

USING CAMERA TRAPS TO DETERMINE GROUP DEMOGRAPHY IN A PARAGUAYAN POPULATION OF *SAPAJUS CAY*

Rebecca L. Smith¹ & Emily S. Briggs¹

¹ *Fundación para la Tierra, Reserva Natural Laguna Blanca, Santa Rosa del Aguaray, San Pedro, Paraguay. E-mail: <rebecca@paralatierra.org>; <esbriggs33@gmail.com>.*

Abstract

The understudied Hooded Capuchin (*Sapajus cay*) is the only representative of its genus in Paraguay. The species is distributed throughout the Upper Paraná Atlantic Forest, a biome that historically covered most of eastern Paraguay but has been reduced to small, isolated fragments by agricultural encroachment. Understanding group composition and demographics is important for monitoring the viability of populations. In this study, video camera traps were used to monitor a single group of Hooded Capuchins during their visits to a provisioning platform in a small Atlantic Forest fragment in Reserva Natural Laguna Blanca, Departamento San Pedro, Paraguay. Video analysis enabled identification and assignment of age classes to all 18 individuals of the group. Sex determination was possible for 8 adults, 2 subadults, and 2 juveniles. This study provides the first information of group demographics and composition of wild Hooded Capuchins in Paraguay.

Keywords: Atlantic forest, group composition, hooded capuchin, paraguay, video camera trapping.

Resumen

El poco estudiado capuchino de Azara (*Sapajus cay*) es el único representante de su género en Paraguay. La especie está distribuida a lo largo del bosque Atlántico del alto Paraná, un bioma que históricamente cubrió la mayor parte del oriente de Paraguay pero que ha sido reducido a fragmentos pequeños y aislados por el avance de la agricultura. Entender la composición de grupo y la demografía es importante para monitorear la viabilidad de las poblaciones. En este estudio, trampas de video cámara fueron utilizadas para monitorear un grupo de capuchinos de Azara durante sus visitas a una plataforma de aprovisionamiento en un pequeño fragmento de bosque Atlántico en la Reserva Natural Laguna Blanca, Departamento San Pedro, Paraguay. El análisis de los videos permitió identificar y asignar clases de edad a 18 individuos del grupo. La determinación del sexo fue posible para 8 adultos, 2 subadultos y 2 juveniles. Este estudio provee la primera información de la demografía y composición de un grupo silvestre de Tufted capuchins en Paraguay.

Palabras clave: Bosque Atlántico, composición de grupo, capuchino de Azara, Paraguay, trampeo con video cámara.

Introduction

The taxonomy of the capuchins has long been debated. All capuchins were historically classified in the single genus *Cebus*, however Elliot (1913) split the capuchins into two groups: those with “heads without tufts on males” and those with “heads with tufts or ridges on males”. Hershkovitz (1949, 1955) agreed with this separation but argued *Cebus apella* should be classed as a member of the tufted group. Hill (1960) reduced the 12 recognized species of tufted capuchin to one, *Cebus apella*, with 16 subspecies. Grooves (2001) recognized 4 species (*C. apella*, *C. libidinosus*, *C. nigrurus* and *C. xanthosternos*) with 13 subspecies. Silva Jr. (2001) argued that, morphologically, the tufted and untufted capuchins displayed sufficient differences to be classified as separate subgenera: *Sapajus* (Kerr 1792) for the tufted or robust species and *Cebus* (Erxleben, 1777) for

the untufted or gracile species. Studies of the mitochondrial genes 12S and cytochrome *b* (Lynch Alfaro *et al.*, 2012) and 10 distinct ALU elements (Martins *et al.*, 2014) have since confirmed that *Sapajus* and *Cebus* diverged around the late Miocene era, possibly as a result of the establishment of the Amazon River (Hoorn *et al.*, 2010; Halsam, 2012). The present sympatry of *Cebus* and *Sapajus* species observed in the Amazon Basin is thought to result from a late Pleistocene invasion of *Sapajus* species from the Atlantic Forest (Lynch Alfaro *et al.*, 2012; Nascimento *et al.*, 2015). Currently, 8 species are recognized within the *Sapajus* genus (*S. macrocephalus* (Spix, 1823), *S. apella* (Linnaeus, 1758), *S. libidinosus* (Spix, 1823), *S. flavius* (Schreber, 1774), *S. xanthosternos*, (Wied-Neuwied, 1826) *S. robustus* (Kuhl, 1820), *S. nigrurus* (Goldfuss, 1809) and *S. cay* (Illiger, 1815)) and are distributed across all countries in

South America except Chile and Uruguay (Lynch Alfaro *et al.*, 2012).

The Hooded capuchin (*Sapajus cay*) formerly known as *Cebus apella cay* (Illiger, 1815) and *C. libidinosus paraguayanus* (Fischer, 1829), is found in south-east Bolivia, northern Argentina, and Brazil (states of Goiás, Mato Grosso, Mato Grosso do Sul) and is the only representative of the genus found in Paraguay (Wallace, 2015). In Paraguay, it occurs in the humid semi-deciduous Upper Paraná Atlantic Forest throughout the east of the country (Lowen *et al.*, 1996; Rylands *et al.*, 2013), but its range does not extend into the Paraguayan Chaco (Stallings, 1985). In Paraguay, the average group size for the capuchin has been estimated at 7 individuals with a population density of 4 groups/km² or 28 individuals/km² (Stallings, 1985). Across its range, very little is known about the Hooded Capuchin and little information exists regarding its reproduction, movement and activity patterns, home range, and social organization (Rylands *et al.*, 2013).

Baseline demographic analysis is essential for monitoring the viability of a population (Lynch Alfaro *et al.*, 2014). Studying fluctuations in demographic factors can help to determine the future viability of small, isolated populations of Neotropical primates (Belle and Estrada, 2005; Strier *et al.*, 2006). The effects of stochastic variation on the fecundity and mortality rates in large populations will be mitigated by the high number of individuals within the population; however, in small or isolated populations such variations can have serious consequences for the viability of the population, increasing extinction risk (Colishaw & Dunbar, 2000). Changes in group size can have effects on behavior and ecology of populations. For example, in muriquis (*Brachyteles arachnoides*), increases in population size have been found to lead to increases in home range size (Strier, 1993). A low proportion of juveniles or infants may indicate reproductive problems in the population (Colishaw & Dunbar, 2000; Lynch Alfaro *et al.*, 2014) and sex ratio imbalances in a group or a population can have a dramatic effect on the future number of breeding males or females (Dunbar, 1988). Modelling of changes in sex ratios on the viability of populations in muriquis (*Brachyteles arachnoides*) have shown that slight deviations in the sex ratio of neonates in favor of males can lead to drastic reductions in population size (Strier, 1993 – 1994). Other studies have shown that changes in demography can lead to changes in levels of competition for mates or even patterns of sex-biased dispersal (Strier, 2003; Jones, 2005; Strier, 2007). Age composition can have a significant effect on the viability of a population. A group made up of mainly young or old females will have a lower birth rate than a group of females in their reproductive prime (Strum & Western, 1982).

Previous studies have highlighted inherent difficulties with the use of spot counts and direct observation as a means of assessing group demography in arboreal primates

(Williamson & Fiestner, 2011), especially in areas where troops are not fully habituated to human presence (Strier, 2007). In order to overcome these issues, alternative methods can be utilized. Motion-activated camera traps are an effective non-invasive method for monitoring primates (Kierulff *et al.*, 2004; Tan *et al.*, 2013; Pebsworth & LaFleur, 2014). Camera traps have been used successfully to confirm species presence (Lhota *et al.*, 2012; Bezerra *et al.*, 2014), provide information on activity patterns (Tan *et al.*, 2013; LaFleur *et al.*, 2014) and investigate life history (Galvis *et al.*, 2014). In this paper, we report how video camera trapping was used to provide the first information on group composition for wild Hooded Capuchins (*Sapajus cay*) in Paraguay.

Methods

Study Site

This study was carried out at Reserva Natural Laguna Blanca (RNLB), San Pedro, Paraguay (23°49'52.0"S 56°17'42.2"W). RNLB is a private nature reserve in eastern Paraguay and is home to two groups of Hooded Capuchins. This 804 ha reserve is located in the transitional zone between the Cerrado and Atlantic Forest ecoregions. The reserve contains a small fragment of 243 ha of young secondary Upper Paraná Atlantic Forest, characterized by deciduous, mesophytic, broadleaf plants (Lowen *et al.*, 1996). Departamento San Pedro experiences average yearly temperatures of 23 to 24°C, and an average yearly rainfall of approximately 1400 mm (Cartes, 2008). The forest fragment has a history of selective logging until 2010 when it was classified as a reserve.

Data Collection

A provisioning station was constructed in an area of the forest where the capuchins were regularly observed. The station consisted of a 2 m high, 0.72 m² triangular platform positioned 50 cm from a *Chrysophyllum gonocarpum* tree (Fig. 1). A Primos Truth Cam Ultra 46 HD Trail Cam (www.trailcampro.com) was secured to the tree with a durable canvas strap. The camera has a 13.72 m detection range and uses an infrared sensor to detect body heat and motion. The camera was set to record 60 seconds of 1,280x720p HD footage per trigger with a 5-second delay between each trigger. Each 60-second video was automatically marked with a date and time stamp.

The platforms were baited with between 5 and 10 kg of whole ears of corn for a preliminary period of 16 trap days between March 10th 2015 and May 30th 2015. A trap day was defined as a full 24-hour period in which the video camera trap was set. During this time, two visits were recorded at the station but the videos were not used in this analysis. For 24 camera trap days between July 4th 2015 and the 4th August 2015, two 106SS model Tomahawk traps were tied to the platform; with the door secured in the open position by plastic cable zipties, and facing the camera trap. Corn pieces and whole bananas were placed



Figure 1. Provisioning Station. a. Video camera trap, b. Baited Tomahawk traps, c. 2 m high, 0.72 m² triangular platform.



Figure 2. Camera trap frames of adult, subadult, juvenile, and infant *S. cay*. 2A is the largest adult male, he has a very robust lower jaw and smaller tufts than the adult female (2B). 2C and 2D show subadult individuals. 2C has a thinner pointed black cap than 2D and 2D has pink marking under her eyes. 2E shows a juvenile who is smaller than the subadults in comparison to the Tomahawk traps. 2F shows the group's only infant being carried by the same female shown in 2B.

both inside the traps and loose in the center of the platform. The Tomahawk traps were baited with 6 kg of bananas and halved ears of corn twice per week and videos were retrieved from the SD memory card on a continuous basis when the station was re-baited.

Data Analysis

All videos in which a capuchin appeared were reviewed on a frame-by-frame basis. Screen shots were taken at all opportunities when the face and body of individuals were clearly visible. Individual identities were assigned to monkeys on each screenshot based on a variety of physical characteristics including: 1) body size, shape, size, and color of tufts 2) shape of the black cap on forehead 3) shape and

coloration of black and white facial masks and 4) distinctive scars or wounds.

A sex was assigned to an individual when a clear image of their genitalia was obtained. Individuals with robust facial features, complete adult dentition, and the largest relative body sizes were scored as “adults” (Fig. 2A and 2B) (Fragaszy *et al.*, 2004). The presence of elongated nipples, indicative of lactation, was used to score the age and sex of one smaller adult female. “Subadults” were classified as individuals approaching adult body size but lacking the characteristic robust facial features and tufts of the adults (Fig. 2C and 2D). “Juveniles” were classified as individuals that were less than three quarters of the average adult size, not including tail length (Fig. 2E) (Oliveira & Langguth, 2006; Bezerra *et al.*, 2014). “Infants” were classed as only those individuals observed being carried by an adult (Fig. 2F).

Results

Over the 24 trap days during which the station was baited the capuchins visited the platform on 11 occasions. A total of 319 videos were obtained, resulting in 196 videos in which at least one capuchin appeared (61.44%). Each individual appeared in the videos at least once during the 11 visits. A group of 18 individuals containing 3 adult males, 5 adult females, 5 subadults (2 females), 4 juveniles (2 males) and 1 infant was identified.

Discussion

Demographic comparisons of wild primate species across forest fragments can be used to monitor the health and life histories of different populations. Rapid and cost effective assessments are necessary to establish baseline demographic information for future spatial and temporal comparisons across populations of a single species. These assessments can be used to compare population densities, reproductive parameters, patterns of natal dispersal, and group fission and fusion events across multiple species (Lynch Alfaro *et al.*, 2014). Our results provide the first detailed demographic information of a group of wild hooded capuchins (*Sapajus cay*) in Paraguay.

The group size of 18 individuals in Reserva Natural Laguna Blanca is higher than the only previous estimate for *Sapajus cay* in Paraguay (average group size: 7 (Stallings, 1985)), though the total group size is more comparable to the average group size across the genus (Table 2). Group sizes and compositions of the eight *Sapajus* species can vary within and across different habitat locations (Tables 1 and 2). The variability of group sizes across the genus may be indicative of site-specific factors such as variable predation rates, access to supplemental food sources, and anthropogenic disturbances such as hunting and agricultural encroachment (Cullen *et al.* 2000; Fragaszy *et al.*, 2004; Hankerson & Dietz, 2014; Izar *et al.*, 2012).

Though few natural potential predators exist in the area, the capuchins were hunted by local people (mainly for meat and infants for the pet trade (Ayala, pers. com.)) until the reserve was granted protected status in 2010. Predation has been found to reduce the number of individuals in a group (Irwin *et al.*, 2009; Hankerson & Dietz, 2014) and affect group composition by increasing the number ratio of adult males to adult females (Hill & Lee, 1998). Even the loss of

one individual per year from the group can have important consequences for group demographic structure (Fragaszy *et al.*, 2004). A reduction in the number of breeding females would likely have a large impact on the future of the group, as the percentage of juveniles and infants in the group is already below the mean for the genus (Table 2).

Table 1. Study results and mean group size and composition across the genus *Sapajus*.

Species	Group Size	-	No. of Adult Males	No. of Adult Females	No. of Subadults	No. of Juveniles	No. of Infants	Source
<i>S. cay</i>	18	-	3	5	5	4	1	This study
Species	Mean Group Size	Group Size Range	Mean No. Males	Mean No. Females	Mean No. Subadults	Mean No. Juveniles	Mean No. Infants	
<i>S. cay</i> (Paraguay)	12.5	7-18	-	-	-	-	-	Stallings, 1985; This Study
<i>S. cay</i> (Brazil)	20.5	20-21	6	6	2	7.5	-	Pinto, 2006; Fernandes Jr., 2013;
<i>S. macrocephalus</i>	8.3	2-21	1.8	2.1	0.65	2.8	0.8	Klein & Klein, 1976; Izawa, 1980; Defler, 1982; Soini, 1986; Rylands <i>et al.</i> , 2013
<i>S. libidinosus</i>	21.8	6-45	3.4	7	1.25	5	2.5	Freitas <i>et al.</i> , 2008; Izar <i>et al.</i> , 2011; Massaro <i>et al.</i> , 2012; Carretero-Pinzón, 2013; Falótico & Ottoni, 2013
<i>S. nigritus</i>	20.6	7-44	2.4	5.6	2.6	6.8	2.5	Lynch & Rímoli, 2000; Di Bitetti & Janson, 2001; Lynch-Alfaro, 2007; Izar <i>et al.</i> , 2011; Garber <i>et al.</i> , 2012; Janson <i>et al.</i> , 2012; Liebsch & Mikich, 2015
<i>S. xanthosternos</i>	14	9-27	2	3	4	4	1	Canale <i>et al.</i> , 2013
<i>S. robustus</i>	15.7	8-23	2	4	1	-	-	Martins, 2010; Mittermeier <i>et al.</i> 2015
<i>S. flavius</i>	40.2	7-77	10	15	-	37	7	Pontes <i>et al.</i> , 2013; Rodrigues, 2013; Bastos <i>et al.</i> , 2015; Mittermeier <i>et al.</i> 2015

Table 2. Study results and percentage group composition across the genus *Sapajus*.

	% Adult Males	% Adult Females	% Subadults	% Juveniles	% Infants
<i>S. cay</i> (Paraguay)	16.67	27.78	27.78	22.22	5.56
<i>S. cay</i> (Brazil)	29.9	29.9	9.91	36.6	-
<i>S. macrocephalus</i>	9.09- 25	20- 50	0 – 20	22.22– 60	0 – 31.25
<i>S. libidinosus</i>	7.14 - 17.78	21.43 - 35.56	0- 21.43	22.22-42.86	17.39- 33.33
<i>S. nigritus</i>	9.52 – 17.86	25 -62.5	0-25	0 -39.28	0-21.43
<i>S. xanthosternos</i>	14.29	21.43	28.71	28.57	7.14
<i>S. robustus</i>	13.3	26.67	6.67	-	-
<i>S. flavius</i>	24.8	37.3	-	92.04	17.4

Species classification based on Lynch Alfaro *et al.* (2012).

Access to supplemental food sources can increase the size of populations. In Parque Nacional de Brasília, Brasília, Brazil, the capuchins have become accustomed to being fed by tourists and their population has increased exponentially (Fragaszy *et al.*, 2004). In Japanese macaques (*Macaca fuscata*) access to supplementary food sources, in the form of human rubbish dumps, has been found to decrease feeding competition and increase female fertility, leading to increases in group size (Asquith, 1989; Muruthi *et al.*, 1991). The forest fragment of RNLB is bordered on two sides by a large crop field. The capuchins have been seen raiding the crops during the season when corn is grown (Pers. obs.). Though the lack of information from various sites across Paraguay prevents a definitive answer, it may be that the group size in RNLB is related to this supplemental food access.

Within Paraguay, encroachment of soy plantations and cattle farming have had devastating effects on the country's native forest and as a result it is becoming more important to assess wildlife populations in isolated fragments (Huang *et al.*, 2007). With less than 13% of this forest remaining (WWF, 2015), continued habitat fragmentation surrounding RNLB and across Paraguay has the potential to further isolate remaining populations of *Sapajus cay*. Habitat fragmentation can have significant impacts on group demographic structure. Initially, habitat fragmentation can lead to unnaturally high densities of primates, increasing feeding competition within and between groups (Strier, 2007). Decreases in available habitat can affect dispersal patterns. For example, red howler monkeys living in small forest fragments show increased rates of female dispersal, leading to an increased troop density within the fragment (Crockett, 1996). In contrast, mantled howler monkeys (*Alouatta palliata*) have been found to remain in their natal groups causing group size to increase as habitat decreases (Crockett, 1998). In RNLB the 414 ha forest fragment is home to two groups of hooded capuchins. At present, there is no information available for the home ranges of this species but home ranges of *Sapajus nigritus* in Iguazú National Park, Argentina have been found to average 161.77 ha (range=81±293 ha, n=7) (Di Bitetti, 2001). If *S. cay* have similar home ranges to *S. nigritus* then the troop density in RNLB is not abnormally high. The higher number of individuals in the group compared to Stallings (1985) average group size of 7 may be a result of the isolated nature of the forest fragment. However, as the forest at RNLB only became cut off from surrounding fragments within the last 10–15 years (Ayala, pers. comm.) future monitoring will be required to establish long term effects of habitat fragmentation on the group's demographic structure.

We have demonstrated that video camera trapping has great potential for rapid demographic assessment of semi- or unhabituated arboreal primates in areas of rugged terrain or with non-sexually dimorphic species. Using tomahawk traps made the food items harder to access, forcing the capuchins to remain within sight of the video camera for long

periods of time to obtain a food reward. These extended visits produced sufficient videos to identify individuals and made determination of sex possible for the majority of subjects. Though we had success over the course of this study, long-term provisioning of wild primates has been known to alter behavior, development and demographic structure (Asquith, 1989; Lyles & Dobson, 1988; Fedigan, 2010), therefore, the use of a baited provisioning platform is recommended only for short-term assessments and not long-term studies of demographic changes.

This novel information on the group composition of wild *Sapajus cay* population in Paraguay provides a baseline from which changes in group structure can be monitored, facilitating future studies on the effects of living in the remnants of the Paraguayan Atlantic Forest, a topic of increasing importance to the conservation of wild primates (Lynch Alfaro *et al.*, 2014).

Acknowledgments

We thank all the people that helped with this project, in particular Jorge Damian Ayala Santacruz for constructing the platform and his continued support throughout. Special thanks must be extended to Sean Coyne, Roxanne Hawkins, Anna O'Riordan, Susan Smith, Stefan Harrison, Karina Atkinson and Paul Smith for their helpful comments on earlier drafts of this paper. Thanks to Jessica Lynch Alfaro for her extremely helpful comments on this paper. Thank you to the Secretaria del Ambiente and Malvina Duarte for their continued and unwavering support of Fundación Para La Tierra's projects. Our sincere appreciation goes to all the Fundación para la Tierra volunteers and interns who assisted with re-baiting the feeding platform and to everyone who supported our YouCaring Fundraising Campaign that facilitated the purchase of the two camera traps.

References

- Asquith, P. J. 1989. Provisioning and the study of free-ranging primates: history, effects and prospects. *Yearb. Phys. Anthropol.* 32: 129–158.
- Bezerra, B. M., Bastos, M., Souto, A., Keasey, M. P., Eason, P., Schiel, N. and Jones, J. 2014. Camera trap observations of non-habituated Critically Endangered wild blonde capuchins, *Sapajus flavius* (formerly *Cebus flavius*). *Int. J. Primatol.* 35: 895–907.
- Bastos, M., Souto, A., Jones, G., Eason, P., Bione, C., Schiel, N. 2015. Vocal repertoire of wild blonde capuchins (*Sapajus flavius*) and contextual use of calls. *Am. J. Primatol.* 77: 605–617.
- Boinski, S., Quatrone, R. P. and Swartz, H. 2000. Substrate and tool use by brown capuchins in Suriname: ecological contexts and cognitive bases. *Am. Anthropol.* 102: 741–761.
- Canale, G. R., Kierulff, M. C. M., and Chivers, D. J. 2013. A Critically Endangered capuchin monkey (*Sapajus*

- xanthosternos*) living in a highly fragmented hotspot. In: *Primates in Fragments*, L. K. Marsh and C. A. Chapman (eds.), pp. 299–311. Springer, New York.
- Carretero-Pinzón, X. 2013. An eight-year life history of a primate community in the Colombian Llanos. In: *Primates in Fragments*, L. K. Marsh and C. A. Chapman (eds.), pp. 159–182. Springer, New York.
- Chapman, C. A. 1989. Primate seed dispersal: The fate of dispersed seeds. *Biotropica* 21: 148–154.
- Chapman, C. A. and Peres, C. A. 2000. Primate conservation in the new millennium: The role of scientists. *Evol. Anthropol.* 10: 16–33.
- Chiarello, A. G. 2000. Conservation value of a native forest fragment in a region of extensive agriculture. *Rev. Bras. Biol.* 60: 237–247.
- Cowlshaw, G. and Dunbar, R. 2000. *Primate Conservation Biology*. The University of Chicago Press. Chicago.
- Crockett, C. M. 1996. The relationship between red howler monkey (*Alouatta seniculus*) troop size and population growth in two habitats. In: *Adaptive Radiation of Neotropical Primates*. M. A. Norconck, A. L. Rosenberger and P. A. Garber. pp. 489–510. Plenum Press, New York.
- Crockett, C. M. 1998. Conservation biology of the genus *Alouatta*. *Int. J. Primatol.* 19: 549–578.
- Cullen Jr., L., Bodmer, R. E. and Pádua, C. V. 2000. Effects of hunting in habitat fragments of the Atlantic Forests, Brazil. *Biol. Conserv.* 95: 49–56.
- Defler, T. R. 1982. A Comparison of intergroup interactions in *Cebus albifrons* and *Cebus apella*. *Primates* 23: 385–392.
- Di Bitetti, M. S. 2001. Home-range use by the tufted capuchin monkey (*Cebus apella nigrurus*) in a subtropical forest of Argentina. *J. Zool.* 253: 33–35.
- Di Bitetti, M. S. and Janson, C. H. 2001. Reproductive socioecology of tufted capuchins (*Cebus apella nigrurus*) in northeastern Argentina. *Int. J. Primatol.* 22: 127–143.
- Dunbar, R. I. M. 1988. *Primate Social Systems*. Chapman and Hall, London.
- Elliot, D. G. 1913. *A Review of Primates*. Monograph Series, New York, American Museum of Natural History.
- Falótico, T. and Ottoni, E. B. 2013. Stone throwing as a sexual display in wild female bearded capuchin monkeys, *Sapajus libidinosus*. *PLoS ONE* 8, (11): e79535.
- Fedigan, L. M. 2010. Ethical issues faced by field primatologists: Asking the relevant questions. *Am. J. Primatol.* 72: 754–771.
- Fernandes Jr., O. 2013. Comportamento alimentar de um grupo de macacos prego *Sapajus cay* (Illiger, 1815), (Primates, Cebidae), em fragmento de Cerrado, Guia Lopes da Laguna, Mato Grosso do Sul. Dissertação de mestrado. Universidade Federal de Mato Grosso do Sul, Mato Grosso do Sul, Brazil.
- Fragaszy, D. M., Visalberghi, E. and Fedigan, L. M. 2004. *The Complete Capuchin: The Biology of the Genus Cebus*. Cambridge University Press, Cambridge.
- Garber, P. A., Gomes, D., and Bicca-Marques, J. 2012. Experimental field study of problem-solving using tools in free-ranging capuchins (*Sapajus nigrurus*, formerly *Cebus nigrurus*). *Am. J. Primatol.* 74: 344–358.
- Galvis, N., Link, A. and Di Fiore, A. 2014. A novel use of camera traps to study demography and life history in wild animals: A case study of spider monkeys (*Ateles belzebuth*). *Int. J. Primatol.* 35: 908–918.
- Groves, C. P. 2001. *Primate Taxonomy*. Washington, DC, Smithsonian Institution Press.
- Halsam, M. 2012. Towards a prehistory of primates. *Antiquity* 86: 299–315.
- Hankerson, S. J. and Dietz, J. M. 2014. Predation rate and future reproductive potential explain home range size in golden lion tamarins. *Anim. Behav.* 96: 87–95.
- Hershkovitz, P. 1949. Mammals of northern Colombia. Preliminary report No. 4: monkeys (Primates), with taxonomic revisions of some forms. *Proc. U.S. Nat. Mus.* 98: 323–427.
- Hershkovitz, P. 1955. Notes on the american monkeys of the genus *Cebus*. *J. Mammal.* 36: 449–452.
- Hill, R. A. and Lee, P. C. 1998. Predation risk as an influence on group size in Cercopithecoïd primates: implications for social structure. *J. Zool. London* 245: 447–456.
- Hoorn, C. F., Wesselingh, H., Ter Steege, M., Bermudes, A., Mora, J., Sevink, I., Sanmartin, A., Sanchez-Meseguer, C., Anderson, J., Figueiredo, C., Jaramillo, D., Riff, F., Stadler, T., Särkinen, T. and Antonelli, A. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330: 927–31.
- Huang, C. Kim, S. Altstatt, A. Townshend, J. R. G. Davis, P. Song, K. Rodas, O. Yanosky, A. Clay, R. and Musinsky, J. 2007. Rapid loss of Paraguay's Atlantic forest and the status of protected areas – a Landsat assessment. *Remote Sens. Environ.* 106: 460–466.
- Irwin, M. T., Raharison, J.-L. and Wright, P. C. 2009. Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically? *Anim. Conserv.* 12: 220–230.
- Izar, P., Verderane, M. P., Peternelli-Dos-Santos, L., Mendonça-Furtado, O., Presotto, A., Tokuda, M., Visalberghi, E. and Fragaszy, D. 2012. Flexible and conservative features of social systems in tufted capuchin monkeys: comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigrurus*. *Am. J. Primatol.* 74: 315–331.
- Izawa, K. 1980. Social behaviour of the wild black-capped capuchin (*Cebus apella*). *Primates* 21: 443–467.
- Janson, C., Baldovino, M. C. and Di Bitetti, M. 2012. The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigrurus*) in Iguazú National Park, Argentina. In: *Long-term field studies of primates*. P. M. Kappeler and D. P. Watts (eds.), pp.185–212. Springer, New York.
- Jones, C. B. 2005. *Behavioral Flexibility in Primates: Causes and Consequences*. Springer Science + Business Media, New York.
- Kierulff, M. C. M., Santos, G. R. dos, Canale, G., Guidorizzi, C. E. and Cassano, C. 2004. The use of camera-traps in a survey of the buff-headed capuchin monkey, *Cebus xanthosternos*. *Neotrop. Primates* 12: 56–59.

- Klein, I. I. and Klein, D. J. 1976. Neotropical primates: aspects of habitat usage, population densities and regional distribution in La Macarena, Colombia. In: *Neotropical Primates: Field Studies and Conservation*. R. W. Thorington and P. G. Heltne (eds.) pp. 70–78. Washington DC: National Academy of Sciences.
- LaFleur, M., Sauter, M., Cuozzo, F., Yamashita, N., Yousouf, I. A. J. and Bender, R. 2014. Cathemerality in wild ring-tailed lemurs (*Lemur catta*) in the spiny forest of Tsimanampetsotsa National Park: camera trap data and preliminary behavioural observations. *Primates* 55: 207–217.
- Lahota, S., Loken, B., Spehar, S., Fell, E., Pospech, A. and Kasyanto, N. 2012. Discovery of Miller's Grizzled Langur (*Presbytis hosei canicrus*) in Wehea forest confirms the continued existence and extends known geographical range of an endangered primate. *Am. J. Primatol.* 74: 193–198.
- Liebsch, D. and Mikich, S. B. 2015. First record of *Eucalyptus* spp. bark-stripping by brown capuchin monkeys (*Sapajus nigritus*, Primates: Cebidae). *Ciênc. Florest.* 25: 501–505.
- Lowen, J. C., Bartina, L., Clay, R. P., & Tobias, J. A. 1996. *Biological Surveys and Conservation Priorities in Eastern Paraguay*. CBS Conservation Publications, Cambridge.
- Lyles, A. M. and Dobson, A. P. 1988. Dynamics of provisioned and unprovisioned primate populations. In: *Ecology and Behavior of Food-Enhanced Primate Groups, Monographs in Primatology* (Vol. 11), J. E. Fa and C. H. Southwick (eds.), pp. 167–198. Liss, New York.
- Lynch, J. W. and Rímoli, J. 2000. Demography of a group of tufted capuchin monkeys (*Cebus apella nigritus*) at the Estação Biológica de Caratinga, Minas Gerais, Brazil. *Neotrop. Primates* 8: 44–49.
- Lynch Alfaro, J. W. L., Izar, P. and Ferreira, R. G. 2014. Capuchin monkey research priorities and urgent issues. *Am. J. Primatol.* 76: 1–16.
- Lynch Alfaro J. W. 2007. Subgrouping patterns in a group of wild *Cebus apella nigritus*. *Int. J. Primatol.* 28: 271–289.
- Lynch Alfaro, J. W., Boubli, J. P., Olson, L. E., Di Fiore, A., Wilson, B., Gutiérrez-Espeleta, G. A., Chiou, K. I., Schulte, M., Neitzel, S., Ross, V., Schwochow, D., Nguyen, M. T. T., Farias, I., Janson, C. H. and Alfaro, M. E. 2012. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J. Biogeogr.* 39: 272–288.
- Lynch Alfaro, J. W., Silva Jr., J. S. E. and Rylands, A. B. 2012. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *Am. J. Primatol.* 74: 273–286.
- Malta, A. de J. R. and Mendes Pontes, A. R. 2013. The simplified novel diet of the highly threatened blond capuchin in the vanishing Pernambuco Endemism Center. In: *Primates in Fragments: Complexity and Resilience, Developments in Primatology: Progress and Prospects*. L. K Marsh and C. A. Chapman (eds.), pp. 245–257. Springer Science + Business Media, Berlin.
- Martins, W. P. 2010. Densidade populacional e ecologia de um grupo macaco-prego-de-Crista (*Cebus robustus*; Kuhl, 1820) na Reserva Natural Vale. Dissertação de Mestrado. Universidade Federal de Minas Gerais, Minas Gerais, Brasil.
- Martins Jr., A. M. G., Amorim, N., Carneiro, J. C., De Mello Alfonso, P. R. A., Sampaio, I. and Schneider, H. 2015. *ALU* elements and the phylogeny of capuchin (*Cebus* and *Sapajus*) monkeys. *Am. J. Primatol.* 77: 369–375.
- Massaro, L., Qing, L., Visalberghi, E. and Frigaszy, D. 2012. Wild bearded capuchins (*Sapajus libidinosus*) select hammer tools on the basis of both stone mass and distance from the anvil. *Anim. Cogn.* 15: 1065–1074.
- Muruthi, P., Altmann, J. and Altmann, S. 1991. Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia* 87: 467–472.
- Nascimento, F. F., Lazar, A., Seuánez, H. N. and Bonvicino, C. R. 2015. Reanalysis of the biogeographical hypothesis of range expansion between robust and gracile capuchin monkeys. *J. Biogeogr.* 42: 1349–1363.
- Oliveira, M. M. and Langguth, A. 2006. Rediscovery of Marcgrave's capuchin monkey and designation of a neotype for *Simia flavia* (Schreber, 1774) (Primates, Cebidae). *Boletim do Museu Nacional do Rio de Janeiro* 523: 1–16.
- Pebsworth, P. A. and LaFleur, M. 2014. Advancing primate research and conservation through the use of camera traps: introduction to the special Issue. *Int. J. Primatol.* 35: 825–840.
- Pinto, M. C. M. 2006. Padrão comportamental de um grupo de macacos-prego (*Cebus apella cay* Illiger, 1815) no Parque Estadual Matas do Segredo, Campo Grande. Dissertação de Mestrado. Universidade Federal de Mato Grosso do Sul, Mato Grosso do Sul, Brazil.
- Rodrigues, K. C. 2013. Padrão de atividades, comportamento alimentar, exploração de habitat e área de vida de um grupo de *Sapajus flavius* (Schreber, 1774) (Primates, Cebidae) em um Fragmento de Floresta Atlântica, Paraíba, Brazil. Dissertação de Mestrado. Universidade Federal da Paraíba. Paraíba, Brazil.
- Rylands, A. B., Mittermeier, R. A., Bezerra, B. M., Paim, R. P. and Queiroz, H. L. 2013. Family Cebidae (Squirrel Monkeys and Capuchins). In: *Handbook of The Mammals of the World Volume 3*, R. A. Mittermeier, A. B. Rylands and D. E. Wilson (eds), pp. 348–413. Lynx Edicions, Barcelona.
- Silva Jr., J. S. 2001. Especiação nos macacos-prego e caiararas, gênero *Cebus* Erxleben, 1777 (Primates, Cebidae). Tesis de Doctorado, Universidade Federal do Rio de Janeiro, Brazil.
- Soini, P. 1986. A Synecological study of a primate community in the Pacaya-Samiria National Reserve, Peru. *Primate Conserv.* 7: 63–71.
- Stallings, J. R. 1985. Distribution and status of primates in Paraguay. *Neotrop. Primates* 6: 52–58.

- Strier, K. B. 1993 – 1994. Viability of an isolated population of muriqui monkeys (*Brachyteles arachnoides*): implications for primate conservation and demography. *Primate Conserv.* 14-15: 43–52.
- Strier, K. B. 2003. Demography and the temporal scale of sexual selection. In: *Sexual Selection and Reproductive Competition in Primates*, C. B. Jones (eds). American Society of Primatologists: Special Topics in Primatology, pp. 45–63.
- Strier, K. B., Boubli, J. P., Possamai, C. B. and Mendes, S. L. 2006. Population demography of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga Reserva Particular do Patrimônio Natural Feliciano Miguel Abdala, Minas Gerais, Brazil. *Am. J. Phys. Anthropol.* 130: 227–237.
- Strier, K. B. 2007. *Primate Behavioral Ecology* (3rd edition). Pearson Education Inc., Boston.
- Strum, S. C. and Western, D. 1982. Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *American Journal of Primatology* 16: 577–593.
- Tan, C. L., Yang, Y. and Niu, K. 2014. Into the night: camera traps reveal nocturnal activity in a presumptive diurnal primate, *Rhinopithecus brelichi*. *Primates* 54: 1–6.
- Van Belle, S. and Estrada, A. 2005. Cambios demográficos en poblaciones del mono aullador negro (*Alouatta pigra*) como consecuencia de la fragmentación del hábitat. *Universidad y Ciencia* 002: 1–9.
- Wallace, R.B. 2015. *Sapajus cay*. The IUCN Red List of Threatened Species. Version 2015.2. <http://www.iucnredlist.org/details/136366/0>. Accessed on 28 July 2015.
- Williamson, E. A. and Feistner, A. 2011. Habituating primates: processes, techniques, variables and ethics. In: *Field and Laboratory Methods in Primatology: A Practical Guide*, 2nd edition, J. M. Setchell and D. J. Curtis (eds.), pp.33–50. Cambridge University Press, Cambridge.
- World Wildlife Fund. 2015. Priority places, South America: Atlantic Forest. http://wwf.panda.org/what_we_do/where_we_work/atlantic_forests/. Accessed 4 August 2011