

ARTICLES

HOWLER AND CAPUCHIN MONKEY DENSITIES IN RIPARIAN FORESTS ON ISLANDS AND ADJACENT SHORES ON THE UPPER PARANÁ RIVER, SOUTHERN BRAZIL

Lucas M. Aguiar¹, Gabriela Ludwig², James J. Roper³, Walfrido K. Svoboda³, Itamar T. Navarro⁴, Fernando C. Passos³

¹ Universidade Federal da Integração Latino-Americana (UNILA), Foz do Iguaçu, Brasil. Email: lucas.aguiar@unila.edu.br; ² Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Centro Nacional de Pesquisa e Conservação de Primatas Brasileiros, Fundação Flora de Apoio a Botânica, João Pessoa, Brasil. ³ Universidade Federal do Paraná (UFPR), Curitiba, Brasil; ⁴ Universidade Estadual de Londrina (UEL), Londrina, Brasil.

Abstract

Three primates (*Alouatta caraya*, *Sapajus nigritus* and *Sapajus cay*) are found in riparian areas of the Upper Paraná River in southern Brazil. Population densities of these three species were estimated from October 2004 through September 2005 by counts on linear transects in riparian forests on two riverine islands and adjacent shores in the states of Mato Grosso do Sul and Paraná. A total of 397 sightings of these species were accumulated in 188 km of traversed transects. *Alouatta caraya* was the most abundant species on the large island (2.56 ind ha⁻¹) and on the Mato Grosso do Sul side (0.84 ind ha⁻¹). This density was greater than twice that of the sympatric *S. cay* (0.31 ind ha⁻¹). *Sapajus nigritus* was the most abundant species on the Paraná side (0.51 ind ha⁻¹) followed by *A. caraya* (0.40 ind ha⁻¹). The folivorous *A. caraya* was the most abundant in flooded forests, while the omnivorous *Sapajus* species were less so. Differences in forests, conservation status, dispersal restrictions and autecology of the primates help explain differences in primate abundance.

Keywords: *Alouatta caraya*, *Sapajus cay*, *Sapajus nigritus*, habitat fragmentation, population survey, primate conservation.

Resumo

Três espécies de primatas (*Alouatta caraya*, *Sapajus nigritus* e *Sapajus cay*) podem ser encontradas nas matas ciliares do Alto Rio Paraná, sul do Brasil. Suas densidades populacionais foram estimadas através do método das transecções lineares em matas ciliares de duas ilhas fluviais e das margens opostas do rio, no limite entre os estados do Mato Grosso do Sul e Paraná, durante outubro de 2004 a setembro de 2005. Obteve-se um total de 397 avistamentos de primatas ao longo de 188 km percorridos. *Alouatta caraya* foi a espécie mais abundante na maior ilha (2.56 ind ha⁻¹) e na margem do Mato Grosso do Sul (0.84 ind ha⁻¹). A densidade da espécie neste local foi maior que o dobro da densidade da espécie simpátrica, *S. cay* (0.31 ind ha⁻¹). *Sapajus nigritus* foi a espécie mais abundante na margem do Paraná (0.51 ind ha⁻¹), seguido de *A. caraya* (0.40 ind ha⁻¹). A espécie folívora, *A. caraya*, foi mais abundante na floresta de inundação, mais conservada, enquanto que *Sapajus*, onívoro, foi mais abundante na floresta de terra firme. Diferenças entre a estrutura das florestas, grau de conservação, restrições para dispersão e autoecologia dos primatas ajudam a explicar as diferenças entre as abundâncias encontradas.

Palavras-chaves: *Alouatta caraya*, *Sapajus cay*, *Sapajus nigritus*, fragmentação florestal, levantamento populacional, conservação de primatas.

Introduction

Fragmentation may result in rapid population growth in mammal species whose population sizes, in other more diverse communities, would have been controlled by competition or predation (Redford, 1992; Peres and Dolman 2000; Terborgh *et al.*, 2001; Link *et al.*, 2010). At least

three hypotheses may explain these increased densities: (1) absence of predators, (2) ecological plasticity and (3) density compensation, in which the effects of isolation result in the elimination of some species (Redford, 1992; Glanz, 1996; González-Solís *et al.*, 2001; Terborgh *et al.*, 2001). For example, in the Amazon, small and medium-sized primate species increase in abundance where larger

species of the family Atelidae are preferentially hunted (Peres and Dolman, 2000). Also, greater densities in *Alouatta* and *Sapajus* species may be found in degraded communities in fragments and islands (Chiarello and Galetti 1994; González-Solís *et al.*, 2001; Ludwig *et al.*, 2005; Martins, 2005; Almeida-Silva *et al.*, 2005; Link *et al.*, 2010).

Islands may serve as natural experiments to examine the effects of isolation on mammal populations (Glanz, 1996; Terborgh *et al.*, 2001). For example, abundance of *Alouatta seniculus* increased in the absence of predators as well as with simplification of forests on artificial islands (Terborgh *et al.*, 2001). Similarly, black-and-gold howler monkey (*Alouatta caraya*) densities are greater on an island than the nearby shores of the Paraná River in Argentina (Rumiz, 1990; Zunino *et al.*, 2001). However, islands in the Paraná River are natural and have primate predators, such as large cats (Aguiar *et al.*, 2007; Ludwig *et al.*, 2007). On the islands of the Paraná River, with rich alluvial soils, two important factors may contribute to high howler population densities: (1) greater productivity of high-quality resources, such as fruits and young leaves, and (2) year-round resource availability (Janzen, 1974; Rumiz, 1990; Zunino *et al.*, 2001; Bravo and Sallenave, 2003).

Although *A. caraya* population studies have taken place in the system of islands of the Middle Paraná River (Rumiz, 1990; Zunino *et al.*, 2001), few studies include other primates in this area (Brown and Zunino, 1994) and in other portions of this river. Given the importance of understanding local variation in primate abundances, the main goal of this study was to examine and compare densities of *A. caraya*, *Sapajus nigritus* and *Sapajus cay* on forested islands and along the adjacent margins of the Upper Paraná River in southern Brazil.

Methods

Study area

Primates were studied in the Upper Paraná River Protected Area in the southern Brazilian Atlantic Forest. Primate abundances were estimated on two islands and along the margins of the river near the city of Porto Rico in Paraná, and near the city of Taquarussu in Mato Grosso do Sul (22°43'60"S and 53°24'18"W; Fig. 1). The region is subtropical, with an average rainfall between 1,200–1,300 mm (Romagnolo and Souza, 2000). Human impact has degraded the forests, although today the area is in process of recovery (Campos and Souza, 2002). The study area comprises two main forest types: alluvial, or flooded forests (*várzeas*), that are found in the islands and flood plains on the Mato Grosso do Sul side of the river; and submontane (higher than 250 m above sea level) on the Paraná side of the river. Alluvial forests flood annually and have low tree diversity and are dominated by pioneer species (Romagnolo and Souza, 2000; Campos and Souza, 2002). The canopy is open and low (10–15 m, emergent to 25 m). Productivity is

high due to the rich alluvial soils and so high-quality forage (leaves) is abundant and relatively constant for folivorous howler monkeys (Rumiz, 1990). *Cecropia pachystachya* is the dominant tree and the main food source for howler monkeys here (Ludwig *et al.*, 2008). Submontane forests are the most diverse and mature forests in the region in areas that do not flood (M. C. Souza, unpublished). However, productivity of resources used by folivorous primates is relatively lower and more seasonal (Rumiz, 1990). The canopy is more closed with trees of 15–30 m. Today, the submontane forest is nearly extinct in this region with only a few fragments remaining (Campos and Souza, 1997).

Primates were counted on two islands and both margins of the river (Fig. 1). Mutum Island is the largest island (1,050 ha), near the river center (1,000 m from Paraná, 700 m from Mato Grosso do Sul) and comprises a mosaic of alluvial forests, swamps, and patches of more preserved forests, and is dominated by the pioneer tree *C. pachystachya*. Carioca Island is smaller (360 ha), 600 m from Paraná, 800 m from Mutum Island, and comprises a mosaic of degraded alluvial forests with few trees and discontinuous canopy with many vines. Humans and feral domestic pigs (*Sus scrofa*) have impacted the island. The shores of Mato Grosso do Sul comprise alluvial forests that are naturally narrow corridors above the dikes formed by the river. Today, they are fragmented and poorly preserved due to an increasing pressure from agriculture, cattle, fire, and human settlements. Farther from the dikes, the forests are rapidly being replaced by pasture and marshes. Finally, the Paraná shore has submontane forests and, despite some anthropic influence, has continuous, wider stretches that retain most of the original forest structure (M. C. Souza, unpublished). Abundant palms (*Acrocomia aculleata* and *Syagrus romanzoffianum*), and agriculture, including corn and cassava, are only on the Paraná side of the river (L. M. Aguiar, personal observation).

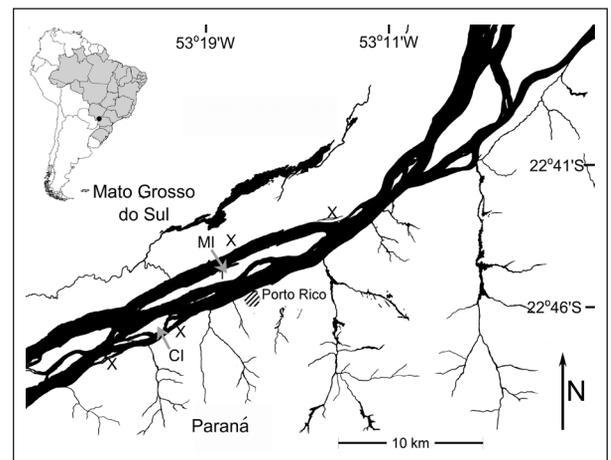


Figure 1. Location of the study area on the Upper Paraná River, southern Brazil. X marks the transect locations on the river shore; MI: Mutum Island; CI: Carioca Island. Porto Rico: nearby city.

Study animals

Three species of primates are found in the region (Aguiar *et al.*, 2007). The black-and-gold howler monkey is found on both shores of the river, and is the only monkey on the islands. The black-horned capuchin (*S. nigritus*) is found on the Paraná side of the river, and Azara's capuchin (*S. cay*) on the Mato Grosso do Sul side of the river. The Paraná river is a barrier for dispersal of both capuchins (Aguiar *et al.*, 2007). Monkeys are seldom hunted in the region and so populations are not responses to hunting pressure (Aguiar *et al.*, 2007). Capuchin taxonomy follows Alfaro *et al.* (2011).

Density estimates

Linear transects with multiple counts (Buckland *et al.*, 1993; Ferrari, 2002) were used to estimate primate density. Due to the narrow riparian forests in various degrees of perturbation, transects were established to accompany the forest habitat and had to vary in length to fit within these patches. Transect lengths were 1500 m on Mutum Island, 560 and 1260 m on Carioca Island, 1000 and 1010 m on the Mato Grosso do Sul shore, and 1000 and 1180 m on the Paraná shore. Transects were walked once or twice each week from October 2004 through September 2005. Transects were walked at an average speed of 0.5 km h⁻¹, between 06:00–12:00 h, and between 14:00–19:00 h. No transect was walked twice in the same day. At each sighting, the perpendicular distance to the trail was measured (Bushnell distance meter or tape), and time, species and numbers of visible individuals were noted (measurable individuals following Marshall *et al.*, 2008). The distance to the most distant individual in each group was measured. The program Distance version 4.1 was used to estimate abundance using the size-biased sampling method, using a probability of 0.15 for significance of regressions between clusters sizes and sighting distances to the clusters (Buckland *et al.*, 1993).

Results

A total of 397 sightings were recorded during about 500 h of walking over 188 km (Table 1). Howler monkey density

varied between 0.40–2.56 ind ha⁻¹, with the lowest densities on the Paraná side and on Carioca Island, and the greatest on the Mato Grosso do Sul side and Mutum Island. Capuchin monkey density varied between 0.31 ind ha⁻¹ for *S. cay* in Mato Grosso do Sul and 0.51 ind ha⁻¹ for *S. nigritus* in Paraná.

Discussion

The flooded, and more conserved forests on Mutum Island are apparently the most favorable local habitats for *A. caraya* such that their density is more than five times that of the other locations. Primate density is similar in the other locations, although capuchin density was greater in more mature and conserved forests (*e.g.*, *S. nigritus* in Paraná) and greater than the density of sympatric howlers. Indeed, howler density was lower than that of the capuchins in mature forests of Paraná and in the most disturbed habitat of Carioca Island. Howler abundance, therefore, may be strongly influenced by productivity (such as flooded forests), while the more generalist capuchins do better in mature forests and more conserved habitats. We suggest that the flooded habitat in Mutum Island is important to maintain the extremely abundant *C. pachystachya* as a very important resource that allows greater population sizes in *A. caraya*. In contrast, while often flooded, Carioca Island apparently cannot support similar population sizes there due to environmental degradation. A similar relationship of abundance, productivity and degradation has been found in the Middle Paraná River (Rumiz, 1990; Brown and Zunino, 1994; Zunino *et al.*, 2001).

Other factors may also influence densities in this study area: 1) low predation and hunting pressure, 2) density compensation (Redford, 1992; Glanz, 1996; González-Solís *et al.*, 2001; Terborgh *et al.*, 2001) and 3) crowding (Lovejoy *et al.*, 1986). First, hunting pressure by humans is low and natural primate predators are less abundant in this region, probably due to the presence of humans. While predation is an important component of primate life histories, predation as a constraint on primate population size has not been clearly demonstrated in most species (Isbell,

Table 1. Sampling effort (distance walked in km), number of sightings, sighting rate (sightings km⁻¹), average group (cluster) size, and density estimate (individuals ha⁻¹) at four sampling locations on the Upper Paraná River, in southern Brazil.

Estimates-statistics	Mutum Is.	Carioca Is.	Paraná		Mato Grosso do Sul	
	<i>A. caraya</i>		<i>A. caraya</i>	<i>S. nigritus</i>	<i>A. caraya</i>	<i>S. cay</i>
Distance	21	49	57	57	61	61
Sightings	99	42	45	52	111	48
Sighting rate	13.2	1.6	1.1	1.59	2.6	0.43
Group sizea	3.1	3.3	3.2	2.8	2.1	1.6
Density	2.56	0.63	0.40	0.51	0.84	0.31
Function	Uni/Cos	Hazard rate	Uni	Uni/Cos	Half-normal	Half-normal/Cos

a Group size (average) was counted on the islands and estimated on the mainland using the program Distance. Coefficient of variation (CV) varied between 15–25%. Effective width varied between 20 m (*S. cay*) and 32 m (*A. caraya* in Paraná).

1994). Density compensation may also allow greater abundance. Since the local primate community is depauperate, with never more than two co-occurring species in any one place, it is possible that reduced competition for resources and isolation due to fragmentation combine to favor increased density. Also, other potential competitors for howlers, such as capuchins and coatis are absent from the islands (Aguiar *et al.*, 2007). This distribution raises the question of why there are not three primate species, and coatis, at any given site, since they are all locally available?. Perhaps the river is an effective barrier for dispersal of capuchins and coatis, or flooded forests may not provide the additional resources (prey, fruit) that these omnivorous species require (Haugaasen and Peres, 2005; Aguiar *et al.*, 2011).

The crowding effect (Lovejoy *et al.*, 1986) may also be important, since these primates are opportunists and generalists, and may have overlapping ranges. They may coexist at relatively high densities in environmentally degraded areas due to dispersal limitation, such as on the islands. This is an important possibility, because it suggests that degraded areas may still provide resources to maintain large or dense populations. Usually, capuchins are more frugivorous and more resource generalists than howlers (Freese and Oppenheimer, 1981; Link *et al.*, 2010). However, *S. cay* is not very abundant (in contrast to howlers), apparently because the flooded forest is not ideal habitat for capuchin species (Peres, 1989; Haugaasen and Peres, 2005). Riparian forest along the river in Mato Grosso do Sul is a narrow corridor and with a relatively small area for foraging. In contrast, *S. nigritus* is more abundant on the Paraná side of the river than is typical (Ludwig *et al.*, 2005; Martins, 2005; Almeida-Silva *et al.*, 2005). On the Paraná side, the riparian forest corridor is wider, with more mature and better-preserved forest including many palm trees where they forage, as well as having cultivated crops that they may also consume (Ludwig *et al.*, 2005). These complex interactions require autecological studies that examine the importance of each resource to better understand how these resources influence abundance patterns.

Therefore, here, the abundance patterns of these three primate species suggest that forest structure and conservation status may be the main influences regulating population size. Greater abundance may be explained by both, immigration and reproduction (Begon *et al.*, 2006). Since howlers can swim (Aguiar *et al.*, 2007) and then find abundant resources, their populations will grow as long as resources are not limiting. If riparian areas are well protected, they can maintain populations of primates and other animals. We suggest that the interactions of density compensation, crowding, low hunting and predation pressures, and the extremely abundant *Cecropia* (for howlers) probably allow the unusually high densities. Although humans have fragmented the habitat, primates are still relatively abundant, which suggests that these are important populations for conservation, in contrast with the lower abundances of these species elsewhere (Ludwig *et al.*, 2005; Moura, 2007).

Thus, populations along the Paraná River are potentially important sources for regional maintenance of these species. We recommend further study to specifically tests the hypotheses presented here and thereby assure conservation of these primates.

Acknowledgments

We thank CNPq for scholarships to L. M. Aguiar, G. Ludwig and F. C. Passos, SESA-PR for their financial support, and the ICMBio for a license provision. The manuscript benefited from the comments of A. G. Chiarello, Z. M. B. Hirano, E. L. A. Monteiro-Filho, J. E. Silva-Pereira, R. F. Moro-Rios and two reviewers.

References

- Aguiar, L. M., Ludwig, G., Svoboda, W. K., Hilst, C. L. S., Navarro, I. T. and Passos, F. C. 2007. Occurrence, local extinction and conservation of primates in the corridor of the Upper Paraná River, with notes on other mammals. *Rev. Bras. Zool.* 24: 898–906.
- Aguiar, L. M., Moro-Rios, R. F., Silvestre, T., Silva-Pereira J. E., Bilski, D. R., Passos, F. C., Sekiama, L. M. and Rocha, V. J. 2011. Diet of brown nosed coatis and crab-eating raccoons from a mosaic landscape with exotic plantations in southern Brazil. *Stud. Neotrop. Fauna Environm.* 46: 153–161.
- Alfaro, J. W., Boubli, J. P., Olson, L. E., Di Fiore, A., Wilson, B., Gutiérrez-Espeleta, G. A., Chiou, K. L., Schulte, M., Neitzel, S., Ross, V., Schwochow, D., Nguyen, M. T. T., Farias, I., Janson, C. H. and Alfaro, M. E. 2011. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J. Biogeogr.* 39: 272–288.
- Almeida-Silva, B., Cunha, A. A., Boubli, J. P., Mendes, S. L. and Strier, K. B. 2005. Population density and vertical stratification of four primate species at the Estação Biológica de Caratinga/RPPN-FMA, Minas Gerais, Brazil. *Neotrop. Primates* 13: 25–29.
- Asensio, N., Arroyo-Rodríguez, V. and Cristóbal-Azkarate, J. 2007. Feeding encounters between a group of a howler monkeys and white-nosed coatis in a small forest fragment in Los Tuxtlas, México. *J. Tropical Ecol.* 23: 253–255.
- Begon, M., Townsend, C. R., Harper, J. L. 2006. *Ecology: from individuals to ecosystems*. Blackwell Publishing, Malden.
- Bravo, S. P. and Sallenave, A. 2003. Foraging behavior and activity patterns of *Alouatta caraya* in the northeastern argentinean flooded Forest. *Int. J. Primatol.* 24: 825–846.
- Brown, A. D. and Zunino, G. E. 1994. Hábitat, densidad y problemas de conservación de los primates de Argentina. *Vida Silvestre Neotropical* 3: 30–40.
- Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L. 1993. *Distance sampling: estimating abundance of biological populations*. Chapman and Hall, London.

- Campos, J. B. and Souza, M. C. 1997. Vegetação. In: *A Planície de Inundação do Alto Rio Paraná: Aspectos físicos, biológicos e socioeconômicos*, A. E. A. M. Vazzoler, A. A. Agostinho and N. S. Hahn (eds.), pp.331–342. EDUEM, Maringá.
- Campos, J. B. and Souza, M. C. 2002. Arboreous vegetation of an Alluvial Riparian Forest and their soil relations: Porto Rico Island, Paraná River, Brazil. *Braz. Arch. Biol. Technol.* 45: 137–149.
- Chiarello, A. G. and Galetti, M. 1994. Conservation of the brown howler monkey in South-east Brazil. *Oryx* 28: 37–42.
- Ferrari, S. F. 2002. Multiple transects or multiple walks? A response to Magnusson (2001). *Neotrop. Primates* 10: 131–132.
- Freese, C. H. and Oppenheimer, J. R. 1981. The capuchin monkeys, Genus *Sapajus*. In: *Ecology and Behavior of Neotropical Primates*, A. F. Coimbra-Filho and R. A. Mittermeier (eds.), pp.331–389. Academia Brasileira de Ciências, Rio de Janeiro.
- Glanz, W. E. 1996. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. In: *The Ecology of a tropical forest: seasonal rhythms and long-term changes*, E. G. Leigh, A. S. Rand and D. M. Windsor (eds.), pp.455–468. Smithsonian Institution Press, Washington.
- González-Solís, J., Guix, J. C., Mateos, E. and Llorens, L. 2001. Population density of primates in a large fragment of the Brazilian Atlantic Rainforest. *Biodiversity Conserv.* 10: 1267–1282.
- Haugaasen, T. and Peres, C. A. 2005. Primate assemblage structure in amazonian flooded and unflooded forests. *Am. J. Primatol.* 67: 243–258.
- Isbell, L. A. 1994. Predation on primates: ecological patterns and evolutionary consequences. *Evol. Anthropol.* 3: 61–71.
- Janzen, D. H. 1974. Tropical Blackwater rivers, animals, and mast fruiting by Dipterocarpaceae. *Biotropica* 6: 69–103.
- Link, A., Luna, A. G., Alfonso, F., Giraldo-Beltran, P. and Ramírez, F. 2010. Initial effects of fragmentation on the density of three Neotropical primates species in two lowland forests of Colombia. *Endang. Species Res.* 13: 41–50.
- Lovejoy, T. E., Bierregaard, R. O., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., Brown Jr., K. S., Powell, A. H., Powell, G. V. N., Schubart, H. O. R. and Hays, M. B. 1986. Edge and other effects of isolation on Amazon forest fragments. In: *Conservation Biology, the science of scarcity and diversity*, M. E. Soulé (ed.), pp.257–285. Sinauer Associates Inc Publishers, Massachusetts.
- Ludwig, G., Aguiar, L. M. and Rocha, V. J. 2005. Uma avaliação da dieta, da área de vida e das estimativas populacionais de *Sapajus nigritus* (Goldfuss, 1809) em um fragmento no Norte do Estado do Paraná. *Neotrop. Primates* 13: 12–18.
- Ludwig, G., Aguiar, L. M., Miranda, J. M. D., Teixeira, G. M., Svoboda, W. K., Malanski, L. S., Shiozawa, M. M., Hilst, C. L. S., Navarro, I. T. and Passos, F. C. 2007. Cougar predation on Black-and-gold howlers on Mutum Island, Southern Brazil. *Int. J. Primatol.* 28: 39–46.
- Ludwig, G., Aguiar, L. M., Svoboda, W. K., Hilst, C. L. S., Navarro, I. T., Vitule, J. R. S. and Passos, F. C. 2008. Comparison of the diet of *Alouatta caraya* (Primates, Atelidae) between a riparian island and mainland on the Upper Paraná River, southern Brazil. *Rev. Bras. Zool.* 25: 419–426.
- Marshall, A. R., Lovett, J. C. and White, P. C. L. 2008. Selection of Line-transect methods of estimating the density of group-living animals: lessons from the primates. *Am. J. Primatol.* 70: 452–462.
- Martins, M. M. 2005. Density of primates in four semi-deciduous forest fragments of São Paulo, Brazil. *Biodiversity Conserv.* 14: 2321–2329.
- Moura, A. C. A. 2007. Primate group size and abundance in the Caatinga Dry Forest, northeastern Brazil. *Int. J. Primatol.* 28: 1279–1297.
- Peres, C. A. and Dolman, P. M. 2000. Density compensation in Neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122: 175–189.
- Redford, K. H. 1992. The empty Forest. *BioScience* 42: 412–422.
- Romagnolo, M. B. and Souza, M. C. 2000. Análise florística e estrutural de florestas ripárias do alto rio Paraná, Taquaruçu, MS. *Acta Botanica Brasílica* 14: 163–174.
- Rumiz, D. I. 1990. *Alouatta caraya*: Population density and demography in northern Argentina. *Am. J. Primatol.* 21: 279–294.
- Terborgh, J., Lopez, L., Nuñez, P. V., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D. and Balbas, L. 2001. Ecological meltdown in predator-free Forest fragments. *Science* 294: 1923–1926.
- Zunino, G. A., González, V., Kowalewski, M. M. and Bravo, S. P. 2001. *Alouatta caraya*: relations among habitat, density and social organization. *Primate Report* 61: 37–46.