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TESIS DOCTORAL

Social and reproductive strategies in a species with a fission-fusion social system "(Ateles belzebuth)

Estrategias sociales y reproductivas en una especie con sistema social fisión-fusión "(Ateles belzebuth)"

MEMORIA PARA OPTAR AL GRADO DE DOCTORA

PRESENTADA POR

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UNIVERSIDAD COMPLUTENSE DE MADRID
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Grupo UCM de Estudio del Comportamiento Animal y Humano

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Tesis doctoral que presenta SARA ÁLVAREZ SOLAS para optar al Grado de Doctor

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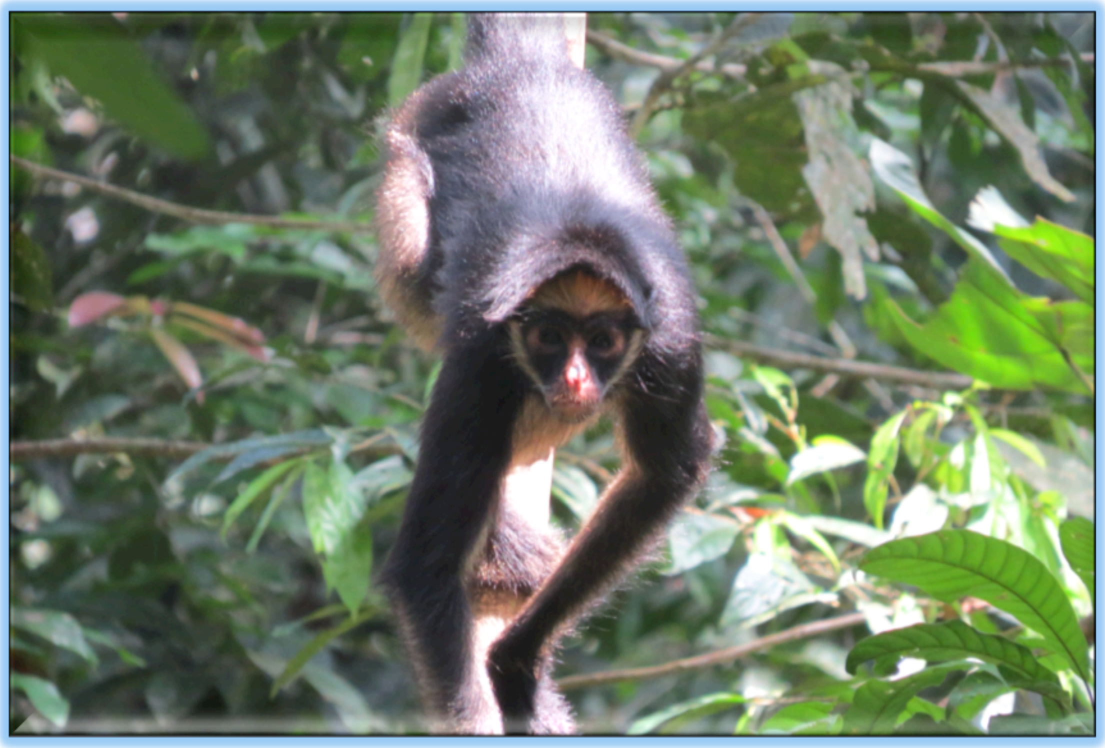

Juvenile male of spider monkey (*Ateles belzebuth*)

SOCIAL AND REPRODUCTIVE STRATEGIES IN A SPECIES WITH A FISSION - FUSION SOCIAL SYSTEM (Ateles belzebuth)

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A mis padres…

y a esos 35 monos araña que formaron parte de este trabajo, porque espero que estudios como éste ayuden a su conservación…

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SUMMARY

SUMMARY

Among primates, several social patterns have been described within many species, highlighting different social systems. The study of those systems is essential to explain the different behavioral strategies of each sex to maximize the reproductive success within the environment where they live in groups. The variety of grouping patterns we studied can be influenced by demographic, ecological and social conditions. Nevertheless, studies of social ethology are very sensitive to the influence of the phylogenetic history of the species belonging to the individuals who make a social group (Di Fiore & Rendall, 1994, Rendall & Di Fiore, 1995; Review: Colmenares, 2002).

There are several theories that try to explain these differences through models that had been built from data collected during years. However, we also have to pay attention to the intraespecific behaviors that individuals present and make these behavioral studies so interesting. This discipline deals with the analysis of all the variables that may contribute to reveal the nature of the relationship between the social behavior of individuals and their ecological environment (Colmenares, 2002, 2014). The socio-ecological model (e.g., Wrangham, 1980; van Schaik 1983, 1989; Dunbar 1988) predicts that food is the limiting factor for the female's reproductive success, while male's is the number of fertile females they access. For females, this factor is linked to the maximization of their reproductive rate and therefore the provision of commodities to their young to ensure their survival (Trivers, 1985; Kappeler & van Schaik, 2004; Lindenfors *et al.,* 2007).

The purpose of this study is to contribute to understand social and reproductive strategies of a primate species, which have not been well documented and are starting to be on the eye of a lot of researchers due to the interesting patterns they present. Recent literature on this species

have built a platform where our study has been able to add a big database, which will contribute to explain their social relationships and the ecological function that influence in their patterns. This research documents the behaviour of a group of spider monkeys, studying in detail their social structure, reproduction, ecological patterns and distribution on their territory.

Study species

The study of species and models is important to understand the social network lattice that makes these systems. Spider monkeys (*Ateles belzebuth*) present several interesting patterns on their natural, ecological and social wild life that are related to the social strategies they develop in the habitat where they live. They have some interesting similarities to the chimpanzee (*Pan troglodytes*), a human close relative. Like in chimpanzee societies, spider monkeys present a fission-fusion social system, where individuals of the group usually travel within smaller subgroups, which change during the day. It seems this is a strategy to avoid competition when high quality resources are scarce and distributed in small patches (Wrangham, 1980; Symington, 1990). Spider monkeys and chimpanzees also share some unusual patterns in primates, such as female dispersal or male boundary patrols. Nevertheless, the study of animals contributes to understand the role that species have within the ecosystem and their importance in the maintenance of the Neotropical rain forest.

Dispersal patterns usually affect the way relationships are built between the members of each sex. Males are the philopatric sex, spending their entire life in the same group. It is expected that males show stronger bonds than females, because they are relatives and they usually show alliances between them. These alliances are also useful to protect their territories, especially within a species when intergroup encounters are usually very aggressive. Males are also found in larger subgroups than females (Aureli & Schaffner, 2008), where average subgroups are nearly as double in number than females (Shimooka, 2005), and is less likely to be encountered alone (Chapman, 1990). Males, within the same community are rarely seen aggressive towards each other (Aureli & Schaffner, 2008). However, between groups it is common to observe disputes, even physical aggressions, when there are inter-group encounters (Aureli *et al.,* 2006; Wallace, 2007). Boundary patrols are usually carried out by groups of males, more often than with females (Shimooka, 2005).

On the other hand, spider monkey females usually travel alone, with their offspring, foraging and monopolizing a good number of resources, limiting factor for the females´ reproductive success, according to the socioecological theory (e.g., Wrangham, 1980; van Schaik, 1983, 1989; Dunbar, 1988). So females are expected to spend less time with other community members than males (Wrangham, 2002) and to travel in smaller subgroups in order to reduce travel cost (van Roosmalen & Klein, 1988; Chapman, 1990). This situation make females vulnerable to a sexual coercion, which has been documented in spider monkeys by several authors, being ovulating females the main recipient of male aggressions (Slater *et al.,* 2009; Symigton, 1987a).

There is a marked asymmetry in investment in parental care by females as these must invest energy in pregnancy, lactation and care of the young. *Ateles belzebuth* females invest disproportionate amounts of energy on their offspring during pregnancy, whose gestation is 7-7.5 months long (Eisenberg, 1973; Di Fiore & Campbell, 2007), but also during care and transportation for several years post-natally (Link *et al.,* 2009). The mayority of female spider monkeys emigrate from their natal community at or around the time of reproductive maturity (Aureli & Schaffner, 2008).

Methods

Our data was collected from a group of wild white-bellied spider monkeys (*Ateles belzebuth*) in Tiputini Biodiversity Station (from

Universidad San Francisco de Quito), in the Western Ecuadorian Amazon. Since 2006 until the end of 2013, all adult males (N=6) and all adult females (N=11) where followed, dawn to dusk, using animal focal sampling (Altman, 1974). All individuals were perfectly identified and the group composition was estimated in 35 individuals. Home range data was collected with GPS (model Garmin 76CSx), recording point every 20 seconds. We collected behavioural data every five minutes and all social interactions (aggression, grooming, proximity…) and feeding bouts was recorded continuously. We also collected *Ad libitum* data, when any interactions or important behaviour happened outside our focal animal.

Aggression and hierarchy

According to literature (Campbell, 2003; Link *et al.*, 2009; Slater *et al.*, 2009; Abondano & Link, 2012), this group of spider monkeys showed very low levels of aggression, being the total number during 7 years of study (8596 hours of data), 442 aggressions. The majority of those agonistic events were male-to-female aggression, where males usually make a display towards the females making her urinate. Some studies (Symington, 1987a; Slater *et al.,* 2009) suggest that the purpose of male aggression towards females might be associated with inducing them to urinate, since males tend to smell the urine of females, likely because it contains clues on their reproductive status (Campbell, 2003). Nevertheless, males formed coalitions often, mainly dyads, to attack females. We didn’t find almost any aggression between males and aggressions by females were very low, being more than half of the time towards their own offspring.

Males context of aggression was found during fusion events, more often than between females, which could be related with social control as an indirect mechanism of sexual coercion by male spider monkeys (Link *et al.,* 2009), where males assert their-term control over females´ reproduction and perhaps discouraging them from mating outsite the group. It has also been proposed that the functionality of these attacks is related to spatial fluidity. Individuals of *Ateles* can spend extended periods of time without seeing each other. In this way males would show its dominance and social control against females just after fusion events and join between individuals (Link *et al.,* 2009). On the other hand, females seem to be aggressive more often in feeding context, which could explain some kind of feeding competition, but the low rates of aggression compare with the time they invest foraging makes that hypothesis difficult to confirm.

Although we found that the more common aggression between individuals was from males to females, as other studies found, we didn’t find any differences between males aggression towards females within all different reproductive states. Campbell (2003) already highlighted a not clear direction towards cycling females, as it has been documented in other studies (Slater *et al.,* 2009). This study remarks that a consequent reproduction or consort-ship after the aggression should not be expected. These aggressions were distributed within all female reproductive states, and even though aggression within estrus period was registered only in the case of two females, this kind of aggressions seems to be not a sexual coercion male´s strategy or at least not an exclusive strategy.

Within the study of hierarchy, it seems that males are dominant over females in terms of the direction of the aggression. Females attack two other females more often than the rest, so it seems their social relationships are at least not as equal as it has been documented (Gibson, 2010). These two females were the last to arrive to the group, so it could be interpreted as some kind of rejection by resident females. However, these females were within the group for a long period of time and even they have one and two infants within the group. This could mean some degree of dominance of some females over others. In contrast, males don’t seem to have a clear dominance between them, or not as those that characterize chimpanzee societies.

Infanticide

Infanticide amongst primates has been most commonly documented within one-male-multifemale societies. Although rare, infanticide has also been reported in many multimale-multifemale societies such as those of spider monkeys (*Ateles spp.*). This explicit expressions of sexual conflict between males and females arises when the reproductive success of one sex is negatively affected by the reproductive strategies of the other sex (Trivers, 1972; Arnqvist & Rowe, 2005; Palombit, 2012).

Field studies in primates show consistent patterns of infanticide by males such as [1] most infants killed are unrelated to the infanticidal male or males, [2] the killing of an infant leads to the returning to reproductive activity for females, and [3] infanticidal males often have reproductive oportunities with these females. Thus, the hypothesis for male infanticide related to sexual selection (see Hrdy, 1979) has been proposed to fit most of the infanticide observed to date in primate societies (see also Palombit, 2012), suggesting that males kill unrelated infants in order to gain reproductive opportunities with anestrous females.

Although, males are presumably related within social groups, resident males control reproductive access to the group´s females and paternity is monopolized by within group males, five confirmed and suspected infanticide events have been witnessed in studies on wild spider monkeys (Gibson *et al.,* 2008; Shimooka *et al.,* 2008; Vick, 2008). Females usually present their offspring to males by approaching and allowing them to inspect the infants (Gibson *et al.,* 2008), and this situation could encourage them sometimes towards any kind of aggressions. However, the five infanticide events documented have been directed towards very young male infants under the age of three months.

Within this study, aggressions towards females with new infants were found in several occasions and in one case, the aggression ended with the dead of the male infant. The event was recorded as a very intense aggression from a male. Thanks to genetic analyses we know now that this male was the father of the infant, who died some days later. Although we cannot confirm he killed the infant, at least we know he attacked the mother intensively and after less than a week the infant died. Nevertheless, 9 months later this female had a new infant. Paternity analysis also revealed that the next offspring that was born to that female was also sired by the same male.

In this research, we also described another suspected case of infanticide in Colombia, where Proyecto Primates is also working, within a group of brown spider monkeys (*Ateles hybridus*). In this event, one subadult male and the mother of the infant were found with several wounds, after hear aggressive vocalizations within the group, and the male infant was found on the ground several hours later, around the same area. He finally survived because the observer carried the infant where his mother was and she recovered him, but it would probably have died if left on his own in the forest floor.

This could be added to five more cases of infanticide and several aggressions towards male infants described in different groups (Symington, 1987b). So, although the sample is still too small and only a few cases of infanticides in spider monkeys have been documented, this could be more common that we previously though and it could be skewed towards males. Infanticide is not well understood in this species, where all males are relatives and the success of a relative infant should be an indirect benefit. However we need more data to evaluate the possibility that this behaviour could be related with the hypothesis of social control, and the regulation of the number of males and females within the group.

Mineral lick

Mineral licks are important areas visited by several Neotropical birds and mammals to consume soil for mineral supplementation or as a detoxification agent. Spider monkeys and howler monkeys are the only platyrrhines that regularly visit mineral licks, and both species visit licks together in higher frequencies than expected by chance alone (Blake, *et al.,* 2010; Link *et al.,* 2011; Link & Di Fiore, 2013).

Voigt et al. (2008) found that mineral licks are richer in five minerals (iron, calcium, magnesium, sodium and potassium) compared to fruits and insects. These minerals are essential for mammalian homeostasis and reproduction. Fruits and insects were similarly rich in sodium, potassium and magnesium, whereas calcium and iron concentrations were higher in fruits than in insects (Voigt *et al.,* 2008). Although a few insectivorous animals eat soil at mineral licks, frugivores and folivores tend to visit mineral licks more often and to be more geophagous (Kreulen, 1985; Voigt *et al.,* 2008; Link *et al.,* 2011), such as howler and spider monkeys. Many fruits, young leaves, and other plant parts consumed by animals contain toxic compounds, and the fact that geophagy is more common among frugivorous and folivorous animals suggests that they may be consuming clays or clay-saturated water in order to buffer these toxic effects.

For arboreal primates, mineral licks are especially risky because they are the only place individuals go down to the ground, which is where predation risk is greater (Janson, 1998; Link & Di Fiore, 2013). Jaguars (*Panthera onca*), pumas (*Felis concolor*) and ocelots (*Leopardus pardalis*) also visit mineral licks (Montenegro, 2004; Matsuda & Izawa, 2008; Mosquera, unpublished data) and these felids include large primates in their diet (Di Diore, 2002; Ferrari, 2009).

Although spider monkeys visit mineral lick areas frequently, a large proportion of visits are “unsuccessful” in the sense that no individual in the subgroup actually descends to the ground to feed on soil at the lick. We evaluate the influence of success of certain individuals according to three subgroups, which usually move in different core areas of the territory. Females with core range areas closer to the lick visited the lick more often than those whose core areas were located farther away. However, the success rate when females that ranged farther apart were presented, was significantly higher than that of other females or males, perhaps due to the greater effort spent in going to the lick. However, this subgroup could also increase the possibility to find bigger subgroups in the mineral lick. For that reason we explore different possibilities.

We also found positive and significant relationships between both subgroup size and the presence of howler monkeys at the lick and the success rate of lick visitation by spider monkeys. The number of individuals in the subgroup is usually more than 10 individuals and successful visits increase with the number of individuals within the subgroup. During these visits, spider monkeys sometimes share the mineral lick with howler monkeys (*Alouata seniculus*), the other unique plathirriny species, which also feeds on clay. Our results showed when both species visit the lick together, the chance of animals actually descending to the ground increased considerably. Moreover, the observations of both species in the mineral lick raise the possibility of some "association" between species being more efficient in looking out for predators together than alone.

West Females individuals seems to use a combination of these variables to visit the mineral lick, having stronger effect/influence of the subgroup, increasing the possibility to consume soil when they were presented. We also found that howler presence is the best predictor of the success of the mineral lick visit.

To test whether the frequency of mineral lick visitation was associated with weather conditions we recorded a daily index that describes cloud cover, precipitation, and luminosity. Prior data collected on this group (Link *et al.,* 2011) showed that weather conditions in the morning preceding lick visits may influence the animals' subsequent behavior. However, data from the present study suggests that the weather conditions do not have as strong an influence on visit success as does the size of the subgroup or the presence of howlers.

Incursion

Boundary patrols has recently been documented in spider monkeys societies (Symington, 1990; Shimooka, 2005; Aureli, *et al.,* 2006; Wallace, 2007, 2008; Link, 2011). During spider monkeys' territorial encounters, aggression has been observed between neighboring groups and parties, primarily by males (Symington, 1990; Shimooka, 2005; Wallace, 2007; Aureli *et al.,* 2006; and this study).

However, Aureli *et al.,* (2006) described seven cases of deep incursions by male Central American spider monkeys into the range of another group; in these cases, animals only fed for a small portion of the time they spent within the neighboring territory, leading Aureli *et al.* (2006) to conclude that these kind of incursions seem not to be motivated by feeding competition.

Here, we document a case where most members of group of white-bellied spider monkeys (*Ateles belzebuth*) collectively made a deep incursion into a neighboring territory. What seemed a territorial boundary patrol at the beginning ended up being the only reported case in which spider monkeys actually use of a mineral lick well within a neighboring group´s territory.

This event, we suggest, is thus best interpreted as a case of an incursion specifically to "use" resources located in another group's territory without the intention to interact with or challenge that group. The direct path they took towards the mineral lick outside of their territory suggests they have spatial knowledge of the area, perhaps due to past experiences, such as prior boundary patrols. It may even be the case that the locations of extra-territory resources are known to one or more of a group's females by virtue of the fact that females are the dispersing sex and may have immigrated in from other groups.

We suggest that this kind of intrusion into neighboring territories might reflect a high level of inter-group competition for key resources and territory. Nonetheless, the underlying explanations behind the decision to visit the mineral lick in a neighboring territory remains largely unexplained.

In **conclusion,** despite of the high number of hours of observation of this study group (8569), we are far from understanding the meaning of all patterns that this species shows in the wild. However, this study is a big step to reveal other new characteristic and important events never documented before, and to support new ideas that have been highlighted within the last years.

This kind of studies are also important towards the conservation of species in the wild because with these researches we could better know their necessities or their distribution for a better management of animal populations, for example. This project is part of a conservation programme of primates that have been running for more than 18 years. Another area where this project is developing their research is in San Juan, Colombia, where the second suspected case of infanticide has been described. This species *Ateles hybridus* is critically endangered and the study site is a fragmented area with a high human impact, where we could compare the changes within their behaviour. Nevertheless, these areas where these two groups live are exposed to different threats, such as oil exploitation, hunting or bush meat, and describing the essential role they play within the ecosystem where they live we could help to protect them.

RESUMEN

RESUMEN

Los sistemas sociales de los primates varían ampliamente tanto entre distintas especies como entre poblaciones de la misma especie. El estudio de estos sistemas nos permite obtener información que ayuda a explicar la relación entre el comportamiento social y la estructura grupal de los animales y el ambiente en el que viven. La presente investigación se centra en el estudio de las conductas y relaciones sociales que se establecen en una especie de la Amazonía Ecuatoriana, el mono araña (*Ateles belzebuth*), con objeto de entender su comportamiento en su medio natural. Esta especie, además, se considera esencial en el mantenimiento de la selva Neotropical, como dispersora de semillas, por lo que han sido objeto de estudio en numerosas investigaciones en los últimos años. Este primate comparte numerosas características con el chimpancé (*Pan troglodytes*), aun tratándose de especies alejadas filogenéticamente y ocupando nichos en puntos geográficos muy distantes. A pesar de ello, el mono araña apenas ha sido investigado, por lo que todavía nos queda mucho para llegar a entender mejor su comportamiento.

Al igual que en las sociedades de chimpancés, el mono araña presenta un sistema social de tipo fisión-fusión, donde los individuos del grupo se desplazan por el territorio en subgrupos más pequeños, cuya composición puede cambiar a lo largo el día. Parece que este sistema social supone una estrategia para evitar la competencia por los recursos cuando los de alta calidad son escasos y están distribuidos en pequeños parches (Wrangham, 1980; Symington, 1990; Aureli & Schaffner, 2008).

Ambas especies también comparten patrones sociales, poco comunes dentro de los primates, como la dispersión de las hembras o los patrullajes de los machos por el límite de los territorios vecinos. Los patrones de dispersión suelen afectar a la forma en que las relaciones se

construyen entre los miembros de cada sexo. Los machos son el sexo filopátrico, pasan toda su vida en el mismo grupo, por lo que se espera que éstos muestren lazos sociales más fuertes que las hembras, ya que están emparentados entre sí. Estas alianzas también son útiles para proteger sus territorios, sobre todo en una especie donde los encuentros entre grupos suelen ser muy agresivos. Por otro lado, las hembras suelen viajar solas, acompañados únicamente de su descendencia, forrajeando y monopolizando así un mayor número de recursos, factor limitante para el éxito reproductivo de las hembras de acuerdo con la teoría socioecológica (Wrangham, 1980; van Schaik 1983, 1989; Dunbar 1988). El forrajeo en solitario puede suponerle a las hembras una mayor vulnerabilidad a la coerción sexual, comportamiento que ha sido documentado en monos araña por varios autores, siendo las hembras en período de ovulación las principales receptoras de agresiones por parte de los machos (Slater *y cols.,* 2009; Symigton, 1987a) .

Nuestros datos se recogieron en un grupo de monos araña de vientre blanco (*Ateles belzebuth*) en la Estación de Biodiversidad Tiputini (Universidad San Francisco de Quito), en la Amazonía ecuatoriana occidental. Desde 2006 hasta finales de 2013 se muestrearon y registraron focales individuales (Altman, 1974) de todos los machos (N = 6) y hembras adultas (N = 11), desde el amanecer hasta el atardecer, con un total de 8569 horas de observación. Todos los individuos del grupo estaban perfectamente identificados (la composición del grupo fue de un total de 35 individuos, con juveniles y crías) y los datos territoriales o *home range* se recogieron con un GPS (modelo Garmin 76CSx), que registraba puntos cada 20 segundos.

Aunque nuestros resultados mostraron que las agresiones más comunes entre los individuos fueron las dirigidas por los machos hacia las hembras, no se encontraron diferencias en la tasa de agresión hacia hembras entre los diferentes estados reproductivos. Además, el contexto donde los machos agredían con mayor frecuencia coincidía con eventos de fusión, lo que podría estar indicando la existencia de una relación entre agresión y “control social”; en este caso, la agresión de los machos podía funcionar como un factor disuasorio frente a la tentación de copular con machos ajenos al grupo (Link *y cols.,* 2009). Por otro lado, no se observa una clara jerarquía social entre los machos, o al menos no del tipo que caracteriza las relaciones jerárquicas en las sociedades de chimpancés.

En el caso de las hembras, a pesar de la baja tasa de agresión que muestran, los eventos agonísticos parecen coincidir con contextos de alimentación. No obstante, es importante destacar que este hecho no es necesariamente indicador de que exista una competencia por los recursos, puesto que las hembras invierten la mayor parte del tiempo forrajeando (Di Fiore *y cols.*, 2008).

Cabe destacar que dos hembras, precisamente aquellas que menos tiempo llevaban en el grupo, fueron diana de la mayoría de estas agresiones. A pesar de que su tiempo de permanencia en el grupo es relativamente largo, teniendo una y dos crías respectivamente durante este período, la alta proporción de agresiones recibidas en comparación al resto podría estar relacionado con cierto rechazo de hembras residentes que llevan más tiempo en el grupo. De este modo, estos resultados mostraron que las relaciones sociales entre las hembras no son tan igualitarias como se había documentado en estudios previos (Gibson, 2010).

Por último, en varias ocasiones se registraron agresiones hacia hembras con crías dependientes y una de las mismas finalizó con la muerte del macho recién nacido. A este evento aislado sumamos otro caso de presunto infanticidio en Colombia (San Juan), otra de las zonas de estudio de Proyecto Primates. Esta especie de mono araña en peligro de extinción (*Ateles hybridus*), que habita en una zona fragmentada muy distinta a nuestro grupo de estudio, también mostró este comportamiento tan poco usual en una especie donde los machos están emparentados entre sí. Aunque la muestra de los datos es demasiado pequeña y sólo existen cinco casos documentados de infanticidios en monos araña, cabe destacar que todas las víctimas fueron machos. Adicionalmente, otros estudios también observaron mayores agresiones hacia crías machos frente a las crías hembras (Symington 1987b). Por tanto, estos dos nuevos casos registrados en este estudio podrían significar que el infanticidio puede ser más común que lo que se había pensado anteriormente, y que este comportamiento podría estar sesgado hacia los machos.

En definitiva, el infanticidio en una especie donde todos los machos están emparentados entre sí no parece tener una explicación adaptativa clara, puesto que el éxito de la cría de un pariente debería ser un beneficio indirecto. Sin embargo, y aunque necesitamos más datos para sacar conclusiones, podríamos evaluar la posibilidad de que este comportamiento esté relacionado con la hipótesis de control social y la regulación del número de machos y hembras en el grupo.

Por otro lado, ambos sexos tienen diferentes estrategias de distribución a lo largo de sus territorios. Las hembras generalmente se mueven en áreas más pequeñas y dentro de sus áreas centrales (*core areas*) con sus crías, mientras que los machos, por lo general, se mueven más y más rápido alrededor de su área de distribución (*home range*). Este comportamiento podría ser otra estrategia de los machos para monopolizar y controlar su grupo dentro de sus grandes territorios, que patrullan y protegen invirtiendo gran cantidad de tiempo.

Dentro de los grandes territorios que ocupan los monos araña, los individuos del grupo se "reúnen" con frecuencia para usar y monopolizar un importante recurso, el saladero. Esta zona es el único lugar en el que los monos araña descienden al suelo para ingerir arcilla, comportamiento que comparten con muchos otros animales. Parece que el consumo de barro se utiliza para adquirir minerales y como agente desintoxicante, aunque sus propiedades siguen siendo objeto de debate (Blake *y cols.,* 2010; Link *y cols.,* 2011; Link & Di Fiore, 2013). En cualquier caso, esta área es esencial para ellos ya que invierten varios horas en grandes subgrupos generalmente, hasta que finalmente ingieren barro del suelo. Los monos araña visitan los saladeros a menudo y varias veces por semana, pero sólo consumen arcilla en algunos de estos encuentros (lo que consideramos éxito de la visita).

Para estudiar los factores que influyen en este consumo, dividimos el grupo de estudio en tres subgrupos en función de su distribución espacial (Link *y cols.,* en preparación): *"Machos", "Hembras del Este" y "Hembras del Oeste".* Nuestros resultados mostraron que las hembras que tenían el territorio central (*core areas*) más alejado del saladero, "*Hembras del Oeste*", eran más eficientes, y su presencia aumentaba la probabilidad de que el grupo consumiera barro. Esto podría deberse a que al invertir más energía por un recorrido mayor aprovecharan mejor la visita, pero también podría influir en la formación de grupos de mayor tamaño cuando estas hembras estaban presentes (puesto que este subgrupo no visitaba el saladero con tanta frecuencia como "*Machos*" y "*Hembras del Este*"). Efectivamente, nuestros resultados mostraron que la probabilidad de practicar geofagia aumentaba con el tamaño de grupo y que las visitas de las "*Hembras del Oeste*" eran en grupos grandes en su mayoría. Sin embargo, también encontramos que cuando los grupos eran medianos y estas hembras estaban presentes, el éxito relativo también era mayor.

Además, estas visitas eran en ocasiones compartidas con otra especie de primate platirrino, el mono aullador (*Alouata seniculus*), que muestra este mismo comportamiento. Cuando ambas especies estuvieron juntas en el saladero, su ingesta fue mayor, lo que podría implicar la existencia de un beneficio mutuo (mutualismo) derivado de la vigilancia, con un incremento del éxito como resultado. Así, parece que un mayor número de individuos y otra especie de primate en la zona son dos variables importantes para el éxito de la visita en el saladero, probablemente porque aumenta la intensidad de la conducta de vigilancia. Del mismo modo que en el caso anterior, parece que las "*Hembras del Oeste*" mostraron una mayor influencia que "*Machos*" y "*Hembras del Este*" en ambas condiciones, aunque especialmente sin aulladores. Sin embargo, cuando controlamos ambas variables (tamaño de grupo y presencia de aulladores), no encontramos diferencias tan claras. Por lo tanto, parece que la "*Hembras del Oeste*" usan una combinación de ambas situaciones, siendo las visitas cuando ellas están presentes las más exitosas. No obstante, el posible "conocimiento" de estas hembras para realizar visitas con variables favorables para aumentar la posibilidad de consumo sigue siendo objeto de estudio.

Finalmente, estudios recientes han documentado la existencia de patrullajes en territorios vecinos (Symington, 1990; Shimooka, 2005; Aureli *y cols.,* 2006; Wallace, 2007, 2008; Link, 2011), con subgrupos formados predominantemente por machos (Symington, 1990; Shimooka, 2005; Wallace, 2007; Aureli *y cols.,* 2006). Sin embargo uno de los eventos registrados de nuestro grupo de estudio aportó un nuevo enfoque a las incursiones a territorios de otros grupos.

El subgrupo que formó parte de esta invasión estaba compuesto por machos y hembras junto con juveniles de corta edad. En esta ocasión, los individuos se desplazaron al territorio vecino donde hicieron uso del saladero de dicho grupo. Aunque resulta difícil hablar de competencia por los recursos alimenticios entre grupos, debido a que el barro es una fuente inagotable, parece al menos claro que el objetivo principal de la incursión en este caso no fue la defensa del propio territorio, sino el uso de un recurso perteneciente a otro grupo. La trayectoria de este recorrido parecía estar muy definida por lo que se podría interpretar que los individuos conocían muy bien el territorio vecino. Esto podría deberse a que reconocían la zona debido a patrullajes pasados o que incluso algunas hembras podrían haber pertenecido a este grupo antes de su migración al grupo actual. De este modo estas hembras podrían haber "mostrado" este saladero al resto de individuos, puesto que conocía el territorio ya que habrían vivido en el mismo durante varios años antes de la migración. Sin embargo, sea cual sea la fuente de información que les permitió conocer este saladero, la razón por la que este grupo se dirige a otro territorio para hacer uso y alimentarse de barro en esta zona, cuando tienen su propio saladero, sigue sin estar clara y son necesarios más datos para poder aclarar y entender este comportamiento tan poco usual.

En conclusión, este estudio constituye una aportación que revela nuevos eventos característicos e importantes de este grupo, nunca antes documentados, y para apoyar las nuevas ideas que se habían puesto de relieve en los últimos años. A pesar del elevado número de horas de observación de este grupo (8569 horas), aún estamos lejos de comprender el significado de todos los patrones que esta especie muestra en la naturaleza. Por este motivo, es importante seguir construyendo una base que nos acerque a un mejor entendimiento de las especies y su relación con el ecosistema en el que viven.

CAPÍTULO 1:

Introducción general y objetivos

INTRODUCCIÓN

Un *sistema social* se puede definir como un conjunto de individuos que permanecen asociados durante períodos de tiempo relativamente prolongados y que interactúan entre sí (Colmenares, 2002). Foley y Lee (1989) propusieron un esquema estructural para la clasificación de los sistemas sociales existentes entre los primates que combina información sobre tres parámetros: el sexo, el parentesco y la estabilidad de la asociación espacial entre los miembros del grupo.

La *socioecología,* por otro lado, enfatiza el papel de la ecología local, en particular, de la presión predatoria y de la abundancia y distribución de los recursos vitales (alimento y parejas sexuales), sobre la organización social de un grupo y las estrategias de interacción que exhiben sus miembros (Wrangham, 1980; van Schaik, 1983, 1989; Dunbar 1988; Sterck *y cols.,* 1997; Overdorff & Parga, 2007; Nystrom & Ashmore, 2008). La teoría socioecológica se apoya en la teoría de la selección sexual (Trivers, 1985; Kappeler & van Schaik, 2004) para articular un conjunto de predicciones acerca de cómo se espera que sean las relaciones sociales entre los individuos de cada sexo.

Los factores limitantes de la reproducción difieren entre los sexos y, en consecuencia, lo esperable es que cada sexo organice sus relaciones de competición y de cooperación con otros congéneres de un modo que refleje esas diferencias. En última instancia, lo que predicen los modelos socioecológicos es la existencia de un patrón de co-variación entre el comportamiento social de los individuos y las características del ambiente trófico y social en el que viven y se reproducen. Este patrón es el resultado de las estrategias de competición intrasexual, de elección de pareja y de conflicto intersexual a través de las cuales los individuos intentan maximizar su eficacia biológica (revisiones: Colmenares, 2002, 2014).

De este modo, el estudio de los sistemas sociales, en este caso de primates, aportan gran información acerca de los pasos de la evolución, llegando incluso a ayudar a comprender mejor nuestro propio comportamiento. Además, su estudio desde una perspectiva comparada nos ayuda a describir la diversidad/semejanza de las estrategias sociales y a construir una base teórica que intente explicar lo que ocurre en la naturaleza. Este conocimiento nos permite plantearnos fines aplicados concretos, como es la gestión de las poblaciones naturales.

En definitiva, los estudios comportamentales que describen los sistemas sociales de primates han contribuido enormemente a profundizar nuestro conocimiento sobre el papel que desempeñan las relaciones sociales en la psicología y la biología de los individuos, al menos en los primates. Para conocer y comprender la calidad de vida de los individuos y su éxito biológico es preciso analizar la red de relaciones sociales que éstos tienen entre sí. Por lo tanto, sus éxitos y sus fracasos a lo largo de su trayectoria vital completa estarán íntimamente ligados a la calidad y cantidad de relaciones sociales que hayan mantenido (revisión Colmenares, 2002).

Finalmente, estos estudios también son esenciales para ayudar a comprender su distribución y la vinculación entre comportamiento y ecología, para poder aprender sobre sus necesidades en el espacio y llegar así a conservar estos animales tan valiosos para el ecosistema en el que viven. El estudio de ambas variables puede ayudar a entender mejor su comportamiento en el medio en el que viven y la gestión de los recursos dentro del ecosistema.

Los monos araña (*Ateles sp.*) tienen un papel ecológico fundamental en el mantenimiento del bosque tropical, puesto que son dispersores de semillas (Link & Di Fiore, 2006; Dew, 2008), de las cuales se alimentan y distribuyen a través de las heces. Este comportamiento los hace indispensables para el mantenimiento de la selva Neotropical.

Muchas especies desaparecen de forma natural por ser incapaces de hacerle frente a nuevos retos ambientales (Tellería, 2012). Estos retos, a menudo provocados por una gran pérdida de hábitat, tienen influencia tanto sobre la organización de los grupos como sobre las relaciones que los individuos tienen que modificar para adaptarse al medio en el que viven. Por este motivo, muchas especies de primates se encuentran en grave peligro de extinción (IUCN). Siguiendo esta línea, este proyecto también trabaja para fomentar la investigación y la conservación de una especie de *Ateles* en peligro crítico de extinción, *Ateles hybridus*, localizada en una zona fragmentada de Colombia, San Juan. Esta especie de mono araña es un buen ejemplo de cómo afecta la acción del ser humano al comportamiento de unos primates que luchan por sobrevivir en una zona muy reducida. El estudio del comportamiento de especies que habitan en diferentes condiciones también ayuda a crear las bases científicas de la conservación de las especies, mostrando el papel que desempeñan cada una de ellas en el funcionamiento de los ecosistemas en los que viven.

Especie de estudio

El mono araña, al igual que el chimpancé, presenta un sistema social de tipo fisión-fusión, en el que los individuos del grupo viajan dentro del territorio en subgrupos que muestran mucha flexibilidad en su composición y que cambian repetidas veces a lo largo del día. Estos subgrupos parecen estar relacionados con la cantidad de frutos disponibles en el bosque, siendo de menor tamaño cuando los recursos son escasos o están distribuidos en pequeños parches (Symington, 1988; 1990; Shimooka, 2003; Aureli & Schaffner, 2008). Este tipo de sistema “segregado” podría perder una de las más importantes ventajas que aporta la vida en grupo, como es la defensa ante el riesgo de depredación (van Shaik, 1983; Dunbar, 1988; Schaffner & Aureli, 2008). Sin embargo al ser una especie de gran tamaño, arborea, ágil y en cierto modo críptica, el riesgo de depredación no es muy elevado. Esta estrategia, por tanto, está directamente relacionada con la adaptación para mitigar los costes de la competición directa por los recursos, cuando éstos son escasos, y los riesgos de depredación cuando están en cantidades elevadas (Di Fiore *y cols.,* 2011).

A pesar de que esta organización segregada es común en ambos sexos, existe grandes diferencias conductuales entre los machos y las hembras en esta especie. De acuerdo con la teoría de la selección sexual (Trivers, 1972), existe una marcada asimetría en la inversión en el cuidado parental por parte de las hembras ya que estas deben invertir energía en la gestación, lactancia y cuidado de las crías. Por el contrario, los machos generalmente solo aportan espermatozoides en el momento de la cópula. Asimismo, las hembras tienen gametos (óvulos) limitados, tiempos extensos entre cría y cría y en general tiene una varianza mucho menor en el éxito reproductivo comparado con la varianza potencial en el éxito reproductivo de los machos. En los monos araña, las hembras invierten una cantidad desproporcionada de energía en sus crías durante la gestación pero también en el transporte, cuidados y lactancia, varios años después del parto (Link *y cols.,* 2009). El período de gestación tiene una duración de entre 7 y 7,5 meses (Eisenberg, 1973; Nunes & Champman, 1997) y las hembras suelen tener crías cada 3 años (Eisenberg, 1973; Champman & Champman, 1990). Las hembras sub-adultas permanecen junto a las madres hasta los 6 años de edad aproximadamente y dejan el grupo para alcanzar la madurez sexual en el grupo al que llegan (Di Fiore & Campbell, 2007).

Este gasto energético lleva a las hembras a quedarse más restringidas en las áreas centrales (*core areas*), de menor tamaño que aquellas que ocupan los machos (Symington, 1988; Shimooka, 2005; Wallace, 2008). Estas áreas generalmente comprenden entre un 20% y un 40% del total del territorio (Symington, 1988; Shimooka, 2005), mientras que los machos suelen moverse por toda la superficie. El tamaño del territorio (*home* range) de los monos araña es en general bastante estable, siendo el tamaño medio de unos 150 a 350 ha (Wallace*.,* 2008).

Además, el recorrido diario suele ser entre 500 a 4500m, siendo los recorridos más cortos en hembras que en machos (Shimooka, 2005; Wallace, 2007, 2008). Los territorios de los grupos de monos araña no suelen solapar con grupos vecinos, aunque en los últimos estudios se ha documentado cierto grado de solapamiento de alrededor de un 10-25% (revisión, Wallace 2008).

Agresión y dominancia

Otro de los factores que los monos araña comparten con los chimpancés, poco común en el resto de los primates, es la filopatria de los machos y la dispersión de las hembras (Di Fiore & Campbel, 2007; Shimooka *y cols.,* 2008). Al estar los machos emparentados entre sí, cabe esperar que las relaciones sociales entre éstos sean más estrechas que aquellas que muestran las hembras. De este modo, los subgrupos a menudo se encuentran formados únicamente por varios machos (Schaffner & Aureli, 2008), siendo sus relaciones las más consolidadas dentro de los grupos de monos araña, aparte de la relación madre-cría (Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988; Symington, 1990). Las agresiones entre machos son prácticamente inexistentes, por lo que no presentan una clara jerarquía social, o al menos no como aquellas que caracterizan a las sociedades de los chimpancés. En el caso de las hembras, las relaciones sociales aparecen documentadas en muchos estudios como igualitarias y sin una linearidad jerárquica (Gibson, 2010).

Las hembras de mono araña a menudo viajan solas junto con sus descendientes, forrajeando en solitario y consumiendo así un mayor número de recursos. De acuerdo con el modelo socioecológico (Wrangham, 1980; van Schaik 1983, 1989; Dunbar 1988), los recursos alimenticios son la principal limitación para el éxito reproductivo de las hembras, mientras que para los machos, su éxito se ve limitado por número de hembras que pueden monopolizar. Sin embargo, esta distribución en solitario de las hembras podría hacerles vulnerables a la coerción sexual. Así, esta estrategia de coerción de los machos hacia las hembras ha sido documentada en varias investigaciones donde se encontró una alta tasa de agresión (Fedigan & Baxter, 1984; Symington, 1987a; Klein, 1974; Campbel, 2008), asociado fuertemente a períodos en los que las hembras estaban ovulando (Symington, 1987a). En estudios más recientes (Campbel, 2003), esta relación entre ovulación y agresión no se muestra tan clara, estando repartidas las agresiones más uniformemente, siendo estos resultados no concluyentes.

Infanticidio

El infanticidio es una de las expresiones de conflicto sexual más notable entre machos y hembras en las sociedades de mamíferos (Hrdy, 1979; van Schaik & Janson, 2000). En monos araña algunos estudios han documentado agresiones de machos a hembras con crías recién nacidas e incluso algunos casos de infanticidio (Gibson *y cols.,* 2008).

Una de las teorías que mejor explica el infanticidio como una estrategia desarrollada por los machos es la hipótesis de la selección sexual. De acuerdo con esta teoría, Hrdy (1979) remarca que para que esta estrategia sea eficaz deben cumplirse una serie de criterios. En primer lugar, las crías víctimas del infanticidio no deben estar emparentadas con el agresor. Segundo, la pérdida de una cría debería estar relacionada con la recuperación del estado de actividad reproductivo (estro) de la hembra, acortando el período entre nacimientos. Por último, esta situación debería aumentar las probabilidades de reproducción del macho con dicha hembra (revisión, van Schaik, 2000).

En los monos araña los machos son el sexo filopátrico y por tanto comparten un porcentaje genético (en mayor o menor medida) con las crías del grupo, por lo que el infanticidio en esta especie no parece ser un comportamiento con una explicación adaptativa clara. El beneficio de un pariente debería suponer un beneficio indirecto para el individuo. Además, la falta de certeza de paternidad en esta especie, donde una hembra copula con varios machos (Campbel, 2008), aumenta el riesgo de eliminar a su propia cría.

Varios casos de agresiones dirigidas por machos hacía crías han sido registradas en otras investigaciones, siendo la tasa de agresión mayor hacia crías macho que hacia crías hembras (Fedigan & Baxter, 1984; Chapman *y cols.,* 1989; Symington, 1987b). Además, se documentaron 5 casos de infanticidio (Gibson *y cols.,* 2008) y en todos ellos la víctimas fueron machos. La razón por la que este comportamiento se presenta en una especie con un sistema social como el de los monos araña sigue siendo objeto de atención.

Saladeros

A pesar de las diferencias entre sexos y los conflictos que pueden manifestar ante muchas situaciones, machos y hembras también se reúnen para monopolizar un importante recurso, el saladero. Lo monos araña son primates arbóreos que rara vez descienden al suelo ya que el riesgo de depredación es mayor (Janson, 1998; Link & Di Fiore, 2013). Sin embargo, los individuos del grupo visitan con frecuencia un lugar específico del territorio, el saladero, donde practican geofagia (ingesta de barro). Felinos de gran tamaño como pumas (*Felis concolor*), jaguares (*Panthera onca*) y otros de menor tamaño como ocelotes (*Leopardus pardalis*), son animales que incluyen grandes primates en su dieta (Di Fiore, 2002; Ferrari, 2009) y su presencia en los saladeros ha sido constatada en diferentes estudios (Matsuwa & Isawa, 2008; Montenegro, 2004; Mosquera, datos preliminares del proyecto cámara trampa). A pesar del riesgo, la frecuencia de visitas es elevada por lo que parece un recurso bastante valioso para el grupo.

Datos previos sobre el mismo grupo de estudio proporcionaron algunos resultados interesantes a través del uso de cámaras trampa (Blake *y cols.,* 2010; Di Fiore & Link, 2013). Estos resultados resaltaron la alta frecuencia de visitas de los monos araña, incluso una tendencia muy elevada de visitas junto con otra especie de primates platirrinos, el mono aullador (*Alouata seniculus*), lo que parecía responder a algún tipo de asociación. El clima y los días soleados podrían ser otras variables características de estas visitas, registrándose más visitas en los días menos lluviosos (Link *y cols.,* 2011). El alto número de visitas y la alta inversión de tiempo resalta lo valioso que son estos saladeros para el grupo, sin embargo, las propiedades de dicha arcilla sigue siendo objeto de debate (Blake *y cols.,* 2010; Link *y cols.,* 2011; Link & Di Fiore, 2013). Estos saladeros no son sólo importantes para estas dos especies de monos platirrinos, si no que también lo son para un gran número de otros mamíferos y aves. Venados, pecarís, murciélagos, puercoespines, numerosas especies de aves junto con muchos otros animales visitan el saladero con frecuencia para ingerir barro. Muchos estudios sugieren que a través de este consumo los animales adquieren minerales necesarios en su dieta y también puede servir como agente desintoxicante (Atwood & Weeks, 2003; Blake *y cols.,* 2010). En primates, Krishnamani y Mahanery (2000) añaden propiedades antidiarreicas y farmacológicas; aunque la completa explicación sigue sin estar clara (Blake *y cols.,* 2010).

En el área en el que se realizó el presente estudio, en la Estación Biodiversidad Tiputini, se analizó la composición del barro encontrado en el saladero. Los resultados indicaron que este barro era rico en 5 minerales: hierro, calcio, magnesio, sodio y potasio (Voigt *y cols.,* 2008). Según Voigt *y cols.,* (2008), estos minerales son esenciales para la regulación de la homeostasis de los mamíferos.

Cabe destacar, que en una dieta compuesta por frutos e insectos los valores de sodio, potasio y magnesio son similares, sin embargo, los valores de hierro y calcio son más ricos en frutos que en insectos (Voigt *y cols.,* 2008). Por este motivo se esperaría que los animales insectívoros, en el caso de este estudio los murciélagos, presentaran una mayor frecuencia de visitas al saladero. No obstante, los resultados revelaron precisamente que los murciélagos que más visitaron los saladeros fueron los frugívoros y los folívoros.

Por otro lado, muchos frutos contienen toxinas, por lo que los animales podrían consumir barro en gran medida como forma de amortiguar los efectos tóxicos de los frutos o de los componentes secundarios (Atwood & Weeks 2003; Blake *y cols.,* 2010).

Dentro de los primates platirrinos que forman parte de este lugar de estudio, sólo los monos aulladores (*Alouata seniculus*) y los monos araña (*Ateles belzebuth*) practican habitualmente la geofagia. Sin embargo, los monos lanudos (*Lagothrix lagotrica*), pertenecientes a la misma familia (Atelinidae), no presentan este comportamiento. De acuerdo con su alimentación, los aulladores tienen principalmente una dieta folívora basada en hojas jóvenes. Por otro lado, monos araña y lanudos tienen una dieta bastante similar basada en frutos en su mayoría y en hojas nuevas cuando hay escasez de frutos (Di Fiore *y cols.,* 2008). La principal diferencia entre los monos araña y los lanudos es que éstos comen frutos ricos en lípidos y en ocasiones se alimentan también de insectos (Link, 2003; Di Fiore, 2002, 2004). Esto podría ser una posible explicación de la ausencia de lanudos en los saladeros, aunque las causas que influyen en la ingesta siguen siendo objeto de estudio.

Incursión y uso del saladero en territorio vecino

En general, los monos araña no comparten su distribución con otros grupos y es habitual observar patrullajes hacia el límite de los territorios vecinos (Symington, 1990; Shimooka, 2005; Aureli *y cols.,* 2006; Wallace, 2007, 2008; Link, 2011), como forma de protección de los mismos. Esta característica es otro patrón que también encontramos en las sociedades de chimpancés. Es frecuente observar subgrupos compuestos predominantemente por machos adultos patrullando los límites de los territorios vecinos (Symington, 1990; Shimooka, 2005; Wallace, 2007; y este estudio), siendo el tamaño del subgrupo mayor en estas zonas que en el interior del territorio propio del grupo (Symington, 1987a, 1990; Wallace, 2007).

Del mismo modo y a pesar de la dificultad de registro de encuentros entre grupos, por la rapidez en la que suceden, varios eventos han sido documentadas (Symington 1988; van Roosmales, 1985; Aureli *y cols.,* 2006; Wallace, 2007) describiéndose incluso agresión física entre los individuos de diferentes grupos. No obstante, en las observaciones registradas durante estas invasiones, los individuos no parecían mostrar una evidente competición por los recursos (Aureli *y cols.,* 2006).

La presente investigación trata de aportar un nuevo enfoque sobre estas incursiones, describiendo un caso que no cumple los patrones generales de un patrullaje, en el que el grupo de estudio hizo uso del saladero de un territorio vecino.

Metodología

Este estudio forma parte de un gran proyecto y programa de conservación, Proyecto Primates, que lleva 18 años desarrollándose en el Parque Nacional Yasuní y Reserva de la Biosfera, en la Amazonía Ecuatoriana. Desde 2006 este proyecto desarrolla su investigación con monos araña (*Ateles belzebuth*) en la Estación Biodiversidad Tiputini (Universidad San Francisco de Quito), una zona de bosque tropical primario, donde los monos araña coexisten con 9 especies de primates más. Del mismo modo, Proyecto Primates lleva a cabo proyectos de investigación y conservación en Colombia (San Juan), con una especie en grave peligro de extinción (*Ateles hybridus*) en un hábitat fragmentado, que nos sirve de referencia para ciertas cuestiones desarrolladas en el presente estudio.

Todos los individuos estaban perfectamente habituados e identificados en un largo proceso previo. Las jornadas de trabajo de los observadores se desarrollaron desde el amanecer hasta el atardecer para realizar el seguimiento durante todo el período de actividad de los individuos (aproximadamente 12 horas), desde los dormideros al despertar hasta los mismos cuando terminan su actividad, en la medida de lo posible. Se realizaron focales de los individuos adultos registrando puntos muestrales cada 5 minutos y recogiendo todas las interacciones sociales y episodios de alimentación de manera continua. Los observadores realizaban los seguimientos de manera individual usando GPS (model Garmin 76CSx), que tomaban puntos cada 20 segundos, para la posterior realización de un mapa de la ruta del individuo focal en ArcGIS. 9.2 (software DNR Garmin). En estos mapas se podía visualizar la composición del grupo en todo momento así como los eventos de fisión y fusión. También se tomaron datos de fenología y frutos de la dieta, factores climáticos y muestras biológicas fecales para el posterior análisis genético en Austin (Texas), dirigido por el Dr. Anthony Di Fiore y Dr. Andrés Link. De este modo, este proyecto supone uno de los estudios de primates Neotropicales más completos de campo con una amplia base de datos, de 8569 horas de observación focal, que fue analizada para obtener los resultados que se presentan en esta investigación.

Objetivos

El objetivo principal de este estudio es documentar las estrategias sociales y reproductivas de un grupo de monos araña (*Ateles belzebuth*) que ha sido objeto de estudio por este equipo de trabajo durante varios años. Esta gran base de datos nos permite intentar describir e interpretar cómo este grupo de la Amazonía Ecuatoriana se comporta en su hábitat natural. De este modo podemos ampliar nuestro conocimiento hacia una especie de primate y su relación con el ecosistema, destacando la descripción de los comportamientos agonísticos que presenta y la relación entre sexos, el uso de los recursos y sus estrategias ecológicas.

Finalmente, esta investigación pretende también aportar y discutir, sobre una base teórica, la explicación de comportamientos poco frecuentes, como es el infanticidio, en una especie donde los machos constituyen el sexo filopátrico o el uso de un saladero en un territorio vecino.

CAPÍTULO 2:

Patterns of aggression and social hierarchy in wild spider monkeys (Ateles belzebuth).

Patterns of aggression and social hierarchy in wild spider monkeys (*Ateles belzebuth*)*

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ABSTRACT

Several features of spider monkey (*Ateles spp.*) and chimpanzee (*Pan troglodytes*) societies exhibit striking convergent features (e.g., high degree of fission-fusion dynamics, male philopatry, territorial boundary-patrols). In both societies social bonds amongst males have been proposed to be particularly strong and females have been described as less social, often spending large amounts of time alone with their dependent offspring. Both male and female chimpanzees have very defined hierarchical relations with dominant males having better access to females and dominant females having access to better territories (e.g., core areas). For spider monkeys, it is still unclear whether their social relations are indeed egalitarian or otherwise organized hierarchically, similar to those described in chimpanzee societies. Here, we build on previous studies on *Ateles* describing the patterns of intragroup aggression within a group of wild spider monkeys and evaluate the presence of hierarchical versus egalitarian relations amongst group members. From 2006 to 2013 we conducted behavioral follows on all adult males (N=6) and adult females (N=11) in one group of white-bellied spider monkeys at the Tiputini Biodiversity Station in Ecuador, completing 8596 hours of focal animal sampling. We recorded all aggressive events in which the focal animal was the recipient or the initiator of aggression and complemented these systematic observations with *ad libitum* data. Although general aggression rates were low compared with other primates, we recorded 442 aggressions (369 where we were able to identify the participants), and 247 of those aggressions were between adult spider monkeys. Males were the initiators of most of the aggression (78%), being most of them directed towards females like it had been described in other studies, while females were the principal recipients of aggression (96%). Male-to-male aggression was very low accounting only for (4%) of aggression. Contrary to the results of previous studies, female-directed aggression was not predominantly against cycling females. Also, approximately 40% of male-to-female aggressions took place in the context of subgroups coming together, suggesting a potential role of aggression in “social-control”. Aggression within members of the same sex was very low, and the number and directionality of aggressive of within-sex encounters was not high enough to reveal hierarchic relations between group members, especially among males. Aggression towards females was strongly biased towards two females who had migrated into the group in the past few years and were nulliparous. This study provides further support for the low rate of male-male aggression in spider monkeys and the fact that most aggression is directed from males to females in a wide variety of contexts suggesting a more comprehensive role of male to females aggression that only related to sexual coercion. Finally, these results denote that the regulation of social relations within group members in spider monkeys differ drastically from those in chimpanzees.

Key Words: Aggressions_ hierarchy_ dominance_ spider monkey_ social control

INTRODUCTION

Most primates, like many other gregarious animals, live in social systems where groups have an ample variety of grouping patterns. These patterns can be influenced by demographic, ecological and social conditions. A social system is the collection of individuals who remain spatially associated for a period of time and they frequently interact amongst them (Colmenares, 2002). Thus group living is a widespread phenomenon within the animal kingdom, which may confer benefits to individuals improving the strategies of defense against predators, the monopolization of resources, and the ability to defend larger or more valuable territories (Terborgh & Janson, 1986; Watts, 2010). These independent factors may well determine the potential competitive regime amongst individual primates, according to the socio-ecological model (Sterck *et al*, 1997).

Among females, resource distribution seems to influence the type of social relationships between them in different species of primates and other mammals (van Schaik, 1989). The ecological model assumes that predation risk forces females to live in groups. When females live together, they compete for resources, and the nature of this competition shapes female social relationships. Within and between-group contest competition leads to four types of female-female social relationships: Dispersing-Egalitarian, Resident-Nepotistic, Resident-Nepotistic-Tolerant, and Resident- Egalitarian (Sterck *et al.*, 1997). According to Sterck *et al.,* (1997), the first prediction of this model concerns associations among social, where frequent coalitions, often but not always exclusively between relatives, should occur with decided agonistic relationships (i.e., with agonistic dominance relationships). A second prediction of the ecological model is that no species should show female dispersal in combination with decided dominance relationships and frequent nepotistic or mutualistic coalitions.

Generally, dominance relationships tend to arise in contexts where individuals or groups are able to effectively monopolize access to a limited and valuable resource. The dominant individual will have "priority of access" to these resources, excluding rivals or competitors, which confers reproductive advantages (Bergstrom & Fedigan, 2010). Dominance is a fundamental aspect of social organization in many species of organisms: birds (Izawa & Watanabe, 2008), gregarious mammals such as elephants (Wittemyer & Getz, 2007), several species of primates such as baboons, cercopithecus, chimpanzees, macaques, marmosets, capuchin monkeys, amongst others (Altmann & Alberts, 2003; Wittig & Boesch, 2003; Singh *et al.*, 2006; Bergstrom & Fedigan, 2010; Greenberg *et al.,* 2010; Klass & Cords, 2011). According to Bergstrom & Fedigan (2010) linearity, strength and stability are essential characteristics of hierarchical relations needed to better understand the changes in dominance relationships, social structure and patterns of reproductive success among social primates.

On the other hand, sex differences in strategies of sexual and social behavior of males and females are interpreted in relation to selective pressures, which affect differently members of each sex (Trivers, 1972; Kappeler & van Schaik, 2004; Lindenfors *et al.*, 2007). Females, maximize their reproductive success depending on their ability to ensure access to adequate food resources, their ability to choose appropriate partner or partners and the ability of provide services to females (and their offspring) with an adaptive value (e.g., food, protection from the aggression of others, etc). However, males maximize their reproductive rate depending on their ability to monopolize a greater number of sexual partners, specifically, their ability to fertilize more eggs. Thus, the strategies of males and females are often in direct conflict (Trivers, 1972; Arnqvist & Rowe, 2005; Palombit, 2012). Females reject mating opportunities with males, while males use aggression, threat and force, as a sexual coercion strategy, increasing the likelihood of these mating with females or decreasing the chances that females mate with other males (Slater *et al.*, 2008; Link *et al.,* 2009). Many studies confirm that aggression directed by males is significantly higher towards cycling females than non-cycling females: in baboons (*Papio sp.*, Bercovitch, 1986; Smuts & Smuts, 1993) in macaques (*Macaca fuscata,* Soltis *et al.,* 1997), gorillas mountain Gorilla (*Gorilla gorilla beringei,* Nadler, 1989), and chimpanzees (*Pan troglodytes,* Goodall, 1986a; Muller *et al.,* 2007; Wrangham, 2002). Sexual coercion also appears in species characterized by female dispersal and fission fusion social systems (Smuts & Smuts 1993; Slater *et al.*, 2008; Link *et al.*, 2009).

Among New World monkeys, spider monkeys stand out for sharing several behavioural and social traits with common chimpanzees (*Pan troglodytes*), which are rather uncommon among mammals generally. These traits include a high degree of fission-fusion sociality, female-biased dispersal, and male cooperation in the context of inter-group competition with the occurrence of territorial boundary patrols. However, in contrast with the large amount of studies on chimpanzees about their social behavior, very little is known about spider monkeys. Chimpanzees are known for their complex social networks. This species has a strongly hierarchical social system (Foster *et al.,* 2009; Wroblewski *et al.*, 2009) with strong bonds and alliances, especially among males, being more gregarious and more social than females. Although in spider monkeys male-male bonding has been observed (Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988; Symington, 1990; Aureli & Schaffner, 2008), the hierarchical or egalitarian nature of their relations is still unclear.

Chimpanzees and spider monkeys are some of the few primate species where males are the philopatric sex while females disperse to other groups after reaching sexual maturity (chimpanzees: Goodall, 1968; Nishida, 1968; Pusey, 1979; spider monkeys: Di Fiore & Campbell, 2007; Link *et al.*, 2009). Males in a social group are closely related, and in general it has been proposed that males have strong social bonds (Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988; Symington, 1990; Aureli & Schaffner, 2008) between them where the mating system mostly involved scramble competition, being the competition for females very subtle (Gibson, 2010). Nevertheless, males display cooperative behaviors to compete against other rival neighboring groups (de Waal, 1982; Watts, 1998; Aureli & Schaffner, 2008). Given that predation avoidance is not a strong selective pressure because they are large-primates (but see Link & Di Fiore 2013), one of the main benefits to live in groups is probably to be the cooperative effort in intergroup competition for resources (Shimooka, 2003). Males patrol the territory to defend access to females and food resources from neighboring communities (Aureli & Schaffner, 2008). They are often found in larger subgroups than females (Aureli & Schaffner, 2008), which average subgroups in *A. belzebuth belzebuth* is nearly double than females (5,4 vs 2,8 individuals) (Shimooka, 2005), and are less likely to be encountered alone (*A. geoffroyi*: Chapman, 1990). Males, within the same community, are rarely aggressive towards each other (Aureli & Schaffner, 2008). The fact that [1] there are no recorded observations of direct competition between males for access to receptive females, [2] the rate of aggression between males is extremely low, and [3] the absence of sexual dimorphism in these primates, suggests a scenario of low competition between males in *Ateles* within their social groups. Adult males, in general, are more affiliative with other males (Fedigan and Baxter, 1984) and grooming is most frequent in male-male dyads (Aureli & Schaffner, 2008), while female-female grooming is the least common (Symington, 1990). Additionally, males usually exchange embraces and pectoral sniffs when they join a new subgroup (fusion), while these behaviors are less frequent between females (van Roosmalen & Klein, 1988).

According to socio ecological theory, female primates that feed primarily on ripe fruits experience strong intragroup contest competition for food as such resources are distributed in discrete, monopolizable patches (van Schaik, 1989; Sterck *et al.*, 1997; Koenig, 2002; Aureli & Schaffner, 2008). They are expected to display unidirectional agonistic, to form alliance and clear dominance relationships. However, although ripe fruit is the main source of food for spider monkeys, they reduce feeding competition with high levels of fission fusion dynamics, characterized by the formation of long and stable social groups are divided into small foraging subgroups (parties) that vary in size and composition (Link *et al.*, 2009). Females usually travel in small subgroups or are found foraging alone (Aureli & Schaffner, 2008; Link *et al.*, 2009) with their offspring. Larger groups incur in higher travel cost because they need to visit more patches to allow every individual to cover their nutritional and energetic needs (Janson & Goldsmith, 1995). Females travel slowly (Shimooka, 2005), especially those with offspring, and spend a longer time travelling between these patches, so they have higher relative travel cost than males (Aureli & Schaffner, 2008). This situation makes females vulnerable to sexual coercion by not having alliances and found no support in small groups or alone where access is limited allies (Wrangham, 2002; Slater *et al.*, 2008). Under this condition, the selection pressure to remain in the natal group and rely on strong bond with kin is low. Dispersal from natal groups may even be favored through the reduction of competition between kin. Thus the value of their relationship is expected to be low (Aureli & Schaffner, 2008). So, interactions among female spider monkeys are largely non-antagonistic and aggressions between them are not common (Aureli & Schaffner, 2008).

One of the patterns most studied in relation to low-intensity aggression in *Ateles*, is male-to-female aggression (Campbell, 2003; Link *et al.*, 2009; Slater *et al.*, 2009; Abondano & Link, 2012). Initial studies suggested that male spider monkeys directed aggression towards females in a context associated with resource competition since it was eventually observed in trees and feeding contexts (van Roosmalen & Klein, 1988). These hypotheses were not supported by subsequent studies in which less than one fifth of the aggression of males towards females occurred in feeding contexts (Symington, 1987a). Symington (1987a) suggested that the function of male aggression towards females might be associated with inducing them to urinate, since males tend to smell the urine of females, probably because this contains information of the reproductive status (Campbell, 2003). The hypothesis that proposes that male aggression toward females have a reproductive function, has been supported by several studies (Symington, 1987a; Campbell, 2003; Slater, *et al.*, 2009), and has even been suggested to have a function of "social control" as an indirect mechanism of sexual coercion by male spider monkeys (Link *et al.,* 2009), where males assert their-term control over females´ reproduction and prehaps discouraging them from mating outsite the group. Slater *et al.* (2009) described that prologed chases not result in inmediate copulation, but sometimes the female victim left the subgroup to travel alone with her male aggressor as a form of male intimidation into a mating consorthips. However, some studies agree that the aggression directed by males to females is not only directed at females who are ovulating but also at infants and even at those females who have babies and therefore are not available reproductively (Campbell, 2003; Link *et al.,* 2009).

Several studies also agree that a high proportion of male-to-female aggression usually occurs right after a “fusion” of two subgroups (two subgroups join together) (Klein, 1974; Aureli & Schaffner, 2007). It has been proposed that the functionality of these attacks is related to spatial fluidity. Spider monkeys can spend extended periods of time in which two individuals don´t come across each other. In this way males would show their dominance and social control against females just after fusion events (Link *et al.,* 2009). They also showed an increase of affiliative behavior, highliting that these events generate tension and these affiliative interactions could play a role in conflict management, reducing that tension and facilite tolerance at reunions (Aureli & Schaffner, 2007).

In all studies of spider monkeys, this type of aggression is usually a consistent pattern in which one or several males aggress a female while they makes vocalizations emitting growl, and chase or force her towards the lower branches of a tree, whereas she vocalize sharply with clear signs of stress (Link *et al.*, 2009). In general, studies that seek to establish dominance relationships in groups of primates (and other social animals) use the results of antagonistic or submissive behaviors between pairs of individuals. In some species such as chimpanzees (*Pan troglodytes*) some vocalizations (the "pant-hoots") have a clear submission component and could be useful for studying dominance (Watts, 2000). In other species the dominance is studied mainly by direct attacks or displacements. The dominance relationships appear when an individual repeatedly wins the fight, the space, females, etc, and become dominant figure in a group. A key concept associated with dominance relationships in social groups, is associated with the "linearity of dominance", ie transitive dominance relationships in a social group. According to the market theory (Noë *et al.*, 1991; Noë & Hammerstein, 1994) the value of potential pattern is based on the services and commodities that partners can offer relative to other group members in different circumstances. Female-male relationships present another source of variation due to changes of female reproductive status. Finally, due to the extremely unusual aggression between members of the same sex, spider monkeys studies have suggested weakly supported hypotheses on the existence of dominance relationships in these primates, females nor males (Symington , 1987a).

The principal aim of this long-term project is to study the patterns of aggression and social hierarchy in a wild population of white-bellied spider monkeys (*Ateles belzebuth*) in Western Amazonia. We compared differences between sexes and within different contexts of aggression. This study documents the development of aggression patterns between sexes and the existence or non-existence of linearity and social hierarchy among them.

METHODS

Study Site

This study took place at the Tiputini Biodiversity Station (TBS) in Yasuní National Park (Ecuadorian Amazon), one of the most biodiverse areas in the world. This area is a primary tropical rainforest, with annual rainfall of generally exceeds 3,000 mm (Di Fiore, 2004), and where 10 primate species live sympatrically.

Study Group

The study group of wild white-bellied spider monkeys (*Ateles belzebuth*) was been studied continuously since 2006. The group consists of six adult males and eleven adult females until the end of the study in December 2013. Including juveniles and infants the group contained 35 individuals.

Behavioural Follows

We conducted behavioral follows of all adult members of MQ-1 group from August 2006 to December 2013 using focal animal sampling (Altmann, 1974), attempting to follow each focal subject from dawn to dusk. We collected behavioral data every five minutes using instantaneous point sampling, and all the social interactions (aggression, grooming…) were recorded.

Every aggression, its participants and the direction of each aggression were registered describing the scenario and the number of individuals that participated during the aggression. We consider coalition when more than one individual simultaneously aggressed a single victim and the aggression were also classified according to the reproductive state of the females aggressed and the context that involved the aggression. We also recorded data *Ad libitum* of interaction, especially aggressions, which the observer could register outside of the focal sample.

Female Reproductive State

Reproductive state of each female was estimated based on the birth of their infants, considering the reproductive states described by other authors (Eisenberg, 1973; Chapman & Chapman, 1990; Campbell & Gibson, 2008). Before birth, the duration of estrus period had been described to last around 4 months as females usually cycle for a few month before conception, e.g. *A. geoffroyi* 3-6 cycles (Campbell & Gibson, 2008), and according to the time where these females were seen copulating. The duration of the gestation is 7.5 months long (Eisenberg, 1973; Di Fiore & Campbell, 2007) and we estimate the pre-ovulation period (anestrus) according to these data. After birth, the lactating period was considered to last around 19 months according to the data reported on previous studies (between 18-20 months: Eisenberg, 1973) and the behaviour observation of these females nursing their offspring.

Context of Aggression

We classified the context of aggression in three different categories according to the behaviour observed during the event. These categories were (1) fusion, defined as the event when two subgroups join together, considering the effect of this situation during 30 minutes and counting the aggression happened within this period of time. Second (2), feeding, considering this context when the aggression happened in a feeding tree; and (3) unclassified, when we do not have enough information to classify the context but it is none of the other two contexts that we mentioned before.

Data Analyses

To analyze the data we used SPSS 15.0 statistic program, using non-parametric measures because our data have a normal distribution but does not meet the criteria of homoscedasticity. To do a descriptive summary of our results we used the whole number of aggressions, including the *Ad Libitum* data. However to do the statistics analysis through rates of aggressions (aggression per hour) we only used focal data, where we have the total numbers of hours of observations for each individual. Within these data we could not identified the individuals in 11 cases (four actors not identified and seven receivers not identified) within focal samples, and 62 events within *Ad libitum* data. We excluded these data from our analyses because they didn´t contribute to understanding the patterns of aggression, but it was included within the total number of aggressions observed during this study. We included data from two additional males (N=8) for the total summary results but we excluded them from the calculation of the rates of aggression because the number of observations of each of these males was much lower than the rest. We considered a single event of aggression when the “attacks” or “threats” were observed between the same individuals, within 20 or 30 minutes.

To analyze the data between sexes we used Mann Whitney U Test. To compare male coalitions (individual single attacks *vs* coalitionary attacks in dyads or groups), each female reproductive state and each context, we used Friedman test (Wilcoxon test was used as a post doc test, using Bonferroni correction to adjust p value to evaluate the differences between pairs (dividing p/number of comparisons)). To evaluate the hierarchy relationships and dominance we used the program Noldus MatMan 1.1 (Noldus Information Technology, 2012), studying the relationship between matrix of Actor/Receiver of aggression and comparing dyads of male-male, female-female and male-female. In this case, we also included *Ad Libitum* data to do the matrixes, because we evaluated the whole number of aggressions. The distribution of those aggressions were analyzed with Chi-squared test in aggression directed by males towards females, and with Two Samples Kolmogorov-Smirnov test in events of aggression directed by females towards other females (because the numbers of aggressions in several cases were less than 5). We also analyzed the differences of the directionality towards females when male and female were actors, to study if both sexes aggressed same females individuals, with a Pearson Correlation.

RESULTS

Overall patterns of aggression

During the study period, 442 aggressions were recorded in 8596 hours of focal animal sampling, 5107 focal hours on females (N=11) and 3488 on males (N=6). Unfortunately we could not identify all the individuals involved in all cases of aggression (in 16,5% of aggression we were unable to identify either actors or receivers of aggression, or both), but we could identify the age and sex of the individuals involved in these aggressions in 369 events (83,5%) and in 301 of those events (68,1%), we could identify also the identity of all the individuals involved.

Rates of aggressions were very low (0,051 aggressions per hour) or approximately one aggression every 19.6 hours of behavioral follows. Within the focal sample data we registered 170 aggressions where individuals were identified and an additional 199 aggressions were registered through *Ad libitum* data. Males were the initiators of aggression in 229 events (62,1%) (110 within the focals and 119 within the *Ad libitum* data), and females were the initiators of aggression in 132 events (35,8%) (57 within focals and 75 in *Ad libitum* data) being 84 of those aggressions (35 focals, 29 *Ad Libitum*) directed towards juvenile and sub-adult individuals (63,6%). Most of those female aggressions were towards their own offspring (85,7% of the total of aggressions towards non-adult individuals). Finally, eight aggressions were initiated by mixed subgroups of males and females (2,2%).

1. Aggressions between Adults

There were 247 aggressions (65,3%) between adults (119 focals and 128 in *Ad libitum* data).

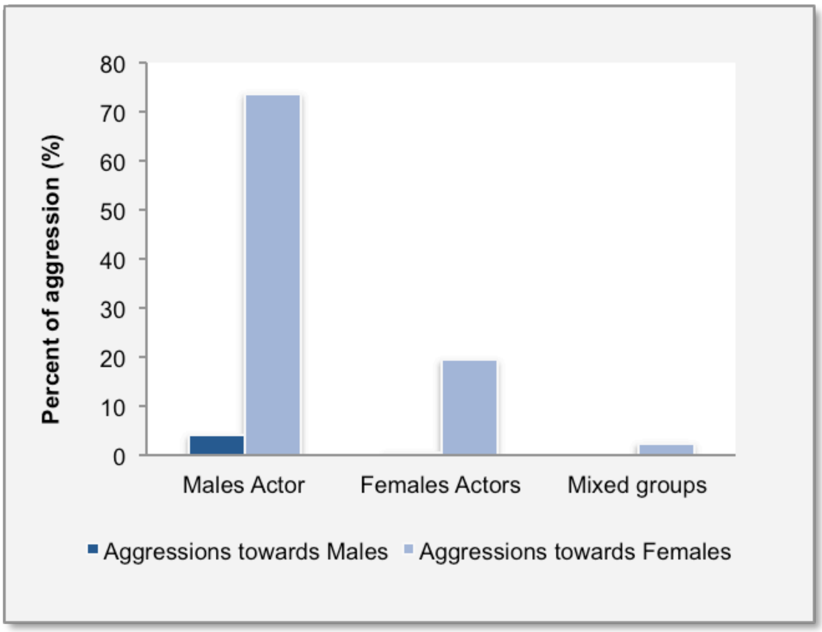


Figure **1. Percent of aggressions between adults, describing differences between sexes.**

Males were the principal actor of this kind of aggression (Fig.1), being the initiators of 182 (90 focals and 92 *Ad libitum*) events (73,7%) directed towards adult females (169 events where we could identify the aggressed female) and only 10 events directed towards other males (4,1%). Females aggressed other adult female in 48 (21 focals and 27 *Ad Libitum*) events (19,4%) and only 1 event towards a male (0,4%). Finally, six aggressions were initiated by mixed subgroups towards females (2,4%).

Rates of Aggression

When we compared the aggression´s rates according to the hours of observation of each individual (focals) we could corroborate the differences between adults (Fig. 2), being males principle actors (Mann Whitney U test, U=0,000, p<0,01) and females were principle receivers (Mann Whitney U test, U=0,000, p<0,01).

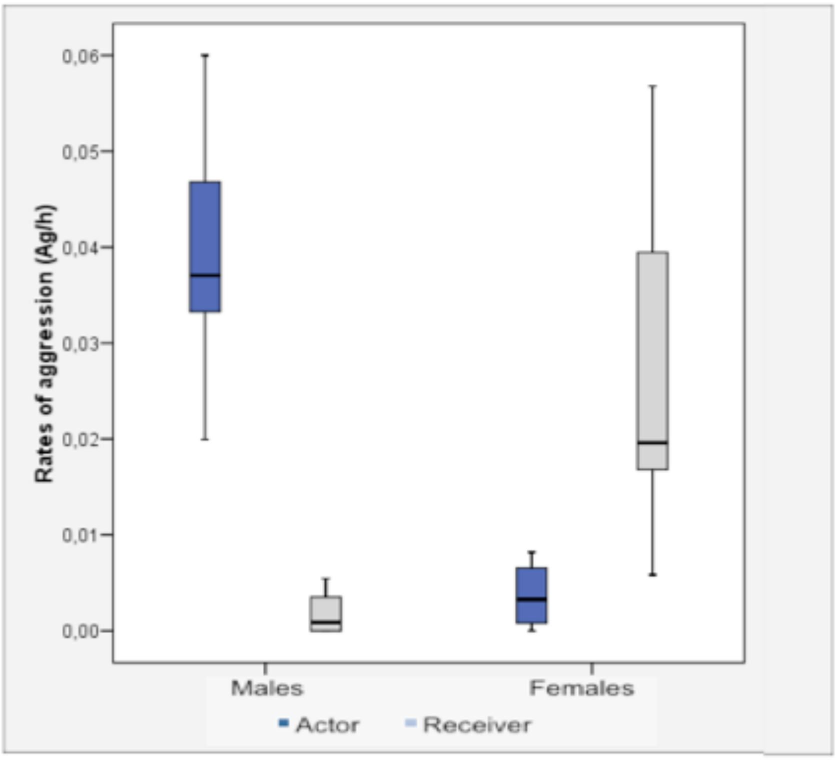


Figure 2. Rates of aggression per hour: female *vs* males total aggressions (actors-receivers).

We also found differences within coalitions (Fig. 3); males attack in dyads and in groups more often than females (Mann Whitney U test, U=0,00 p<0,01)

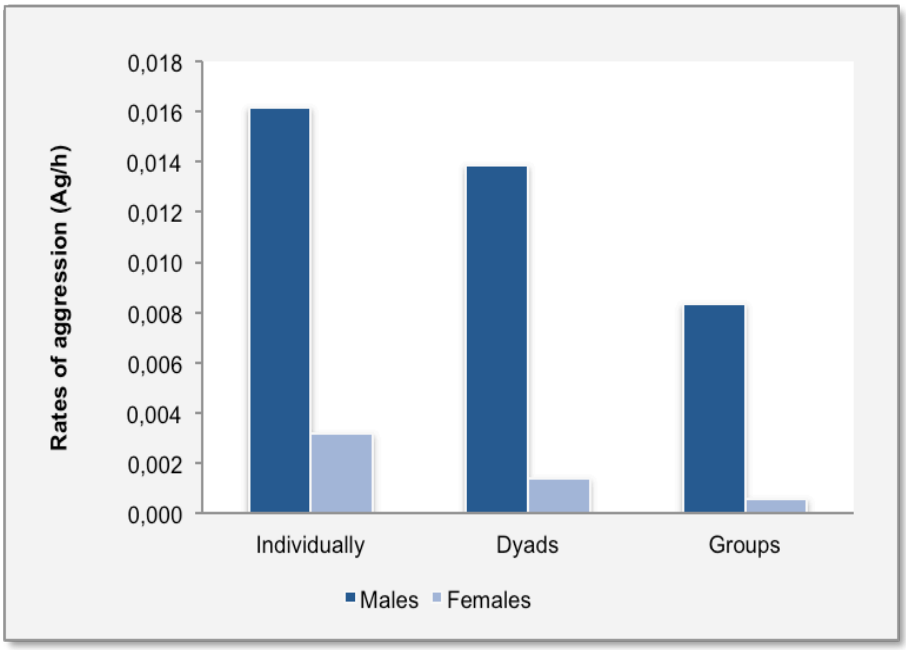
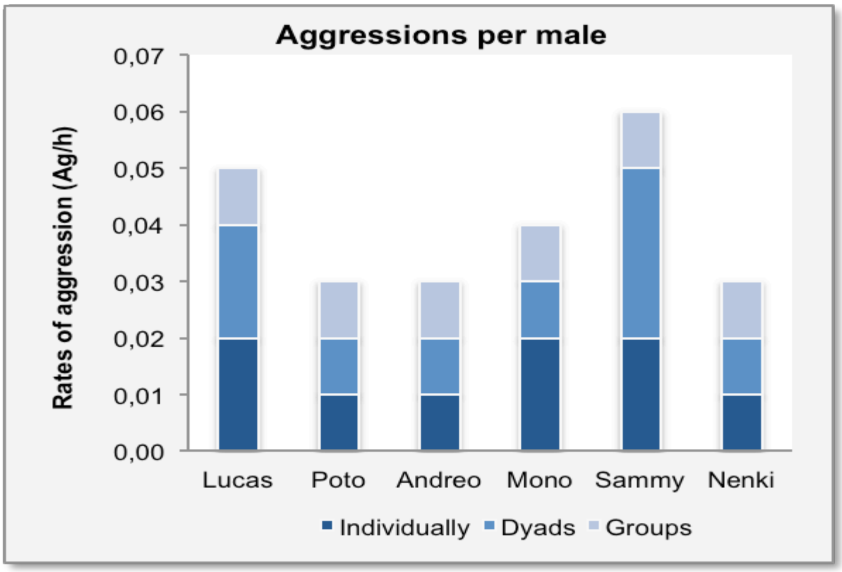


Figure 3. Males´ rates of aggression per hour: individually aggressions, coalition in dyads and in groups.

Male aggression was studied in detail (Fig. 4) evaluating the frequency of male coalitions (attacks from at least two males). We found significant differences when we compare the three categories (individually, dyads and groups; Friedman, X^2=7,36; p<0,05) but the post hoc analysis didn't show significant differences between pairs. However, individual attacks and in dyadic attacks were more frequent (No differences between Individually-Dyads: post hoc, Wilcoxon, Z=-1,21; p>0,05) than attacks in groups of >2 males (Individually-Groups: post hoc, Z=-2,2, p=0,028).



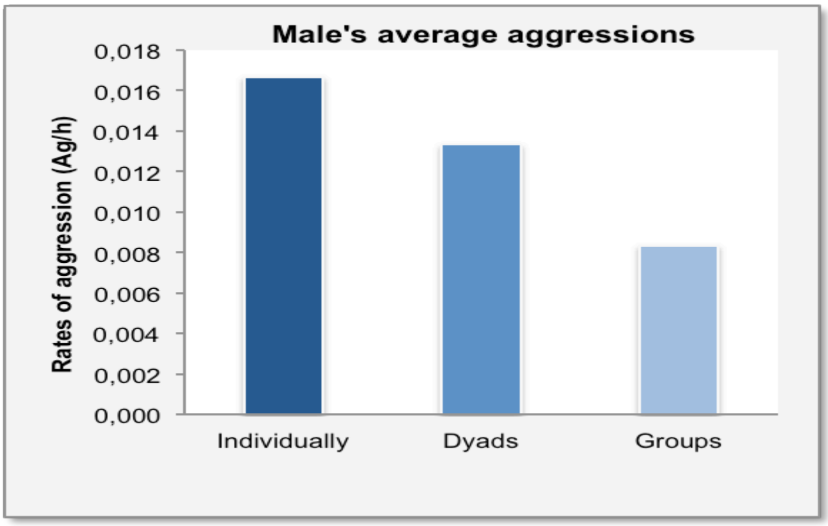


Figure 4. Rates of aggression of each male: individually, with two aggressors (dyads), more than two (groups) and in mixes groups, per male (top), on average (down).

When we analyzed the total number of aggressions, including non-adults individuals, the number of agonistic situation where females were actors increased because they often directed aggression towards their offspring. However, females initiated aggression significantly less than males (males: 0,044 ± 0,006; females: 0,014 ± 0,004; Mann Whitney U test, U=5, p<0,01). When considering aggression directed to subadults, juveniles and infants, there were no differences between male and female aggressions (Mann Whitney U test, U=31,5, p>0,05). Females also aggressed their own offspring in general, only in 5 cases they aggressed other non-adult individuals.

2. Context of Aggression

The context of aggression (Fig. 5) where males were actors were: 6 (2,6%) in sexual context (copulation), feeding context 25 events (10,9%), fusion context 87 (38,0%), 11 situations (4,8%) with both context (feeding and fusion) and indeterminate context (unclassified) were 101 events (44,1%), considering focal and *Ad libitum* data. Where females were actors: 37 of those aggressions were in feeding context (28,0%), 21 in fusion context (15,9%), one situation (0,7%) with both context (fusion and feeding) and 73 unclassified context (55,3%).

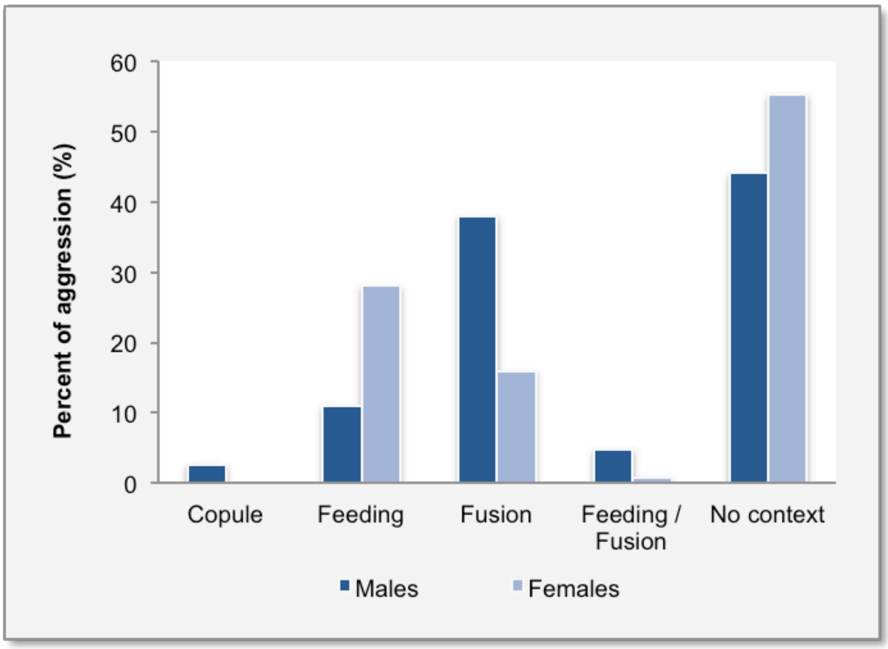


Figure 5. Males and Females percent of aggression according to the context

Rates of Aggression

When we analyses the differences between sexes according to the context we found that males usually aggress in fusion context, more often than females, while females aggressed more often in feeding context than in fusion context (Fig. 6).

There were differences within the three contexts: fusion, feeding and unclassified (Friedman, males, X^2= 6,3; p<0,05; females, X^2= 6,5; p<0,05); although there were not significant differences in the analyses post hoc. We only found a tendency between feeding and fusion context in males, being the number of aggression within fusion context higher than feeding (Wilcoxon, Z=-2,21, P=0,028). In females we found significant differences being less common fusion than unclassified context (Wilcoxon, Z=-2,43, P=0,015).

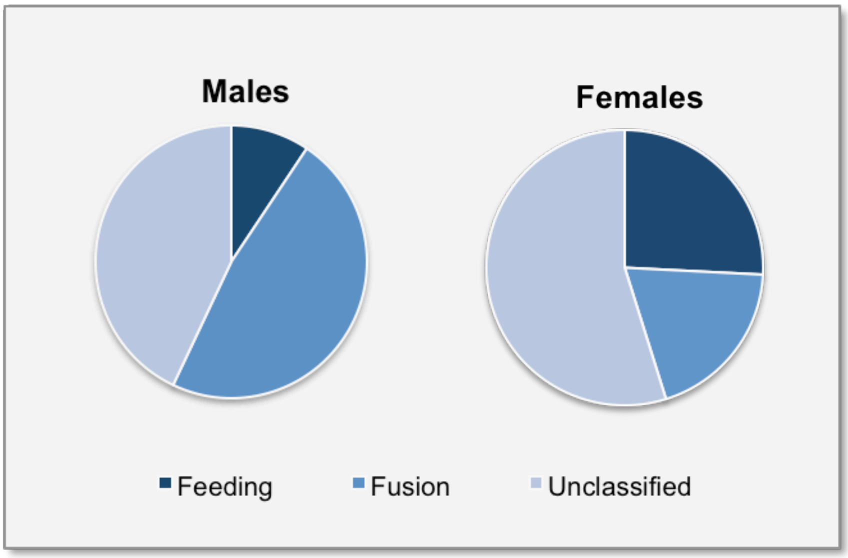


Figure 6. Male´s and female´s rates of aggression according to the context of those aggressions

Between males and females we found significant differences within the fusion context (males: 0,017 ± 0,003 *vs* females: 0,003 ± 0,001, Mann Whitney U test, U=0,00; p<0,01) but we didn´t find significant differences within feeding context (males: 0,003 ± 0,001 *vs* females: 0,004 ± 0,001, Mann Whitney U test, U=30; p>0,05) and other context (males: 0,016 ± 0,004 vs females: 0,009 ± 0,002, Mann Whitney U test, U=18; p>0,05).

For males, aggression is often initiated within a fusion context, while for females, aggressions more often takes place within a feeding context (Fig. 7). However, it is worthwhile to note that a large proportion of aggression initiated by both males and females takes place outside fusion and feeding contexts.

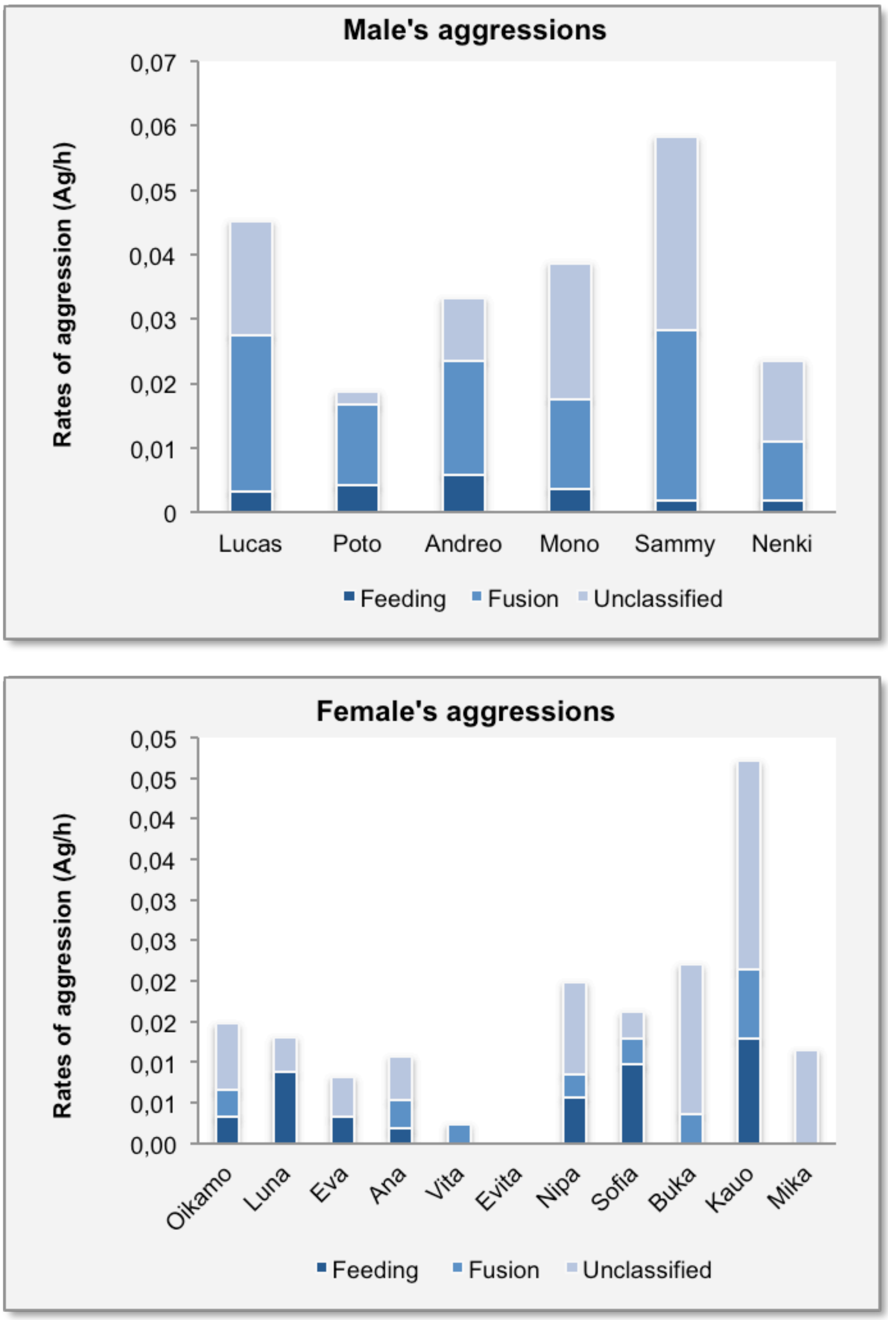


Figure 7. Rates of aggressions of each individual according to the context

Females also directed aggressions towards juveniles and sub-adults (26 events towards adults and 35 towards non-adults) and most of those aggressions (N=30) were towards their own juveniles and sub-adults (21 own juveniles and 9 own sub-adults).

3. Female Reproductive States

We studied female directed aggression by males and evaluated if aggression was skewed toward a particular reproductive state, more specifically when females were in estrous and thus potentially fertile. Males directed aggression towards females with dependent infants (within the first three months of life) in 30 occasions (17,8%), towards females in anestrus period 32 times (18,9%), towards female in estrus 23 times (13, 6%), and on 29 occasions (17,2%) when females were pregnant, 41 times (24,3%) when females were nursing their offspring (lactating) and when we couldn´t determinate the reproductive state in 14 times (8,3%) of those aggressions (Fig. 8).

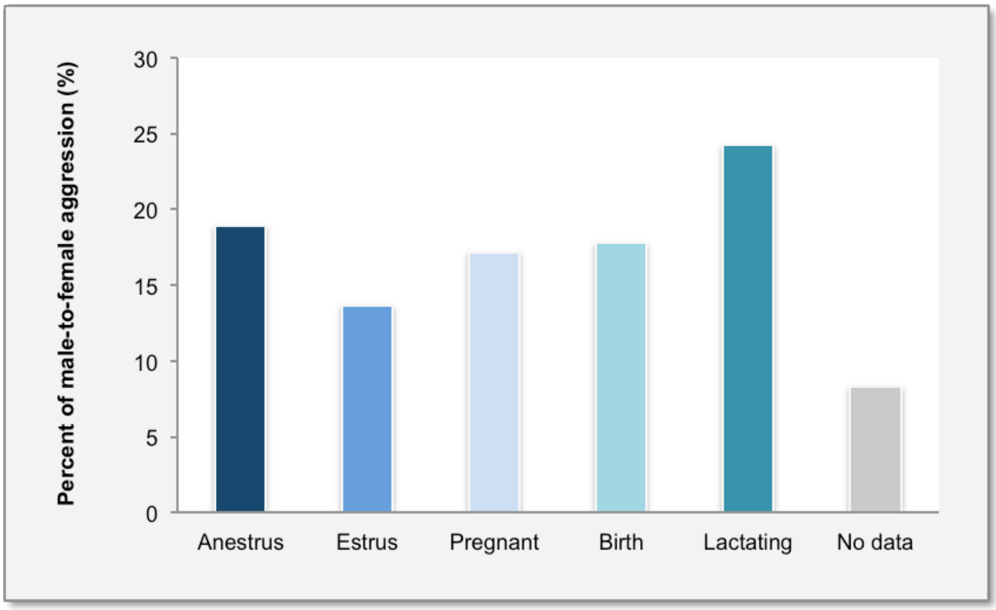


Figure 8. Percent of aggressions of males directed to females according to the females reproductive states

Rates of Aggression

In contrast with other studies where female directed aggression by males has been suggested to act as sexual coercion with most of male aggression directed to females during their estrus period (Slater *et al.,* 2009), we found no differences between aggressions and the reproductive state of female spider monkeys (Friedman, X^2= 7,57; p=0,11). We analyzed the aggressions that female received by males according to the time we observed each individual and we found significant differences between each female. It is noteworthy that within estrus period (X^2=11,64 p<0,01), two females, Vita and Evita, showed the highest rates of aggression, however, aggressions towards other females during this period was not different from other reproductive states. During the gestation period we also found differences (X^2=6,2, p<0,05) and Sofia, Evita and Mika didn't show aggressions and it was higher towards Vita, Nipa and Kauo. During birth (new infants within their 3 first months of life) we found differences because not all of them show aggressions (X^2=11,36, p<0,05). We didn´t find significant differences within anestrus period (X^2=0,82; p>0,05), gestation (X^2=5,73; p>0,05) and lactating (X^2=0,00, p>0,05), where almost all females received aggressions (also the longest periods, see fig. 10).

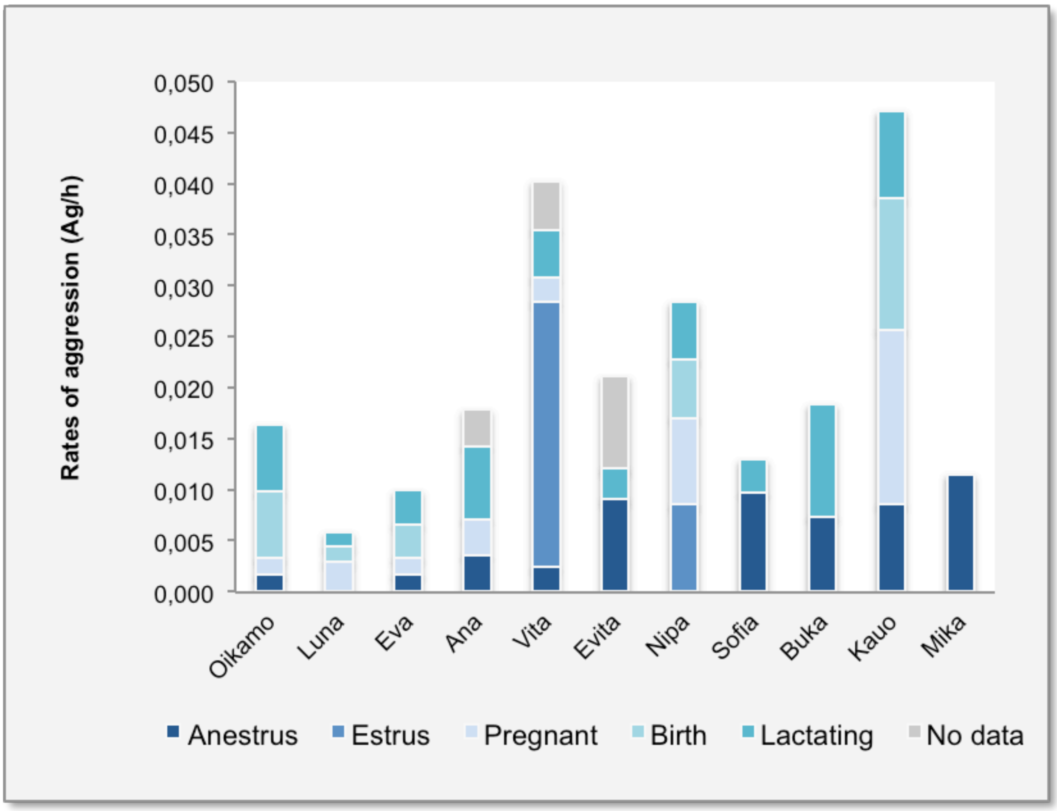
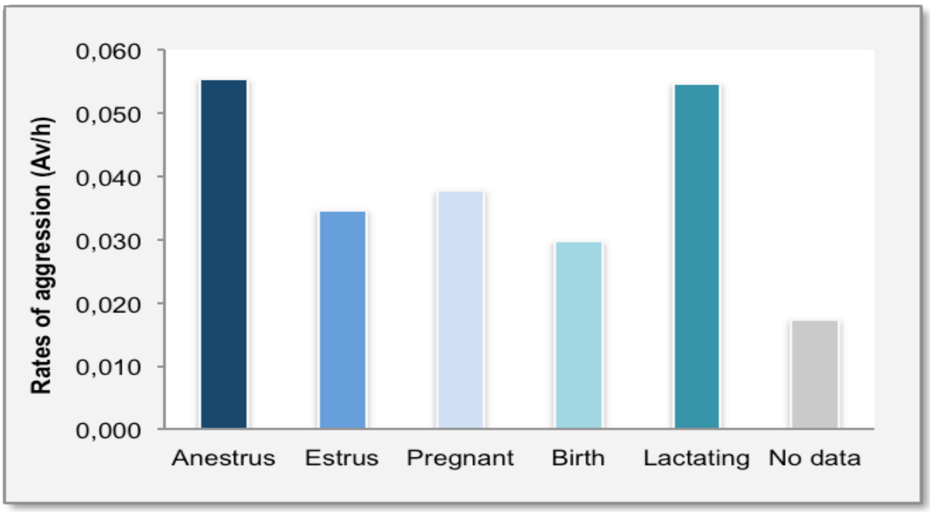


Figure 9. Aggressions receiver according to the reproductive state per female.

In total we found the distribution of aggression that we can see in the figure 10, although we must emphasize that if we consider the period of time of each state there is several differences about the length (i.e while lactation period or anestrus period are the medium 12 and 19 months respectively, the period of time that we consider as birth (new infant) and estrus, are only 3 and 4 moths). When we consider this factor of time and we divided per month, we found some differences. However, we didn't find any differences within each reproductive state, anyway (Friedman, X^2=3,71, p>0,05).



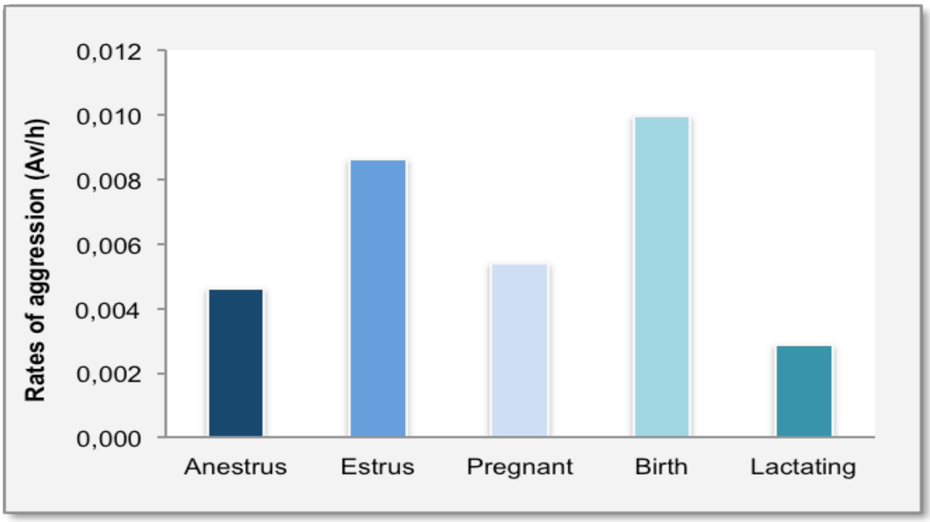


Figure 10. Rates of aggression of females according to the reproductive state (top). Rates of aggression of females per month according to the reproductive state (down)

4. Dominance relationships

This group of spider monkeys didn't show too many interactions between them, especially agonistic behavior. Dominance relationship between males was not evident, at least not by aggressions, because there were just 8 aggressions between them (aggressions with individual identified) (N=6) within 8596 hours of observation. It seems there is not a clear dominance or linearity within the males relationships. However, when we compare the relationships between females (N=11) we found a tendency of dominance or linear hierarchy through the aggressions. The value of Landau´s *h* (in this case equal to Kendall´s linearity index K, because the matrix holds and odd number of subject) equals 0,35, which is almost significant (X^2=27,35, df=20,20, p=0,058), show a tendency of a linear ordering of dominance relationships. Two females (Vita and Evita) were clearly more attacked by other females than the rest and they only aggressed other females one time each (Fig. 11).

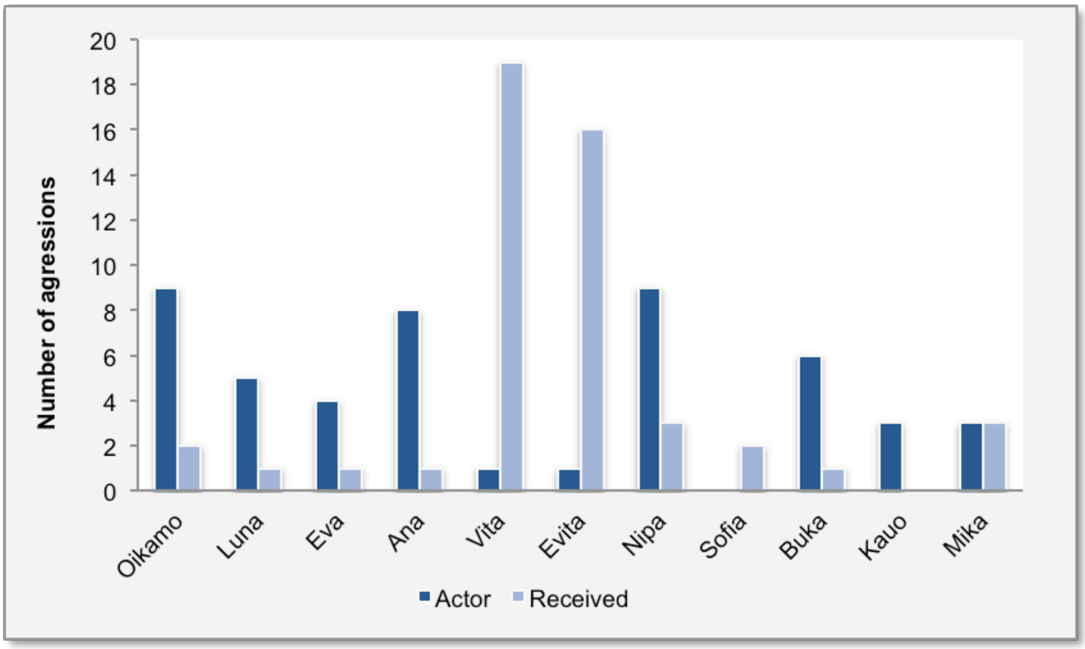


Figure 11. Female aggressions made and received by other females (Focal and *Ad libitum* data)

It is also interesting that this tendency to aggresse these two females is not an objective by males (Fig. 12), i.e males aggressed females in a more distributed way (Chi-squared, X^2=16,85, p>0,05); while female aggressions are focus on them (Two Samples Kolmogorov-Smirnov Test, Z= 1,92; p<0,01). There is not a correlation between female individuals aggressed by males than by other females (Pearson Correlation = 0,54; p>0,05).

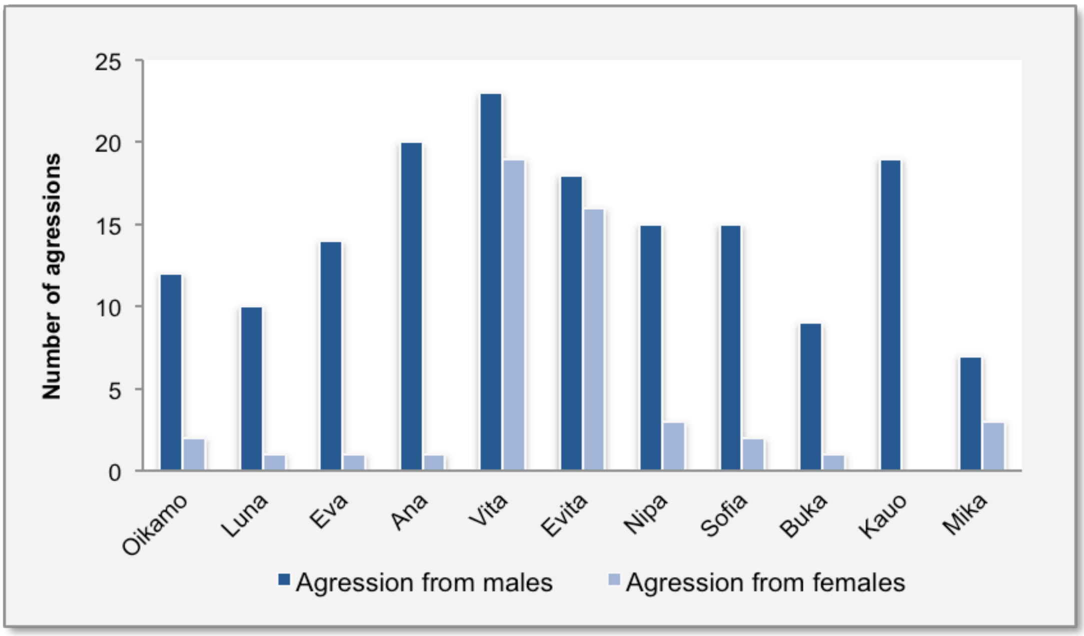


Figure 12. Distribution of total of aggressions received by females from males and from other females (Focal and *Ad libitum* data).

Finally, we analyzed the male-female matrix, and as we expected, we found male clear dominance towards females. The value of Landau´s *h* (in this case equal to Kendall´s linearity index K, because the matrix holds and odd number of subject) equals 0,68, which is significant (X^2=88,29, df=24,14, p<0,01), so we accept the alternative hypothesis of a linear ordering of dominance relationships. So, there were male/female dominant relationships with male being dominant over females.

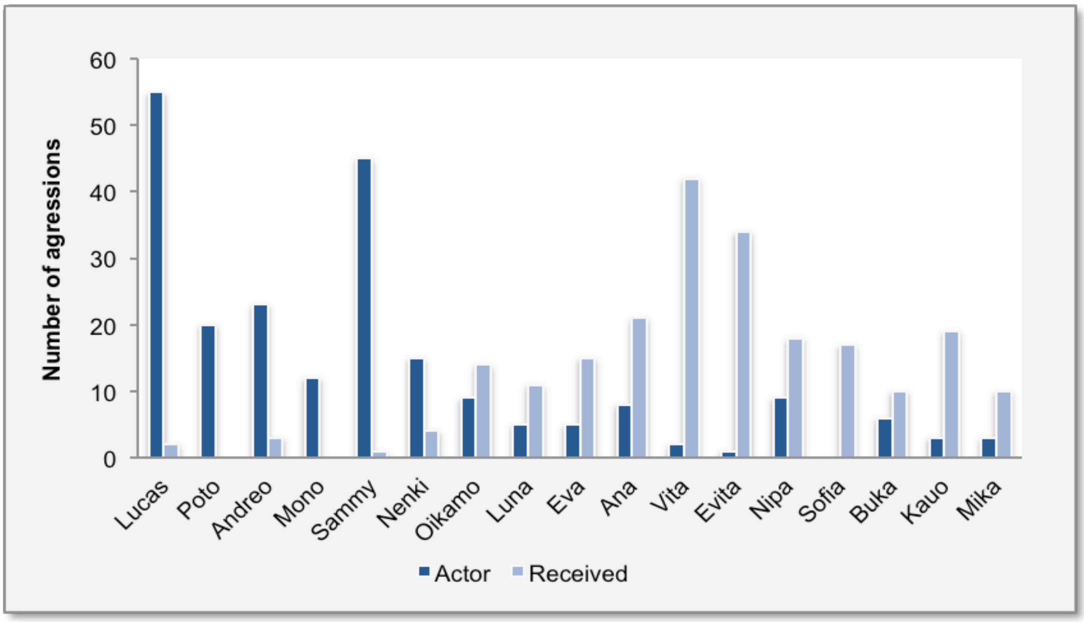


Figure 13. Distribution of total of aggressions made and received (Focal and *Ad libitum* data).

We can see in the Table 1 the relationships between each pair of dyads (through matrixes) according to he program Noldus MatMan 1.1 (Noldus Information Technology, 2012) to measure linear hierarchy.

Table 1. Analyses of linearity and hierarchy (Matman 1.1) between males, females and males-females through agonistic behavior within the group

		Females-to-Females	Males-to-Females
N	6	11	17
Matrix Total	8	49	221
Total number of relationships	15	55	136
Linearity index	0,66	0,49	0,73
Expected value of h or h´	0,43	0,25	0,17
P	0,28	0,06	0,00
Directional consistency index	1,00	0,88	0,95

DISCUSSION

Aggressions between Adults

Based on 8596 hours of focal animal data collected over a period of more than seven years of study, we can conclude that the aggression amongst spider monkeys is extremely low (442 agonistic behaviors, 0,051 rates of aggression per hour). The majority of aggression in this study was initiated by males and directed towards females (182 aggressions), being the rates of aggression between adults almost 10 times higher in males than females (males: 0,039 ag/h *vs* females: 0,006 ag/h). Within aggression towards non-adult individuals, aggressions were also very low and we didn't find significant differences between males and females, although those, contrary to the rest of the results, were higher in females (males: 0,005 ag/h *vs* females: 0,008 ag/h). In our study, females only aggressed males on one occasion.

In primates with a high-degree of fission-fusion dynamics and female dispersal males are in general more gregarious than females, and males are also more sociable with other males than with females (Fedigan & Baxter, 1984; Symington, 1990; Slater *et al.,* 2009). It is possible that the low number of aggression within the genus *Ateles* is due to the fact that males are the philopatric sex (Di Fiore *et al.,* 2009) and thus expected to be closely related to each other. Under this scenario, competition for resources (e.g., females) might be low or might be reduced through kin selection (Hamilton, 1964) an inclusive fitness, and thus this may explain their cooperative behaviors to defend their territories from rival groups of males (Aureli & Schaffner, 2008). This should be a good strategy to build alliances with relatives, making the variability of the reproduction success lower than other primate species (Strier *et al.,* 2011; Di Fiore & Link unpublished data). According to Fedigan and Baxter (1984), low rates of aggression between males, indicate an unusually low degree of male-male competition within polygamous primates. Likewise, female-female rates of aggression could be interpreted as a competition for feeding resources (Slater, *et al.,* 2009).

Among primate societies, it has been documented that males sometimes cooperate by forming coalitions to attack females (Watts, 1998). Although in spider monkeys, in general, males attacked individually, alliances with more than one male involved, used to be very frequent (Campbell, 2003; Slater *et al.,* 2008). In our study, males also usually cooperated to attack females, being equally frequent as individual attacks, and less frequent with more than two males. When males cooperated in this kind of coalitions, all of them participated with vocalizations, threat or displays, in general towards females, making them even urine, most of the cases. Although less common, these coalitions had been reported in other primate societies, such as capuchin monkeys (*Cebus sp*.) or chimpanzees (*Pan troglodytes*), to attack females within the group or even to defend their territories (Fedigan & Baxter, 1984; Watts, 1998, 2000; Leca *et al*., 2002).

Two males, Lucas and Sammy, were the two individuals who were involved in a greater number of antagonistic events. They were also the two individuals who attack females in dyads (coalition) more often, although we didn’t find significant differences. Moreover, these two males attacked together several times and Lucas is in fact, the only non- relative male within the group. Another interesting anecdote is that Sammy was the father of the most of the infants born between 2010 and 2011. However, in contrast with this information, Lucas was the only male who has not been father yet (Di Fiore and Link, unpublished data). In general, these results suggest males collaborate to control or monopolize females, forming coalitions to threat them.

Context of Aggression

It is also noteworthy that the context where aggression took place is often different between the sexes. Males aggressed more often within fusion context, when two subgroups join together, which may serve as a strategy of social control, controlling females´ reproduction and perhaps discouraging them from mating outside the group (Link *et al.,* 2009). Females seems to compete more often within feeding context, although the context are more distributed, and most of their aggression was directed towards their offspring. The context of aggression within the *Ateles* genus had been associated with feeding (van Roosmalen & Klein, 1988) and fusion context (Aureli & Schaffner, 2007) by other authors before. Aureli and Schaffner (2007) affirmed that their study showed the first evidences of conflicts after fusion. We found something similar in our study, being fusion context an important event for males, which involved a lot of number of aggressions, where they were actors, and we also found that for females, feeding context tend to be more frequent than fusion. Not only have spider monkeys been described as engaging in conflicts after a fusion, also chimpanzees have too (Baxter & Feedigan, 1984; Aureli & Schaffner, 2007). It is possible that aggressions after a fusion were a mechanism to confirm male dominance towards females (Fedigan & Baxter, 1984) or any kind of indirect sexual coercion (Link *et al.,* 2009) or even social control.

Aggressions within feeding context were more common in females (although not significantly higher than males, probably because the number of aggressions in general was lower), while fusion context was not very common in events where they were actors. It seems more important for females feeding context than fusion context but we cannot say there is a remarkable feeding competition because this kind of aggression is not high compare with the time they invest foraging (Di Fiore *et al.,* 2008). These results were also found in other studies with *Ateles* (Campbell, 2003), being aggressions between females more common within feeding context. Witig and Boesh (2003) described a similar pattern in chimpanzees, where females aggressed more frequently in feeding context. In this case, this tendency could be related to the dominance and hierarchy of chimpanzee societies, structure not as clear in spider monkeys. However, the reproductive success of females are determined by the access of feeding resources and the tendency of aggress some females more often than others, could be a representation of feeding competition, although it is not a clear pattern in spider monkeys.

Additionally, we registered six events of aggression during copulation where male aggressed the female, which could be part of sexual coercion or forced copulation, as it had been reported in other studies (Gibson *et al.,* 2008; see infanticide chapter).

Female Reproductive State

In contrast with other studies (Slater *et al.,* 2009), male aggression was not mainly directed towards females in estrous period. In this case these aggressions were distributed within all female reproductive state, and even aggression within estrous period was only in case of two females. There were some aggressions when females had a new infant, within the first three months of live, so these kinds of aggression seems to be not a sexual coercion male´s strategy. Campbell (2003) also documented higher taxes of aggressions during gestation period, or not estrous period in spider monkeys, highlighting that these attacks were not focused on the ovulation period. In this case, it seems males use aggression to monopolize females as a strategy of social control instead of sexual coercion, or at least not result in inmediate copulation. We added one state, when the infant have until 3 moths of life, and although we didn’t find significant differences with the rest of the states, these attacks were longer and very intense in several cases (personal observations, see infanticide case), compare with other event of aggressions observed in this group. In these cases, the female will invest around three years caring the infant (Eisenberg, 1973; Campbell & Gibson, 2008), so the reproductive objective not seems to be the reason. Moreover, when we divided the rates of aggressions between the number of months that each period was considered, to dilute the effect of finding more aggression during longer periods of time just because the duration (i.e longer periods, more opportunities of aggression), the differences were still not significant, but the rates of aggressions within the first three months of the infants life (birth state) increased compared with the other states (see fig. 9). However, females usually present their offspring to males by approaching and allowing them to inspect the infants (Gibson *et al.,* 2008), and this situation could encourage them sometimes towards any kind of aggressions.

However, in the majority of events of aggressions females urine when males threat them, so it could give them information about their reproductive state (Fedigan & Baxter, 1984; Symington, 1987a; Campbell, 2003; Slater *et al.,* 2008). So, although we didn't find significant differences between states, sexuality is probably an important component, although not the unique reason.

Dominance relationships

Conclusively, it seems that males are dominant over females in terms of the direction of the aggression, but they don't have a clear hierarchy between males, or at least not as clear as those that characterize chimpanzee societies, since they don't present aggressions between them. Males, according to other studies (Gibson, 2010), don't seem to compete directly, or they compete in an indirect and subtle way. However, a very interesting result, which had not been documented in other studies, is that they present aggressions focus only two females, who didn't aggress the rest of females (only one time each), so females seem to compete between them. These two females were the last to arrive and these aggressions could be interpreted as some kind of rejection to new females. However, several aggressions were documented when these females had been within the group for a long time. These females were not individuals, who had been aggressed by males at a higher level than other females (no correlation between males and females aggressions towards other females), which could be mean that they are vulnerable for any kind of aggression. This result, although the data of aggression is small, could suggest that the relationships between females are at least not as equality as it had been thought (Gibson, 2010), or at least no so clear, and it could be part of an intragroup competition for resources (Slater *et al.,* 2009). Females are in general more solitary than males (Campbell, 2003), so this could be the reason why this subtle dominance was not perceived clearly, because they don't interact very often.

Although, the exact relationships between dominance and reproductive success of male´s spider monkeys is still unknown, it had been suggested that males compete for access to females, being males with higher rank of dominance able to be more efficient monopolizing a larger number of ovulating females than subordinate males (Symington, 1987a). However, little is known about hierarchy and dominance in spider monkeys because their low rates of aggressions and submissive behavior between them. In our case, we could observe a similar pattern of dominance by males towards females that those which had been proposed by Fedigan and Baxter (1984) and Symington, (1987a), where males aggressed females in higher rates, compare with the rest of dyads.

From socio-metric matrixes of agonistic behavior, derived from a data set of approximately seven years, we observed male dominance over females. Between males, the aggressions were almost non-existent, supporting other studies where no clear dominance were reported between males, being rare or absent intracommunity male-male aggression (Fedigan & Baxer, 1984; van Roosmalen & Klein, 1988). It had also been documented that female primates that feed mainly ripe fruits, which is the case of spider monkeys (Di Fiore & Campell, 2007), usually experience strong intragroup contest competition for food, especially when the resources are distributed in small patches (socio-ecology theory, van Schaik, 1989; Sterck *et al.,* 1997; Koenig, 2002). These females are expected to display unidirectional agonistic behavior and form dominance relationships, being philopatry favored until these conditions (Aureli & Schaffner, 2008). However, in spider monkeys, this competition is reduced with high levels of fission-fusion dynamics, forming small subgroups or foraging alone with their offspring (Fedigan & Baxter; 1984; Symington, 1988; Aureli & Schaffner, 2008, this study). Scramble competition is experienced when food patches cannot be monopolized and individuals lose access to resources because other had already used it (Janson & Van Schaik, 1988). In this kind of competition females are expected to spend less time with other community members than males (Wrangham, 2000), as in this study group. So, it is possible that the relationships that we found between females in this study, where they aggressed two females more often than the rest, were due to this kind of competition, not being very intense, towards the two females who last arrived.

In contrast with other primate studies, as capuchin or chimpanzee societies, our results didn´t show a clear dominance between males and females (Watts, 2000; Leca *et al.,* 2002; Wittig & Boesch, 2003; Bergstrom & Fedigan, 2010). According to several authors, we found low rates of aggression but it was significantly higher by males towards females (Fedigan & Baxter, 1984; Symington, 1987a; Campbell, 2003; Slater *et al.,* 2008; Slater *et al.,* 2009, Link *et al.* 2009), which could be interpreted as dominance of one sex to the other.

CONCLUSIONS

In conclusion, we found that agonistic events within this group of spider monkeys were extremely low. Most of the aggressions were made by males towards females being these events almost 10 times higher than aggressions made by females. We didn't find almost any aggression between males nor by females towards males, and females aggressed two females significantly more often than the rest. Sub-adults and juveniles were aggressed by adults with no differences between sexes but females usually aggressed their own offspring.

Males usually formed coalitions with other males, especially in dyad, to attack or threat females. These alliances are common within species where males are the philopatric sex, because they are relatives.

Males also seems aggressed more often than females within fusion context, when two groups joined together, which could be a strategy of social control, to monopolize females and avoid that they leave the group within this kind of fission-fusion dynamics. In contrast, females tend to aggress within other context, especially within feeding context, which could be the result for a subtle scramble competition for resources.

In contrast with other studies, (excluding Campbell study (2003)), we found no differences in the rates of aggression by males towards females within their different reproductive states. Even within estrous period, only two females were aggressed but not the rest of them. When females have a new infant, we found several aggressions by males within the first three months of the infant´s life, and although these aggressions was not significantly different with other states, when we divided the rates of aggressions between the number of months that we consider each state, new infant (birth state) was higher than the other states relatively. It seems males not only aggressed as a strategy of sexual coercion, or at least not as a direct strategy and could be a form of social control.

Finally, we analyze the patterns of dominancy and linearity hierarchy, through matrixes of dyads male-male, female-female and male-female. We found that males do not have any kind of dominancy or direct hierarchy. However, females showed a tendency of linearity focus their aggression in the last two females who arrived to the group. These two females were within the group several years so it seems, females probably do not have a clear equality relationships that have been documented in other studies. This linearity could be interpreted as a competition for resources and a rejection of resident females, being higher than we previously thought. However, the small number of aggressions between them made it not possible to evaluate the differences in the context between only adult females. Males also showed a clear dominancy towards females being these individuals the receiver of the majority of those aggressions. These results support the conclusion of other studies where females are the dispersal sex.

CAPÍTULO 3:

Male-Directed Infanticide in Spider Monkeys (Ateles spp.)

Male-directed infanticide in spider monkeys (*Ateles spp.*)*

*Co-authors in this study:

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ABSTRACT

Infanticide is considered one of the most conspicuous expressions of sexual conflict amongst mammals. It has now been observed in at least 35 primate species and seems more widespread amongst primates than previously thought. Here we describe two suspected cases of intra-group infanticide in wild spider monkeys that augment five prior cases of observed or suspected infanticide in this genus that have been reported. Contrary to the typical pattern of infanticide seen in most primate societies, where infants are killed by conspecifics independent of their sex, all seven cases of observed or suspected infanticide in spider monkeys have been directed towards male infants within their first weeks of life. Moreover, although data are still scant, infanticides seem also to be perpetrated uniquely by adult males against infants from their own social groups and are not associated with male takeovers or a sudden rise in male dominance rank. Although the slow reproductive cycles and large lactation/pregnancy ratio of spider monkeys might be expected to generally favour the presence of infanticide because of the potential to shorten females' interbirth intervals, infanticide is nonetheless uncommon among spider monkeys and patterns of male-directed infanticide are not yet understood. We suggest that given the potentially close genetic relationships among adult males within spider monkeys groups and the need for males to cooperate with one another in territorial interactions with other groups of related males, infanticide may only be expected to occur in rare cases where the level of intragroup competition among males outweighs that of competition between social groups. Finally, we also suggest that infanticide in spider monkeys may be more prevalent than previously thought, given that it may be difficult for observers to witness cases of infanticide or suspected infanticide that occur soon after birth in taxa that are characterized by high levels of fission-fusion dynamics. Early, undetected, male-biased infanticide could have strong influences on the composition of spider monkey social groups and contribute to the female-biased adult sex ratios that have commonly been reported for this genus.

Keywords:
Male sexual strategies_ infanticide_ aggression_ spider monkeys

INTRODUCTION

Infanticide is considered one of the most conspicuous expressions of sexual conflict between males and females in mammalian societies (Hrdy, 1979; van Schaik & Janson, 2000). Sexual conflict arises when the reproductive success of one sex is negatively affected by the reproductive strategies of the other sex (Trivers, 1972; Arnqvist & Rowe, 2005; Palombit, 2012). In general, sexual conflict occurs because among primates (as among most mammals) the critical resources that limit reproductive success differ for males versus females (Trivers, 1972). For females, fitness is limited primarily by access to the foods needed to support pregnancy and lactation, while for males, who typically invest far less than females in each individual offspring, fitness is limited primarily by their ability to copulate with fertile females (Trivers, 1972).

Although infanticide and its implications for primate socioecology are still debated (van Schaik & Janson, 2000), it is generally accepted that male infanticide can impose an important constraint on female reproduction. In wild primates, females not only invest a disproportionate amount of energy in parental care but also are either pregnant or lactating during most of their reproductive lives and are thus unavailable for fertilization by males. On the other hand, males are relatively freed from such reproductive constraints and, all else being equal, are expected to benefit from allocating their time and energy toward acquiring additional mating opportunities for siring additional offspring. Under such conditions, a strategy that prematurely returns anestrous females to reproductive condition would be beneficial for males, especially when male-male competition is intense (Palombit, 2012). Thus, infanticide in primates and in mammals generally, is more common in those taxa with long periods of juvenile dependency and for whom substantial post-natal maternal investment is commonplace (van Schaik & Janson, 2000).

Infanticide perpetrated by males is thus often considered one of the major factors shaping both the nature of intersexual social relations for primates (e.g., the formation of strong social bonds or “friendships” between particular males and females (Palombit 2000; 2009), as well as the evolution of primate societies (Sterck *et al.,* 1997; van Schaik & Kappeler, 1997). Hrdy (1979) noted that for infanticide to be an effective male reproductive strategy, certain conditions are expected to be met. First, most infants killed are expected to be unrelated to the infanticidal male or males. Second, the killing of an infant should result in a mother’s more rapid return to reproductive activity. And third, infanticidal males should enjoy an increase chance of mating with these females following infanticide. An early meta-analysis of data available from field studies of primates indeed suggests that these three conditions are commonly met (van Schaik, 2000), providing support for the sexual selection hypothesis, i.e., that males kill unrelated infants in order to gain reproductive opportunities with anestrous females.

A more recent review of male-perpetrated infanticide in primates has compiled reports of infanticide occurring in least 56 populations of 35 different primate species, including all major primate radiations (Palombit, 2012), suggesting that the behavior is even more widespread than previously thought. A number of patterns emerge from this meta-analysis. First, infanticide is generally more common in harem-type (one-male and multi-female) societies, where the intensity of mating competition and reproductive skew is high. Nonetheless, it has been now witnessed in almost all types of primate societies, including multimale-multi-female groups, groups with cooperative breeding, and monogamous societies, amongst others (Palombit, 2012). Second, infanticide has been witnessed to be initiated both from resident as well as external males, and in some societies such as those of chimpanzees, infanticides have been reported to be directed against infants from neighboring groups (Arcadi & Wrangham, 1999). Finally, there is little evidence of sex-biased infanticide in primates (but see Hiraiwa-Hasegawa, 1987); rather, infanticide seems to be directed to infants regardless of their sex, supporting the notion that the main purpose of infanticide is to bring females back into reproductive activity.

Infanticide in Spider Monkeys

Spider monkeys (genus *Ateles*) live in multimale-multifemale social groups characterized by extremely flexible association patterns (Symington, 1990; Aureli & Schaffner, 2008; Ramos-Fernández *et al.,* 2011). Dispersal tends to be strongly female-biased (Shimooka *et al.,* 2008; Di Fiore *et al.,* 2009; Di Fiore *et al.,* 2011) while males remain philopatric, reaching sexual maturity and reproducing in their natal groups. As a result, adult males within a group tend to be related and to form strong bonds, whereas females are unrelated and are often found foraging alone. This sociality is thought to be an adaptation for mitigating the costs of direct competition for food when high-quality resources are scarce and occur in small patches and for minimizing the risks associated with situations of predation pressure when this is elevated (Aureli & Schaffner, 2008; Asencio *et al.,* 2008; Link & Fiore, 2013; Hartwell *et al.,* 2014).

Among spider monkeys, intragroup aggression takes place at relatively low rates and generally takes the form of low intensity aggression directed from males to females (Campbell, 2003; Slater *et al.,* 2008; Link *et al.,* 2009; Abondano & Link, 2012). Only two cases of lethal intragroup aggression, stemming from two independent studies of *Ateles geoffroyi*, have been reported, and, in both cases, coalitions of adult males directed lethal aggression towards a subadult male (Campbell, 2006; Valero *et al.,* 2006). Even though the adult males within a spider monkey group are [1] presumably related to one another, [2] collectively defend reproductive access to a group's females against extragroup males, and [3] are successful at collectively restricting paternity to males within their groups, nonetheless five confirmed or suspected cases of intragroup infanticide have been witnessed in studies of wild spider monkeys (Gibson *et al.,* 2008; Shimooka *et al.,* 2008; Vick, 2008). All five of these events have been directed towards very young male infants under the age of three months.

Although little evidence of sex-biased aggression toward infants has been reported among primates, ever since the earliest studies on wild spider monkeys, researchers have reported a consistent pattern of rare but relatively higher rate of aggression towards infant males than towards infant females. For example, Fedigan and Baxter (1984) observed that immature males (juveniles and infants) received aggression at a much higher rates than females, and Chapman *et al.* (1989) reported six cases of open wounds being seen on infant and juvenile males in *Ateles geoffroyi* in Santa Rosa, Costa Rica. Symington (1987b) also observed more injuries on male juveniles than on females juveniles, a phenomenon also reported in earlier studies (Klein, 1974; Carpenter, 1935), and she noted that the rate of disappearance of male offspring was five times higher than the rate of disappearance of female offspring. In fact, Chapman *et al.* (1989) suggested that aggression biased towards males could also have an impact on sex ratios, which tend to be female-biased in early age and become even more evident in adults.

To date, five cases of observed or suspected infanticide have been witnessed in long term studies of spider monkeys. In a long term study on *Ateles belzebuth* in Tinigua Park, in Colombia, observers reported the case of a young male who was lethally injured, with several large deep lacerations all over its body. Based on the nature of the wounds, the researchers concluded that the injuries were the result of conspecific attack; nonetheless the perpetrator of this infanticide was not recognized (Shimooka *et al.,* 2008). Another case of infanticide was witnessed during a long term study on *Ateles belzebuth chamek* at Manu National Park, in Peru, where an adult male directed an attack towards an adult female and her male infant; after intense fighting the infant was severely injured and died soon thereafter (Gibson *et al.,* 2008). Another directly-observed case of male-directed infanticide was perpetrated by an adult male in a population of *Ateles geoffroyi* at Punta Laguna, Mexico, and two additional cases of suspected infanticides have also been reported for this population, (Gibson *et al.,* 2008). In these cases, researchers observed severely injured male infants who subsequently died within a few days.

Here, we report two additional cases of suspected or attempted infanticide in spider monkeys from two different long term studies on *Ateles belzebuth belzebuth* and *Ateles hybridus*, each one were directed towards male infants. After describing the events, we discuss the potential factors that may help explain male-directed infanticide in wild spider monkeys and its proposed implications for spider monkey´s socioecology.

METHODS

Data for this study were extracted from ongoing longitudinal studies of two different species of wild spider monkeys: *Ateles belzebuth belzebuth* at the Tiputini Biodiversity Station (TBS) in Ecuador and *Ateles hybridus* at site of San Juan de Carare in Colombia. The Tiputini Biodiverstity Station site (0°38´22´´S, 76°09´00´´W) is located in a pristine western Amazonian rainforest within the Yasuní Biosphere Reserve and comprises ~650 hectares of terra-firme and seasonally flooded forests that is contiguous with a much larger expanse of minimally-disturbed primary forest. At the TBS site, we have studied a well-habituated group of white-bellied spider monkeys since 2005 and have conducted over 8000 hours of focal animal sampling on individually-recognized animals. The San Juan de Carare site (6°42´53´´N, 74°08´33´´W) is located in the Magdalena River Basin in central Colombia and consists of several fragments of primary and regenerating forest embedded within a matrix of pastures for cattle ranching and natural flooded savannahs and marshes. At the SJ site, we have studied two social groups of brown spider monkeys since 2008 and have collected over 6000 hours of observational data through focal animal sampling of known individuals.

In both sites, the research groups are fully habituated to the presence of researchers, and individuals can be recognized based on facial or anogenital marks as well as distinctive morphological features (e.g., broken fingers, scars). At the TBS site, the body of the infant male that died from suspected infanticide was recovered, while the young injured male at SJ was recovered from the ground and returned to its mother by the research team a couple of hours after the attack (see below). Genetic analyses (PCR-based microsatellite genotyping) were performed following Di Fiore *et al.* (2009) Primate Molecular Ecology and Evolution Laboratory at the University of Texas at Austin for the infant recovered at the TBS site, and parentage analysis was performed to determine the sire of the deceased infant as well as the sire of the subsequent infant born to the same female.

RESULTS

Case 1: Tiputini Biodiversity Station, Ecuador. Suspected Infanticide

On August 9 of 2010, a day after having been observed without an offspring, an adult female ("Kauo") gave birth to a male offspring and was observed in the adjacent area of a mineral lick that the study group visits frequently (Link *et al.,* 2011). The next day S. Alvarez observed the female with an infant, without hair in the salt lick area once more. The female was resting in close proximity to two of the group males for a couple hours prior to attempting to go to the ground and eat soil. About an hour later one of the males directed intense aggression towards the female. Although there were several males around, only one of the males attacked her repeatedly, attempting to throw her to the ground, and the other males vocalized and made began shaking branches all around. Throughout the encounter, the female emitted high-pitched “squeal” vocalizations, while holding onto the trunk of an understory tree close to the ground. She attempted to escape from the males, but they persistently followed her. The aggressive interaction lasted for roughly one hour, and the male made physical contact with the female by slapping her several times. The observer did not witness direct aggression towards the infant during this encounter, and the infant remained clinging to its mother, but it is possible that it may have been injured during the attacks. A week later, on the 17PthP of August, the same male infant was found by S. Alvarez on the forest floor a couple hundred meters away from a subgroup of spider monkeys that contained several individuals, including the male who had attacked the female a week earlier. The infant was found on the forest ground in between some branches. He was crying and had several open wounds. On his right arm, he had a long and deep cut approximately 62 mm in length and his upper arm bone was broken. The infant´s tail also had several lacerations on it, including an open cut of ~95 mm in length, and he had two deep cuts (6 x 17 mm and 44 x 11 mm) on his back (Figure 1). The deep injuries might have reached and affected its internal organs. Twelve hours later the infant died. The next day the female was observed again going to the salt lick with some other spider monkeys.

Approximately nine months later, this female gave birth to a new infant female, so the conception must have occurred one to two months after the suspected lethal aggression took place, given that the gestation period for spider monkeys is approximately seven months long. Unexpectedly, the male who had directed most of the observed aggression to the female (although not necessarily the one who killed it) was identified as the father of the offspring. Paternity analysis also revealed that the next offspring born to that female was sired by the same male ("Sammy").

Case 2: San Juan de Carare, Colombia. Attempted Infanticide

At ~09:30 on October 3, 2012, while searching for one of our study groups of *Ateles hybridus*, J. Paez heard several loud aggressive vocalizations (e.g., grunts and squeals) from spider monkeys, followed by repeated barks (alarm calls) emitted by an adult female spider monkey (Dl). When she reached the group all members of the subgroup were moving extremely fast in a single-file straight line. All known members of the group were present, except (Dy), an small infant male, who was usually carried ventro-laterally by his mother (Du). The adult female (Du) had several blood stains on her back. One of the subadult males (Vt) also had an injury in his lower left leg, and abundant blood was coming out on his forehead. (Vt) moved away from the females who attempted to get closer to him as he stopped to rest and repeatedly licked his wounds. By midday, an adult male, Rk also approached the subadult male, Vt, and licked his wounds. During the following hours the adult female (Dl) seemed to frequently check for the infant by looking at her own back. Several other individuals directed affiliative behaviors towards the adult female: at 11:41 another adult female came into proximity to (Dl) and embraced her; at 11:43 her oldest son (Db) also approached and groomed his mother for approximately 15 minutes. At midday, J. Paez returned to the place where the aggression took place in the early morning (ca. 300 m away) and found the small infant male on the forest floor, crying. He was unable to move as he had a severe wound in his left leg. J. Paez recovered the infant and took it back to a tree next to where his mother was located and placed it on the forest floor. The infant squealed, calling immediate attention from his mother, who came down to retrieve him. The females and the rest of the group began moving shorlty thereafter, and the small infant repeatedly squealed, probably due to his injuries. Although the infant male survived, its injuries seemed severe enough that we suspect it would have died if left on his own on the forest floor.

Sex-biased infant survival

During approximately nine and five years of continuous study at TBS and SJ, we have recorded 26 and 10 births, respectively. At TBS, only 2 infants (1 male and an unsexed offspring) have been observed just after birth and have gone missing in the first weeks of life. At SJ, four infants (all males) have disappeared in the first two months, and another one was severely injured and only survived due to the intervention of researchers that found him abandoned in the forest floor and took him back to his mother (see description in Case 2). Thus, data on infant survival also support the hypothesis of male-directed infanticide in spider monkeys (Table 1).

DISCUSSION

Both cases of suspected infanticide described in this study support the hypothesis that infanticide in spider monkeys is mainly (if not uniquely) targeted towards infant males. These two cases add to five previous reports of observed or suspected infanticide in spider monkeys. In all but one of these seven cases, aggression was directed towards a young male animal within its first weeks of life (Table 2).

Attempting to explain the factors underlying male-directed potential infanticide in spider monkeys poses some challenges. First, although long term studies on spider monkeys now account for several tens of thousands of contact hours with habituated animals, only seven infanticide attempts or events have been reported (Table 2). Nonetheless, the fact that seven out of seven infanticides were directed towards young males suggests that in spider monkeys infanticide might be driven by different underlying principles to those proposed in the general sexual selection hypothesis for infanticide (Hrdy, 1979). Second, although those infanticide events that have been directly observed by researchers were initiated by adult males, for several other cases observers have been unable to recognize the identity or age-sex category of the aggressor. Thus, although data is still scant regarding infanticide in spider monkeys´ societies, and given the extremely low rates at which infanticide is observed in this taxon, it seems it may play a very relevant role in spider monkeys sociality. Thus, it still worthwhile to attempt to infer about how and why infanticide takes place in these societies, and more specifically, why infanticide might commonly be directed towards males.

In the first description of infanticide in spider monkeys, Gibson *et al.* (2008) suggested several reasons for expecting the occurrence of this behaviour in spider monkeys. First, spider monkeys females only begin reproducing after age 7 or 8, after a lengthy juvenile period, and they have long inter-birth intervals of ca. 3 years, that can be significantly reduced (to only 9 to 10 months) after the loss of a young infant (Table 1). Second, Campbell and Gibson (2008) propose that the secretive mating tactics of spider monkeys (see Gibson, 2010) may have the consequence of promoting aggression from those males that were not a female´s consortship partners during her receptive period. Although this may well be true, the secretive mating in isolation from other males might also act in favour of paternity confusion (see below). Third, only a few female spider monkeys in each social group are receptive each year (e.g. from 1 to 5 out of 11 females in the study groups at TBS, n = 8 years), and for most of the time, only one or two females are potentially cycling at the same time. Thus competition for females within the group could potentially be high as the operational sex ratio is strongly tilted towards males, and sexual coercion might be expected to take place, especially if driven by those males for whom mating opportunities are limited (e.g., subadults) (Gibson *et al.,* 2008).

On the other hand, Gibson *et al.* (2008) also suggest female spider monkeys use a variety of tactics to forestall sexual coercion. First, females mate with several males and sometimes engage in post-conception mating (Hrdy, 1979). Second, females ‘‘present’’ neonates to mature males (perhaps potential sires) by approaching them and pushing the infants toward the males' or by sitting next to the males and allowing them to inspect the infants (Gibson *et al.,* 2008). In summary, the relatively slow reproductive biology of spider monkeys coupled with their fluid grouping patterns and secretive mating tactics might favour the occurrence of infanticide as well as the evolution of female counter strategies.

Other aspects related to spider monkey social behavior and grouping patterns might seem to argue against any potential benefits males might receive through male-directed infanticide. First, the fact that males within the social group are presumably closely related to each other (Di Fiore *et al.,* 2009), coupled with preliminary evidence of no extra-group paternity in spider monkeys, suggest that intra-group infanticide would not be an adaptive strategy within spider monkeys societies. If males kill their own offspring, or that of their kin, they would be acting against their own reproductive success or their inclusive fitness (Hamilton, 1964). Second, in populations where intergroup competition is high between social groups of spider monkeys, and where intergroup encounters and "warfare" (Aureli *et al.,* 2006) is largely resolved against the group of males with lower numbers (Link, 2011; Link & Di Fiore, unpub. data), it might be expected that each male born into the group should become a partner in the near future regarding inter-group competition. Thus, we suggest that male-directed infanticide might be best explained when [1] the possibility that a male might have low chances of being the offspring´s sire (although anecdotally, the male who aggressed the female with offspring at TBS was actually the sire of her offspring) or when [2] there exists a higher level of competition between males within a social group compared to competition between social groups (large operational sex ratio). Under this scenario, there may be some incentive to eliminate future rivals (competitors for mates within social groups), especially if their support in intergroup encounters is not particularly valuable. Finally, we cannot rule out that infanticide in spider monkeys reflects a maladaptive and pathological behavior, as has been described for one male in the spider monkey population at SJ who repeatedly killed howler monkey infants (Rimbach *et al.,* 2012). In a similar way to that described by Valero *et al.* (2006)

regarding intra-group lethal attacks towards subadult males in spider monkeys, male directed infanticide in spider monkeys might be associated with the relation between within-group and between-group male to male competition.

Regardless of its adaptive significance, male directed infanticide could have a strong effect on the population structure of spider monkeys social groups. Most field studies on wild spider monkeys studies have found a clear pattern of unequal sex ratios, specifically with adult females outnumbering adult males (Table 3), and these biased sex ratios have sometimes been discussed in terms of spider monkey females practicing adaptive sex-ratio manipulation (e.g., with females biasing the sex ratio of their offspring towards females, the dispersing sex, in response to local resource competition). Even in the case of a natural sex-biased ratio at birth, the occurrence of male-directed infanticide in *Ateles* should strengthen the effect of skewing the female to male ratios in adult populations.

Finally, the fact that most infanticides in spider monkeys have taken place when infant males are just a few weeks old suggests that it is probably difficult for researchers to accurately estimate the true frequency with which infanticide occurs in spider monkey societies, as well as the true sex ratio at birth in natural populations. That is, given that spider monkeys live in very fluid societies, and given that there are no evident signs for detecting pregnancy in females, it seems unlikely that researchers would be able to accurately document how often infant males are killed in the very first weeks of life. In conclusion, infanticide in spider monkeys is far from being understood, and although rare, now seems more common among spider monkeys and widespread across their current distribution. The unique patterns of male-directed infanticide require further study in order to better understand the underlying principles of this behaviour, which seems to not be completely explained by the sexual hypothesis for infanticide (Hrdy, 1979) and might reflect some unique aspects of the complex sociality of wild spider monkeys.

APPENDIX

Figure 1. Description of the infant´s wounds.

Table 1. Number of infants born since the start of the long-term projects on wild spider monkeys at Tiputini Biodiversity Station (TBS) and San Juan (SJ).

		FEMALES	MALES	UNKNOWN
SJ	Born	4	6	0
	Died < 3 months	0	5*	0
TBS	Born	19	6	1
	Died < 3 months	0	1	1

* One infant was severely wounded and recovered by field assistants, but would most probably have died.

Table 2. Infanticide cases reported in spider monkeys.

Site	Species	Date	Sex	Estimated age	Infanticide	Next birth	Author
Punta Laguna, Mexico	A. geoffroyi	Jun 5, 2000	Male	2 weeks	Observed	9 months	Gibson *et al.,* 2008
Punta Laguna, Mexico	A. geoffroyi	Jan 9, 2001	Male	4 weeks	Suspected	9 months	Gibson *et al.,* 2008
Punta Laguna, Mexico	A. geoffroyi	Mar 22 2001	Male	3 months	Suspected	8 months	Gibson *et al.,* 2008
Cocha Cashu, Peru	A. b. chamek	May 10, 2006	Male	4 weeks	Observed	N.D.	Gibson *et al.,* 2008
Tinigua Park, Colombia	A. b. belzebuth	?	Male	2 weeks	Observed	N.D.	Shimooka *et al*., 2008
TBS, Ecuador	A. b. belzebuth	Aug 10, 2010	Male	2 days	Suspected	9 months	This study
San Juan, Colombia	A. hybridus	Oct 3, 2012	Male	?	Attempted	?	This study

Table 3. Group size and ♂:♀ ratio in spider monkeys. Modified from Shimooka *et al.* 2008.

Study Site	Species	Size	# Adult Males	# Adult Females	References
Ilha de Maraca, Brazil	A. b. belzebuth	19 - 23	6	8	Nunes & Chapman (1997)
La Macarena, Colombia	A. b. belzebuth	27	5	12	Klein (1972)
La Macarena, Colombia	A. b. belzebuth	20	3	11	Klein (1972)
Rio Tawadu, Venezuela	A. b. belzebuth	33	3	15	Catellanos & Chanin (1996)
Tinigua, Colombia	A. b. belzebuth	30	5	10	Shimooka (2003)
Yasuni, Ecuador	A. b. belzebuth	28	5	14	Dew (2001)
Yasuni, Ecuador	A. b. belzebuth	31	5	11	Di Fiore, Link and Spehar (unpublish data)
TBS, Ecuador	**A. b. belzebuth**	**35**	**4-6**	**10-12**	**This study**
Lago Caiman, Bolivia	A. b. chamek	55	15	15	Wallace (unpublish data)
Cocha Cashu, Paru	A. b. chamek	37	5	15	Symington (1987a)
Cocha Cashu, Paru	A. b. chamek	40	5	16	Symington (1987a)
BCI, Panama	A. geoffroyi	21 - 24	5	10	Campbell 2000
Punta Laguna, Mexico	A. geoffroyi	20	4	7	Ramos Fernandez *et al*. (2003)
Punta Laguna, Mexico	A. geoffroyi	40	10	13	Ramos Fernandez *et al.* (2003)
Santa Rosa, Costa Rica	A. geoffroyi	42	4	18	Chapman *et al.* (1989)
San Juan, Colombia	**A. hybridus**	**15-17**	**1-3**	**6**	**This study**
San Juan, Colombia	**A. hybridus**	**13-14**	**1-2**	**5**	**This study**
Quinchas, Colombia	A. hybridus	26	3	11	Link *et al* (2012)
Voltzburg, Surinam	A. paniscus	18	3	8	van Roosmalen (1985)

CAPÍTULO 4:

Influence of subgroup size and inter-specific associations on successful access to mineral licks by spider monkeys

Influence of subgroup size and inter-specific associations on successful access to mineral licks by spider monkeys*

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ABSTRACT

Mineral licks are important areas visited by several Neotropical birds and mammals to consume soil for mineral supplementation or as a detoxification agent. Spider monkeys and howler monkeys are the only platyrrhines that regularly visit mineral licks, and both species visit licks together in higher frequencies than expected by chance alone. Although spider monkeys visit mineral lick areas frequently, a large proportion of visits are "unsuccessful" in the sense that no individual in the subgroup actually descends to the ground to feed on soil at the lick. Here, we evaluate the influence of [1] certain individuals in the mineral lick, [2] subgroup size, [3] the presence of howler monkeys and [4] weather conditions at the mineral lick on spider monkeys' decisions to descend and feed. Mineral lick visits were recorded from July 2010 through March 2013 through direct follows and camera trapping, and we considered a visit 'successful' when at least one individual consumed soil at the lick (although on most 'successful' visits, the majority of subgroup members come down to feed). We recorded a total of 182 mineral lick visits, of which 55 were successful. Females with core range areas closer to the lick visited the lick more often than those whose core areas were located farther away. However, the relatively success rate when females that ranged farther apart was present, was significantly higher (~50%) than that of other females (~34%) or males (~36%) presence, perhaps due to the greater effort spent in going to the lick. We also found positive and significant relationships between both subgroup size and the presence of howler monkeys at the lick and the success rate of lick visitation by spider monkeys. This study further supports the hypothesis that mineral licks are perceived as risky areas by spider monkeys (Link & Di Fiore, 2013) and that both mineral lick visitation and the success of visits largely depend on reducing predation risk by being in large numbers or by being associated with howler monkeys.

Key Words: Mineral lick_ subgroup size _ howler monkeys _spider monkeys_ successful visits

INTRODUCTION

Mineral licks are specific areas where several species usually visit to engage in geophagy. Geophagy – the consumption of soil or clay – has been documented in several species of animals including deers, peccaries, bats, monkeys, porcupine and different bird species (Blake *et al.,* 2010). For some Neotropical primates, mineral licks are the only place where they typically arboreal animals descend to the ground. These sites are considered 'risky areas' because primates who come down to the ground are more vulnerable to being preyed upon by terrestrial predators such as puma or jaguar (Izawa, 1993; Matsuda & Izawa, 2008; Link *et al.,* 2011; Link & Fiore, 2013). Some studies have documented primates engaging in intensive vigilance behavior when visiting mineral licks, which can include spending several hours around the area before descending to feed only for a few minutes (Izawa, 1993; Link *et al.,* 2011). Spider monkeys also most often visit mineral lick under certain weather conditions (dry and sunny days with little wind) that might increase their chance of detect predators, and tend to visit in tandem with other species (Janson, 1998; Blake *et al.,* 2010; Link *et al.,* 2011).

The purpose of eating clay at licks is still unclear, although several hypotheses, none of which are mutually exclusive, have been proposed for explaining geophagy in primates: 1) detoxification of plant toxin and secondary compounds, 2) provision of supplemental minerals, 3) anti-diarrheal properties and 4) the enhancement of pharmacological properties of plant compounds (Krishnamani & Mahaney, 2000). A full explanation has not been achieved, probably because there are multiple factors, which could be influencing this behavior (e.g. seasonality, social patterns, location, etc).

Several studies that have analyzed clay composition at mineral licks in comparison to other sites and other elements in the diet. For example, for the same study area where our research was conducted (the Tiputini Biodiversity Station), Voigt et al. (2008) found that mineral licks are richer in five minerals (iron, calcium, magnesium, sodium and potassium) compared to fruits and insects. These minerals are essential for mammalian homeostasis and reproduction. Fruits and insects were similarly rich in sodium, potassium and magnesium, whereas calcium and iron concentrations were higher in fruits than in insects (Voigt *et al.,* 2008).

Although a few insectivorous animals eat soil at mineral licks, frugivores and folivores tend to visit mineral licks more often and to be more geophagous (Kreulen, 1985; Voigt *et al.,* 2008; Link *et al.,* 2011). Many fruits, young leaves, and other plant parts consumed by animals contain toxic compounds, and the fact that geophagy is more common among frugivorous and folivorous animals suggests that they may be consuming clays or clay-saturated water in order to buffer these toxic effects.

In other species, such as moose (*Alces alces*), Risenhoover and Peterson (1986) found that mineral licks are important sodium sources. Several studies on vertebrate geophagy have found seasonal variation in the use of mineral licks (Jones & Hanson, 1985; Sanders, 1999; Atwood & Weeks, 2003). The two main hypotheses to explain temporal variation in geophagy refer to either (1) observations of seasonal variation in animal diet (possibly associated with periods of fruit availability and scarcity), which might influence the concentrations of plant secondary metabolites or seasonal shortages of key mineral nutrients or (2) animals' need to supplement the diet with certain minerals during particular life history episodes (e.g. pregnancy or lactation) (Brightsmith, 2004; Voigt *et al.,* 2008).

Studies with camera traps (Link *et al.,* 2011) found that the relationship between seasonality and lick visitation approaches significance for spider monkeys but not for howler monkeys, however, the direct relationship with immediate weather conditions was significant for both species. Several hypotheses, none of which are mutually exclusive, have been proposed as to why mammals and birds may prefer to visit mineral licks on sunny days rather than during rainy or overcast days (Link *et al.,* 2011). First, bad weather condition, as rainy or windy days could be associated with a general decrease in animal activity. Second, it may be that the mineral composition and concentration in soils recently washed by heavy rains are different than on drier days. The accumulation of water at mineral licks may also lead to animals' preference to visit licks during drier periods when water from other dietary sources is scarce. Finally, weather conditions are likely to influence the ability to detect predators (Brightsmith, 2004), which in turn may influence animals' decisions about when to visit mineral licks.

Among primates, spider monkeys and howler monkeys are the only platyrrhines that regularly visit mineral licks, and both species visit licks together in higher frequencies than expected by chance alone (Blake *et al.,* 2010; Link *et al.,* 2011). Woolly monkeys also belong to the same family, but these three species differ in some aspects of their diet, which could influence mineral lick visits and use. Howler monkeys are folivorous, foraging mainly on new leaves, while woolly monkeys and spider monkeys, are mainly frugivorous, although they also eat new leaves, especially when fruits are scarce (Di Fiore & Campbell, 2007). Not all ingested fruits and new leaves are shared or are consumed at the same frequency. There is an important differences between these species' diets: woolly monkeys consume insects (Di Fiore, 2004), while spider monkeys and howler monkeys rarely include these food items (Link, 2003; Di Fiore *et al.,* 2009; Di Fiore *et al.* 2011). Only howler monkeys and spider monkeys visit mineral licks regularly.

For arboreal primates, mineral licks are especially risky because they are the only place individuals go down to the ground, which is where predation risk is greater (Janson, 1998; Link & Di Fiore, 2013). Jaguars (*Panthera onca*), pumas (*Felis concolor*) and ocelots (*Leopardus pardalis*) also visit mineral licks (Montenegro, 2004; Matsuda & Izawa, 2008; Mosquera, unpublished data). These felids include large primates in their diet (Di Diore, 2002; Ferrari, 2009). Predation of spider monkeys by jaguars and pumas has been reported in Tinigua National Park, (Colombia), and in both instances spider monkeys were on the ground or visiting a mineral lick (Matsuda and Izawa, 2008). Primates develop antipredatory strategies to minimize predation risk (Kappeler & van Schaik, 2002). For example, spider and howler monkeys spend large periods of time being vigilant before coming down to the floor at licks (Izawa, 1993; Link *et al.,* 2011; Link & Di Fiore, 2013). Spider monkeys seem to respond to the high potential risk of predation at mineral licks by increasing the average size of their subgroups when visiting these areas (Link & Di Fiore, 2013). Also, specific location of mineral licks used by spider monkeys and howler monkeys have been related with predation risk, being these areas least risky to come down to the ground to feed on clay (Izawa, 1993; Link & Di Fiore, 2013).

Our study was focused on a group of habituated white-bellied spider monkeys (*Ateles belzebut*h), which has been studied since 2005. This group visited regularly a single mineral lick located in their home range. All individuals of this group are well habituated to observers, enabling us to study their behaviors closely, even in the mineral lick. In this study, we aimed to characterize the pattern of mineral lick visitation by spider monkeys (*Ateles belzebuth*) and better understand the factors influencing visit “success” (actual soil consumption). We particularly investigated whether successful visits were influenced by certain individuals, the number of individual spider monkeys present in the lick, with the presence of howler monkeys, and/or with particular weather conditions.

METHODS

Study Site

This study is part of the Proyecto Primates research and conservation program that has been in progress for 18 years in the Yasuní National Park and Biosphere Reserve in the Ecuadorian Amazon. The study area covers a series of rolling hills and drainages on the north side of the Río Tiputini and consists largely of undisturbed moist tropical rain forest that receives an annual rainfall of more than 3,200 mm (Di Fiore & Rodman, 2001; Di Fiore, 2004). Data were collected at the Tiputini Biodiversity Station from July 2010 to March 2013.

Mineral Lick Characteristics

The mineral lick visited by our study group is a small cave where animals enter to eat soil and drink water (Link *et al.,* 2011). It is centrally located in the home range of our study group. Animals use branches and fallen tree trucks to access the cave.

Behavioral Follows

We conducted behavioral follows from dawn to dusk on one group of spider monkeys from July 2010 to March 2013 using focal animal sampling (Altmann, 1974), attempting to follow focal subjects from dawn until dusk. During focal follows, we recorded subgroup composition and the location of the focal subject every 20 seconds using a Garmin 76CSx GPS equipped with a high sensitivity antenna. Every 15 minutes, we also recorded the size and composition of the focal animal's subgroup. Individuals were identified using facial traits and genital markings. During this study, the group contained six adult males and eleven adult females. Including sub-adults, juveniles and infants the total groups consisted of 35 individuals. Data collection at the mineral lick was challenging because the observer had to remain in the same location during the duration of the visit to prevent alarming the animals. A visit was considered successful when at least one individual went down to the ground to feed on clay (or went inside the cave). During visits to the mineral lick, usually all individuals present ingest soil, (but sometimes we could not identify the whole group). The visits were only considered for the analysis when the individuals spent more than 30 minutes around the mineral lick area to eliminate the possibility that they were in that area only transiently as part of daily travel.

Influences of Individuals on Successful Mineral lick Visits

Using previous data (Link *et al.,* unpublished data), we divided the subgroup in three categories according to the individual home range (see map). 1) Males, who range evenly around the entire territory; 2) East females, who mostly range around the eastern part of the territory, close to the mineral lick; and 3) West females, who mostly range around the western part of the territory, farther from the lick (investing more energy to arrive to the area).

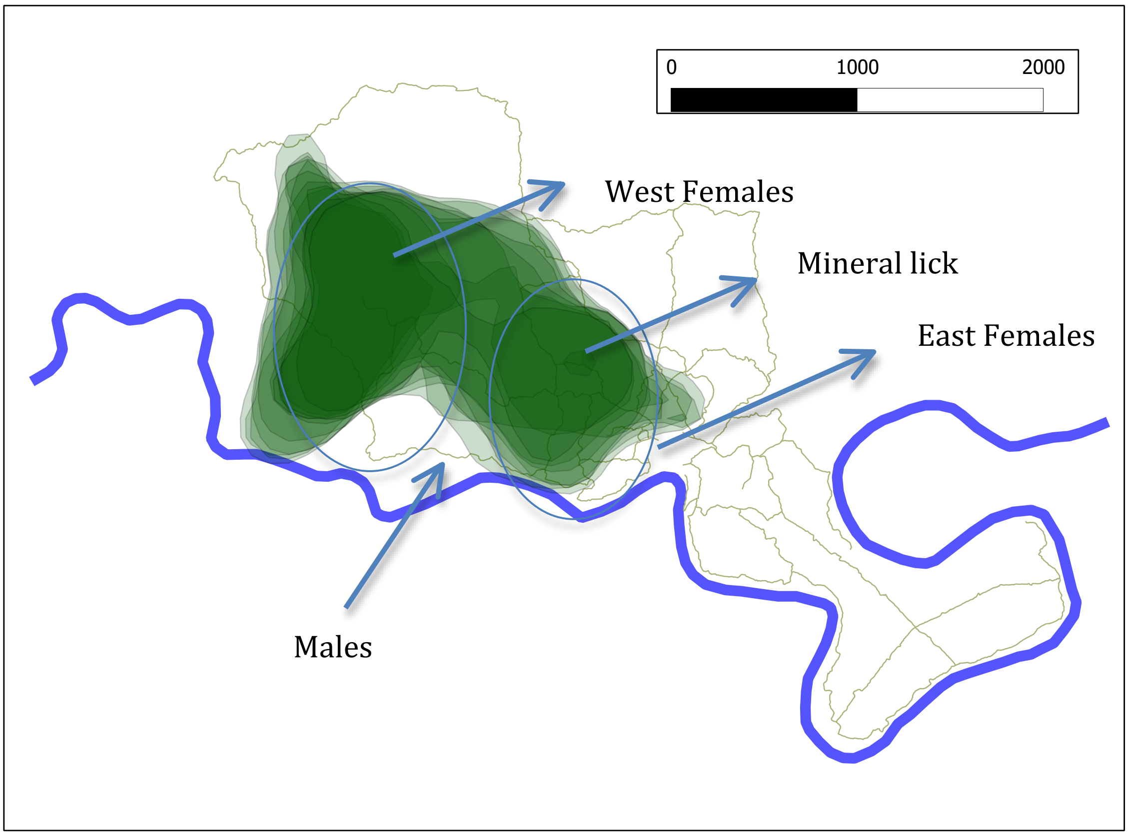

Figure 1. Map of the Tiputini trail system and the home range of the group within 2006-2008 1) Males move around the whole territory; 2) East females move close to the mineral lick; and 3) West females move farther from the lick.

We studied the differences between the set of visits of each subgroup (Males, East Females and West Females), to compare if individuals of each subgroup are influencing differently of the success of those visits (i.e if some individuals have higher impact of the success of the whole subgroup, which is visiting the mineral lick).

Influence of Subgroup Size on Lick Visit Success

We study two measurements to analyse the influence of subgroup size. First, we study the whole number of events exploring if the number of individuals in each event of visitation is influencing in successful visits. We considered all subjects we found in the subgroup (including juveniles and infants) because all of them were vigilant and their presence could be a key factor in the success of the visit.

Second, we analyse the differences of the set of visits of each subgroup, Males, East Females and West Females. We studied if the presence of any individuals of each one are affecting differently according to subgroup size. To consider the influence of subgroup size per adult we classified the subgroup found in the mineral lick in three categories: 1) small subgroup, less than 10 individuals; 2) Medium, between 10 to 20 individuals; and 3) Big subgroup, more than 20 individuals.

Influence of Inter-specific Associations with Howler monkeys (*Alouata seniculus*) on Lick Visit Success

As we study the influence of subgroup size, we evaluate the whole number of events of visitation studying if the howler presence is influencing in the success of the visit. On the other hand, we also registered in the set of visits per individual, when each subject was in the presence or absence of howler monkeys, studying if this factor was equally affecting, independently of the presence of individuals from each subgroup.

Influence of Weather on Lick Visit Success

To test whether the success of mineral lick visitation was associated with weather conditions we recorded a daily index that describes cloud cover, precipitation, and luminosity: 1 dark/rain; 2 dark/overcast; 3 clear/overcast; 4 partly cloudy; and 5 sunny. Climatic conditions were recorded continuously throughout the day whenever the observer noted a conspicuous change in cloud cover, precipitation and/or luminosity.

Combined Influence of All Variables

To evaluate the three variables in the mineral lick visitation success of the study group together, we scored successful and unsuccessful events 1) according to the number of individuals, 2) with and without howlers, and 3) comparing with the average value of the daily index of weather condition. These data were considered for each visitation event to evaluate the influence of these variables on the “success” of each visitation.

Data Analysis

To analyze the data we used the SPSS 20.0 statistical package. We used parametric measures because our data were normally distributed and met the criteria of homoscedasticity. We used Linear Mixed Models to compare the set of visits and their success of those visits between individuals of each subgroup, Males, East Females and West Females. We analyze the data with these models to control the effect of the whole subgroup visiting the lick over each individual (adult) per event, avoiding the pseudo-replication of the data. The visitation of each adult is not completely independent measurement because we are considering the presence (and influence) of any adult of each subgroup in the mineral lick, none of which are mutually exclusive with other subgroup´s individuals. So, we analyze the data with Linear Mixed Models to control the common factor of each event. We used the Bonferroni correction to adjust p value within the model to evaluate the differences between pairs.

On the other hand, to analyze the influence of different variables in each event; number of individuals in the subgroup which is visiting the mineral lick, presence of howlers and weather condition, we used Logistic Regression Models comparing successful and unsuccessful visits. We study each variable separately to evaluate which one is affecting more the success of the visits; and together to consider if the combination of all variables better explain the probability to consume soil. We also used Lineal Mixed Models to compare if these variables affect differently depending of the presence of the individuals of each subgroup.

RESULTS

1. Influences of Individuals on Successful Mineral Lick Visits

When we compared the frequency and success of visits within the set of visits of each subgroups (Fig.1), we found that individuals from East females subgroup (which have their core territory closer to the mineral lick), visit the mineral lick more often, followed by males (Linear Mixed Model, F=26,42; p<0,01; Differences between means: Males-East Females: -12,05; p<0,05; Males-West Females: 20,17; p<0,01; East Females-West Females: 32,21; p<0,01). However, although individuals from West females subgroup visit the lick with less frequency, when we evaluate the percentage of success of those visits we found that they have the highest relative visitation success (Linear mixed model, F=25,28; p<0,01; Differences between means: Males-East Females: 2,14; p=0,92; Males-West Females: -13,5; p<0,01; East Females-West Females: -15,64; p<0,01). So, when individuals from West Females are present in the mineral lick, the subgroup in the lick usually ingest clay. We didn’t find any differences between Males and East females´ success.

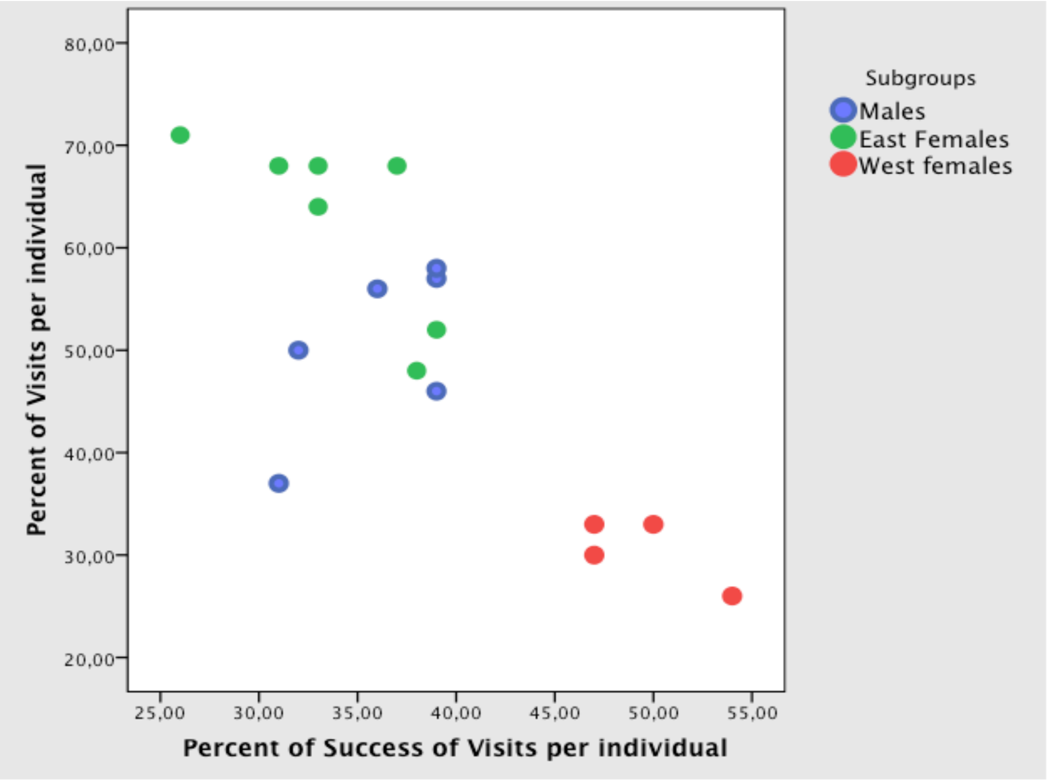

Figure 1. Visits and success of those visits within the three subgroups (Males, East females and West females)

2. Influence of Subgroup Size on Lick Visit Success

When we analyzed the relationship between the number of individuals and the success of visits, we found that successful visits are usually associated with a higher number of individuals within the subgroups visiting the lick (Logistic Regression, B=0,10; p<0,01) (Fig. 2). However, this variable only explain 15,3% of the successful events (R^2 = 0,153).

We could also see in the figure 2 that the average size of individuals when they have successful visits is 20 individuals, being less number within unsuccessful visits.

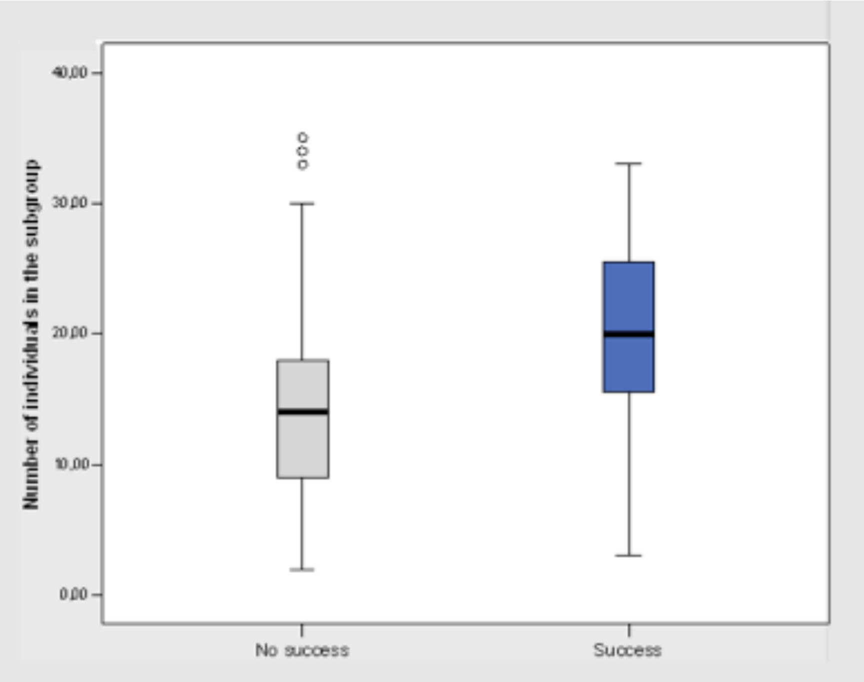

Figure 2. Number of individuals found in the mineral lick in no successful visits and successful visits

When we analyzed the data per individual, (comparing individuals from each subgroup), we found that Males and East Females visit the lick in small subgroups more often than West females (F= 25,37; p<0,01; Differences between means: Males-West Females: 8,65; p<0,01; East Females-West Females: 7,71; p<0,01; no differences between Males-East Females) and within medium subgroups (F= 46,01; p<0,01; Differences between means: Males-East Females: -5,38; p<0,01; Males-West Females: 15,46; p<0,01; East Females-West Females: 20,84; p<0,01), while when West females are present, the subgroup size is usually bigger (F=62,77; p<0,01; Differences between means: Males-West Females: -24,11; p<0,01; East Females-West Females: -28,55; p<0,0; no differences between Males-East Females).

We found the same tendency from each subgroup increasing the success with the number of individuals (Linear mixed model, F= 84,61; p<0,01). However, we also observed that there were some differences between subgroups (F= 2,96; p= 0,06). When we analyzed each category of group size separately, we could confirm that within medium size category, West females individuals have more influence, showing higher success when they are present than the other two subgroups (Fig.3). When the size is small or big, the individuals of each subgroup are not influencing differently.

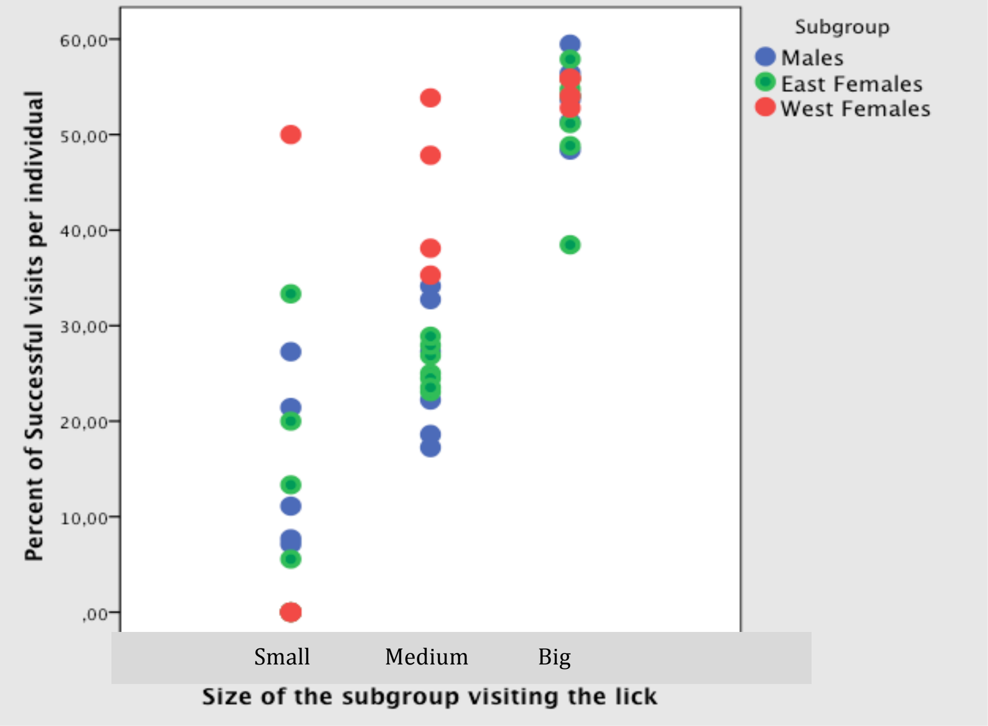

Figure 3. Visits according to the number of individuals found in the mineral lick, comparing the three subgroups categories (Males, East females and West females).

3. Influence of Inter-specific Associations with Howler monkeys (*Alouata seniculus*) on Lick Visit Success

When we compared visits with and without the presence of howler monkeys (Fig.4) we found significant differences within successful visits (Logistic Regresion, B= -2,34; p<0,01), increasing the probability of success when howler monkeys are present in the lick. Spider monkeys usually go to the mineral lick alone, but when they share those visits with howler monkeys, the successful visits increase considerably. This variable explains almost 30% of the successful events ($R^2 = 0,285$) (higher than the group size).

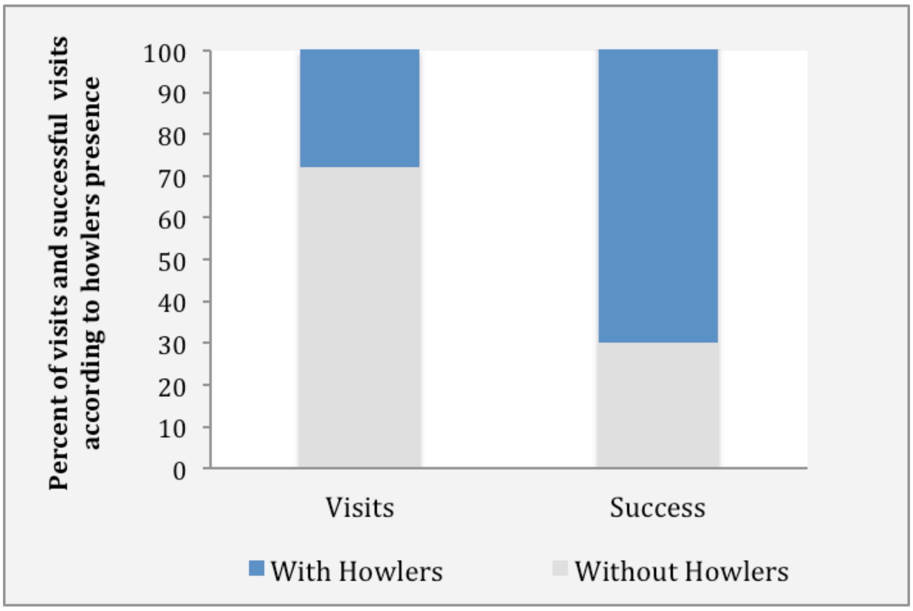

Figure 4. Visits and successful visits with and without howlers

Comparing data with and without howlers within the set of visits by each subgroup, we found the same tendency to increase success with howlers presence (Linear Mixed Model, F=981,98; p<0,01) but also we found differences between subgroups (F=24,65; p<0,01; Differences between means, Males-East Females: 1,78; p=0,85; Males-West Females: -10,75; East Females -West Females: -12,53) and the intersection between subgroups and howler presence (F= 7,35; p<0,01).

We could observed that West females showed the highest success, and especially when there are no howlers in the lick they showed significant differences compare to Males and East Females (Fig. 5). So, again, when individuals from West female subgroup are present in the mineral lick, with and without howlers (but especially without howlers), the probability that the whole subgroup visiting the lick ingest soil increase.

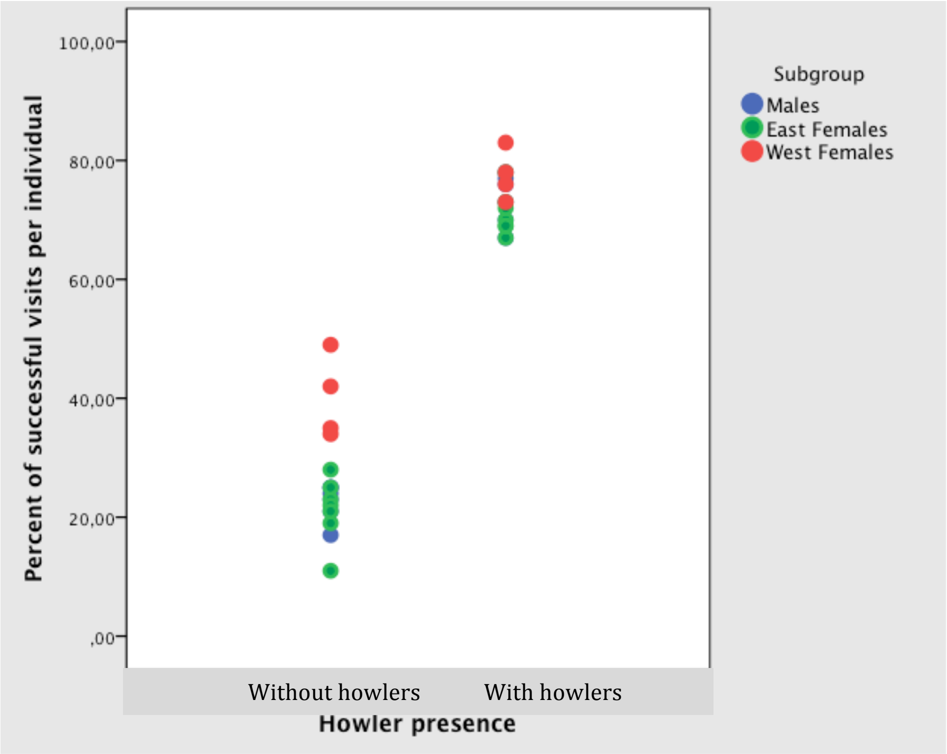

Figure 5: Percent of successful visits with and without howlers within each subgroup

When we control size variable, without howlers (because with howler we didn´t have all categories of size in all individuals), the differences were less clear, just finding differences between Males and East Females (Linear Mixed Model, F= 4,94; p<0,01; Differences between means: Males-East Females: 14,63; p<0,05). So, West Females used big subgroups to compensate howler absence. When Males are present had more influence than East Females in this condition, having higher relatively success within smaller subgroups.

4. Influence of Weather on Lick Visit Success

When we analyzed the relationships with the success of visits in the mineral lick with the weather conditions, we didn't find any relationship (Logistic Regression, B= 0,07; p= 0,75). The weather seems not be a variable that determined the success of visits in spider monkeys in this case.

5. Combined Influence of All Variables

We analyzed the three variables that could be influencing the success of visits at the mineral lick and the interaction with howlers and number of individuals. Under this situation we didn’t find significant differences within the interaction howlers*number of individuals and weather (Logistic Regression, B=0,25; p=0,81), so we excluded these two of the model. Considering only number of individuals and howlers presence we found that the constant variable, “success” depend of those (B= -3,45; p<0,01) and this regression model explained around 40% of the variation in mineral lick visitation success (R^2=0,395). So, howler presence (B= -2,49; p<0,01) and big subgroups (B= 0,11; p<0,01) are two important characteristics that increase the probability of success. However, we could also remark that it seems howler presence is a better predictor of successful visits than higher number of individuals, since this variable explained more variance in its model respectively.

DISCUSSION

When individuals with core territories located farther from the mineral lick, that invest more energy getting there, are present, the success of the whole subgroup visiting the lick increase. Other individuals that have the mineral lick closer of their core territory do not invest too much energy to get there, so the probability to find them in the mineral lick is higher. However, these individuals seem to have less influence over the group´s success. With these results, we could suggest that individuals, who have to travel farther to arrive to the lick, try to use these events to consume soil with higher probability because they are spending more energy. However, the reason could also be related with the fact that when these individuals are present, which frequency to find them in the mineral lick is the lowest, the probability that the number of individual in the lick was higher, also increase. So, this variable could be the one which is affecting instead of the presence of West Females. For this reason we also explore other different possibilities.

Influence of Subgroup Size on Lick Visit Success

Our results showed that the proportion of successful visits increases with the number of individuals. This result supports the vigilance hypothesis, which suggests that the risk of going down to the ground makes animals more cautious around mineral lick sites. Some felids, predators of primates, have been reported visiting these areas, so it seems mineral lick are potential dangerous areas.

Spider monkeys have a fission-fusion social system, and usually travel separately in smaller subgroups, however, when visiting the mineral lick they prefer medium or big subgroups. Individuals on our study group usually wait until the subgroup is large enough to go down, probably to be sure they can monitor the whole area to make sure they can go down without any danger. Before going to the ground they spent large amounts of time (Link *et al.,* 2011; personal observations) visually scanning the area with several individuals going up and down observing the ground around the cave. They usually spent more than three hours in that lick area until they go down (Link *et al.,* 2011), so it seems vigilance is very important in that area. Spider monkeys do not usually visit the lick in small subgroups (less that 10 individuals), although there were rare occasions when they visited the lick and even descended to consume clay in a very small subgroup (two occasions without howlers and four with howlers).

The subgroup that usually visits the lick in these small subgroups is the East females´ individuals, probably because they have their core territory closer to the lick and it easier to find them alone with their offspring, followed by males which mineral lick is part of the area they are usually distributed. Although visits were only considered to be those cases when animals spent more than 30 minutes in the vicinity of the mineral lick area (i.e., excluding times when they just past through the area on a travel route), for individuals from these two subgroups are probably easier to check the area and wait some time to see if someone else is around, just in case some time later the group decides to go down to practice geophagy. Effectively, how we mention before, it seems that when West females are present the group in the mineral lick is also bigger than with Males and East Females, therefore this situation could make the success increase. However, when we analyze the group size in the mineral lick separately, we confirm that the relatively success of visits within big size is the same from each subgroup. We could also remark that within medium group size with West Females presence, the probability to consume soil also increase, so it seems that individuals from West Female subgroups have higher effect to success than the other two.

Influence of Inter-specific Associations with Howler monkeys (*Alouata seniculus*) on Lick Visit Success

Howler monkeys and spider monkeys are the only primates that regularly visit the mineral licks and consume soil in these areas, and these species visit licks together more often than expected by chance (Blake *et al.,* 2010; Link *et al.,* 2011). It appears they tolerate each other because they are usually close, and waiting for a long time around the cave. Indeed, on several occasions we witnessed juveniles of the two different species playing together and adults of the two species sitting in contact with one another (Link et al., unpublished data). Moreover, the observations of both species in the mineral lick raise the possibility of some “association” between species being more efficient in looking out for predators together than alone.

Although spider monkeys usually visit the mineral lick alone (more often than with howlers), our results showed when both species visit the lick together, the chance of animals actually descending to the ground increased considerably. Both species usually spent some time vigilant near the cave until they go down together and may even go inside the cave at the same time. Howlers usually go inside first, but without any problem can be together with spider monkeys inside the cave. The individuals within a group of howler monkeys collectively spent less time eating clay than spider monkeys, but this is probably because their group sizes are smaller. This association between the species is only notable when the animals are around the lick; in different scenarios, members of the two species usually avoid each other and although sometimes juveniles play together, they tend to spent a very short period of time at any sites other than the lick.

Again, when we compared each subgroup, we could see (Fig. 5) that when individuals from West Females subgroup are present, within both conditions but especially without howlers, the success also increased. We control the size variable in the condition without howlers to evaluate if this effect is due to both variables together. In that scenario, we didn't find any differences between individuals from West Females compare with the other two subgroups. In contrast, we found that Males have more influence to success over East Females in howler absence. While Males have more relative success within smaller subgroups, West Females trying to combine big subgroups without howlers to increased their success.

So it seems, West Females individuals have more influence than the rest but probably because they are using a combination of the other two variables, howlers presence and big number of individuals when they are present. However, the relationship with these two variables and their presence, seem to have also more influenced than other individuals of the other two subgroups. These females seem to be more efficient probably because the energy they spent going to the lick, but the way they anticipate big subgroup and howlers presence is still unclear.

Influence of Weather on Lick Visit Success

Good weather conditions could be correlated with the success of visits if it is easier for animals to detect predators with more light and without wind or rain (Brightsmith, 2004). Prior data collected on this group (Link *et* *al.,* 2011) showed that weather conditions in the morning preceding lick visits may influence the animals' subsequent behavior. However, data from the present study suggests that the weather conditions do not have as strong an influence on visit success as does the size of the subgroup or the presence of howlers.

Combined Influence of All Variables

Evaluating the regression logistic model built to analyze all variables within events (not by individuals), we could confirm that howler presence and big number of individuals in a subgroup, have significant positive effects on visit success and the combination of both better explain the successful visits (almost 40%). It seems that the association with howler monkeys have a stronger effect since the percent of explanation of this model is higher (almost 30%) than subgroup size (13%).

CONCLUSIONS

In conclusion, we found that some individuals seem to have more influence than other on the successful mineral lick visits. When individuals from West females subgroup were present, the relatively success compared with the other two subgroups, increased. It seems they probably invest more energy getting there, since their core territory is farther, so they maximize the time.

Our results also support the hypothesis that mineral licks are risky areas, since both a larger number of individuals in the subgroup and the presence of howler monkeys increased the chance of animals descending. With these two conditions and individuals from the West Female subgroup present in the lick, we found the highest possibilities of soil consumption. However the way these females match with this scenario more often than the other two subgroups is still unclear.

Although previously data of this group suggested that sunny days are a favorable condition to visit the lick, it seems is not a clear condition to success or no success during those visits.

Finally, we could conclude that the combination of both a bigger subgroup and howler presence better predict the success of their visits, being howlers presence stronger predictor than the size of the subgroup.

These factors are all important in the evolution of the patterns of successful visits, but the frequency of their visitation is too high to not consider other possible explanations. There are several times when spider monkeys visit the mineral lick area in large subgroups and under favorable weather conditions, but they do not go down. This may suggest that social interactions at mineral lick sites are also important for maintaining and strengthening social bonds and that licks are not simply places visited for the resources they contain. Groups with a fission-fusion social system may use places such as mineral licks as a “meeting point”. Social interactions (grooming, playing, embracing) were very common in this area, and the spider monkeys invest a lot of time and energy going to this area. It would be very interesting to gather more data on social interactions, but it seems mineral lick visits could play an important social role, in maintenance of group bonds and group dynamics.

CAPÍTULO 5:

Deep incursion and use of a mineral lick within a neighboring territory in white-bellied spider monkeys (Ateles belzebuth).

Deep incursion and use of a mineral lick within a neighboring territory by a group of white-bellied spider monkeys (*Ateles belzebuth*)*

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ABSTRACT

Only in chimpanzee and spider monkeys societies do members of a social group jointly conduct territorial boundary patrols and deep incursions into rival neighboring territories. Boundary patrols are usually made by subgroups of adult males, although on occasion, mixed parties of males and females may travel in silence into their neighboring groups´ territories. For spider monkey living in western Amazonian forests, mineral licks seem to be valuable areas where they feed on clay in order to acquire minerals not contained in their diet or as a detoxification agent. Here, we document a case where most members of group of white-bellied spider monkeys (*Ateles belzebuth*) collectively made a deep incursion into a neighboring territory. What seemed a territorial boundary patrol at the beginning ended up being the only reported case in which spider monkeys actually use of a mineral lick well within a neighboring group´s territory. This particular event raises the question as of how do neighboring groups know, if they do, of these resources in the territory of an adjacent group and why did they decide to use it, when a safer mineral lick is often used within their own territory. We suggest that this kind of intrusion into neighboring territories might reflect a high level of inter-group competition for key resources and territory. Nonetheless, the underlying explanations behind the decision to visit the mineral lick in a neighboring territory remains largely unexplained.

Key words: boundary patrol -mineral lick- intrusion- inter-group competition - spider monkeys

INTRODUCTION

Boundary territorial patrols and deep incursions into neighboring territories have been documented in several chimpanzee societies that have been subjects of long term studies (Goodall 1986b; Manson & Wrangham, 1991; Wrangham, 1999; Boesch & Boesch-Achermann, 2000; Watts & Mitani, 2001; Wilson & Wrangham, 2003; Mitani & Watts, 2005). In most populations, boundary patrols are relatively rare events, occurring once every 10–23 days (Goodall, 1986b; Boesch & Boesch-Achermann, 2000; Watts & Mitani, 2001; Mitani & Watts, 2005). During patrols, chimpanzees move along the boundaries of their territory or make deep incursions into their neighbors' territories while on patrol. Patrols generally include, on average, 8–13 individuals and are primarily executed by adult males, with some extent of female participation varying across sites (Goodall, 1986b; Boesch & Boesch-Achermann, 2000; Watts & Mitani, 2001; Mitani & Watts, 2005). Patrolling individuals remain quiet and refrain from performing conspicuous acoustic and olfactory displays like those characteristics of the territorial behavior of other mammals (Mitani & Watts, 2005). Although this behavior had been described as a distinctive and unique aspect of wild chimpanzees, *Pan troglodytes* (Mitani & Watts, 2005), it has also recently been documented in spider monkeys societies (Symington, 1990; Shimooka, 2005; Aureli, *et al.,* 2006; Wallace, 2007, 2008; Link, 2011). During spider monkeys' territorial encounters, aggression has been observed between neighboring groups and parties, primarily by males (Symington, 1990; Shimooka, 2005; Wallace, 2007; Aureli *et al.,* 2006; and this study). Symington (1990) also documented some cases of antagonistic aggressions between group, noting that party size in boundary areas tends to be larger than in the interior of a community's range, so it is possible that increased party size reflects a defensive response to the potential threat of aggression from members of neighboring communities. Wallace (2007) also described a similar pattern at Lago Caiman, Bolivia, where subgroup size was larger in cells bordering the territory boundary than in more central areas. Adult males travel faster and over longer distances than do adult females, lending further support to the argument that male spider monkeys monitor or patrol their territory (Shimooka 2005; Wallace, 2007). Intercommunity disputes, accompanied by physical aggression, has been reported at several sites for several species of spider monkeys (Symington, 1988; van Roosmalen, 1985; Wallace, 2007; Link, 2011), and Aureli *et al.* (2006) have described several deep incursions with an isolated event of intercommunity aggression directed towards females by male spider monkeys. Dunbar (1988) and Wallace (2007) argue that male spider monkeys are territorial in order to defend females rather than other important resources. In fact, Symington (1987a) proposed that males cooperate not to gain immediate access to reproductive opportunities but rather to maintain the integrity of the group´s range. Adult males may well be most concerned with defending adult females, but from a female perspective, in so doing they will also be defending resources, so they would need to defend the territory during periods of fruit scarcity with more intensity (Wallace, 2007). In a similar pattern to that displayed by chimpanzees (Wilson *et al.,* 2004), Aureli *et al.* (2006) suggested in their study that their observations of deep incursions by spider monkey might not be driven by feeding competition or access to key areas of higher fruit productivity, as the patrolling males spent virtually no time feeding during the incursions into neighboring territories. The little feeding they did in the neighboring territory was mainly done after they encountered neighboring monkeys and was on types of food also available in their own territory, suggesting that foraging was not the main reason explaining these raids.

Mineral licks, are important areas visited by several Neotropical mammals and birds to consume soil for mineral supplementation and/or as a detoxification agent (Voigt *et al.,* 2008; Blake *et al.,* 2010; Link *et al.,* 2010). For spider monkeys these areas are frequently visited by high number of individuals, where they often assemble in larger subgroups than in the rest of their territory and spend long periods of time (Link & Di Fiore, 2013). Spider monkeys and howler monkeys (*Alouatta seniculus*) are the only platyrrhines that typically visit licks, and they invest several hours per visit around the area until they go down to the ground to feed on clay. For arboreal primates, mineral licks are especially risky because these are the only sites where they go down to the ground where the risk of predation risk is presumed to be greater (Janson, 1998; Link *et al.,* 2011). Each group of spider monkeys usually has a mineral lick in their territory, and the intensity of visits is very high, up to several times per week (Link, *et al.,* 2011; see mineral lick chapter). Spider monkeys often make long calls in the early morning, which has been interpreted as a mechanism to facilitate interactions between group members and provide a means of social coordination in fission-fusion societies. Subgroups that emitted loud calls, especially those that responded to distant calls, were much more likely to experience an increase in subgroup size within an hour after calling than those that did not (Spehar & Di Fiore, 2013). Although they not always feed on clay in their visits, they usually spend a lot of time in those areas, so it has been suggested that mineral licks are a valuable resource for spider monkeys, at least in western Amazonia.

Here, we describe a unique case of a deep incursion and use of the mineral lick, by a group of white-bellied spider monkey (*Ateles belzebuth*) into a neighboring territory in western Amazonia and discuss its potential implications.

METHODS

Data were collected at Tiputini Biodiversity Station in Yasuní National Park, Biosphere Reserve in the Ecuadorian Amazon. The study group (MQ-1) is a group of wild white-bellied spider monkeys (*Ateles belzebuth*), which has been habituated and followed since 2006. All group members can be individually identified on the basis of variation in age, sex, and distinctive pattern of pelage and pigmentation on the face and genitals. Data collection was made attempting to follow each adult subject from dawn to dusk using focal animal sampling (Altman, 1974). The adults within the groups – six males and eleven females – were followed taking instantaneous point samples of their behavior every five minutes. Additionally, detailed notes on social interactions and feeding bouts were collected continuously during follows. Important social behaviors, such as grooming or aggression among non-focal animals was recorded through *ad libitum* sampling.

The observers used datalogging GPSs (model Garmin 76CSx), which took location points every 20 seconds from the beginning of each focal sample. Daily maps were drawn by downloading the data using the software DNR Garmin and importing the data into ArcGIS 9.2. over a template of the TBS trail system. Locations of fusion events (when two subgroups joined together) and fission events (splitting of individuals from a subgroup) were highlighted. These data and maps thus detail the composition of the subgroup containing the focal individual across the duration of the follow.

In order to monitor spider monkey activity at the mineral lick located in the territory of spider monkey group MQ-6, which occupies a territory adjacent to that of our main study group, we used a video camera trap equipped with a motion and heat sensor. This allowed us to evaluate if this mineral lick was active and if it was being visiting by individuals from our main study group or by other individuals.

Finally, we also used the location data from one male spider monkey fitted with a GPS collar to check if this subject visited the MQ-6 mineral lick on other occasions, even when not followed by our research team.

RESULTS

One of common behavior usually displayed by spider monkeys on days when they are going to visit the mineral lick is to emit long call vocalizations early in the morning. On March 11th, 2011, part of the MQ-1 study group started to vocalize at around 06:27; these vocalizations were not a typical long distance calls, but rather alarm calls (a.k.a., “repeat barks”). The researchers, L. Abondano and S. Alvarez, located a subgroup containing three adult females with their offspring near a mineral lick located at the center of MQ-1’s home range. Within a few minutes, three adult males and three more adult females approached from the eastern part of MQ-1’s home range and joined these three females. The observers then heard many vocalizations coming from the East and Southwest; these vocalizations were more typical long calls, probably from other members of the MQ-1 social group as that emanated from within MQ-1’s home range. These 9 adults and their offspring started to move away from the mineral lick area, and traveled rapidly towards the northern portion of their home range. At around 09:00, the animals were joined by another female from the study group and her two offspring and they continued towards northwest rapidly. Some minutes later three other males joined them and one of the females left the subgroup. At that point, all six adult males were present in the group. The group paused for around an hour to forage and rest. There were a lot of social interactions while they were resting. Some juveniles were playing for a long time and males were resting close to each other, especially two males, Sammy and Lucas, who were resting in contact for most of the time. During this pause (around 10:00) one female with her offspring left the subgroup.

At 10:40 the remainder of the group continued moving northwest rapidly. Some time later, around 12:00, one of the females and her juvenile male left the subgroup. Half an hour later, the entire subgroup of 6 adult males, 5 adult females, 3 subadult females, 1 subadult male, and 4 juveniles, crossed the farthest reaches of their home range that we had observed them using in 6 prior years of observation. The subgroup continued moving very quickly, well outside of the TBS trail system. Up till now, the animals’ behavior was reminiscent of a “boundary patrol” and took them into the territory of another group (MQ-3). We expected the males to “fission” from the rest of the group and to leave the females behind, as usually happened in other patrols (Link & Di Fiore, unpublished data), but instead, the entire subgroup kept moving very close to one another, sometimes with females leading the way. After a time, the animals started to turn towards the West, leaving MQ-3's territory and moving towards the territory of yet another group, MQ-6 territory (Figure 2). The males moved very close to one another, at a distance of about 5 to 10 meters between them. They kept moving northwest (Figure 1), and they traveled very low in the canopy. They were not vocalizing at all, and no other long calls (VLCs) were heard after they started moving northwest.

At 13:50, when the group was about 1 km to the North of the trail system (and over 1 km from what we had presumed was the limit of MQ-1's territory based on six years of prior observation), the monkeys stopped and rested for a few minutes. They were vigilant, looking towards the ground, and one of the adult males (Lucas) did some branch-shaking displays towards the observers. They then started to move very low, approaching the ground and then retreating up very quickly, similar to behaviors seen when they visit the ML-1 mineral lick within their home range.

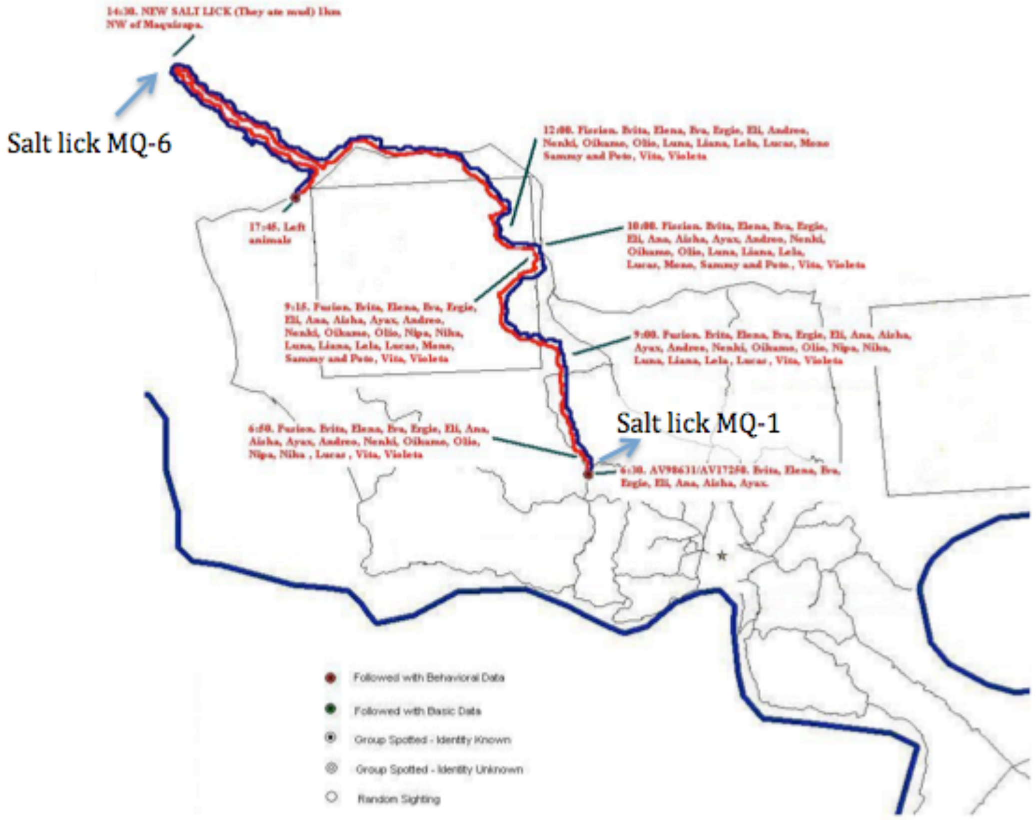

Figure 1. Track of part of the group of MQ-1 within the Tiputini trail system on 11^{th} of March of 2011.

About 15 minutes later, one females with her offspring (Eva and Ergie) were seen climbing back up from the ground with their faces completely covered with mud, so the researchers could confirm that they were indeed using a mineral lick. All individuals started going up to the trees with their faces and feet covered with mud; although mineral lick was difficult to observe as it was located in a narrow canyon, it was evident that all of the subgroup members used the lick. The subgroup remained in the area for about an hour – a much shorter time than the ~4 hours animals spent, on average, around the ML-1 mineral lick within their own territory. At some point, a long-distance vocalization was heard at about 400 m away, coming from the North, but the individuals from MQ-1 did not respond and continued going down to the lick.

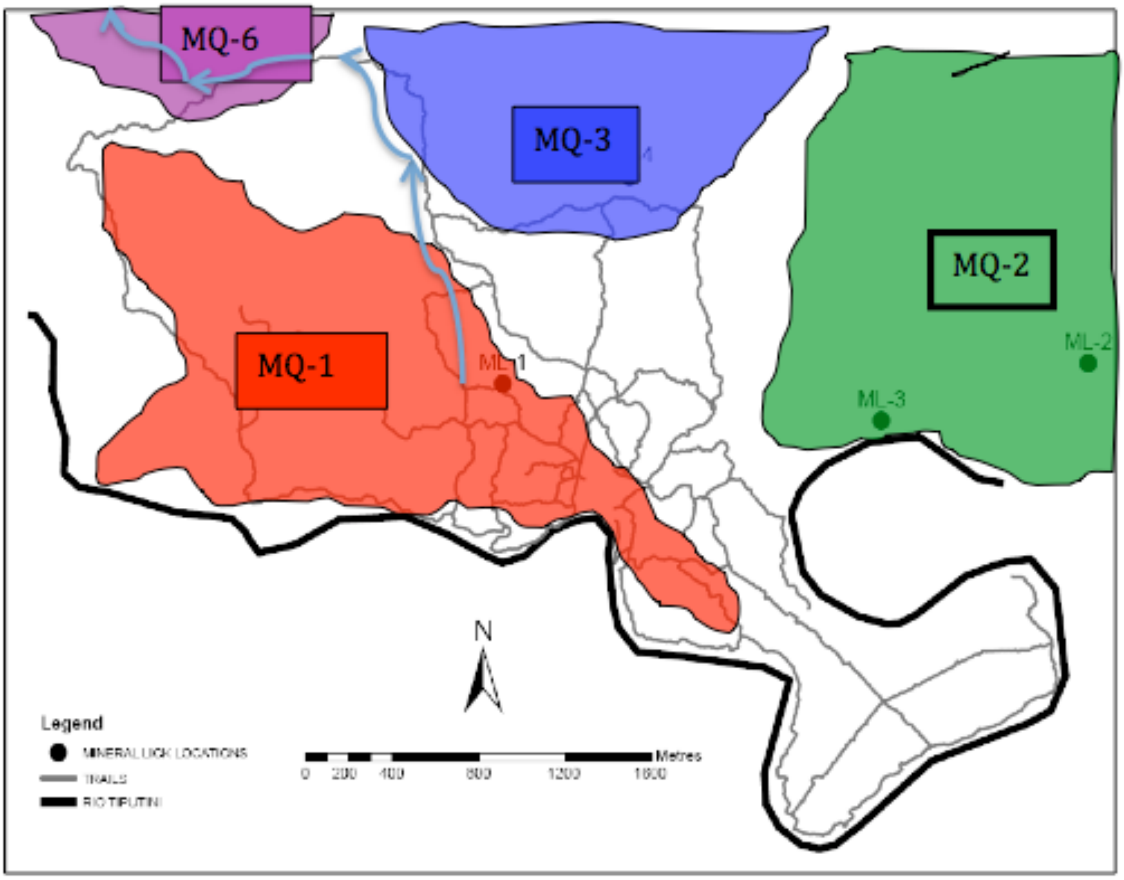

Figure 2. Territory of each group of spider monkeys within the Tiputini trail system.

The subgroup left the mineral lick area at 15:34, and started to head back to their territory backtracking along nearly the same route they used to get there. Nonetheless, they moved much more slowly, resting and eating fruits on their way back. On the return, they also vocalized much more, including contact vocalizations (“whinnys”) and long calls. They arrived back at their limit of their territory around 17:45.

Following this event, we set a video camera trap and the newly identified mineral lick for four months, and we could see that this mineral lick was active (we recorded at least six episodes of clay consumption) and that it was used by other spider monkeys that we did not recognize individually. Unfortunately, with the conditions of this mineral lick, it was very difficult to identify the individuals eating in the lick in the video, although it seems clear they were not from MQ-1. Additionally, using data from one male from the MQ-1 group who was fitted with a GPS collar until ten months after the incursion, we could also confirm that at least this one individual visited the newly recognized mineral lick on one another occasion.

DISCUSSION

In this brief report, we describe a unique case of a deep incursion into a neighboring group’s territory and use of a neighboring group’s mineral lick by one group of spider monkeys. Mineral licks, in general, seem to be very important resources for western Amazonian spider monkeys; they are frequently used, and animals invest a large amount of time being vigilant and resting in large subgroups around lick sites (Link & Di Fiore, 2013; see mineral lick chapter).

Aureli *et al.* (2006) described seven cases of deep incursions by male Central American spider monkeys into the range of another group; in these cases, animals only fed for a small portion of the time they spent within the neighboring territory, leading Aureli *et al.* (2006) to conclude that these kind of incursions seem not to be motivated by feeding competition. This idea has also received support in chimpanzee studies, where chimpanzees spent only a small portion of their time during raids engaged in feeding behavior (Wilson *et al.,* 2004). However, the deep incursion here described included the use of the mineral lick of another group, which suggests that such areas not only play a key role in the grouping patterns of spider monkeys, but maybe also in their intergroup relations. This case also constituted an example of animals engaging in a very directed movement towards a specific and far off location, as the focal subgroup, with 18 individuals all moving almost directly towards the target and then back into their territory using a route that was completely unfamiliar to the observers. Indeed, in 6 prior years of tracking members of this group, we had never seen the animals range anywhere within more than a kilometer from the mineral lick site, which they approached directly. The direct track followed by the animals would seem to suggest that they had a very clear notion of the spatial location of this resource.

In contrast to the behavior of the MQ-1 group of spider monkeys around their own mineral lick, where they usually spend, on average, ~ 4 hours resting and being vigilant around the lick prior to coming down to the ground, in this case they only spent around an hour, total, in the neighboring group's mineral lick area. They arrived in silence and did not spend a large amount of time being vigilant before coming down to eat soil. They fed on clay at the lick and did not respond to the long distance vocalization that came from north of the lick while they were at the site.

Nevertheless, the subgroup composition in this case was very different from the male-dominated parties that we have and other have usually observed during patrols (Symington, 1990; Shimooka, 2005; Wallace, 2007; and this study). In addition to all adult males from the MQ-1 group, five adult females and several subadult animals and juvenile of both sexes were also present, which is not common during incursions or boundary patrols (Link & Di Fiore, unpublished data). Such a subgroup composition would seem to leave some animals vulnerable should they encounter animals from a neighboring group, especially such encounters are generally aggressive (Symington 1988; van Roosmales, 1985; Aureli *et al.,* 2006; Wallace, 2007; this study, data in preparation). This event, we suggest, is thus best interpreted as a case of an incursion specifically to "use" resources located in another group's territory without the intention to interact with or challenge that group. Here, the subgroup included young animals, the animals did not spend a lot of time in outside of their own territory, they moved fast towards the other group's mineral lick, and after using those resources they came straight back into their own territory. The direct path they took towards the mineral lick outside of their territory suggests they have spatial knowledge of the area, perhaps due to past experiences, such as prior boundary patrols. It may even be the case that the locations of extra-territory resources are known to one or more of a group's females by virtue of the fact that females are the dispersing sex and may have immigrated in from other groups.

Finally, it is important to highlight that these rare events are very difficult to describe because during patrols and incursions into neighboring territories, individuals often move quickly and quietly. Under these conditions, it is difficult for observers to follow and document the entire series of events in a patrol.

CONCLUSIONS

The significance of the use of a mineral lick in a neighboring territory is difficult to interpret in terms of intergroup resource competition, given that mineral licks (and the clay contained therein) are relatively unlimited resources. Nonetheless, this case of deep incursion and visit to this neighboring mineral lick strongly suggests that the target and the trajectory used by this subgroup of spider monkeys was clearly intended to reach this particular area. A group's knowledge of a neighboring group's territory could be related to past boundary patrols or incursions, where they recognize and discover resources that other groups are using at the same time as they are defending their own territories and inspecting neighboring areas. On the other hand, some females that may have been born in neighboring groups and migrated into the study group after reaching sexual maturity might have retained knowledge of the spatial location of this mineral lick. So they maybe know this territory because they used to live there and could have shown this resource to the rest of actual the group.

However, the reason as of why our main study group (MQ-1) decided to visit, and more surprisingly use this mineral lick, when safer mineral licks are frequently used within their own territory, is still unclear and further data on this type of events is needed to better understand this unusual behavior.

CAPÍTULO 6:

Discusión general y conclusiones

DISCUSIÓN

En el presente estudio hemos analizado las estrategias sociales y reproductivas de una especie de primate, el mono araña, *Ateles belzebuth*, en su medio natural. Los miembros de este grupo de la Amazonía ecuatoriana mostraron una tasa de agresión entre sus miembros sorprendentemente reducida, siendo las agresiones entre machos casi inexistentes. En el caso de las hembras, aunque muy escasas, las agresiones fueron dirigidas principalmente hacia sus propias crías y las que se produjeron entre hembras adultas tuvieron como diana a dos de ellas. Por otro lado, las agresiones mostradas por los machos se dirigieron hacia las hembras, con ataques que a menudo se realizaron en díadas. A diferencia de lo que se ha descrito en otros estudios (Symington, 1987a; Slater *y cols.,* 2009), estas agresiones de los machos no fueron dirigidas hacia hembras que estuvieran ovulando, como predice la hipótesis de la coerción sexual (Slater *y cols.,* 2009), sino hacia hembras en cualquier condición reproductiva. Por tanto, hasta las hembras que estaban amamantando a sus crías recién nacidas fueron agredidas por los machos. De hecho, en este estudio se documentan dos casos, uno observado en el grupo de estudio de Ecuador y otro en un grupo de Colombia (San Juan), que describimos como posibles casos de infanticidio.

Por otro lado, a pesar de que ambos sexos muestran diferentes estrategias que a menudo entran en conflicto, los monos araña también se reúnen para monopolizar y hacer uso de un recurso valioso como puede ser el saladero. Los resultados de este estudio ponen de relieve que los distintos subgrupos vecinos exhiben diferentes estrategias y que los que tienen el territorio central (*core áreas*) más alejado son más exitosos en sus visitas. De este modo, parece que estos sujetos tienen mayor influencia sobre el resto en la probabilidad de consumo de arcilla en los saladeros. Esto podría significar que los individuos son capaces de detectar las condiciones que son más favorables para visitar el saladero;

entre las que se podrían destacar un elevado número de individuos y la presencia de monos aulladores. Por último, el grupo de estudio mostró un comportamiento singular, que no se había descrito hasta ahora, consistente en el uso de un saladero ubicado dentro del territorio de un grupo vecino.

Agresión y dominancia

El análisis de la voluminosa base de datos disponible (i.e., 8569 horas de observación) confirmó lo que se había documentado en otros estudios (Campbell, 2003; Link *y cols.*, 2009; Slater *y cols.*, 2009; Abondano & Link, 2012), que el mono araña (*Ateles belzebuth*) no muestra una alta tasa de agresión. Se registraron un total de 442 agresiones que suponen una tasa de 0,051 por hora. Debido a las dificultades que presenta el territorio en el que viven y la altura y rapidez a la que estos individuos se desplazan, por no hablar de su rapidez, no siempre se pudo determinar la identidad de los individuos implicados. Así, el sexo y la edad de los individuos se pudo establecer en 369 encuentros agonísticos, y en 301 de éstos se reconoció, además, la identidad de los sujetos. De este modo y a pesar del bajo número de agresiones observadas (ya que estos datos se recogieron durante 7 años) pudimos hacer inferencias de lo que estas agresiones suponen para un grupo de monos araña de vientre blanco en la Amazonía Ecuatoriana.

En el caso de las relaciones sociales entre los machos, llama la atención la ausencia casi completa de agresiones entre ellos. Los machos no muestran una jerarquía social diferenciada, como ocurre, por ejemplo, en las sociedades de chimpancés, o al menos no se manifiesta a través de la agresión. La conclusión es, por tanto, que sus relaciones de dominancia son igualitarias, como también se describe en otras investigaciones (Gibson, 2010). Los machos, que son el sexo filopátrico en esta especie (Shimooka *y cols*., 2008; Di Fiore *y cols*., 2009), desarrollan fuertes alianzas entre ellos ya que están emparentados entre sí y permanecen toda su vida en el mismo grupo natal (Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988; Symington, 1990). Este es probablemente el motivo de que apenas se registren agresiones entre los machos. En este contexto tiene sentido que las interacciones entre ellos sean sobre todo de carácter afiliativo y que se observen subgrupos de machos en los que la cooperación en la defensa del territorio y en los contextos de agresión intergrupal suele ser un patrón recurrente (Aureli & Schaffner, 2007; Link, 2011).

Sin embargo, lo que nos llama más la atención en este estudio es lo que ocurre en el caso de las hembras. Sabemos que éstas en general son más solitarias que los machos y que suelen forrajear sólo en compañía de su descendencia (Aureli & Schaffner, 2008; Link *y cols.*, 2009). Esta situación hace a las hembras vulnerables a la coerción sexual; de hecho, la principal diana de la agresión de los machos son las hembras. Además, la predicción es que las relaciones entre hembras se espera que sean débiles y que apenas ocurran interacciones entre ellas. Dado que las hembras de mono araña presentan dispersión del grupo natal (Di Fiore & Campbell, 2007; Shimooka *y cols.,* 2008; Di Fiore *y cols.,* 2009) y suelen viajar con sus crías, lo esperable es que las relaciones de dominancia apenas estén diferenciadas, una situación que favorece la reducción de competencia entre parientes (Wrangham, 1980; Dunbar, 1988). Sin embargo, a pesar de que las agresiones entre hembras adultas registradas en las observaciones focales fueron muy bajas (48 agresiones observadas donde se pudo identificar la identidad de las hembras), las observaciones disponibles en la base de datos nos permiten detectar la existencia de un sesgo hacia dos hembras en concreto. Además, estas dos hembras fueron las únicas que participaron como actores en un único encuentro agonístico. Sin duda se trata de un suceso notable. Debemos añadir, que estas dos hembras no fueron objeto de agresión por parte de los machos, éstos no mostraron preferencias individuales en la dirección de sus agresiones hacia las hembras. Por ello debemos descartar que estas hembras fueran foco de agresión para cualquier individuo por algún motivo, puesto que sólo lo fueron de las otras hembras adultas. No obstante, cabe destacar que a pesar de que el tiempo de permanencia de estas dos hembras en el grupo es relativamente largo, donde tuvieron una y dos crías respectivamente, fueron las dos últimas hembras que llegaron al grupo, lo que podría estar relacionado con algún tipo de rechazo por parte de las hembras residentes que llevan más tiempo. En cualquier caso, aunque con una tasa de agresión tan reducida poco podemos afirmar acerca de lo que hemos observado, sí podemos señalar que probablemente las relaciones entre las hembras no sean tan igualitarias como se había documentado hasta ahora (Gibson, 2010).

Un factor que promueve relaciones asimétricas (no igualitarias) es la existencia de un régimen de competición directa o indirecta por los recursos que, según el modelo socioecológico (Wrangham, 1980; van Schaik, 1983, 1989; Dunbar 1988; Sterck *y cols.*, 1997; Overdorff & Parga, 2007; Nystrom & Ashmore, 2008), constituyen el factor limitante de reproducción en las hembras. Esta situación podría estar afectando en este caso, al menos en lo que Wrangham (2000) define como competición indirecta (*scramble competition*), donde los parches de alimento no pueden ser monopolizados o están siendo usados por otros individuos del grupo (Janson & van Schaik, 1988). Esta posibilidad también podría testarse mediante el estudio de los contextos de agresión en hembras; por ejemplo, donde los contextos de alimentación parecen ser más frecuentes que los contextos de fusión. Sin embargo, la baja tasa de agresión con respecto al tiempo que estas hembras emplean forrajeando (Di Fiore *y cols.,* 2008) no permite evaluar esta hipótesis.

Por otro lado, la mayoría de las agresiones observadas fueron dirigidas por los machos hacia las hembras (un total de 182 agresiones), con tasas de 0,039 ag/h en los machos y de 0,006 ag/h en las hembras, es decir, casi 6 veces más. Como ya se había descrito en estudios anteriores (revisión: Campbel, 2003, Link *y cols.,* 2009; *Slater y cols.,* 2009; Abondano & Link 2012), los machos fueron efectivamente los principales actores de la agresión, observándose una marcada jerarquía de un sexo (el masculino) sobre el otro (el femenino). Además, el principal contexto de estas agresiones coincidía con los eventos de fusión, patrón documentado también en el estudio de Klein (1974) y Aureli y Schaffner (2007), lo que podría interpretarse como una forma de control social (Link *y cols.,* 2009). Según esta interpretación, los machos podrían estar utilizando la amenaza en parte como una forma de “pastoreo” de las hembras para evitar que éstas migren a otros grupos (Link *y cols.,* 2009).

De acuerdo con nuestros resultados, también observamos coaliciones a la hora de agredir a una hembra siendo en muchos casos (con la misma frecuencia que las agresiones individuales) ataques en díadas. Las agresiones en grupos de más de un macho también fueron comunes aunque en menor medida. Dentro de las coaliciones diádicas, hubo dos machos en particular que protagonizaron la mayoría de estas agresiones. Hay que destacar este resultado ya que precisamente uno de los machos más activos en este tipo de agresiones diádicas hacia las hembras fue el que más crías tuvo durante el año 2011 (resultados mostrados gracias a los análisis genéticos realizados en Nueva York y en Austin, Di Fiore y Link, comunicación personal).

A diferencia de los estudios que habían documentado este comportamiento como una forma de coerción sexual, en la que los machos agreden a hembras principalmente en estado de ovulación (Symigton, 1987a; Slater *y cols.,* 2009), en el presente trabajo no observamos este efecto. En algunos casos, tras la agresión del macho, la hembra orinó y el agresor mostró interés oliendo la orina segundos después, probablemente para obtener información sobre el estado reproductor de la hembra (Symington, 1987a; Campbell & Gibson, 2008). No obstante, nuestros resultados no confirman la hipótesis de que los machos usen la agresión para aumentar las probabilidades de cópula (Campbell, 2003), puesto que la agresión puede ocurrir en cualquier estado reproductivo. De hecho, las hembras con crías recién nacidas fueron agredidas en repetidas ocasiones, siendo este un comportamiento llamativo en este grupo. Las hembras a menudo presentan sus crías a los machos y les permiten inspeccionarlas (Gibson *y cols.,* 2008), y este acercamiento podría aumentar las probabilidades de agresión. Por otro lado, la agresión a estas hembras, no disponibles para la reproducción ya que están amamantando a sus crías (y el período entre nacimientos suele ser de unos 3 años (Eisenberg, 1973; Champman & Champman, 1990), no corresponde a una estrategia de “coerción sexual” donde los machos busquen la inminente reproducción con la hembra.

Infanticidio

En ocasiones, la agresión de los machos hacia las hembras con cría resulta letal para ésta. Este fenómeno ha sido documentado al menos en cinco ocasiones en el mono araña y también se observó en este estudio. A pesar de la baja frecuencia con la que se produce este tipo de ataques, es importante documentar su ocurrencia ya que resulta paradójico que en un sistema social en el que los machos están emparentados entre sí, éstos se involucren en un comportamiento aparentemente maladaptativo. Además, en el caso observado en este estudio, el agresor fue precisamente el padre biológico de la cría (comprobado a través de estudios genéticos) y, tras el infanticidio, la hembra redujo el intervalo entre nacimientos, teniendo la siguiente cría 9 meses después (7-7,5 meses de gestación, Eisenberg, 1973; Campbel, 2003, Campbell & Gibson, 2008).

Este estudio también describe otro presunto caso de infanticidio en Colombia, en un grupo de mono araña marrón (*Ateles hybridus*). En esta ocasión, aunque la cría sobrevivió por la ayuda humana prestada, ya que se reintrodujo a la cría al subgrupo donde estaba su madre, el resultado seguramente hubiera sido la muerte de la cría tras la agresión del macho.

El registro de este tipo de eventos en una especie como el mono araña no siempre es fácil. Esta especie tiene un sistema social de tipo fisión-fusión, por lo que los observadores pueden pasar semanas sin ver a parte de los miembros del grupo mientras siguen a sus compañeros. Durante este estudio hubo dos ocasiones en las que dos hembras que habían sido identificadas con crías en uno de los días de muestreo, fueron vistas algún tiempo después, pero sin crías. Nunca sabremos el motivo de su desaparición, y aunque las hembras con crías recién nacidas reciben una atención prioritaria durante los primeros días tras el parto, muchas veces las condiciones climáticas, el terreno o la simple dificultad de su seguimiento hacen imposible una monitorización ininterrumpida. En esos momentos, esas crías podrían haber sido víctima de un evento de infanticidio, pero lamentablemente eso nunca lo sabremos.

Nuestra impresión es que casos de infanticidio como los descritos es probable que sean más frecuentes de lo que se piensa. Uno de los motivos por los que pensamos que el infanticidio podría actuar como sesgo y control social de la proporción de hembras y machos en el grupo, es porque la proporción de sexos en la edad adulta está sesgado hacia un mayor número de hembras (Chapman *y cols.,* 1989). Sabemos que la *sex ratio* en el mono araña está sesgada hacia las hembras (revisión Chapman *y cols.,* 1989), pero parece que este sesgo se hace más marcado en la edad adulta (p. ej., Klein, 1972; van Roosmalen, 1985; Symington, 1988; Chapman, 1990; Nunes & Chapman, 1997; Ramos-Fernández & Ayala-Orozco, 2003; este estudio). Según Chapman *y cols.* (1989), en todos los estudios revisados, el sesgo hacia las hembras aumenta desde que las crías son inmaduras hasta la edad adulta.

Además, Symington (1987b) señaló que las heridas observadas en crías macho fueron más comunes que en crías hembra (una observación también documentada en otros estudios, p. ej., Klein, 1974; Carpenter, 1935) y que la desaparición de crías macho fue cinco veces superior a la desaparición de crías hembra. Chapman *y cols.* (1989) señalan que estas heridas (o agresiones) sesgadas hacia los machos también podrían estar influyendo en la *sex ratio* que muestra el mono araña en la edad adulta, causando una proporción desfavorable a los machos ya desde edades tempranas. Nuestros resultados apoyarían esta idea, puesto que en los dos presuntos casos de infanticidio descritos en este estudio, las crías afectadas fueron machos.

Saladeros

En muchos casos, las relaciones entre los miembros de un grupo están influidas por el tamaño del territorio y la distribución de los individuos dentro del mismo. En el caso del mono araña, los territorios son muy amplios, en efecto, el *home range* total de un grupo puede ser de 150 a 350 ha en promedio (Wallace, 2008). En nuestro grupo de estudio, con un total de 35 individuos, de los que contamos con seis machos adultos y once hembras adultas, la superficie total del territorio fue de 450 ha (Link *y cols.,* datos en preparación), uno de los territorios más amplios documentados hasta la fecha. En el mono araña, las hembras suelen ocupar áreas más pequeñas y concentrarse en sus áreas centrales (*core áreas*) (Symington, 1988; Shimooka 2005), mientras que los machos suelen moverse por zonas más amplias (Symington, 1988; Shimooka, 2005; Wallace, 2007) y visitan los límites de los territorios con mayor frecuencia (Chapman, 1990; Shimooka, 2005; Wallace, 2008).

En el grupo de estudio se observa una clara zonificación de las hembras; hubo dos subgrupos de hembras que ocuparon varias zonas diferentes del territorio, siendo fieles a estas zonas a lo largo del tiempo (Link *y cols.,* datos en preparación). Los machos, en cambio, ocupaban todo el territorio de forma más homogénea. Se les podía encontrar con igual probabilidad tanto en puntos del oeste como del este. Las hembras formaron al menos dos subgrupos de fácil clasificación, las "*Hembras del Este*" y las "*Hembras del Oeste*". A pesar que las hembras se encuentran la mayor parte del tiempo viajando en solitario, lo cierto es que sí podemos destacar una clara segregación en cuanto a las relaciones territoriales. Cuatro hembras mostraron una clara preferencia por el territorio situado al oeste, mientras que el resto, siete hembras, se localizaban en general en un territorio más al este o central.

Esta división se refleja además en las visitas que el grupo realizó al saladero, un recurso aparentemente muy valioso para el grupo. Mientras que el subgrupo de "*Hembras del Este*" tenía el saladero muy próximo o incluso dentro del “territorio central” que solían frecuentar; las “*Hembras del Oeste*” tenían el “territorio central” muy alejado y el trayecto hasta el mismo probablemente les suponía una mayor inversión de energía.

Los saladeros se consideran áreas muy importantes para muchas especies tanto de mamíferos como de aves. Aunque no está muy clara la explicación, se cree que el consumo de este barro puede aportar minerales o servir como agente desintoxicante (Atwood & Weeks, 2003; Blake *y cols.,* 2010). En dos de los primates platirrinos de la Amazonía Ecuatoriana, el mono araña de vientre blanco (*Ateles belzebuth*) y el mono aullador rojo (*Alouata seniculus*), los saladeros parecen ser zonas de alto riesgo (Link *y cols.,* 2011; Di Fiore & Link, 2013), donde se ha documentado la presencia de grandes felinos que incluyen primates en su dieta (Montenegro, 2004; Matsuwa & Isawa, 2008; Mosquera, datos preliminares del proyecto cámara trampa). Por este motivo, esta hipótesis se relaciona con una alta inversión de tiempo de vigilancia, antes de bajar al suelo y consumir arcilla (Link & Di Fiore, 2013). Aunque los monos araña visitan el saladero con frecuencia, no todos los encuentros conllevan asociado la ingesta de barro (registramos 182 visitas y 55 finalizaron en consumo), por lo que este estudio trata de estudiar los factores que podrían incidir en este consumo.

Nuestros resultados mostraron que existen ciertas características que pueden estar influyendo en el consumo de arcilla en el saladero. En primer lugar, las “*Hembras del Oeste*” parecen tener un mayor efecto en el éxito de la visita (ingesta de barro), siendo su presencia un factor que podría estar incrementando la posibilidad de consumo del grupo. Estas hembras podrían ser más eficaces, influyendo en las visitas, debido a que su llegada al saladero supone un mayor gasto energético ya que tienen un recorrido mayor desde sus áreas centrales. No obstante, esta relación podría deberse también a que al ser el subgrupo que menos visita el saladero, su presencia podría aumentar la posibilidad de formar grupos grandes, y ser este factor el que realmente influye en el éxito de la visita.

Efectivamente, nuestros resultados mostraron que el número de individuos parecía influir en el éxito de la visita, aumentando las probabilidades de consumo al aumentar el número de individuos que componía el subgrupo de visita. En muy pocos casos se tuvo éxito cuando el tamaño de grupo era pequeño y las visitas se suelen hacer con un tamaño de más de 10 individuos. La media de individuos en el grupo presente en el saladero en eventos de éxito era de 20 individuos, mientras que sin consumo era de 14 de media.

Como se ha visto en anteriores análisis del comportamiento en los saladeros, los monos araña (*Ateles belzebuth*) de la Amazonía Ecuatoriana parecen necesitar muchas horas de conductas de vigilancia y descanso alrededor de la zona del saladero, lo que parece deberse a que estas zonas son consideradas como áreas de alto riesgo (Link *y cols.,* 2011; Di Fiore & Link, 2013). En este caso, el número de individuos podría ayudar a una mejor detección de los peligros siendo más “seguro” bajar al suelo a ingerir barro cuando el tamaño de grupo es grande y varios individuos pueden estar vigilando mientras otros sujetos bajan al suelo e ingieren arcilla. Además, en este saladero podría ser especialmente importante la vigilancia puesto que es una pequeña cueva, donde los monos araña se adentran, siendo altamente vulnerables a cualquier ataque terrestre. Como se ha mencionado anteriormente, a pesar de que por su tamaño y agilidad estos primates no tienen muchos depredadores, jaguares, pumas y ocelotes, grandes felinos que contienen estos primates en su dieta, han sido documentados en los saladeros, a través de cámaras trampa (Montenegro, 2004; Matsuwa & Isawa, 2008; Mosquera, datos preliminares del proyecto cámara trampa).

Esta relación positiva entre tamaño de grupo y consumo ocurría cuando estaban presentes individuos de cualquiera de los subgrupos. Teníamos tres tamaños de subgrupo, pequeño (1) menor de 10 individuos, mediano (2) de 10 a 20 y grande (3) mayor de 20 individuos. Cabe destacar, que a pesar de que los individuos del subgrupo “*Hembras del Oeste*” solían coincidir con la formación de grupos grandes; cuando los grupos eran medianos y estas hembras estaban presentes en el saladero, el éxito relativo también aumentaba en comparación con la presencia de "*Machos*" y "*Hembras del Este*". Este resultado parece confirmar que no sólo el grupo grande está influyendo en la probabilidad de consumo de barro, si no que la presencia de "*Hembras del Oeste*" parece ser también un factor que influye en este éxito.

Otro factor notable y que también ha sido descrito en otros estudios y en datos previos de este proyecto (Blake *y cols.,* 2010; Link *y cols.,* 2011; Di Fiore & Link, 2013) es la asociación, al menos pasiva, que estos primates parecen establecer en el saladero con los aulladores (*Alouata seniculus*). En este caso, también aumenta la posibilidad de éxito cuando los aulladores están presentes. Los monos araña visitan los saladeros con mayor frecuencia sin aulladores. Sin embargo, su presencia aumenta notablemente la probabilidad de consumo de barro (en el ~67% de las visitas con éxito compartían la visita con esta otra especie de primate). Estos resultados podrían sugerir que esta asociación les ayuda a aumentar el número de "vigilantes" ante una posible amenaza de un depredador, y como en el caso del número de individuos, la mayor facilidad de detección de este peligro puede ayudar a descender al suelo con mayor "seguridad".

Al comparar esta relación entre los datos individuales de los distintos subgrupos, encontramos la misma relación positiva entre presencia de aulladores y consumo, pero el éxito relativo fue mayor con la presencia de "*Hembras del Oeste*" en ambas condiciones, pero especialmente cuando los aulladores no estaban presentes.

No obstante, cuando controlamos ambas variables, el tamaño de grupo y la presencia de aulladores, observamos que esas diferencias entre subgrupos ya no son tan evidentes, lo que parece indicar que las "*Hembras del Oeste*" usan una combinación de ambos factores en sus visitas. En cualquier caso, el mecanismo que pudiera subyacer a la posible capacidad de estas hembras de “predecir” cuándo se producirán estas condiciones, sigue siendo objeto de estudio.

Por último, a pesar de que datos previos (Link *y cols.,* 2011) mostraron que las mañanas con climas más cálidos fueron más frecuentes en días de visita, pudiendo ser estas condiciones importantes a la hora de visitar el saladero, en este estudio no encontramos diferencias significativas en los días con y sin éxito, por lo que el clima no parece influir en el consumo de arcilla.

Al analizar en conjunto todas las variables o factores estudiados, no observamos interacción y la presencia de aulladores parece ser el mejor predictor del éxito de la visita.

Incursión y uso del saladero en territorio vecino

Finalmente, y en relación a la importancia que estas zonas tiene sobre los grupos de monos araña, cabe destacar un evento (único documentado), en el que el grupo de estudio realizó una incursión dentro de un territorio vecino y consumió arcilla del saladero de este grupo. En esta invasión, no sólo los machos formaron parte del subgrupo, como suele ocurrir en los patrullajes que los monos araña realizan por la defensa de su territorio (Symington, 1990; Shimooka, 2005; Wallace, 2007), sino que cinco hembras con sus juveniles y crías formaron parte del subgrupo (18 individuos en total). Aunque este grupo de estudio ha sido observado en otras incursiones en grupos mixtos (Link *y cols.,* datos en preparación), el objetivo de esta intrusión no parece tener un objetivo de defensa territorial, si no que realizó un trayecto directo y claro hacia el saladero de otro grupo donde consumieron arcilla.

Los individuos se movieron con rapidez y casi en línea recta hacia el norte de su territorio, alejándose incluso varios kilómetros de su frontera. La ruta realizada fue muy definida siendo un recorrido aparentemente conocido por los individuos del subgrupo, por sus movimientos directos hacia este lugar del territorio vecino. En un punto de este trayecto empezaron a moverse despacio y por debajo del estrato arbóreo por donde suelen desplazarse. Debido al difícil acceso de los observadores a este saladero, no se pudo visualizar claramente la ingesta de arcilla, pero los individuos se desplazaron por el suelo subiendo al estrato superior con el rostro cubierto de barro. Este comportamiento lo realizaron minutos después de llegar, siendo la duración total del uso del saladero de aproximadamente una hora, mientras que en su propio territorio emplean de media unas 4 horas. Durante el consumo de barro se escuchó una vocalización que venía de lejos (hacia el norte), probablemente del grupo cuyo territorio estaban invadiendo, y aunque no influyó en el comportamiento que estaban realizando bajando al suelo, abandonaron la zona tras haber consumido arcilla con bastante rapidez. Al regresar a su territorio, una vez se habían alejado del saladero, se desplazaron despacio e incluso se alimentaron de otras fuentes de alimentación de este territorio vecino.

Resulta difícil interpretar este evento como un episodio de competición por los recursos entre grupos, debido a que los saladeros constituyen una fuente inagotable de barro. No obstante, parece claro que la trayectoria del subgrupo tenía un objetivo específico, el saladero, y por tanto, no sólo la defensa del territorio forma parte de estos eventos, si no que parece que los recursos también podrían estar influyendo en estas incursiones.

Por otro lado, dada la trayectoria directa al saladero podríamos suponer que los individuos del subgrupo tenían un amplio “conocimiento” del territorio vecino. Esto podría deberse a que identificaron la zona en anteriores patrullajes o incluso que algunas hembras pudieran provenir de este grupo antes de migrar al grupo actual. En esta situación podría ser que estas hembras conocieran el territorio por haber vivido en él antes de alcanzar la madurez sexual y llevar a cabo su migración y que éstas hubieran “mostrado” la ubicación del saladero al resto del grupo. En cualquier caso, la razón por la que este subgrupo hizo uso del saladero del territorio vecino, siendo considerado un área de riesgo, cuando podrían usar el propio ya conocido, todavía es una pregunta a la que no hemos encontrado respuesta.

Limitaciones del estudio

El seguimiento de monos araña es una labor complicada que a menudo resulta un reto para los observadores, especialmente cuando el territorio es poco conocido o nuevo y el tránsito de personas por estos lugares es prácticamente inexistente, haciendo del lugar de paso aún más silvestre y salvaje y por tanto más difícil de penetrar. Las rutas que los individuos emplean a lo largo de los meses suelen ser los mismos, habiendo zonas de paso claras y siendo así algo más sencillo para el observador. Aunque sea de uno mismo, el paso día tras día permite conocer más el terreno, tenerlo muchas veces más despejado o incluso reconocer mejor los lugares de cruce, por ejemplo, entre riachuelos, que en algunos momentos pueden ser de gran ayuda.

En general es importante que el mismo observador realicé los seguimientos mes tras mes, como ocurre en el caso de Proyecto Primates, teniendo investigadores con una larga experiencia y largos períodos de trabajo de campo. De este modo solucionamos muchos problemas de metodología. Si bien es cierto que es posible que aparezcan ciertas variaciones inter-observador o incluso intra-observador, el descarte de los primeros datos, o meses de “entrenamiento” y la enorme cantidad de horas que tenemos en esta base de datos hace que los posibles e inevitables errores se diluyan considerablemente. Del mismo modo, los datos utilizados para esta investigación en concreto no poseen mucho margen de error en cuanto a las diferencias en toma de datos se refiere. En la mayoría de los casos se tuvieron en cuenta eventos determinados como agresiones y visitas al saladero, lo cuál reduce mucho la posibilidad de error, junto con dos situaciones aisladas (infanticidio o incursión y uso del saladero en territorio vecino) donde se realizó un registro descriptivo detallado. Por último, el análisis del territorio se analizó con el registro de puntos del GPS, por lo que no pudo cometerse más error que el propio “desajuste técnico” que pudiera tener el aparato.

Amenazas y conservación

Este estudio aporta una gran fuente de información clave para una mejor comprensión de las relaciones sociales y las estrategias de un grupo con un sistema social de tipo fisión-fusión. Una especie con patrones similares al chimpancé y esencial en el mantenimiento del bosque tropical. Un grupo cuyo hábitat peligra por vivir sobre un suelo que alberga petróleo bajo tierra, tan codiciado por la especie humana. Pero no sólo el petróleo es el mayor de sus problemas, si no la reducción del hábitat debido a los asentamientos, concentrando a los grupos en pequeños parches de bosque (Michalski & Peres, 2005; revisión, Ramos-Fernández & Wallace, 2008; Tellería, 2012). Esto ocurre con la otra especie de monos araña estudiada por Proyecto Primates en Colombia, donde se documentó el segundo supuesto caso de infanticidio documentado en esta investigación. *Ateles hybridus,* una especie de primate en peligro crítico de desaparición y foco de atención para este proyecto y su programa de conservación, se localiza en una zona de San Juan (Colombia) en tan sólo 60 ha de territorio. Si recordamos el dato de nuestro grupo de estudio en Ecuador, donde un solo grupo de monos araña tiene un territorio de más de 450 ha, parece evidente que las diferencias comportamentales serán muy marcadas. En esta zona de Colombia, dos grupos luchan por sobrevivir ante la fuerte reducción de su hábitat que el ser humano ha provocado con su expansión. Un lugar donde incluso los miembros de este grupo presentan un comportamiento mucho más terrestre probablemente por la escasez de recursos y la fuerte competición entre los individuos del grupo y con los grupos vecinos, del mismo modo que presentan un comportamiento mucho más agresivo (Link, datos en preparación). El objetivo futuro de este estudio es llegar a comparar ambos grupos para conocer estas variaciones comportamentales de adaptación.

Otra de las causas más evidentes de reducción de este tipo de primates, como de muchos otras especies animales, es la llegada de la caza junto con los asentamientos que con el tiempo desarrollan nuevas formas y técnicas de batida. Debido al gran tamaño de los primates de la familia *Ateles* es frecuente que estos primates sean *target* dentro de las comunidades cazadoras rurales, siendo vulnerables ante una fuerte presión de caza (Ramos-Fernández & Wallace, 2008; de Thoisy *y cols.,* 2009). Por este motivo, y por la baja densidad encontrada debido a esta presión, Proyecto Primates incluso estableció su nueva toma de datos en un lugar más remoto (Estación Biodiversidad Tiputini), donde la observación de primates resultara algo más sencilla que en la primera zona de estudio donde este proyecto comenzó su investigación. Por este motivo, y por la gran importancia que tienen estas especies para los ecosistemas en los que habitan, es esencial llevar a cabo este tipo de investigaciones, donde la divulgación de los datos puede ayudar a reducir el impacto que tiene el ser humano sobre sus poblaciones. De este modo también se intenta al menos concienciar a la población humana de la inminente desaparición de las especies si no frenamos nuestro comportamiento devastador, que seguro traerá graves consecuencias negativas en el futuro.

CONCLUSIONES

En conclusión, los estudios descritos en esta tesis aportan información de primera mano que contribuirá a aumentar la base de conocimiento sobre la biología de estas especies. Tanto su estudio en términos de evolución como su importancia para el mantenimiento del bosque tropical, hacen de esta especie un interesante eslabón, foco de estudio y divulgación.

Esta investigación muestra ciertas características que aún no tienen una explicación evidente dentro del estudio del comportamiento y que llama a la necesidad de seguir trabajando en el estudio de la especie. No obstante, nuestros datos, junto con los estudios de los últimos años, nos ayudan a empezar a comprender y evaluar cómo se comporta esta especie en su medio natural.

Nuestros resultados mostraron una bajísima tasa de interacción, respecto a encuentros agonísticos, que no parece reflejar una marcada jerarquía, por lo menos entre los machos. Por el contrario, las hembras no mostraron una relación tan igualitaria como se había documentado anteriormente, siendo dos hembras diana de la agresión dentro de las hembras adultas y el contexto de agresión en muchos casos coincidió con episodios de alimentación. La baja tasa de agresión con respecto al tiempo que las hembras emplean forrajeando no permite afirmar una competición por los recursos clara, ya que las hembras en general son más solitarias. Sin embargo, al ser las dos hembras que llegaron más tarde al grupo diana de estas agresiones podría estar relacionado con cierto rechazo por parte de las hembras que llevan más tiempo.

Por otro lado, sí parece evidente la dominancia de los machos sobre las hembras quienes fueron actores del mayor número de agresiones, dirigidas en la mayoría de los casos hacia hembras adultas. A pesar de que este comportamiento había sido descrito como una estrategia de coerción sexual, siendo las hembras foco de agresión cuando estaban ovulando; en nuestro estudio no se vieron estas diferencias, siendo igual de probables las agresiones en cualquier estado reproductivo. Por tanto, no parece claro que estas agresiones busquen de manera directa el apareamiento con dichas hembras, ya que incluso encontramos agresiones a hembras con crías recién nacidas.

En este estudio, describimos además dos casos de posible infanticidio hacia dos crías macho, que se sumaron a los cinco únicos eventos documentado sobre este conducta en monos araña. Un comportamiento que aparentemente podría considerarse maladaptativo en una especie donde los machos están emparentados entre sí. No obstante, los diferentes casos que encontramos en la literatura sobre agresiones hacia crías macho, junto con estos sucesos descritos en esta investigación, empiezan a construir una base que podría indicar que este comportamiento es más frecuente de lo que se pensaba y que podría estar sesgado hacia los machos. Estos resultados podrían reflejar un mecanismo de “control social” regulando el número de hembras y machos en el grupo.

Por último, varias investigaciones han estudiado el papel de los saladeros en diferentes especies relacionando su visita con una función de adquisición de minerales o desintoxicación. En este caso, nuestro objetivo era estudiar la influencia de diferentes factores sobre el consumo de barro en el alto número de visitas que los monos araña realizan al saladero. Nuestros resultados mostraron que las hembras con el “territorio central” más alejado y que por tanto probablemente invierten más energía en su recorrido, eran más eficientes, aumentando además la probabilidad de consumo del grupo en las visitas donde estas hembras estaban presentes. Por otro lado, el número de individuos presente en el saladero influía positivamente en la visita, siendo más exitosas las visitas con un mayor número de individuos. Del mismo modo, parece establecerse una clara asociación, al menos pasiva, con otra especie de primate que visita el saladero. Aunque su frecuencia conjunta es menor que la frecuencia de visita de monos araña en solitario, la probabilidad de consumo aumentaba notablemente con la presencia de aulladores. El último factor estudiado fue el clima, que a pesar de haberse observado que tiene influencia sobre la posibilidad de visita al saladero, no parece tener influencia sobre el éxito de la misma. Por tanto, un alto número de individuos y la presencia de otra especie de primates en el saladero podría ayudar en la detección de alguna amenaza o riesgo de depredación, haciendo que el descenso para el consumo de barro sea probablemente más “seguro”. Cabe destacar, que el mejor predictor para el consumo parece ser la presencia de aulladores.

Finalmente, nuestro grupo de estudio realizó una incursión en el territorio vecino que aportó un enfoque diferente a lo que se había documentado en los patrullajes de monos araña. Todos los machos y cinco hembras con su descendencia se desplazaron por el territorio de otro grupo marcando una trayectoria directa y aparentemente conocida por los individuos que formaban el subgrupo, para hacer uso del saladero localizado en el territorio vecino. Este posible conocimiento del territorio podría ser fruto de experiencias pasadas como patrullajes o incluso podría ser el grupo de origen de algunas hembras. En cualquier caso, esta incursión parece mostrar que el objetivo de este evento no era la defensa del territorio sino el uso de este saladero, que podría manifestar cierta competición por los recursos. No obstante, la razón por la que hicieron uso de este saladero y no del suyo propio no deja de ser una incógnita.

El estudio de las relaciones y estrategias sociales y reproductivas que los monos araña presentan nos acerca a la comprensión de una especie que vive dentro de un hábitat que se encuentra amenazado. Entendiendo un poco más sus necesidades, su importancia y el equilibrio que estas especies aportan al resto de los ecosistemas podemos ayudar a planificar gestiones que ayuden a mantener las diferentes poblaciones. Gracias a los datos de diferentes proyectos de investigación, hoy sabemos que el Parque Nacional Yasuní es uno de los lugares más biodiversos del planeta y que la actual lucha para frenar la explotación de este lugar ha unido a muchos investigadores para hacer de la divulgación el punto de partida hacia la conservación. A pesar que los pasos son pequeños y que aún nos queda mucho por hacer, pequeños logros pueden ayudar a concienciar sobre la situación de nuestros bosques, y de este modo quizá, aunque sólo “quizá”, futuras generaciones puedan ser testigos de la gran riqueza que todavía posee nuestro planeta Tierra.

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