

ARTICLES

ECOLOGICAL OBSERVATIONS ON THE PRIMATES OF THE AREA DE CONSERVACIÓN PRIVADA PANGUANA, PERUVIAN AMAZONIA

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We report results from the first systematic survey and ecological observations of primates of the Área de Conservación Privada Panguana (ACPP), located in Peruvian Amazonia between the Sira Mountains, the eastern slopes of the Andes and, the Gran Pajonal. Seven primate species (*Leontocebus leucogenys*, *Saimiri boliviensis peruviensis*, *Cebus yuracus*, *Aotus nigriceps*, *Alouatta seniculus*, *Plecturocebus discolor*, *Pithecia inusta*) were encountered during the study. Their group sizes were within ranges reported for the same or for related species at other sites, but tended to range at the lower end of group size values. No habitat preferences were detected except for *L. leucogenys* and *S. boliviensis peruviensis* who were more frequently encountered around or within forest gaps. Plant species or genera consumed during our observations coincide with species and genera reported from other areas, and several are also used by humans. ACPP is an important natural refuge in a landscape otherwise that is increasingly altered by human activities.

Keywords: *Leontocebus leucogenys*, *Saimiri boliviensis peruviensis*, *Cebus yuracus*, *Alouatta seniculus*, *Plecturocebus discolor*, *Pithecia inusta*, group size, habitat use, diet

Resumen

Reportamos los resultados del primer estudio sistemático y observaciones ecológicas de los primates del Área de Conservación Privada Panguana (ACPP), ubicada en la Amazonía peruana entre los Cerros de El Sira, los vertientes orientales de los Andes, y el Gran Pajonal. Encontramos siete especies de primates (*Leontocebus leucogenys*, *Saimiri boliviensis peruviensis*, *Cebus yuracus*, *Aotus nigriceps*, *Alouatta seniculus*, *Plecturocebus discolor*, *Pithecia inusta*). El tamaño de los grupos estuvo dentro del rango reportado para las mismas especies o especies relacionadas en otros lugares, pero tendieron hacia los valores inferiores. No se encontraron preferencias de hábitat, salvo en *L. leucogenys* y *S. boliviensis peruviensis*, que fueron encontradas con mayor frecuencia cerca o dentro de claros del bosque. Especies o géneros de plantas consumidas durante las observaciones coinciden con especies o géneros reportados para otras áreas, y varios de ellos son también explotados por humanos. ACPP es un refugio natural en un paisaje cada vez más alterado por actividades humanas.

Palabras clave: *Leontocebus leucogenys*, *Saimiri boliviensis peruviensis*, *Cebus yuracus*, *Alouatta seniculus*, *Plecturocebus discolor*, *Pithecia inusta*, tamaño grupal, uso de hábitat, dieta

Introduction

Founded in 1968, Panguana is the oldest biological research station in Peru. In 2011, it was officially recognized by the Peruvian Ministry of the Environment as a private conservation concession, the Área de Conservación Privada Panguana (ACPP; <https://en.wikipedia.org/wiki/Panguana>). It is located in western Amazonian lowlands, but rather isolated from the major tracts of Amazonian forests due to its position between the Cerros de El Sira (Sira Mountains) to the east, the eastern slopes of the Andes to the west, and the Gran Pajonal to the south (Fig. 1).

This isolation makes it an interesting place for biological research, and more than 180 papers have been published on its flora and fauna. However, primates at ACPP have only been cursorily mentioned in the context of a mammal survey that reports the presence of eight primate species in the area (Hutterer et al., 1995), and in a very short study of *Leontocebus leucogenys* (= *Saguinus fuscicollis leucogenys*) (Podloucky, 1978).

Neotropical primate communities are very variable with regards to richness and composition, with rainfall being a major determinant of this variation (Peres and Janson,

1999). Probably due to the shielding effect of the Sira Mountains, ACPP has a long season of reduced rainfall, compared to other lowland Amazonian sites (Fig. 2). Given the strong influence of seasonality on primate ecology (Brockman and van Schaik, 2005; Terborgh, 1983), this makes Panguana an interesting place for studying the ecology of the local primate community. Furthermore, ACPP is located in a region of increasing human impacts on the environment and information on its primate community is important in the context of conservation efforts. Therefore, this study aimed at providing basic ecological information on primates at ACPP, as a starting point for future detailed studies. Specifically, we report data on group size and habitat use of primates at ACPP.

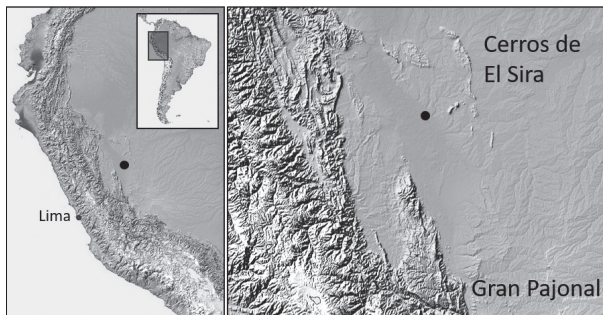


Figure 1. Geographic location of the study area. The black dot indicates the location of ACP Panguana. Map after NASA, <http://photojournal.jpl.nasa.gov/jpeg/PIA03388.jpg>, downloaded on 8 November 2016.

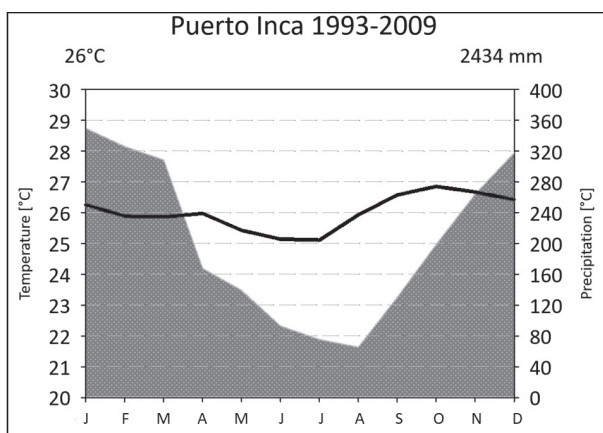


Figure 2. Climate diagram for the nearest meteorological station, Puerto Inca (09°22'53" S 74°57'39" W; 200 m a.s.l.), 1993-2009. Data from Servicio Nacional de Meteorología e Hidrología (SE-NAMHI; www.senamhi.gob.pe).

Methods

Study site and period

ACPP lies in the Huánuco department of Peru, on the south bank of the Río Yuyapichis (=Llullapichis), a tributary of the Río Pachitea, at 09°37'S 74°56'W and an altitude between 220 and 260 m a.s.l. (Kovařík et al., 2015).

Average temperature at the nearest meteorological station (Puerto Inca, 30 km from Panguana) is 26°C, and annual precipitation 2,434 mm, with about 2.6 times more rainfall in the wet season from October to March compared to the dry season from April to September (Fig. 2). The Cerros de El Sira with elevations up to 2,500 m are situated about 40 km to the east, and the eastern slopes of the Andes about 150 km to the west of ACPP. Since these two mountain ranges meet at the Gran Pajonal in the south, the principal connection of the forests at ACPP with other tracts of Amazon rainforest is in the north.

ACPP covers an area of around 12.5 km². The hilly terrain is covered with little disturbed primary *terra firme* forest, characterized as evergreen seasonal rain forest of the preandine Hylaea (Ellenberg, 1959; Hutterer et al., 1995), and with secondary forest of different ages. It is interspersed with creeks and small permanent ponds. Cattle meadows limit the forest in some areas, the Río Yuyapichis limits the study area in the north. Pampas Verde, a village of the indigenous Asháninka, is the nearest human settlement at about 3 km from the study area. The next small city, Yuyapichis, is situated at a distance of about 4 km on the opposite bank of the Río Pachitea. Within the area of ACPP, a section of ca. 1 km² with existing paths was selected for the study. Paths were used to define five (non-independent) trails of about the same length (3 km) that were used for surveying and habitat characterization. Data were collected by the first author (MG) between 23 February 2016 and 28 March 2016, and between 5 May 2016 and 6 July 2016.

Primate observations

Hutterer et al. (1995) had recorded eight primate species in the area of the ACPP. We re-assigned the species occurring in Panguana in the light of recent taxonomic changes (Table 1). To collect data on primates, MG walked the five defined trails either from starting to end point or in the opposite direction five times per direction in the morning and afternoon, respectively. Thus, every trail was walked 20 times by the totally 100 walks. Walks took place from 0630 h to 1000 h and from 1400 h to 1700 h at a speed of about 1 km/h. The order of walked trails and the walking direction (starting to end point or end to starting point) were varied systematically. Upon encountering primates, on the following data were recorded: species, number of individuals sighted, habitat type (forest or gap), ranging height in trees (of the majority of animals during encounter), predominant canopy height, height of the highest tree, geographic position (recorded with a Garmin GPSMAP 64s), and time of day. Tree height was categorized in 5 m bins (5-10 m, 10-15 m etc.). Areas with very young secondary vegetation and canopy heights of <5 m were defined as gaps. We recorded habitat type as gaps if primates ranged inside or at the edge (i.e., within 5 m) of a gap.

Table 1. Primates of ACPP. Light grey cells: primate species encountered during this study.

Family	Primate species reported by Hutterer et al. (1995)	New taxonomic assignment	References for new assignments
Callitrichidae	<i>Saguinus fuscicollis</i>	<i>Leontocebus leucogenys</i>	Matauschek et al., 2011; Rylands et al., 2016
Aotidae	<i>Aotus nigriceps</i>	<i>Aotus nigriceps</i>	
Cebidae	<i>Cebus albifrons</i>	<i>Cebus yuracus</i>	Boubli et al., 2012; Ruiz-Garcia et al., 2010
	<i>Saimiri sciureus</i>	<i>Saimiri boliviensis peruviensis</i>	Lynch Alfaro et al., 2015
Atelidae	<i>Alouatta seniculus</i>	<i>Alouatta seniculus</i>	
	<i>Lagothrix lagothricha</i>	<i>Lagothrix lagothricha poeppigii</i>	Aquino et al., 2015a
Pitheciidae	<i>Callicebus cupreus</i>	<i>Plecturocebus discolor</i>	Byrne et al., 2016
	<i>Pithecia monachus</i>	<i>Pithecia inusta</i>	Marsh, 2014

When an exact count of individuals was not possible (either due to large group size and/or to wide group spread), group size was estimated. Precaution was taken to exclude counting the same group during the same walk. When primates were encountered outside of systematic trail walks, or, due to decreasing visibility, more than 25 m away from trails, we classified observations as chance encounter. We used the same protocol as during systematic observations. To avoid biasing results, data from chance encounters were used only for descriptive purposes, not in quantitative analyses.

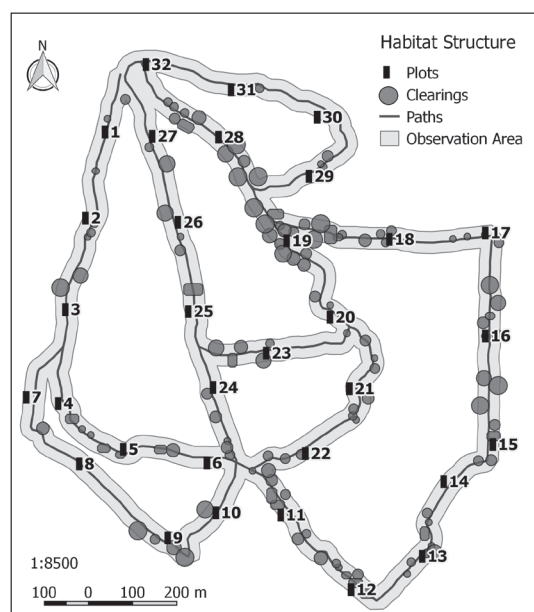
Habitat characterisation

To characterise the habitat, 32 10 m x 20 m plots were established every 200 m along survey trails and their position with regard to the trail varied systematically, if possible (Fig. 3). Within each plot, mean tree height and the height of the highest tree were estimated (5 m bins). The DBH (diameter at breast height) of all trees with DBH ≥ 5 cm was measured with a measuring tape. From this, we calculated the basal area and the number of small trees (DBH 5-10 cm), number of medium trees (DBH 10-20 cm), number of large trees (DBH ≥ 20 cm). To estimate canopy cover, MG took photographs from ground level (Ganzhorn et al., 2011): one picture from the centre of every plot and one from each corner. Finally, MG noted size and position of all gaps within a distance of <25 m from the trails, as well as their gross shape (circular or rectangular) and estimated size in 50 m² bins.

Data analyses

We used QGIS 2.16.1 (QGIS Development Team, 2016) for all geostatistical data management. We imported geographic coordinates of paths, primate observations, habitat plots and gaps from the Garmin GPSMAP 64s. To compute the study area, we created a buffer of 25 m along both sides of trails. We manually added sized and positioned gaps to scale at the given positions and added a buffer of 5 m to all gaps, because primates that were observed in this radius were noted as ranging in a gap. For describing habitat use of primates, we assigned all location records to the nearest habitat plot. For determination of borders between plot areas, we used Voronoi polygons. To calculate plot

area sizes and total area of gaps within the observation or plot areas, we clipped the layers. We transferred the photographs of canopy covers from the plots to binary images so that black pixels could be counted. We performed both with GIMP 2.8.16 (GNU Image Manipulation Program; Kimball et al., 2012). We pooled results for each plot.

**Figure 3.** Location of survey trails and habitat plots.

Statistical analyses

For statistical analyses we only used systematic survey data, the significance level (p-value) for all analyses was 0.05. To test whether primates used the two principal habitat types (forest, gaps) according to availability or exhibited preference for one or the other, we performed exact binomial tests and used a Bonferroni correction to adjust significance levels ($p^* = 0.01$). To account for co-variation between habitat variables, we computed a principal component analysis (PCA). Habitat properties (predominant canopy height, height of highest tree, basal area, canopy cover, number of small, medium and large trees, and percentage of area covered by gaps) were used as variables. Since the first two factors resulting from the PCA accounted for only 44% of variance and correlations between the variables were low

(between -0.29 and 0.51), we tested the influence of habitat properties on primate occurrence separately with a Spearman's rho rank correlation test. Again, we used a Bonferroni correction to adjust significance levels ($p^*=0.0065$). Beforehand, we checked habitat properties for normal distribution using Shapiro-Wilk normality test. We conducted the PCA in STATISTICA 12.0 (StatSoft, Inc., 2014) and all other statistical tests in R 3.3.1 (R Core Team, 2016).

Results

We obtained a total of 279 observations of seven primate species (*A. seniculus*, *A. nigriceps*, *C. yuracus*, *L. leucogenys*,

P. inusta, *P. discolor*, *S. boliviensis*). One hundred seventy-eight observations were made during systematic surveys, 101 observations were chance encounters. We observed *Cebus yuracus* only during systematic surveys, *A. nigriceps* only during chance encounters, and never encountered *L. lagotricha*. Numbers of observations differed largely between species, ranging from a total of two observations of *A. nigriceps* and *C. yuracus* to a total of 116 observations of *L. leucogenys*. Mean group size varied from 2.5 individuals in *P. discolor* to 22 individuals in *S. boliviensis* (Table 2). Maximum group size ranged between 4 and 8 individuals for all species except *S. boliviensis*, for which the highest count was 40 individuals.

Table 2. Observed primate group sizes at the ACP Panguana and closely related species at other locations. We pooled the data from systematic surveys and chance encounters, as means did not differ from each other. SE: standard error; n: number of sightings; Max.: maximum; NA: not available; * mode.

Group size at ACP Panguana					Group size at other locations/regions				
Species	Mean (SE)	Mode	Max.	n	Species	Group Size		Location/region	Reference
						Mean	Range		
<i>Leontocebus leucogenys</i>	3.8 (0.2)	4	8	112	<i>Leontocebus</i> sp.	5	2-9	3°S (northern Peru) to 18°S (southern Bolivia)	Freese et al., 1982
					<i>Leontocebus illigeri</i>	6*	2-10	Pacaya-Samiria National Reserve, Peru	Soini, 1987
<i>Aotus nigriceps</i>	NA	NA	4	2	<i>A. nigriceps</i>	2.8 ± 0.6	2-4	Río Urubamba and Río Tambo, Peru	Aquino et al., 2013
						3.6	2-4	upper Rio Urucú, Brazil	Peres, 1993
<i>Saimiri boliviensis peruviansis</i>	22.0 (19.3)	20	40	25	<i>S. b. peruviansis</i>	32	12-50	Pacaya-Samiria National Reserve, Peru	Soini, 1986
						53.7	45-75	Manu National Park, Peru	Boinski et al., 2003; Mitchell, 1994
<i>Cebus yuracus</i>	NA	NA	4	2	<i>S. b. boliviensis</i>	15.6 ± 3.1	13-19	Río Urubamba and Río Tambo, Peru	Aquino et al., 2013
						8.3	5-10	Pacaya-Samiria National Reserve, Peru	Soini, 1986
<i>Cebus yuracus</i>	NA	NA	4	2	<i>C. yuracus</i>	10.3 ± 2.9	6-13	Río Urubamba and Río Tambo, Peru	Aquino et al., 2013
							9-15	Huánuco and San Martín, Peru	Aquino et al., 2017
<i>Alouatta seniculus</i>	3.6 (1.0)	3	6	8	<i>A. seniculus</i>	5.5	2-13	Pacaya-Samiria National Reserve, Peru	Soini, 1986
						5.6 ± 2.1	4-8	Río Urubamba and Río Tambo, Peru	Aquino et al., 2013
<i>Alouatta seniculus</i>	3.6 (1.0)	3	6	8	<i>A. seniculus</i>	5 ± 1.9	3-9	Chontayacu, Chinchao and Alto Huallaga, Peru	Aquino et al., 2015b
							2-5	Huánuco and San Martín, Peru	Aquino et al., 2017
<i>Plecturocebus discolor</i>	2.5 (0.2)	2	5	39	<i>P. discolor</i>	3.5 ± 0.6	2-6	Tiputini Biodiversity Station, Ecuador	Dacier et al., 2011; Van Belle et al., 2016
<i>Pithecia inusta</i>	3.4 (0.3)	3	7	39	<i>Pithecia isabela</i>	4 ± 1.5	2-8	Pacaya-Samiria National Reserve, Peru	Soini, 1988
					<i>Pithecia monachus</i> -group	1.9-5.2	2-8	Western Pando, Bolivia different locations	Izawa and Yoneda, 1981; Norconk & Setz, 2013

The observation area had a total size of 35.7 ha, 82% of which were covered by forest and 18% by gaps (including a 5m buffer around gaps). We observed *L. leucogenys* ($p < 0.0001$) and *S. boliviensis* ($p = 0.0089$) more often in gaps than expected by chance. *Pithecia inusta* ($p = 0.0156$) and *P. discolor* ($p = 0.0484$) seemed to prefer gaps, however, values were not significant when p-levels were adjusted. *Alouatta seniculus* ($p = 1$) did not show a preference. For *A. nigriceps* and *C. yuracus*, the number of sightings was too low to examine habitat preferences.

The frequency of sightings of *S. boliviensis* correlated with the size of the area covered by gaps ($\rho = 0.51$, $p = 0.003$). We also noted the following trends: frequency of sightings of *S. boliviensis* and basal area ($\rho = 0.37$, $p = 0.0375$), and frequency of sightings of *P. inusta* and maximum tree height ($\rho = 0.43$, $p = 0.0133$); in both cases, p-values are higher than the adjusted p-values. There was no other significant correlation of trend. We observed feeding on 14 plant species directly and found residuals from six plant species below sites where we had spotted primates (Table 3).

Table 3. Plant species recorded in the diet of primates at ACPP. fl: flower; fr: fruit. *A. n.*: *Aotus nigriceps*; *A. s.*: *Alouatta seniculus*; *C. y.*: *Cebus yuracus*; *L. l.*: *Leontocebus leucogenys*; *P. d.*: *Plecturocebus discolor*; *P. i.*: *Pithecia inusta*; *S. b.*: *Saimiri boliviensis*; d: direct feeding observation; r: feeding residuals encountered below place of primate sighting.

Family	Species	Local name	Part consumed	Primate species							
				<i>L. l.</i>	<i>A. n.</i>	<i>S. b.</i>	<i>C. y.</i>	<i>A. s.</i>	<i>P. d.</i>	<i>P. i.</i>	
Acanthaceae	<i>Mendoncia cf. lindavii</i>		fl								r
Anacardiaceae	<i>Spondias mombin</i>	Ubo grande	fr								d
Anacardiaceae	<i>Spondias</i> sp.	Ubo chico	fr								d
Annonaceae	<i>Annona</i> sp.	Anonilla	fr			d					d
Annonaceae	<i>Mosannonna raimondii</i>		fr					d			r
Arecaceae	<i>Astrocaryum</i> sp.	Huicongo	fr								r
Arecaceae	<i>Attalea phalerata</i>	Shapaja	fr			d					
Arecaceae	<i>Iriartea deltoidea</i>	Cashapona	fr								r
Arecaceae	<i>Oenocarpus bataua</i>	Ungurahui	fr								r
Bombacaceae	<i>Quararibea</i> sp.	Sapote	fr	r							
Fabaceae	<i>Dipteryx odorata</i>	Shihuahuaco	fr			d					
Fabaceae	<i>Inga</i> sp. 1	Shimbillo	fr			d					
Fabaceae	<i>Inga</i> sp. 2	Shimbillo	fr			d					
Fabaceae	<i>Inga</i> sp. 3	Shimbillo	fr		i						d
Malvaceae	<i>Malvaviscus concinnus</i>		fl, fr			d					
Malvaceae	<i>Theobroma cacao</i>	Cacao	fr	d							
Moraceae	<i>Ficus</i> cf. <i>pertusa</i>		fr					d			
Moraceae	<i>Ficus</i> sp.		fr	d	d	d					
Moraceae	<i>Naucleopsis glabra</i>	Cacahuillo	fr	r							
Myrtaceae	indet.		fr			d					

Discussion

We encountered all primate species reported by Hutterer et al. (1995) except for the largest one, *L. lagothericha*. This species has not been seen in the area of ACPP (Juliane Diller, pers. comm.; Carlos Vásquez Módena, pers. comm.) within the last 50 years. It was listed by Hutterer et al. (1995) based on skulls obtained 10 km east of Panguana and hunters seen with dead woolly monkeys outside the area. Apparently, *Lagothrix lagothericha* went locally extinct, probably due to hunting. Although hunting of primates is prohibited by Peruvian law, large species like *L. lagothericha* are heavily hunted for bushmeat throughout Amazonia and consequently become generally rare or locally extinct (Aquino et al., 2016; Peres, 1990). *Cebus yuracus* was present in the area 20-50 years ago but had not been seen for almost 20 years (Carlos

Vásquez Módena, pers. comm.). This species seems to recover, probably due to the increase in size of the protected area since the creation of ACPP in 2011.

For all species except *C. yuracus* (which was only encountered twice) group sizes observed at ACPP are within ranges reported for the same or for related species at other sites, but tended to range at the lower end of group size values. Carlos Vásquez Módena (pers. comm.) reported that group size of capuchins in the area had always been small 20-50 years ago and that they usually travelled together with *Saimiri* groups. In the absence of data on factors that might affect group size (e.g. habitat productivity), we refrain from discussing causes of the trend towards smaller group sizes of primates at Panguana.

The only species to show obvious habitat preferences were *L. leucogenys* and *S. boliviensis*. The higher encounter rates of these highly insectivorous primates close to or within gaps might relate to a higher abundance of insects (Fowler et al., 1993). However, *Leontocebus nigrifrons* does not show increased prey foraging success in young secondary forest compared to primary forest, despite probably higher abundance, at least of katydids in the former (Kupsch et al., 2014).

Almost all plant species consumed by primates during our study come from genera that have been reported to be part of the diet of primates at other sites. Given the short study period, the list of species likely represents only a small fraction of what is actually used. Several plant species are actually also exploited as food, construction material or medicine by humans (Duke and Vasquez, 1994).

In sum, our study provides the first systematic data on the primates of the ACP. These data must be considered as preliminary and do not allow to draw far-reaching conclusions. In any case, this area warrants further study, on one hand due to its geographic location, on the other hand because its protection status converts it into an important natural refuge within an otherwise increasingly altered landscape.

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References

- Aquino, R., Cornejo, F. M. and Heymann, E. W. 2013. Primate abundance and habitat preferences on the lower Urubamba and Tambo rivers, central-eastern Peruvian Amazonia. *Primates* 54: 377–383.
- Aquino, R., Cornejo, F. M., Cortés Ortiz, L., Encarnación C., F., Heymann, E. W., Marsh, L. K., Mittermeier, R. A., Rylands, A. B. and Vermeer, J. 2015a. *Monkeys of Peru. Pocket identification guide*. Conservation International, Arlington.
- Aquino, R., Zárate, R., López, L., García, G. and Charpentier, E. 2015b. Current status and threats to *Lagothrix flavicauda* and other primates in montane forest of the Región Huánuco, Peru. *Primate Conserv.* 29: 31–41.
- Aquino, R., López, L., Arévalo, I. and Daza, J. 2016. Diversidad y abundancia de primates y sus amenazas en el interfluvio de los ríos Napo y Putumayo, Amazonía peruana. *Rev. peru. Biol.* 23: 243–252.
- Aquino, R., García, G., Charpentier, E., López, L. 2017. Estado de conservación de *Lagothrix flavicauda* y otros primates en bosques montanos de San Martín y Huánuco, Perú. *Rev. Peru. Biol.* 24: 25–34.
- Boinski, S., Kauffman, L., Westoll, A., Stickler, C. M., Cropp, S. and Ehmke, E. 2003. Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). *Behaviour* 140: 1421–1467.
- Boubli, J. P., Rylands, A. B., Farias, I. P., Alfaro, M. E. and Lynch Alfaro, J. 2012. *Cebus* phylogenetic relationships: a preliminary reassessment of the diversity of the untufted capuchin monkeys. *Am. J. Primatol.* 74: 381–393.
- Brockman, D. K. and van Schaik, C. P. 2005. *Seasonality in primates. Studies of living and extinct human and non-human primates*. Cambridge University Press, Cambridge.
- Byrne, H., Rylands, A. B., Carneiro, J. C., Lynch Alfaro, J. W., Bertuol, F., da Silva, M. N. F., Messias, M., Groves, C. P., Mittermeier, R. A., Farias, I., Hrbek, T., Schneider, H., Sampaio, I. and Boubli, P. J. 2016. Phylogenetic relationships of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy based on molecular evidence. *Front. Zool.* 13: 1–26.
- Dacier, A., de Luna, A. G., Fernandez-Duque, E. and Di Fiore, A. 2011. Estimating population density of Amazonian titi monkeys (*Callicebus discolor*) via playback point counts. *Biotropica* 43: 135–140.
- Duke, J. A. and Vasquez, R. 1994. Amazonian ethnobotanical dictionary. CRC Press, Boca Raton.
- Ellenberg, H. 1959. Typen tropischer Urwälder in Peru. *Schweiz. Z. Forstwesen* 3: 169–187.
- Fowler, H.G., Silva, C.A. and Venticinque, E. 1993. Size, taxonomic and biomass distributions of flying insects in central Amazonia: forest edge vs. understory. *Rev. Biol. Trop.* 41: 755–760.
- Freese, C. H., Heltne, P. G., Castro R., N. and Whitesides, G. 1982. Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *Int. J. Primatol.* 3: 52–90.
- Ganzhorn, J. U., Rakotondrany, S. J. and Ratovomana, Y. R. 2011. Habitat description and phenology, In: *Field and laboratory methods in primatology. A practical guide*, J. M. Setchell and D. J. Curtis, D.J. (eds.), pp. 51–68. Cambridge University Press, Cambridge.
- Hutterer, R., Verhaagh, M., Diller, J. and Podloucky, R. 1995. An inventory of mammals observed at Panguana Biological Station, Amazonian Peru. *Ecotropica* 1: 3–20.
- Izawa, K. and Yoneda, M. 1981. Habitat utilization of nonhuman primates in a forest of the western Pando, Bolivia. *Kyoto Univ. Overseas Res. Rep. New World Monkeys* (1981): 13–22.

- Kimball, S., Mattis, P. and GIMP Development Team. 2012. *GNU Image Manipulation Program 2.8.16*. <http://www.gimp.org>.
- Kovařík, F., Teruel, R., Lowe, G. and Friedrich, S. 2015. Four new scorpion species (Scorpiones: Buthidae) from Amazonian Peru. *Euscorpius* 210: 1–40.
- Kupsch, D., Waltert, M. and Heymann, E. W. 2014. Forest type affects prey foraging of saddleback tamarins, *Saguinus nigrifrons*. *Primates* 44: 403–413.
- Lynch Alfaro, J. W., Boubli, J. P., Paim, F. P., Ribas, C. C., da Silva, M. N. F., Messias, M. R., Röhe, F., Mercês, M. P., Silva Júnior, J. S., Silva, C. R., Pinho, G. M., Koshkarian, G., Nguyen, M. T. T., Harada, M. L., Rabelo, R. M., Queiroz, H. L., Alfaro, M. E. and Farias, I. P. 2015. Biogeography of squirrel monkeys (genus *Saimiri*): South-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. *Mol. Phylogen. Evol.* 82B: 436–454.
- Marsh, L. K., 2014. A taxonomic revision of the saki monkeys, *Pithecia* Desmarest, 1804. *Neotrop. Primates* 21: 1–163.
- Matauschek, C., Roos, C. and Heymann, E. W. 2011. Mitochondrial phylogeny of tamarins (*Saguinus*, Hoffmannsegg 1807) with taxonomic and biogeographic implications for the *S. nigricollis* species group. *Am. J. Phy. Anthropol.* 144: 564–574.
- Mitchell, C. L. 1994. Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). *Behaviour* 130: 169–190.
- Norconk, M. A. and Setz, E. Z. 2013. Ecology and behavior of saki monkeys (genus *Pithecia*). In: *Evolutionary biology and conservation of titis, sakis and uacaris*, L. M. Veiga, A. A. Barnett, S. F. Ferrari, and M. A. Norconk (eds.), pp. 262–271. Cambridge University Press, New York.
- Peres, C. A. 1990. Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* 54: 47–59.
- Peres, C. A. 1993. Structure and spatial organization of an Amazonian terra firme forest primate community. *J. Trop. Ecol.* 9: 259–276.
- Peres, C. A. and Janson, C. H. 1999. Species coexistence, distribution, and environmental determinants of neotropical primate richness: a community-level zoogeographic analysis, In: *Primate communities*, J. G. Fleagle, C. H. Janson and K. E. Reed (eds.), pp. 55–74. Cambridge University Press, Cambridge.
- Podloucky, R., 1978. Freilandbeobachtungen an südamerikanischen Braunrückentamarins (*Saguinus fuscicollis leucogenys*) im peruanischen Amazonasregenwald. *Kurzfasungen der Vorträge, 52. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde*, Frankfurt.
- QGIS Development Team. 2016. *QGIS Geographic Information System*. Open Source Geospatial Foundation. <http://qgis.osgeo.org>.
- R Core Team. 2016. R: *A Language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ruiz-Garcia, M., Castillo, M. I., Vasquez, C., Rodriguez, K., Pinedo, M., Shostell, J. and Leguizamon, N. 2010. Molecular phylogenetics and phylogeography of the white-fronted capuchin (*Cebus albifrons*; Cebidae, Primates) by means of mtCOII gene sequences. *Mol. Phylogen. Evol.* 57: 1049–1061.
- Rylands, A. B., Heymann, E. W., Lynch Alfaro, J., Buckner, J. C., Roos, C., Matauschek, C., Boubli, J. P., Sampaio, R. and Mittermeier, R. A. 2016. Taxonomic review of the New World tamarins (Primates: Callitrichidae). *Zool. J. Linn. Soc.* 177: 1003–1028.
- Soini, P. 1986. A synecological study of a primate community in the Pacaya-Samiria National Reserve, Peru. *Primate Conserv.* 7: 63–71.
- Soini, P. 1987. Ecology of the saddle-back tamarin *Saguinus fuscicollis illigeri* on the Rio Pacaya, northeastern Peru. *Folia Primatol.* 49: 11–32.
- Soini, P. 1988. El huapo (*Pithecia monachus*): dinámica poblacional y organización social. *Informe de Pacaya* 27: 1–24.
- StatSoft, Inc. 2014. *STATISTICA für Windows (Software-System für Datenanalyse)*, Version 12.0. URL www.statsoft.com.
- Terborgh, J. 1983. *Five New World primates. A study in comparative ecology*. Princeton University Press, Princeton.
- Van Belle, S., Fernandez-Duque, E. and Di Fiore, A. 2016. Demography and life history of wild red titi monkeys (*Callicebus discolor*) and equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador: A 12-year study. *Am. J. Primatol.* 78: 204–215.