., Robinson, S. K., Blake, J. G. & Bierregaard, R. O., 1990. Birds of four neotropical forests. In: *Four Neotropical Rainforests*: 237–

269 (A. H. Gentry, Ed.). Yale Univ., New Haven.

- Kattan, G. H., 1992. Rarity and vulnerability: the birds of the Cordillera Central of Colombia. *Conservation Biology*, 6: 64–70.
- Kratter, A., 1997. Bamboo specialization by Amazonian birds. *Biotropica*, 29: 100–110.
- Peterson, A. T. & Watson, D. M., 1998. Problems with areal definitions of endemism: the effects of spatial scaling. *Diversity and Distributions*, 4: 189–194.
- Phillimore, A. B. & Owens, I. P. F., 2005. Are subspecies useful in evolutionary and conservation biology. *Proceedings of the Royal Society B*, 273: 1049–1053.
- Pinto, O., 1944. *Catálogo de aves do Brasil (2ª parte)*. Secretária da Agr., Ind. e Com., São Paulo, Brasil.
- 1978. Novo catálogo das aves do Brasil (1ª parte).
 São Paulo, Brasil.
- Pitman, C. A., Terborgh, J., Silman, M. R. & Nunez P., 1999. Tree species distributions in an upper amazonian forest. *Ecology*, 80: 2651–2661.
- Rabinowitz, D., Cairns, S. & Dillon, T., 1986. Seven forms of rarity and their frequency in the flora of the British isles. In: *Conservation Biology: the science of scarcity and diversity*: 182–204 (M. E. Soulé, Ed.). Sinauer Associates, Sunderland, Massachusetts.
- Remsen, J. V. & Parker, T. A., 1983. Contribution of river–created habitats to bird species richness in Amazonia. *Biotropica*, 15: 223–231.
- Ridgely, R. S. & Tudor, G., 1989. *The birds of South America. Vol. 1, The Oscines Passerines*. Univ. of Texas, Austin, Texas.
- 1994. The birds of South America. Vol. 2 The Suboscines Passerines. Univ. of Texas, Austin, Texas.
- Roma, J. C., 1996. Composição e vulnerabilidade da avifauna do leste do estado do Pará, Brasil.

M. A. Thesis, Univ. Federal do Pará/Museu Paraense Emílio Goeldi, Bélem, Pará.

- Rosenberg, G. H., 1990. Habitat specialization and foraging behavior by birds of Amazonian river islands in northeastern Peru. *Condor*, 92: 427–443.
- Terborgh, J., 1974. Preservation of natural diversity: the problem of extinction prone species. *Bioscience*, 24: 715–722.
- Terborgh, J. & Winter, B., 1980. Some causes of extinction. In: Conservation Biology: and evolutionary–ecological perspective: 119–133 (M. E. Soulé & B. A. Wilcox, Eds.). Sinauer, Sunderland, Massachussets.
- Thomas, C. D. & Mallorie, H. C., 1985. Rarity, species richness and conservation: butterflies of the Atlas Mountains in Morocco. *Biological Conservation*, 33: 95–117.
- Vicentini, A., 2004. A vegetação ao longo de um gradiente edáfico no Parque Nacional do Jaú. In: Janelas para a Biodiversidade no Parque Nacional do Jaú: Uma estratégia para o estudo da biodiversidade na Amazônia: 105–125 (S. H. Borges, S. Iwanaga, M. R. Pinheiro & C. C. Durigan, Eds.). Fundação Vitória Amazônica / WWF–Brasil / USAID, Manaus.
- Whitney, B. & Alvarez, J. A., 1998. A new *Herpsilochmus* antwren (Aves: Thamnophilidae) from northern Amazon Peru and adjacent Ecuador: the role of edaphic heterogeneity of *terra firme* forest. *Auk*, 115: 559–576.
- Willis, E. O., 1979. The composition of avian communities in remanescent woodlots in southern Brazil. *Pap. Avulsos Zool.* (São Paulo), 33: 1–25.
- Yu, J. & Dobson, F. S., 2000. Seven forms of rarity in mammals. *Journal of Biogeography*, 27: 131–139.
- Zimmer, K. J. & Whittaker, A., 2000. Species limits in Pale–tipped tyrannulets (*Inezia*: Tyrannidae). *Wilson Bulletin*, 112: 51–66.

Annex 1. Bird species and subspecies included in the analysis of rarity of Jaú National Park avifauna distributed in Rabinovitz et al.'s seven forms of rarity of (1986). Nomenclature of species follows the recommendations of the Brazilian Ornithological Records Committee (http://www.cbro.org.br).

Annex 1. Especies y subespecies de aves incluidas en el análisis de rareza de la avifauna del Parque Nacional de Jaú agrupadas en las siete formas de rareza según Rabinovitz et al. (1986). La nomenclatura de especies sigue las recomendaciones del Comité de Registros Ornitológicos de Brasil (http://www.cbro.org.br).

Rarity form 1

Restricted geographic distribution, habitat specialists, small population sizes

Crypturellus cf. duidae, Chordeiles pusillus esmeraldae, Phaethornis rupurumii amazonicus, Nonnula amaurocephala, Eubucco richardsoni nigriceps, Frederickena unduligera unduligera, Thamnophilus nigrocinereus cinereoniger, Myrmotherula klagesi, Formicivora grisea rufiventris, Myrmoborus lugubris stictopterus, Conopophaga aurita inexpectata, Formicarius analis zamorae, Grallaria varia cinereiceps, Automolus rubiginosus venezuelanus, Schiffornis major duidae, Ramphocaenus melanurus duidae, Polioptila guianensis facilis, Schistochlamys melanopis aterrima, Lanio fulvus peruvianus.

Rarity form 2

Restricted geographic distribution, habitat specialists, large population sizes

Tinamus major serratus, Odontophorus gujanensis buckleyi, Nyctiprogne leucopyga latifascia, Selenidera nattereri, Picumnus lafresnayi pusillus, Veniliornis affinis orenocensis, Myrmotherula haematonota pyrrhonota, Myrmotherula ambigua, Hypocnemis cantator flavescens, Hypocnemoides melanopogon occidentalis, Hylopezus macularius diversus, Deconychura longicauda connectens, Synallaxis rutilans confinis, Todirostrum maculatum anectans, Heterocercus flavivertex, Hylophilus ochraceiceps ferrugineifrons, Microcerculus bambla albigularis, Tachyphonus surinamus brevipes, Hemithraupis flavicollis aurigularis.

Rarity form 3

Restricted geographic distribution, habitat generalists, small population sizes

Topaza pyra pyra, Percnostola minor minor, Myrmeciza disjuncta, Hylexetastes stresemanni stresemani, Dolospingus fringilloides.

Rarity form 4

Wide geographic distribution, habitat specialists, small population sizes

Pipile cumanensis cumanensis, Mitu tuberosum, Leptodon cayanensis cayanensis, Harpagus bidentatus, Geranospiza caerulescens caerulescens, Leucopternis melanops, Busarellus nigricollis nigricollis, Spizaetus ornatus ornatus, Leptotila rufaxilla dubusi, Touit huetii, Amazona kawalli, Deroptyus accipitrinus accipitrinus, Opisthocomus hoazin, Coccycua minuta minuta, Tapera naevia naevia, Lophostrix cristata cristata, Nyctibius aethereus longicaudatus, Nyctibius bracteatus, Lurocalis semitorquatus semitorquatus, Caprimulgus cayennensis cayennensis, Glaucis hirsutus hirsutus, Threnetes leucurus leucurus, Campylopterus largipennis largipennis, Chrysolampis mosquitus, Polytmus theresiae leuchorous, Galbula galbula, Notharchus ordii, Micromonacha lanceolata, Pteroglossus pluricinctus, Taraba major semifasciatus, Thamnophilus schistaceus heterogynus, Thamnomanes ardesiacus obidensis, Pygiptila stellaris occipitalis, Myrmotherula multostriata, Myrmotherula assimilis assimilis, Dichrozona cincta, Microrhopias quixensis microstictus, Hylophylax punctulatus punctulatus, Xiphorhynchus kienerii, Cranioleuca vulpina vulpina, Ancistrops strigilatus strigillatus, Hyloctistes subulatus subulatus, Xenops milleri, Sclerurus caudacutus brunneus, Onychorhynchus coronatus castenaui, Neopipo cinnamomea cinnamomea, Attila citriniventris, Tityra inquisitor albitorques, Pachyramphus surinamus, Phoenicircus nigricollis, Perissocephalus tricolor, Cephalopterus ornatus, Pipra filicauda filicauda, Vireolanius leucotis leucotis, Atticora melanoleuca, Eucometis penicillata penicillata, Tachyphonus phoenicius, Euphonia plumbea, Euphonia chrysopasta chrysopasta, Emberizoides herbicola sphenurus, Saltator grossus grossus, Saltator maximus maximus, Psarocolius bifasciatus yuaracares, Molothrus oryzivorus oryzivorus, Sturnella militaris militaris.

Annex 1. (Cont.)

Rarity form 5

Restricted geographic distribution, habitat generalists, large population sizes

Penelope jacquacu orienticola, Psophia crepitans ochroptera, Aratinga pertinax chrysogenys, Pyrrhura melanura melanura, Brotogeris chrysoptera tenuifrons, Pionopsitta barrabandi barrabandi, Amazona autumnalis diadema, Phaethornis malaris insolitus, Thalurania furcata nigrofasciata, Momotus momota microstephanus, Pteroglossus azara azara, Thamnophilus aethiops polionotus, Thamnophilus amazonicus cinereiceps, Myrmotherula cherriei, Terenura spodioptila signata, Myrmoborus myotherinus ardesiacus, Schistocichla leucostigma infuscate, Gymnopithys leucaspis laterallis, Rhegmatorhina cristata, Hylophylax poecilinotus duidae, Phlegopsis erythroptera erythroptera, Myrmothera campanisona dissors, Xiphocolaptes promeropirhynchus orenocensis, Dendrocolaptes certhia radiolatus, Xiphorhynchus obsoletus notatus, Automolus infuscatus badius, Xenops minutus remoratus, Sclerurus rufigularis brunnescens, Todirostrum chrysocrotaphum guttatum, Zimmerius gracilipes gracilipes, Tolmomyias assimilis neglectus, Terenotriccus erythrurus venezuelensis, Cnemotriccus fuscatus duidae, Lepidothrix coronata carbonata, Hylophilus brunneiceps, Hylophilus hypoxanthus hypoxanthus, Thryothorus coraya griseipectus, Cyphorhinus arada transfluviatilis, Tangara chilensis coelicolor, Cyanerpes cyaneus dispar.

Rarity form 6

Wide geographic distribution, habitat specialists, large population sizes

Crypturellus undulatus yapura, Nothocrax urumutum, Ictinia plumbea, Buteogallus urubitinga urubitinga, lbycter americanus, Falco rufigularis rufigularis, Orthopsittaca manilata, Aratinga leucophthalma callogenys, Touit purpuratus viridiceps, Pionus fuscus fuscus, Amazona festiva festiva, Crotophaga major, Crotophaga ani, Glaucidium brasilianum ucayale, Nyctibius grandis grandis, Hydropsalis climacocerca schomburgki, Phaethornis bourcieri bourcieri, Trogon curucui peruvianus, Trogon violaceus ramonianus, Pharomachrus pavoninus pavoninus, Notharchus macrorhynchos hyperrhynchus, Notharchus tectus tectus, Monasa nigrifrons nigrifons, Chelidoptera tenebrosa tenebrosa, Campephilus rubricollis rubricollis, Sakesphorus canadensis loretoyacuensis, Cercomacra tyrannina tyrannina, Sclateria naevia argentata, Nasica longirostris, Xiphorhynchus picus picus, Berlepschia rikeri, Mionectes macconnelli macconnelli, Hemitriccus minor pallens, Camptostoma obsoletum napaeum, Phaeomyias murina wagae, Inezia subflava subflava, Tolmomyias poliocephalus poliocephalus, Platyrinchus platyrhynchos platyrhynchos, Lathrotriccus euleri lawrencei, Knipolegus poecilocercus, Pitangus sulphuratus sulphuratus, Philohydor lictor lector, Conopias trivirgatus berlepschi, Tyrannopsis sulphurea, Attila cinnamomeus, Pachyramphus castaneus saturatus, Gymnoderus foetidus, Chiroxiphia pareola regina, Hylophilus semicinereus viridiceps, Atticora fasciata, Stelgidopteryx ruficollis ruficollis, Thryothorus leucotis albipectus, Polioptila plumbea plumbea, Turdus fumigatus fumigatus, Habia rubica peruviana, Tachyphonus cristatus cristatellus, Tachyphonus luctuosus luctuosus, Ramphocelus nigrogularis, Ramphocelus carbo carbo, Thraupis palmarum melanoptera, Chlorophanes spiza caerulescens, Hemithraupis guira nigrigula, Sicalis columbiana goeldii, Paroaria gularis gularis, Psarocolius decumanus decumanus, Cacicus haemorrhous haemorhous, Lampropsar tanagrinus tanagrinus.

Rarity form 7

Wide geographic distribution, habitat generalists, small population sizes

Crypturellus cinereus, Accipiter bicolor bicolor, Buteo nitidus nitidus, Harpia harpyja, Spizaetus tyrannus serus, Herpetotheres cachinnans cachinnans, Micrastur mirandollei, Micrastur semitorquatus semitorquatus, Strix huhula huhula, Asio stygius stygius, Nyctibius leucopterus, Caprimulgus rufus rufus, Chlorestes notata, Elaenia ruficeps, Myiornis ecaudatus miserabilis, Rhytipterna immunda, Pachyramphus rufus rufus.

Common species

Wide geographic distribution, habitat generalists, large population sizes

Crypturellus soui sou, Crypturellus variegatus, Rupornis magnirostris magnirostris, Daptrius ater, Milvago chimachima cordatus, Micrastur ruficollis concentricus, Micrastur gilvicollis, Aramides cajanea cajanea, Patagioenas speciosa, Patagioenas cayennensis cayennensis, Patagioenas plumbea wallacei, Patagioenas

Annex 1. (Cont.)

subvinacea purpureotincta, Leptotila verreauxi brasiliensis, Geotrygon montana Montana, Ara ararauna, Ara macao macao, Ara chloropterus, Pionites melanocephalus melanocephalus, Pionus menstruus menstruus, Amazona amazonica, Amazona farinosa farinosa, Piaya cayana cayana, Piaya melanogaster melanogaster, Megascops choliba crucigerus, Megascops watsonii usta, Pulsatrix perspicillata perspicillata, Nyctibius griseus griseus, Nyctidromus albicollis albicollis, Caprimulgus nigrescens, Phaethornis ruber nigricinctus, Florisuga mellivora mellivora, Anthracothorax nigricollis, Chlorostilbon mellisugus subfurcatus, Hylocharis sapphirina, Hylocharis cyanus viridiventris, Amazilia versicolor milleri, Amazilia fimbriata fimbriata, Heliodoxa aurescens, Heliothryx auritus aurita, Heliomaster longirostris longirostris, Trogon viridis viridis, Trogon rufus sulphureus, Trogon melanurus eumorphus, Galbula albirostris chalcocephala, Galbula leucogastra, Galbula dea brunneiceps, Jacamerops aureus aureus, Bucco tamatia tamatia, Bucco capensis, Malacoptila fusca, Monasa morphoeus peruana, Capito auratus, Ramphastos tucanus cuvieri, Ramphastos vitellinus culminatus, Melanerpes cruentatus, Colaptes punctigula guttatus, Celeus grammicus grammicus, Celeus elegans jumanus, Celeus torquatus occidentalis, Dryocopus lineatus lineatus, Campephilus melanoleucos melanoleucos, Cymbilaimus lineatus intermedius, Thamnophilus murinus murinus, Megastictus margaritatus, Thamnomanes caesius glaucus, Myrmotherula brachyura brachyuran, Myrmotherula axillaris axillaries, Myrmotherula longipennis longipennis, Myrmotherula menetriesii pallida, Herpsilochmus dorsimaculatus, Cercomacra cinerascens cinerascens, Hypocnemis hypoxantha hypoxantha, Pithys albifrons peruvianus, Hylophylax naevius naevius, Formicarius colma colma, Dendrocincla fuliginosa neglecta, Dendrocincla merula bartleti, Deconychura stictolaema secunda, Sittasomus griseicapillus amazonus, Glyphorynchus spirurus rufigularis, Dendrexetastes rufigula devillei, Dendrocolaptes picumnus validus, Xiphorhynchus guttatus guttatoides, Philydor pyrrhodes, Mionectes oleagineus oleagineus, Corythopis torquatus anthoides, Hemitriccus zosterops zosterops, Hemitriccus minimus, Tyrannulus elatus, Myiopagis gaimardii guianensis, Myiopagis caniceps cinerea, Ornithion inerme, Cnipodectes subbrunneus minor, Platyrinchus coronatus coronatus, Myiobius barbatus barbatus, Legatus leucophaius leucophaius, Conopias parvus, Empidonomus varius rufinnus, Tyrannus melancholicus melancholicus, Rhytipterna simplex frederici, Myiarchus tuberculifer tuberculifer, Myiarchus ferox, ferox, Ramphotrigon ruficauda, Tityra cayana cayana, Pachyramphus marginatus nanus, Cotinga cayana, Lipaugus vociferans, Laniocera hypopyrra, Xipholena punicea, Neopelma chrysocephalum, Tyranneutes stolzmanni, Piprites chloris tschudii, Xenopipo atronitens, Dixiphia pipra pipra, Pipra erythrocephala erythrocephala, Schiffornis turdina amazona, Cyclarhis gujanensis gujanensis, Hylophilus thoracicus griseiventris, Troglodytes musculus albicans, Microbates collaris collaris, Turdus albicollis phaeopygus, Coereba flaveola minima, Tangara mexicana boliviana, Tangara punctata punctata, Tangara velia iridina, Dacnis flaviventer, Dacnis cayana cayana, Cyanerpes caeruleus microrhyncha, Euphonia chlorotica amazonica, Euphonia rufiventris, Sporophila angolensis torridus, Caryothraustes canadensis canadensis, Cyanocompsa cyanoides rothschildii, Psarocolius viridis, Cacicus cela cela, Icterus chrysocephalus.