DEMOGRAPHY, HABITAT USE AND ACTIVITY BUDGET OF A WILD GROUP OF BLACK-FACED BLACK SPIDER MONKEYS (*ATELES CHAMEK*) IN LAS PIEDRAS, SOUTH-EASTERN PERÚ

Liselot Roos Lange^{1, 2} and Nicola Marie Robson³

¹Association for Research and Conservation in the Amazon (ARCAmazon), Jr. Billinghurst 433, Puerto Maldonado, Madre de Dios, Peru. E-mail <liselotlange@gmail.com> ² Junglekeepers Peru, Jr. Junin 17C-18, Puerto Maldonado, Madre de Dios, Peru. ³Faculty of Health and Medical Sciences, University of Surrey, Stag Hill, Guildford GU2 7XH, United Kingdom. E-mail <nickirobson.uk@gmail.com>

Abstract

Spider monkeys are one of the main seed-dispersal agents in the Amazonian ecosystem and therefore help regenerate the rainforest. The black-faced black spider monkey (*Ateles chamek*) is internationally recognized as Endangered, and its range is limited to Peru, Bolivia and Brazil. Spider monkeys are a difficult genus to study and little is known about their populations in the wild. Here we present the results of a study on demography, habitat use, activity budget and preliminary notes on ranging pattern and diet of a wild group of *A. chamek* studied in a floodplain forest in south-eastern Peru. The group (in total eight to nine individuals) had a home range of approximately 1.6 km² (160 hectares) with a daily path length of approximately 1,200 m. The group was encountered at canopy levels above 20 m in height 75.2% of the time and rarely descended to lower forest levels. There was a weak but significant positive correlation between the number of encounters with individuals of the study group and the number of feeding trees in an area (R² = 0.38, N = 93, P > 0.001). The majority of their diet consisted of fruits, followed by leaves. Resting accounted for 41.9% of their activity budget, with foraging accounting for 30% and traveling 23.8%. Most findings of this study are consistent with other studies on the species, but we found that the group size in our study was unusually small. However, this did not seem to have an influence on home range size or activity budget.

Keywords: spider monkey, Ateles, demography, home range, activity budget, habitat use, ranging pattern, diet.

Resumen

Los monos araña son uno de los principales agentes de dispersión de semillas en el ecosistema amazónico y por lo tanto ayudan a regenerar la selva. El mono araña negro (*Ateles chamek*) está reconocido internacionalmente como En Peligro, y su área de distribución se limita a Perú, Bolivia y Brasil. Los monos araña son un género difícil de estudiar y se sabe poco sobre sus poblaciones en estado silvestre. Aquí se presentan los resultados de un estudio sobre demografía, uso del hábitat, presupuesto de actividades y notas preliminares sobre la pauta de distribución y la dieta de un grupo silvestre de *A. chamek* estudiado en un bosque de llanura inundable en el sudeste del Perú. El grupo (en total, ocho o nueve individuos) tenía un área de distribución de aproximadamente 1.6 km² (160 hectáreas) con una longitud de recorrido diario de aproximadamente 1,200 m. El grupo se encontró en niveles de copas de más de 20 m de altura el 75,2% del tiempo y rara vez descendió a niveles inferiores del bosque. Hubo una correlación positiva, débil pero significativa, entre el número de encuentros con los individuos del grupo de estudio y el número de árboles en que se alimentan en una zona (R² = 0,38, N = 93, P > 0,001). La mayoría de su dieta consistió en frutos, seguidos de hojas. El descanso representó el 41,9% de su presupuesto de actividades, la búsqueda de alimento el 30% y los viajes el 23,8%. La mayoría de los hallazgos de este estudio son consistentes con otros estudios sobre la especie, pero encontramos que el tamaño del grupo en nuestro estudio era inusualmente pequeño. Sin embargo, esto no pareció tener influencia en el tamaño del área de distribución o en el presupuesto de actividades.

Palabras clave: mono araña, *Ateles*, demografía, rango de hogar, presupuesto de actividad, uso de hábitat, patrón de recorrido, dieta.

Introduction

Spider monkeys (genus *Ateles*, Fig. 1) represent some of the most charismatic and ecologically-important primates found in the neotropical rainforest. The genus *Ateles* consists of seven species (following Groves, 2001; Morales-Jiménez *et al.*, 2015) which occur in tropical forests ranging from Mexico to Bolivia (Collins, 2008). However, *Ateles* are under serious threat from both habitat loss and poaching. Little is known about the demography and behavior of distinct populations, as *Ateles* are a particularly hard genus to study due to their preference for higher canopy levels. *Ateles* have evolved distinct morphological characteristics which allow them to thrive in the highest level of the forest canopy (Campbell *et al.*, 2005; Rosenberger *et al.*, 2008; Hooper, 2014). Many aspects of their

physiology are distinct from other primates and are specialized for movements such as below-branch suspension and brachiation, rather than leaping and quadrupedal travel (Fontaine, 1990; Rosenberger *et al.*, 2008; Lindshield and Rodrigues, 2009). For instance, skeletal modifications to the wrist and elbow, and the absence or reduction of the thumb, all assist *Ateles* in these suspensory activities which are essential for life in the canopy (Rosenberger *et al.*, 2008; Lindshield and Rodrigues, 2009). In addition to specialized forelimbs, *Ateles* also possess a prehensile tail that can support the animal's entire body weight (Youlatos, 2008).



Figure 1. An example of *Ateles chamek* with its distinct morphological characteristics, e.g. the long limbs and prehensile tail. Photo credit: Liselot Lange (2016).

Ateles usually prefer primary, closed-canopy forests (Michalski and Peres, 2005; Wallace, 2008; Salvador *et al.*, 2011), and they are found to spend more than 70% of the time in the higher canopy levels above 25 m (Van Roosmalen, 1985; Wallace, 2008). Ateles may be restricted to the highest canopy levels due to dietary and physical specialization. *Ateles* are extremely frugivorous (Campbell *et al.*, 2005; Wallace 2008), and ripe fruit is seldom found in lower forest levels (Campbell *et al.*, 2005). Furthermore, their shoulder joint modifications and elongated forelimbs do not allow for terrestrial quadrupedism, making it harder for *Ateles* to visit the ground (Campbell *et al.*, 2005). They are believed to descend to the forest floor only for drinking, visiting clay licks, eating soil or decaying wood, and during social conflicts (Campbell *et al.*, 2005).

Ateles exhibit a larger home range than other primates in the same habitat due to the distribution of fruit patches (Takahashi, 2008; Defler, 2010). Home ranges of *Ateles* have been recorded between 32 and 900 ha with daily path lengths between 500 and 5,600 m (McFarland Symington, 1988a; Wallace, 2006, 2008; Spehar, Di Fiore and Link, 2010; González-Zamora *et al.*, 2012, 2015; Velázquez-Vázquez *et al.*, 2015).

The activity budget of *Ateles* is often described using four mutually exclusive categories: resting, foraging, traveling, and other (see Table 1) (McFarland Symington, 1988a; Wallace, 2001). On average, social behaviors account for less than five percent of *Ateles* activity budgets (Slater, Schaffner and Aureli, 2007, 2009), which is less than for most primates. The largest portion of *Ateles* daily activity budget (nearly half) consists of resting (White, 1986; McFarland Symington, 1988a; Nunes, 1995; Wallace, 2001). Traveling accounts for between 14.8 and 32.6% of the activity budget, and foraging between 18 and 50.5% (Chapman, Chapman and McLaughlin, 1989; Wallace, 2006). Time spent resting and traveling is likely influenced by levels of fruit abundance and distribution.

Ateles feed 70 to 90% of the time on large-seeded fruits (Di Fiore *et al.*, 2008; Felton *et al.*, 2008). *Ateles* are very important seed dispersal agents as they rarely masticate the seeds and instead swallow them whole, therefore contributing to the regeneration of forests (Link and Di Fiore, 2006; González-Zamora *et al.*, 2012; Link *et al.*, 2012). In times of fruit scarcity, *Ateles* complement their diet with leaves, flowers, seeds, decaying wood, clay, soil, and a very small percentage of invertebrates (Di Fiore *et al.*, 2008; Rylands and Mittermeier, 2013).

Spider monkeys are of particular interest to primatologists because they exhibit a fission-fusion social structure similar to that of chimpanzees, which is unique among Neotropical primates (Anaya-Huertas and Mondragón-Ceballos, 1998). This structure involves the division of a group, that can consist of over 50 individuals, into temporary subgroups (Shimooka et al., 2008). Subgroups fluctuate in size and composition throughout the day, averaging three to four individuals at a time (Van Roosmalen, 1985; Chapman, 1988; Shimooka, 2005; Lange, 2016). Due to the clumped distributions of their primary food sources (González-Zamora et al., 2008) and the fact that Ateles often deplete fruit supplies in their feeding trees (Chapman, 1988), this social system evolved to reduce intragroup competition for food resources (Asensio et al., 2008; Spehar and Di Fiore, 2013). Therefore, group fission is evoked when fruit is scarce, and conversely, fusion occurs in instances of high fruit availability (Asensio et al., 2008; Aureli and Schaffner, 2008). Hence, subgroups need to visit fewer food patches to find sufficient food (Aureli and Schaffner, 2008).

Most research on spider monkeys has been conducted in protected areas (González-Zamora *et al.*, 2008), and little is known about their behavioral ecology in unprotected areas (Hagell, Whipple and Chambers, 2013). In this study, we report the demography, habitat use, activity budget and preliminary notes on ranging patterns and diet of *Ateles chamek* in an area not part of a national park or reserve.

Methods

Study site

This study was conducted at the Las Piedras Amazon Center (LPAC), a 4,465-hectare ecotourism and conservation concession run by the non-governmental organization (NGO) the Alliance for Research and Conservation in the Amazon (ARCAmazon). The site is located in the Madre de Dios department of Peru (-12.0709367 S, -69.5005917 W), approximately 65 km from the town of Puerto Maldonado and 55 km from the border with Brazil. The site consists of terra firme and floodplain forest ranging from 200 to 400 m in elevation along the Las Piedras River. Our research was conducted between May 2016 and December 2017. During this time, minimum temperature averaged 22°C, maximum temperature 35°C, humidity levels averaged between 60 and 90% and average daily rainfall between 10 and 220 mm (Weather Underground, 2019; World Weather Online, 2019). Field work was based out of the research center at LPAC, which takes up less than one hectare of the land and consists of sleeping platforms and communal areas. The concession contains approximately 37 km of mapped trails, some of which were used to observe the focal group in the north-east of the concession. A stream (the Loboyoc) cuts from the south-west to the north-east of the concession and joins with the Las Piedras River. The stream is traversable by the study group which has multiple crossing points along its course. Within the concession, multiple groups of spider monkeys are found without any major geographical boundaries separating the groups. This study solely focused on one of the groups in the north-east of the concession.

The river shed of Las Piedras is an extraction forest, and most concessions are used for the exportation of Brazil nuts and timber. Hunting (mostly illegal) is a common practice in the concessions surrounding LPAC, as the region does not lie within a national park or reserve and there is little protection for wildlife. ARCAmazon acquired the LPAC-concession in April 2015 with the aim to preserve the land and create a corridor for flora and fauna while forming alliances with other NGOs and landowners. Ten species of non-human primates are found within the concession (Lange, 2016).

Subjects

The focal group consisted of eight well-habituated, individually recognizable *Ateles chamek* at the start of the study (May 2016). As there had been tourism in the years before the study, the spider monkeys had become accustomed to the presence of humans. There were three adult males (Ezra, Luca, Scar) and five females, where we group both subadult and adult females into one category (Juno, Mami, Manchas, Flor, Rose). The individuals were identified by facial characteristics and were given names to ease data collection and communication in the field. Throughout the study, the group's composition fluctuated due to death and newborn individuals. In August 2016 an infant male (Leaf) was born to Juno. Later in June 2017, the oldest female (Manchas) passed away from natural causes. The remains were discovered in a decomposing state, after which it was discovered that the subject's left ankle and foot were missing. Post-mortem examination showed the animal had worn teeth and brittle bones; indicators of old age. The individual also had a healed fracture of the left humerus, but did not show limitations in movement whilst alive. Around the same time of this death, a female infant (Maya) was born to Mami. By the end of the study (December 2017), the group consisted of three adult males (Ezra, Luca, Scar), two (sub)adult females (Flor, Rose), two lactating females (Juno, Mami), one juvenile male (Leaf), and one infant female (Maya).

Data collection

The data on Ateles chamek were collected through focal follows of the study subjects. Follows took place in surveys between 05:00 and 19:00, covering all hours in which Ateles are known to be active. Existing trails within the concession were walked at a slow speed (between one and two km/h) to locate the study group. Upon encountering a subgroup or the entire group, a random individual was chosen for the focal observations. In this study data were collected only on adult individuals, as the infants and juveniles' behavior is strongly correlated with their mother's behavior. Data were collected on adult males, sub and adult females (without offspring), and lactating females (with offspring). Behavioral data were collected on the focal individual every fifth minute, using instantaneous focal sampling (Altmann, 1974). For gathering data on their activity budget, the following categories were used; traveling, resting, foraging, and other (Table 1). The forest level use of the focal individual was also recorded every fifth minute (between the ground and 10 m high, between 10 m and 20 m high, or above 20 m high). The focal animal was followed for one hour, until out of sight for more than ten minutes, until no longer possible to follow, or until the sun set and the focal settled at a sleeping site. After one hour of following a focal individual, a new individual was selected. The focal individual's movements were recorded by creating a track with a handheld GPS-system (GARMIN 64s).

Data were also collected on diet by recording and identifying food items consumed by the spider monkeys (fruits, flowers, leaves, bark, clay or invertebrates). Additionally, ad libitum data were taken on social interactions and group composition. Finally, all feeding trees and sleeping sites were marked with the GPS-system.

Activity categories	Description
Traveling	Moving for more than thirty seconds or between trees
Resting	Sleeping, being stationary or small movements less than thirty seconds
Foraging	The looking for, handling of, or ingestion of food or water
Other	Behaviors not fitting into any of the other categories, e.g. social interactions between individuals, interaction with observers, defecating and/or urinating

Table 1. Description of the used activity categories.

Data analysis

All GPS data were uploaded into the computer software Basecamp (Garmin Ltd., 2019). By creating a polygon of the outer points of A. chamek encounters and follows, we calculated the home range (in ha) and created a map presenting habitat usage (Fig. 2). Additionally, a second map was created showing the distribution of the feeding trees and sleeping sites within the home range (Fig. 3). A non-parametric regression analysis was used to verify whether a correlation exists between grid-cell use and the number of feeding trees present within that cell. An estimation of the encountered subgroups' daily path length was made by calculating their average speed during a follow and multiplying this by average time spent traveling per day. The group's activity budget was calculated by combining the frequency of behavior in all samples. The activity budgets of adult males, (sub)adult females (without offspring) and lactating females (with offspring) are compared through descriptive analyses. No statistical analyses were applied due to the small sample size. All food items consumed were categorized (fruits, flowers, bark, clay and invertebrates) and frequency of consumption of each category was expressed as a percentage of all feeding observations throughout the study.

Results

A total of 1,519 instants, obtained from 149 focal follows, were analyzed. On average the focal follows lasted 45.60±20.11 minutes.

Demography

Total group size fluctuated between eight and nine individuals over the course of the study due to one death and two newborns. Observed subgroup size ranged from one to nine individuals, with an average of 4.63±1.92 members. The subgroups also varied in composition (Fig. 2). The most common type of subgroup consisted of one or more females with their offspring, which accounted for 41.2% of encounters. The second most common group observed was both males and females with offspring, which accounted for 31.9% of subgroups. Interestingly, while 10.9% of observed subgroups consisted of males only, female-only subgroups without offspring were never encountered. The percentage of solitary encounters were low, with solitary females and males accounting for only 3.4 and 3.6% of subgroups respectively. For the group as a whole, male to female ratio at the start of the study was 1:1.67, but this decreased to 1:1.25 by the end of the study.



Figure 2. A histogram showing the relative frequency of *A. cha-mek* subgroup types encountered (n= 119 encounters).

Habitat use

The group occupied forest levels higher than 20 m for 75.2% of the time, levels between 10 and 20 m for 23.2% of the time and were rarely found below 10 m. The home range was approximately 160 ha, consisting entirely of floodplain forest. Figure 3 shows the intensity of area use within the home range and includes bordering areas (represented in white) rarely or not visited by the study group.

A significant positive correlation was found between the number of feeding trees within a cell and the frequency of *Ateles chamek* encounters within that cell (R2 = 0.38, N = 93, P < 0.001). Figure 4 shows the distribution of 79 feeding trees and four sleeping sites that were located throughout the study period.



Figure 3. One-hectare grid map of the approximately 160 ha home range of the focal *Ateles chamek* group at the Las Piedras Amazon Center, Peru, showing the frequency of encounters within each cell.



Figure 4. One-hectare grid map with the distribution of feeding trees and sleeping sites throughout the home range of the focal *Ateles chamek* group at the Las Piedras Amazon Center, Peru.

Preliminary notes on ranging pattern

On average, the individuals encountered traveled two hours and 47 minutes per day and their speed was approximately 440 m per hour. This means the group's estimated daily path length was 1,200 m per day. More in-depth research is required to determine whether subgroup size has an influence on ranging patterns.

Activity budgets

The activity budget of the spider monkeys consisted of 41.9% resting, 23.8% traveling, 30% foraging and 4.3% other behaviors. The category 'other' consisted of 3.8% social interactions between group members, for instance affiliative behaviors such as playing and handling other female's offspring, and also agonistic behaviors such as aggressive chases. The remaining time was spent on behaviors

such as urination, defecation, and interaction with observers. Our results (see Figure 5) show that lactating females (with offspring) spent the least time resting out of the three age-sex classes of *A. chamek*, and (sub)adult females (without offspring) spent most time resting. In regard to traveling, adult males traveled most and lactating females (with offspring) least. Lactating females (with offspring) spent far more time foraging than the other two age-sex classes, with adult males spending the least amount of time foraging. Lastly, adult males demonstrated other behaviors more frequently, such as interactions with observers and social behaviors.

Preliminary notes on diet

A total of 383 records of foraging events were analyzed for the study period. The majority of the group's diet consisted of fruits (84.4%, n=325), with leaves being the second most consumed item (9.7%, n=37). The group supplemented these food items with small amounts of seeds, flowers and bark. One instance of geophagy was observed where a lactating female (with offspring) consumed clay from an arboreal ant nest.



Figure 5. Differences in activity budgets between three different age-sex classes of *Ateles chamek*.

Discussion

The total size of this particular group (eight to nine individuals) is unusually small at this site. Other (sub)groups within the concession with larger numbers of individuals (usually between 15 and 20) were sighted and we have no clear understanding of why the study group in particular is so small. Despite no clear geographical boundaries existing within the concession, no interactions were recorded between the study group and other *Ateles* groups. Previous research on the genus and species report larger group sizes, between 15 and 50 individuals per group (Van Roosmalen, 1985; McFarland Symington, 1988a; Shimooka et al., 2008). However, one long-term study by Ramos-Fernandez et al. (2005) followed a group of Ateles geoffroyi of a similar size (8 adults); this group lived within a fragmented forest, and the habitat was likely a major limitation on their group size. The average subgroup size that we found was, however, very similar to other studies (van Roosmalen, 1985; Chapman, 1988; Shimooka et al., 2008). Therefore, it appears that subgroup size is not correlated with group size. We propose that a possible reason for subgroup size to be around this number is to maximize safety. It is possible that smaller subgroups are less likely to detect a potential predator whilst more likely to be predated upon. Furthermore, it is likely that smaller subgroups are less capable of defending their territory against rival Ateles groups. The subgroup composition also stayed similar to groups with more individuals (Chapman 1990), where females with offspring were the most common composition of subgroups. This is expected, as females without offspring are known to display maternal behaviors towards other female's offspring, potentially to practice motherhood themselves and, therefore, stay close to these females (Slater et al. 2007). The male to female ratio within the focal study group was found to be lower than most other groups studied (Chapman, et al. 1989), however, we do not consider this surprising due to the extremely small size of the focal group.

The home range that we found is similar to the home ranges reported in other studies (McFarland Symington, 1988a; Wallace, 2008). We had anticipated a much smaller home range considering the small size of this group compared to group size in other studies on the genus. Campos et al. (2014) state that there is a positive relationship between primate group size and home range size, and it would be reasonable to assume that a smaller group would experience less competition for resources and thus would not have to travel as far to meet resource demand. Therefore, their equally sized home range could be explained by a potential fruit scarcity in the focal group's home range, causing them to travel further to find sufficient resources. By conducting a more in-depth study on the ecology of their home range (through botanical plots) we could more accurately reveal whether fruit abundance has an influence on home range size in this case. In contrast to Campos, Wallace (2008) found that home range size did not correlate with resident Ateles group size, and therefore there may be other factors contributing to home range size other than group size and food availability. For instance, noise disturbance and the presence of humans could force communities to retreat to less disturbed areas (Kirkby et al., 2000; González-Zamora et al., 2012), hence increasing home range size. We expect that a construction project that took place at the Las Piedras Amazon Center (within the group's home range) during the study could have caused the group to range further than expected. However, comparative data from after the

construction period is required to determine whether home range size and ranging patterns were affected.

Daily path lengths for spider monkeys appear to vary largely (Symington *et al.*, 1988a, Nunes, 1998). Our findings present a shorter average daily path length than the average reported by Symington *et al.* (1988a) and Nunes (1998), however this is likely due to the larger group size of the groups in those studies (18 to >35 individuals). Larger group size would likely mean the spider monkeys need to cover more distance on a daily basis to find sufficient resources, hence explaining why the study group has shorter daily path lengths.

During the study we observed one feeding event of geophagy, in which a lactating female (with offspring) consumed clay from an arboreal ant's nest. The main reasons for soil consumption by animals are to supplement the animal's diet with minerals otherwise unobtainable, and that the consumption of soil supposedly aids in detoxification and alleviation of gastrointestinal problems (Link et al., 2011). It appears that geophagy is more common during particular life history events like lactation or pregnancy (Link et al., 2011, Pebsworth, et al., 2018). Whereas other studies report Ateles spp. consume clay at clay licks, we did not identify any clay licks within the group's home range. Arboreal ant nests and termitaria could be a source of minerals for primates in areas where there are fewer or no clay licks available. The mineral composition of termitaria and ant nests is usually even higher than that of topsoil (Veiga and Ferrari, 2007). This allows Ateles to obtain minerals whilst staying in the canopy. Further research is required to better understand the physiological factors driving geophagy in spider monkeys, to gain insight into the increased consumption of clay during specific life events and finally to understand the use of arboreal ant nests and termitarium for clay consumption.

Lactating females (with offspring) rested least out of the different age-sex classes. We expected lactating females to spend the most time resting in order to compensate for the exertion of carrying and nursing a young. However, time spent resting can sometimes serve as a pool from which time needed to accomplish other behaviors can be drawn (Dunbar, 1988). In this case, it is possible that resting time was substituted for foraging time as the lactating females spent the most time foraging. We assume that this is due to the energy demands for lactating females being higher than those without a dependent young.

Although the study site is not located within any government-protected area, no noticeable differences were found in the habitat use and activity budget of the study group in comparison with studies conducted within governmental-protected areas. Further research is required on the populations of *Ateles* along the Las Piedras River shed to create large-scale conservation strategies for this region.

Acknowledgements

We thank the staff at ARCAmazon and LPAC for all support provided throughout the study and all volunteers and research assistants that helped with data collection and analysis.

References

- Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour*, 49(3): 227–266.
- Anaya-Huertas, C. and Mondragón-Ceballos, R. 1998. Social behavior of Black-Handed Spider Monkeys (*Ateles geoffroyi*) reared as home pets. *Int. J. Primatol.* 19(4): 767–784.
- Asensio, N., Korstjens, A.H., Schaffner, C. M., Aureli, F. 2008. Intragroup aggression, fission-fusion dynamics and feeding competition in Spider Monkeys. *Behaviour*. 145(7): 983–1001.
- Aureli, F., Schaffner, C. M., Verpooten, J., Slater, K. and Ramos-Fernández, G. 2006. Raiding parties of male Spider Monkeys: Insigths into human warfare? *Am. J. Phys. Anthropol.* 131: 486–497.
- Aureli, F. and Schaffner, C. M. 2008. Social interactions, relationships and the social system of spider monkeys. In: *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles*, C. J. Campbell (ed.), Rev. ed., pp. 236–265, Cambridge University Press, Cambridge, New York.
- Bello, R., Rosemberg, F., Timson, S. and Escate, W. 2017. Importancia del monitoreo postliberación de monos araña (*Ateles chamek*) reintroducidos en el sureste de la Amazonia peruana. In: *La primatología en Latinoamérica 2*, B. Urbani, et al. (eds). Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas.
- Campbell, C. J., Aureli, F., Chapman, C. A., Ramos-Fernández, G., Matthews, K., Russo, S. E., ... Vick, L. 2005. Terrestrial behavior of *Ateles* spp. *Int. J. Primatol.* 26(5): 1039–1051.
- Campos, F. A., Bergstrom, M. L., Childers, A., Hogan, J. D., Jack, K. M., Melin, A. D., ... Fedigan, L. M. 2014. Drivers of home range characteristics across spatiotemporal scales in a Neotropical primate, *Cebus capucinus*. *Anim. Behav.* 91: 93–109.
- Chapman, C. A. 1988. Patch Use and Patch Depletion by the Spider and Howling Monkeys of Santa Rosa National Park, Costa Rica. *Behaviour*. 105(1): 99–116.
- Chapman, C. A. and Chapman, L. J. 1990. Reproductive biology of captive and free-ranging spider monkeys. *Zoo Biol.* 9: 1–9.
- Chapman, C. A., Chapman, L. J. and McLaughlin, R. L. 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia*. 79: 506–511.
- Chapman, C. A., Fedigan, L. M. and Chapman, L. J. 1989. Post-weaning resource competition and sex ratios in spider monkeys. *Oikos*. 54(3): 315–319.

- Chapman, C. A. and Lefebvre, L. 1990. Manipulating foraging group size. Spider monkey food calls at fruiting trees, *Anim. Behav.* 39: 891–896.
- Collins, A. C. 2008. The taxonomic status of spider monkeys in the twenty-first century. In: *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles,* C. J. Campbell (ed.), Rev. ed., pp. 50–80. Cambridge University Press, Cambridge.
- Defler, T. R. 2010. *Historia Natural de Los Primates Colombianos*. 2nd ed. Universidad Nacional de Colombia, Bogotá.
- Di Fiore, A., Link, A. and Dew, J. L. 2008 Diets of wild spider monkeys. In: *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles,* C. J. Campbell (ed.), Rev. ed., pp. 81–137. Cambridge University Press, Cambridge.
- Dunbar, R. I. M. 1988. *Primate social systems*. Croom Helm, London and Sydney.
- Estrada, A., Luecke, L., Van Belle, S., Barrueta, E., Meda, M. R. 2004. Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan sites of Calakmul and Yaxchilán, Mexico and Tikal, Guatemala. *Primates.* 45(1): 33–39.
- Fedigan, L. M., Fedigan, L., Chapman, C. A., Glander, K. E. 1988. Spider Monkey home ranges: A comparison of radio telemetry and direct observation. *Am. J. Primatol.* 16: 19–29.
- Felton, A. M., Felton, A., Wood, J., Lindenmayer, D. B. 2008 Diet and feeding ecology of *Ateles chamek* in a bolivian Semihumid Forest: The importance of Ficus as a staple food resource. *Int. J. Primatol.* 29: 379–403.
- Fontaine, R. 1990. Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi. Am. J. Phys. Anthropol.* 82: 485–508.
- Garmin Ltd. 2019. Garmin BaseCamp. Available at: https:// www.garmin.com/nl-NL/shop/downloads/basecamp.
- Gibson, K. N. 2010. Male mating tactics in spider monkeys: Sneaking to compete. *Am. J. Primatol.* 72(9): 794–804.
- Gómez-Posada, C. and Londoño, J. M. 2012. *Alouatta seniculus*: Density, home range and group structure in a bamboo forest fragment in the Colombian Andes. *Folia Primatol.* 83(1): 56–65.
- González-Zamora, A., Arroyo-Rodríguez, V., Chaves, Ó. M., Sánchez-López, S., Stoner, K. E., Riba-Hernández, P. 2008. Diet of Spider Monkeys (*Ateles geoffroyi*) in Mesoamerica: Current knowledge and future directions. *Am. J. Primatol.* 70: 1–13.
- González-Zamora, A., Arroyo-Rodríguez, V., Oyama, K., Sork, V., Chapman, C. A., Stoner, K. E. 2012. Sleeping sites and latrines of Spider Monkeys in continuous and fragmented rainforests: Implications for seed dispersal and forest regeneration. *PLoS ONE*. 7(10): 1–11.
- González-Zamora, A., Arroyo-Rodríguez, V., Escobar, F., Oyama, K., Aureli, F., Stoner, K. E. 2015. Sleeping-tree fidelity of the spider monkey shapes community-level seed-rain patterns in continuous and fragmented rain forests. *J. Trop. Ecol.* 31(4): 305–313.

- Groves, C. P. 2001. *Primate Taxonomy*. Smithsonian Press, Washington, London.
- Hagell, S., Whipple, A. V. and Chambers, C. L. 2013. Population genetic patterns among social groups of the endangered Central American spider monkey (*Ateles geoffroyi*) in a human-dominated landscape. *Ecol. Evol.* 3(5): 1388–1399.
- Hooper, J. 2014. An assessment of enrichment strategies for sanctuary-housed spider monkeys (*Ateles geoffroyi*). Master's dissertation, Oxford Brookes University, Oxford, UK.
- Kirkby, C. A., Doan, T. M., Lloyd, H., Farfán, A. C., Arriaga, W. A., Marín, A. P. 2000. "Project Tambopata 1" Tourism development and the status of neotropical lowland wildlife in Tambopata, south-eastern Peru: recommendations for tourism and conservation. Unpublished report, TReeS-RAMOS.
- Lange, L. R. 2016. Conservation of Peruvian primates and behaviour of Peruvian black spider monkeys (*Ateles chamek*) in south-eastern Peru. Master's dissertation, Oxford Brookes University, Oxford, UK.
- Lindshield, S. M. and Rodrigues, M. A. 2009. Tool use in wild spider monkeys (*Ateles geoffroyi*). *Primates.* 50: 269–272.
- Link, A., Galvis, N., Fleming, E., Di Fiore, A. 2011. Patterns of mineral lick visitation by Spider Monkeys and Howler Monkeys in Amazonia: Are licks perceived as risky areas? *Am. J. Primatol.* 73: 386–396.
- Link, A., Galvis, N., Marquez, M., Guerrero, J., Solano, C., Stevenson, P. R. 2012. Diet of the Critically Endangered Brown Spider Monkey (*Ateles hybridus*) in an inter-andean lowland rainforest in Colombia. *Am. J. Primatol.* 74(12): 1097–1105.
- Link, A. and Di Fiore, A. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. *J. Trop. Ecol.* 22(3): 235–246.
- Link, A. and Di Fiore, A. 2013. Effects of predation risk on the grouping patterns of White-Bellied Spider Monkeys (*Ateles belzebuth belzebuth*) in western Amazonia. *Am. J. Phys. Anthropol.* 150: 579–590.
- McFarland Symington, M. 1987. Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behav. Ecol.Sociobiol.* 20(6): 421–425.
- McFarland Symington, M. 1988a. Demography, ranging patterns, and activity budgets of Black Spider Monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. *Am. J. Primatol.* 15: 45–67.
- McFarland Symington, M. 1988b. Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour*. 105: 117–134.
- Michalski, F. and Peres, C. A. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biol. Conserv.* 124(3): 383–396.
- Morales-Jiménez, A. L., Disotell, T. and Di Fiore, A. 2015. Revisiting the phylogenetic relationships, biogeography, and taxonomy of spider monkeys (genus *Ateles*) in light of new molecular data. *Mol. Phylogenet. Evol.* 82: 467–483.

- Nunes, A. 1995. Foraging and ranging patterns in White-Bellied Spider Monkeys. *Folia Primatol.* 65: 85–99.
- Nunes, A. 1998. Diet and feeding ecology of *Ateles bel*zebuth belzebuth at Maracá ecological station, Roraima, Brazil. *Folia Primatol.* 69: 61-76.
- Pebsworth, P. A., Huffman, M. A., Lambert, J. E., Young, S. L. 2018. Geophagy among nonhuman primates: A systematic review of current knowledge and suggestions for future directions. *Am. J. Phys. Anthopol.* 168 (S67): 164-194.
- Ramos-Fernández, G., Mateos, J. L., Miramontes, O., Cocho, G., Larralde, H., Ayala-Orozco, B. 2004. Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behav. Ecol. Sociobiol.* 55(3): 223–230.
- Ramos-Fernández, G. 2005. Vocal communication in a fission-fusion society: Do Spider Monkeys stay in touch with close associates? *Int. J. Primatol.* 26(5): 1077–1092.
- Rosenberger, A. L., Halenar, L., Cooke, S. B., Hartwig, W. C. 2008. Morphology and evolution of the spider monkey, genus Ateles. In: Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles, C. J. Campbell (ed.), Rev. ed., pp. 81–137. Cambridge University Press, Cambridge, New York.
- Rylands, A. B. and Mittermeier, R. A. 2013. Family Atelidae. In: Handbook of the Mammals of the World - Volume 3 Primates. R. A. Mittermeier, A. B. Rylands and D. E. Wilson (eds), pp. 484–549. Lynx Edicions, Barcelona.
- Salvador, S., Clavero, M. and Leite Pitman, R. 2011. Large mammal species richness and habitat use in an upper Amazonian forest used for ecotourism. *Mamm. Biol.* 76(2): 115–123.
- Scheel, M. H. and Edwards, D. 2012. Captive spider monkeys (*Ateles geoffroyi*) arm-raise to solicit allo-grooming. *Behav. Processes*. 89: 311–313.
- Shimooka, Y. 2005. Sexual differences in ranging of *Ateles belzebuth belzebuth* at La Macarena, Colombia. *Int. J. Primatol.* 26(2): 385–406.
- Shimooka, Y., Campbell, C. J., Di Fiore, A., Felton, A. M., Izawa, K., Link, A. Nishimura, A., ... Wallace, R. B. 2008. Demography and group composition of *Ateles*. In: *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles*, C. J. Campbell (ed.), Rev. ed., pp. 329-348. Cambridge University Press, Cambridge, New York.
- Slater, K. Y., Schaffner, C. M. and Aureli, F. 2007. Embraces for infant handling in spider monkeys: evidence for a biological market? *Anim. Behav.*, 74: 455–461.
- Slater, K. Y., Schaffner, C. M. and Aureli, F. 2009. Sex differences in the social behavior of wild Spider Monkeys (*Ateles geoffroyi yucatanensis*). Am. J. Primatol. 71: 21–29.
- Spehar, S., Di Fiore, A. and Link, A. 2010. Male and female range use in a group of white-bellied spider monkeys (*Ateles belzebuth*) in Yasuní National Park, Ecuador. *Am. J. Primatol.* 72: 129–141.
- Spehar, S. N. and Di Fiore, A. 2013. Loud calls as a mechanism of social coordination in a fission-fusion taxon, the white-bellied spider monkey (*Ateles belzebuth*). *Behav. Ecol. Sociobiol.* 67(6): 947–961.
- Takahashi, J. 2008. A literature review of the spider monkey, Ateles sp., with special focus on risk for extinction. Degree

project, Swedish University of Agricultural Sciences, Uppsula, Sweden.

- Van Roosmalen, M. G. M. 1985. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazonica*. 15: 0–234.
- Veiga, L. M. and Ferrari, S. F. 2007. Geophagy at termitaria by Bearded Sakis (*Chiropotes satanas*) in southeastern Brazilian Amazonia. *Am. J. Primatol.* 69: 816–820.
- Velázquez-Vázquez, G., Reyna-Hurtado, R., Arroyo-Rodríguez, V., Calmé, S., Léger-Dalcourt, M., Navarrete, D. A. 2015. Sleeping sites of Spider Monkeys (*Ateles geoffroyi*) in logged and unlogged tropical forests. *Int. J. Primatol.* 36(6): 1154–1171.
- Wallace, R. B. 2001. Diurnal activity budgets of Black Spider Monkeys, *Ateles chamek*, in a southern Amazonian tropical forest. *Neotrop. Primates*. 9(3): 103–107.
- Wallace, R. B. 2005. Seasonal variations in diet and foraging behavior of *Ateles chamek* in a southern Amazonian tropical forest. *Int. J. Primatol.* 26(5): 1053–1075.
- Wallace, R. B. 2006. Seasonal variations in Black-Faced Black Spider Monkey (*Ateles chamek*) habitat use and ranging behavior in a southern Amazonian tropical forest. *Amer. J. Primatol.* 68: 313–332.

- Wallace, R. B. 2008. Factors influencing spider monkey habitat use and ranging patterns. In: *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles,* C. J. Campbell (ed.), Rev. ed., pp. 138–155. Cambridge University Press, Cambridge, New York.
- Weather Underground. 2019. *Monthly climate history of the Puerto Maldonado International Airport, Peru.* Website: www.wunderground.com. Accessed 22 April 2019.
- White, F. 1986. Census and preliminary observations on the ecology of the black-faced black spider monkey (*Ateles paniscus chamek*) in Manu National Park, Peru. *Am. J. Primatol.* 11: 125–132.
- World Weather Online. 2019. Puerto Maldonado Monthly Climate Averages, Madre de Dios, Peru. Website: www. worldweatheronline.com. Accessed 22 April 2019.
- Youlatos, D. 2002. Positional behavior of Black Spider Monkeys (*Ateles paniscus*) in French Guiana. *Int. J. Primatol.* 23(5): 1071–1093.
- Youlatos, D. 2008. Locomotion and positional behavior of spider monkeys. In: *Spider Monkeys: Behavior, Ecology* and Evolution of the Genus Ateles, C. J. Campbell (ed.), Rev. ed., pp. 185–219. Cambridge University Press, Cambridge, New York.