

Sex Differences in the Social Behavior of Wild Brown Spider Monkeys (*Ateles hybridus*) at a forest fragment in the Magdalena River Valley, Colombia

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Abstract

Spider monkeys live in multimale multifemale groups where females are responsible for parental care, hence having higher energetic costs than males, therefore females' reproductive success is limited by food availability. On the other hand male spider monkeys reproductive success is limited by the number of females available for mating. Thus, male and female social strategies in spider monkeys have been proposed to be quite different. Spider monkeys have fission-fusion dynamics, which have been suggested to reduce intragroup competition for food in females, who tend to be solitary. Males are philopatric and tend to have stronger affiliative behaviors that help them to cooperatively maintain group coercion and face high intergroup competition. We studied a group of brown spider monkeys (*Ateles hybridus*) in a forest fragment in the Magdalena Middle Valley (Colombia) to determine if individuals are flexible in their social behavior when stressful conditions are increased due to reduced resource availability and high primate densities in a limited space. Our results for activity budgets were consistent and similar to those observed in other studies (Fedigan & Baxter, 1984; Slater et al., 2009), where females tend to allocate more time feeding than males to cope with the higher energetic demands that nursing

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infants require. We found that affiliative behaviors are predominant amongst males, and there is a clear pattern of male-to-female directed aggressions. These affiliative behaviors help males to reinforce their bonds in intergroup encounters for territorial defense, and female-directed aggressions may be acting as a mechanism of “social control” as part of an indirect form of sexual coercion (Link et al, 2009). Female affiliative social behaviors are higher than those observed for other species of *Ateles* in undisturbed forests (Slater et al., 2009), suggesting that stressful conditions due to low resource availability is forcing them to employ stress release mechanisms. The fact that there are very few differences between fragmented and continuous forests, imply that spider monkeys have high flexibility in their social behavior to respond to low resource availability. Nonetheless, it is thought that this might change in the near future, as fragmentation continues to increase, probably altering the social dynamics of this critically endangered species.

Key words: *Ateles*, social behavior, aggression, fragmentation, sex differences

Introduction

Spider monkeys live in a multimale-multifemale social system, where the mating system is characterized by being promiscuous (Carpenter, 1935). As in most primates, female spider monkeys are responsible for parental care, therefore females’ energetic cost for reproduction is higher than that of males’ (Coelho, 1986; Coelho at al., 1979; Altmann & Samuels, 1992; Leonard & Robertson, 1997; Key & Ross, 1999). In this scenario, female reproductive success is mostly limited by resource availability, while male reproductive success will largely depend on the number of estrous females available for mating. Spider monkeys have unique grouping patterns characterized by being very flexible as stable social groups generally travel and forage in smaller subgroups that frequently change their size and composition (Klein 1972; Symington 1987, 1990). This “fission-fusion” grouping patterns have been proposed to optimize individual fitness as they allow member of the social group to join or leave a subgroup under different social and ecological scenarios (Lehmann & Boesch, 2004). In groups with fission fusion grouping patterns (Wrangham, 1977; Symington, 1987) females might benefit because foraging in smaller groups implies less resource competition (Lehmann, 2007), and for males because competition for

access to mating females is reduced (Strier, 1994; Fedigan & Baxter, 1994). This is important due to the fact that females have to invest more energy in offspring and nursing, therefore reducing competition for resources will imply less energetic cost in travelling long distances to find food; and it also reduces competition amongst males for ovulating females, hence creating stronger affiliative bonds within the group (Strier, 1994; Link *et al.*, 2009).

In societies such as chimpanzees and spider monkeys, affiliative bonds are also thought to be stronger within males than within females, given that females are the dispersing sex while males are philopatric (Symington, 1987, 1988; Vigilant *et al.* 2001; Di Fiore & Campbell, 2007; Shimooka *et al.*, 2008; Di Fiore *et al.*, 2009). This type of social structure turns out in males who are more social amongst them, and less social females, who tend to be more solitary, reducing intragroup competition for resources (Lehmann, 2007). Given that spider monkeys live in a polygamous mating system where there is no conspicuous sexual dimorphism (Carpenter, 1935) sexual differentiation in social behavior becomes important in determining the social structure of the group.

Previous studies in other *Ateles* species have shown marked differences between male and female social behavior (Fedigan & Baxter, 1984; Shimooka, 2005; Slater *et al.*, 2009; Link *et al.*, 2009). In general terms, males present wider home ranges and a higher number of affiliative interactions amongst them than females, and a clear pattern of male to female directed aggressions from males; which indicates that there are clear differences in the social behaviors between both sexes.

All of these previous studies have been held in continuous forests where resources such as food and spatial availability are not limited. Nonetheless, in forest fragments where there are limited resources, females will be affected by the low resource and spatial availability; hence they will be restricted in their foraging activities generating a more intense competition regime amongst them. Understanding how same-sex associations and different-sex associations towards food search and food consumption may indicate to which extent are these monkeys changing their behavior due to processes associated with habitat disturbance and intervention. These patterns will help to determine the species' behavioral flexibility and their strategies to tolerate the stressful conditions of living in a reduced forest fragment.

As one of the 25 most endangered primate species in the world (Palacios and Morales-Jimenez, 2007), it is urgent to determine how is fragmentation and habitat degradation affecting the remaining wild population, since *Ateles hybridus* has been identified as a critically endangered species, comprising a very restricted distribution in Colombia and Venezuela, and experiencing a decline of 80% over the past 45 years because of hunting and habitat loss primarily (IUCN, 2008). Very little is known about their biology, since only recently *Ateles hybridus* was recognized as a species (formerly known as *Ateles belzebuth hybridus*), by Collins and Dubach (Collins, 1999; Collins and Dubach, 2000).

In this comparative study we studied the social behavior of spider monkeys in a forest fragment. We assessed for the differences in social behavior of male and female spider monkeys in order to understand their behavioral flexibility when exposed to fragmentation and more intense competitive regimes. To achieve this, we aimed our study in (1) determining the behavioral patterns of male and female brown spider monkeys and quantifying their social interactions (e.g. affiliative bonds or antagonistic behaviors), that could mitigate (or not) the increased levels of direct competition within them; and (2) studying the general behavioral ecology of spider monkeys in forest fragments (e.g., diet, ranging behavior) and compare them with patterns observed in continuous forests of other studies.

Methods

Subjects and Study Site

We collected behavioral data from June 2009 to July 2010, in the private landfarm of San Juan de Carare, located at the east bank of the Magdalena River, in Santander department of Colombia (6°50'N, 74°18'O). The study site is a 60 hectare rainforest fragment recently isolated from other forest fragments along the San Juan River. The forest fragment is within a matrix of pastures for cattle ranching and seasonally flooded savannas. Although two groups of brown spider monkeys (SJ-1 and SJ-2) are found in the fragment, this study focused on only one of them.

Ecological and behavioral data were collected from one habituated group (SJ-1) of brown spider monkeys (*Ateles hybridus*) in the forest fragment, comprising six

adult females, five adult males, and a total of 18 individuals including sub-adults, juveniles and infants. Due to the disappearance of one adult male and one adult female around April 2010, during the last three months of the study there were only five adult females and four adult males in the study group.

Data Collection

Spider monkeys were followed from dawn to dusk and twenty-minute focal animal samples were used to record detailed behavioral data on all adult members of the study group. Focal subjects were chosen randomly amongst the adult and subadult members of the group and excluding juveniles and infants. Subsequent samples on the same individual were done with at least one hour from the end of the first focal sample, and all individuals of the subgroup were sampled before repeated samples of the same individual were attempted. Incomplete focal samples that had less than half ($n = 5$) of the sample's instantaneous records were not included in the analyses. In each 20 minute focal sample, we recorded instantaneous records at two minute intervals on the main activity of the focal animal using four basic categories: moving, resting, feeding and socializing. In between the 2-min instantaneous records of each focal sample we recorded all social interactions involving the focal animal through an all-occurrence sampling. We estimated the rate of occurrence of several affiliative and antagonistic social behaviors, such as approaches, embraces, arm-wrapping and aggression and assessed for differences in the rate in which males and females initiated or received each of these behaviors. Finally, for each focal sample we recorded detailed data on subgroup composition.

In this study we assessed for the rates of particular behaviors previously used to evaluate differences on the social behavior of male and female spider monkeys (Fedigan & Baxter 1986; Slater et al. 2009). Within affiliative behaviors we calculated the rate of approaches, embraces, arm-wrappings and grooming between all potential dyads in the study group. Approaches were considered when a spider monkey came within < 2 meters from another adult individual, and proximity was the time spent in this distance range after the approach. Embraces included those events where one individual placed both arms around another individual, in a non-sexual context, and differs from arm-wrapping as the latter takes place primarily during

coalitionary aggression involving two individuals who wrap their arms around each other by their shoulders.

We included all aggressive interactions, such as chases, lunges, threats, as antagonistic behaviors. In spider monkeys aggression often occurs when one or more individuals force another individual to move towards the ground along a tree trunk, often accompanied by displays, grunt vocalizations of branch movement or showing their teeth to the victim (Link et al. 2009). Chases were those events in which one individual rapidly followed another individual making him move rapidly from their position in a sense of escaping from the attacker. Lunges were those cases in which one individual directed its arm violently to another individual, and threats were defined as those events in which an individual initiated social displays by shaking branches or showing teeth towards another individual although it didn't involve any movement of the attacker towards the victim.

Data analysis

Sex differences in the proportion of time spent by male and female spider monkeys moving, resting, feeding and socializing were derived from the two-minute instantaneous records for each individual. In order to control for the lack of independence between points collected in a single focal sample, for each focal sample we calculated the number of 2-min instantaneous samples spent by the focal in of the four activity categories, and treated each focal sample as a datum for analyses. All affiliative and agonistic behaviors described above were considered social activities. In order to test for differences in the time spent by males and females in each activity, we performed a Mann-Whitney U-Test adjusting the level of significance through a Bonferroni's correction, thus establishing a critical value at $P < 0.001$.

In order to assess for differences on the rates of social events initiated and received by male and female spider monkeys, we calculated the number of times each affiliative and agonistic event took place within each focal sample, and noted the directionality of each event. We replicated the methods described by Slater et al., (2009) using the sum of the rates across all the group's dyads in order to obtain the hourly rates of each type of social behavior. Data for hourly rates were normalized using the $\sqrt{(x+0.5)}$ transformation (Keppel & Wickens, 2004), where x corresponds to the average rate of a particular social behavior. After transformations were done, we

did a one-way ANOVA in order to assess for significant differences in the hourly rates and percentage of time spent in each social activity, followed by Tukey's HSD Test to assess for differences between the type of dyads involved in the interactions. In cases where there were no data for more than one type of dyad, such as the rate of arm-wrappings or the percentage of time observed playing, we did independent t-tests.

For those behaviors for which we could measure their exact duration, such as time in proximity and grooming, we calculated the percentage of time each focal spent in that specific behavior. For each type of dyad (e.g., male to male) we calculated the average percentage of time spent in proximity or grooming. For statistical analyses these percentages were normalized using the arcsine transformation (Fowler et al., 1998). A one-way ANOVA was used with a *post hoc* Tukey's HSD Test to test for differences in the interactions amongst dyads. All statistical analyses were done in SPSS 15.0 program.

Results

We collected a total of 1448 focal samples, distributed in 815 samples on females and 633 samples on males, corresponding to approximately 272 and 211 focal animal hours, respectively. We found no differences in the proportion of time male and female spider monkeys spent in each activity (Fig. 1), except in the category for "Others" which includes displays to the observer predominantly ($U = 0.00$, $p = 0.006$). Nonetheless, the results on differences between males and females in the time they spent feeding, nearly reached significance ($U = 2.00$, $p = 0.017$).

We found a clear pattern for aggression within brown spider monkeys at San Juan. Males initiate most of the aggression, corresponding to nearly 80% ($N = 67$) of all aggression recorded in the study group, and in a similar pattern to that described for spider monkeys elsewhere (Fedigan & Baxter 1994; Slater et al 2009; Link et al 2009). In fact, female directed aggression by males accounted for most antagonistic interactions observed in this study. Males received only a minor proportion of the aggression and only 3 cases of male-to-male aggression were recorded during the study period. Within affiliative events, males initiated approaches, embraces and

grooming more frequently than females, but females also initiated many of the affiliate interactions within spider monkeys (Fig 2).

From the data collected on the average hourly rates across males and females of the study group, we found that male-to-female approaches are significantly higher than the average rate of approaches initiated by females, and males have overall higher rates of initiating approaches than females do (Fig. 3a.). Despite that the number of male-to-female approaches almost doubles any other type of interaction of this type, males tend to spend more time in proximity with other adult males compared to the time spent in proximity between females and between mixed-sex dyads. Female-female dyads spent the lower percentage of time in proximity (Fig. 4a.). our results evidence that grooming generally takes place predominantly when at least one male is involved in the interaction, meaning that this behavior is relatively uncommon between adult females (Fig. 3b.). Although average hourly rates are higher for female-to-male grooming interactions (for the number of events and duration) (Table I), Figure 4b. shows that there is a tendency for males to spend more time grooming other males than any other type of dyad. Embraces amongst individuals show no significant differences between the sexes, but females tend to embrace males less frequently (Fig. 3c.).

Hourly rates for antagonistic social events show the same patterns observed in Figure 2, with a pronounced tendency towards female directed aggression by males which differs significantly from rates of aggression amongst any other type of dyads ($p < 0.05$) (Fig. 3d.).

Arm-wrapping was an uncommon behavior within the members of our study group, where we observed that only same sex partners displayed this behavior (N=4, two for each same sex dyad), having no significant differences between them ($p=0.600$). Social play was more common between two males than in opposite sex dyads, and was never observed amongst two adult females (Table I).

Discussion

Sex differences in activity budgets

Overall, male and female brown spider monkeys at San Juan de Carare had similar activity patterns. Except for behaviors such as displays to observers included within the “others” behavioral category, there were no statistical differences in the proportion of time that males and females spent during moving, resting, feeding and socializing. Nonetheless, the differences in the proportion of time male and female spider monkeys invest in feeding near reached significance, evidencing a similar pattern to that described for spider monkeys in previous studies (Slater et al. 2009). The fact that females tend to invest more time in foraging activities in spider monkeys and other taxa has been suggested to be influenced by the fact that feeding resources is one of the most important variables constraining female reproductive success (Lee, 1987; Sterck et al., 1997). Activity budgets obtained for brown spider monkeys at San Juan are relatively similar and within the range of most other wild spider monkey populations living in undisturbed habitats (Di Fiore et al., 2008).

Sex differences in social behavior

The behavior of male and female brown spider monkeys living in a small forest fragment characterized by having an extremely high primate population density (Link et al. 2010), closely resembled that observed at other populations of spider monkeys studied in undisturbed forests of Central and South America (Fedigan & Baxter 1984; Link et al., 2009; Slater et al., 2008, 2009). The most clear and consistent behavioral pattern observed was that female directed aggression by male spider monkeys was the most common form of aggression, accounting for over 75% of all aggression events observed during this study. Female directed aggression generally takes place with a stereotyped pattern of aggression by which one or several males direct “low intensity aggression” (sensu Link et al. 2009) towards one female who attempts to escape and is often chased down the tree trunk even to the forest floor. Aggression can take place in the form of chases, grabbing, open mouth threats and even soft bites that do not seem to have the intention of inflicting an injury to the aggressed female. These aggressions occasionally takes place in sexual contexts where males aggress females before and/or after copulation is observed, more often than in feeding contexts, suggesting that male to female aggressions do not respond to a food competition interest. During female directed aggression females evidence stress and often defecate and vocalize while being chased or threatened by males (Link et al., 2009; Slater et al., 2009).

Female directed aggression is common within brown spider monkey societies and consistent with the general aggression patterns described for all other species of spider monkeys (*Ateles geoffroyi*: Campbell, 2003; Fedigan & Baxter 1984; Slater et al., 2009; McDaniel 2004; *Ateles belzebuth*: Klein, 1972; Symington, 1987; Link et al. 2009; and *Ateles paniscus*: van Roosmalen & Klein, 1988). The generalized pattern of female directed aggression by males in all species of extant spider monkeys suggests it might be an ancestral behavior within the spider monkey lineage. Cooperative aggression from males to females has been suggested to act as a mechanism of “social control” as part of an indirect form of sexual coercion (Link et al, 2009), and is part of the repertoire of cooperative behaviors displayed by spider monkey males that have been suggested to allow the group’s males to “gain long term reproductive benefits by maintaining the integrity of the community range” (Symington, 1987).

During our study on brown spider monkeys at San Juan, male directed aggression was relatively rare, accounting only for approximately 10% of all observed aggression. Nonetheless, most of these aggressions were directed towards the youngest members of the group both by other adult males and females. High intensity aggression (sensu Link et al., 2009) towards subadult males has been reported at some other populations of spider monkeys (Campbell, 2006; Valero, 2006). Previous studies on wild primates where males are philopatric and where there is a high degree of fission-fusion dynamic, such as chimpanzees *Pan troglodytes*, spider monkeys *Ateles spp.* and even on a small scale in human societies (Fedigan & Baxter, 1984; Hohmann & Fruth, 2002; Newton-Fisher, 2002; Strier et al., 2002; Slater et al., 2009), have evidenced that males tend to have stronger affiliative bonds amongst them, than with females or between females. It has been proposed that these affiliative interactions between males play an important role in maintaining strong bonds and group coercion needed in a context of high inter-group competition (Link et al., 2009). Di Fiore (2009) has also suggested that in philopatric systems, the non-dispersed sex has higher genetic relatedness than the dispersed sex; therefore, stronger affiliative bonds between male spider monkeys may be the result of their higher relatedness, hence kin relationships could be playing a role in these type of interactions (Silk, 2005).

The pattern of affiliative interactions between male and female brown spider monkeys at San Juan revealed a different pattern to the pattern observed in other

studies (Slater et al., 2009). Males are the most common initiators of the approaches and in fact females rarely initiate approaches or embraces towards adult males. Nonetheless, female-to-male grooming events had a higher rate than any other type of dyad. We suggest that this behavior of females might act as a mechanism to reduce tension and possible aggressions from males (Aureli, 1999; Wittig et al., 2008).

Grooming, as a way to release stress, has been observed in other primate species and even humans (Aureli et al., 1999; Wittig et al., 2008). This could explain why in a small fragmented forest, with high population density and limited space, females have higher grooming rates than in undisturbed forests where female-to-female affiliative interactions are very rare, almost absent (Slater et al., 2009). Higher rates of female-to-female aggression in feeding contexts (Slater et al., 2009) suggest that female spider monkeys compete principally for food resources, and in forest fragments limited access to fruits can become a stressful situation. Therefore female grooming can also act as a way to cope with stressful situations such as increased intragroup competition for food.

Overall, the social behavior of male and female spider monkeys greatly resemble that of other studied population, even when considering the differences in human intervention and habitat disturbance amongst sites. At the small 60 h forest fragment in San Juan there are still two groups of spider monkeys: SJ-1 (our focus study group) and SJ-2. The fact that there are no big differences in the males' behavioral patterns between fragmented and undisturbed forests, suggest that given that there is still another group present in the fragment, the pressure of males for defending their resources (females available for mating and territory), maintains their social behavior relatively unaltered. Nonetheless, females might be starting to evidence different behavioral patterns to those expected in undisturbed habitats, having higher grooming rates that could be acting as a stress release mechanism to cope with the increased intragroup competition. Given that brown spider monkeys are considered to be critically endangered, and that a large proportion of its population is currently living in habitat with increasing fragmentation and habitat disturbance, it is relevant to increase our understanding on the effects of these processes on spider monkey social behavior and structure, as well as to know how flexible spider monkeys are to adapt to different ecological and social scenarios. This understanding will result key in the designing and implementation of successful conservation strategies to

prevent endangered species, such as the brown spider monkey to continue on their population decline and verge to extinction.

Acknowledgements

We are extremely grateful with the Lalinde and de Greiff families for supporting our research on the primate community at San Juan. Felipe Alfonso and Rebecca Rimbach for helped us with the data collection, and Dr. Pablo R. Stevenson and Gabriela de Luna for their comments and guidance during data analysis. We greatly appreciate the generous financial support received from Ecopetrol Biodiversity Grants, Fundacion Proyecto Primates, the Primate Society of Great Britain and Idea Wild.

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Tables and Figures

Table I. Mean (\pm S.E.M.) values for hourly rates and percentage of time spent in social interactions across all possible dyads. Comparisons where done with a One-Way ANOVA, with an *a posteriori* Tukey HDS Test (superscript letters). Comparisons for mean values with only two types of interactions (Hourly rates for Arm-wrapping and Percentage of time spent in Play) where performed using an Independent *t*-Test.

Behavior	Male actor		Females actor		One-way ANOVA	t-test
	Male receives	Female receives	Male receives	Female receives		
Approach (hourly rate)	0.56 \pm 0.08 ^{a,b}	1.02 \pm 0.22 ^a	0.43 \pm 0.05 ^b	0.26 \pm 0.05 ^b	F=7.74, P=0.002	-
Embrace (hourly rate)	0.18 \pm 0.05	0.17 \pm 0.05	0.04 \pm 0.02	0.13 \pm 0.03	F=2.81, P=0.069	-
Grooming (hourly rate)	0.50 \pm 0.10	0.46 \pm 0.09	0.54 \pm 0.15	0.18 \pm 0.11	F=2.48, P=0.094	-
Arm-wrapping (hourly rate)	0.012 \pm 0.008	0.000 \pm 0.000	0.000 \pm 0.000	0.007 \pm 0.007	-	t (11)=0.54, P=0.600
Aggression (hourly rate)	0.03 \pm 0.02 ^a	0.49 \pm 0.17 ^b	0.03 \pm 0.01 ^a	0.04 \pm 0.03 ^a	F=8.85, P=0.001	-
Grooming (% of time)	2.43 \pm 0.43	2.41 \pm 0.66	2.74 \pm 1.54	1.23 \pm 1.10	F=0.10, P=0.397	-
Proximity (% of time)	5.49 \pm 1.38	4.54 \pm 1.53		2.47 \pm 0.83	F=2.99, P=0.059	-
Play (% of time)	0.06 \pm 1.38	0.04 \pm 1.53		0.00 \pm 0.00	-	t (45)=1.11, P=0.273

Fig. 1. Mean percentage of the activity budget that males and females spent in different behaviors in the overall observation time. Level of significance modified using Bonferroni's correction (* $P < 0.001$).

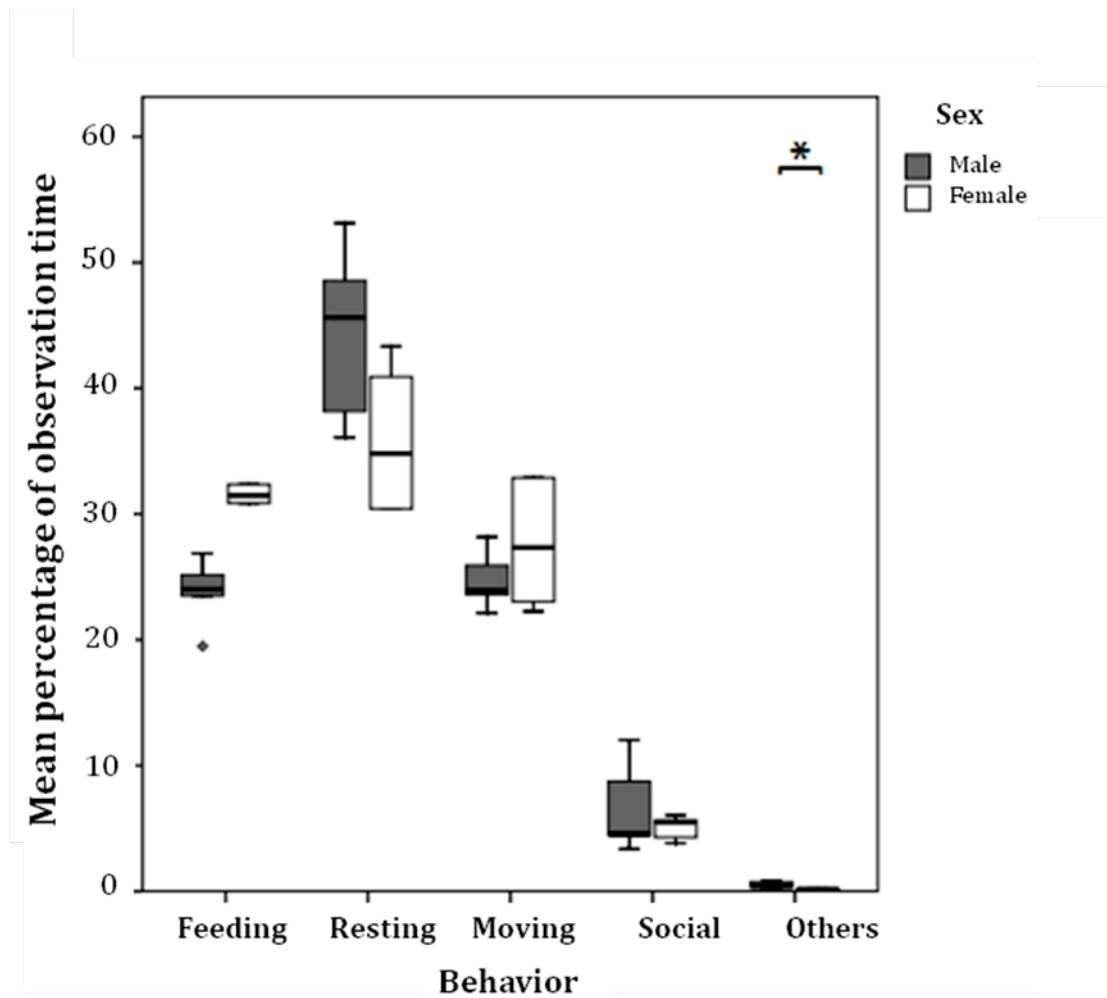


Fig. 2. Social events of males' and females' interaction to same sex and opposite sex individuals. Percentages (y-axis) and total number of events (in brackets) recorded for affiliative (Approaches, Embraces and Grooming), and antagonistic (Aggressions) events.

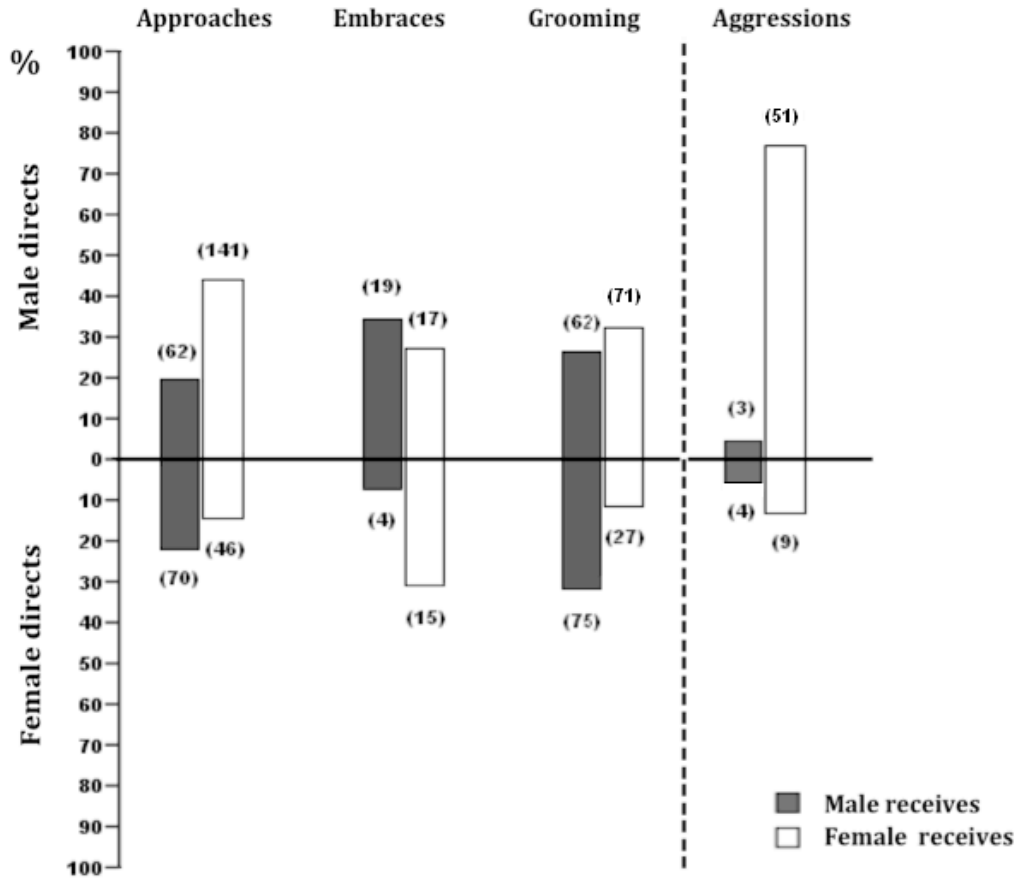


Fig. 3. Average rate of (a) Approaches, (b) Grooming, (c) Embraces and (d) Aggressions per Hour.

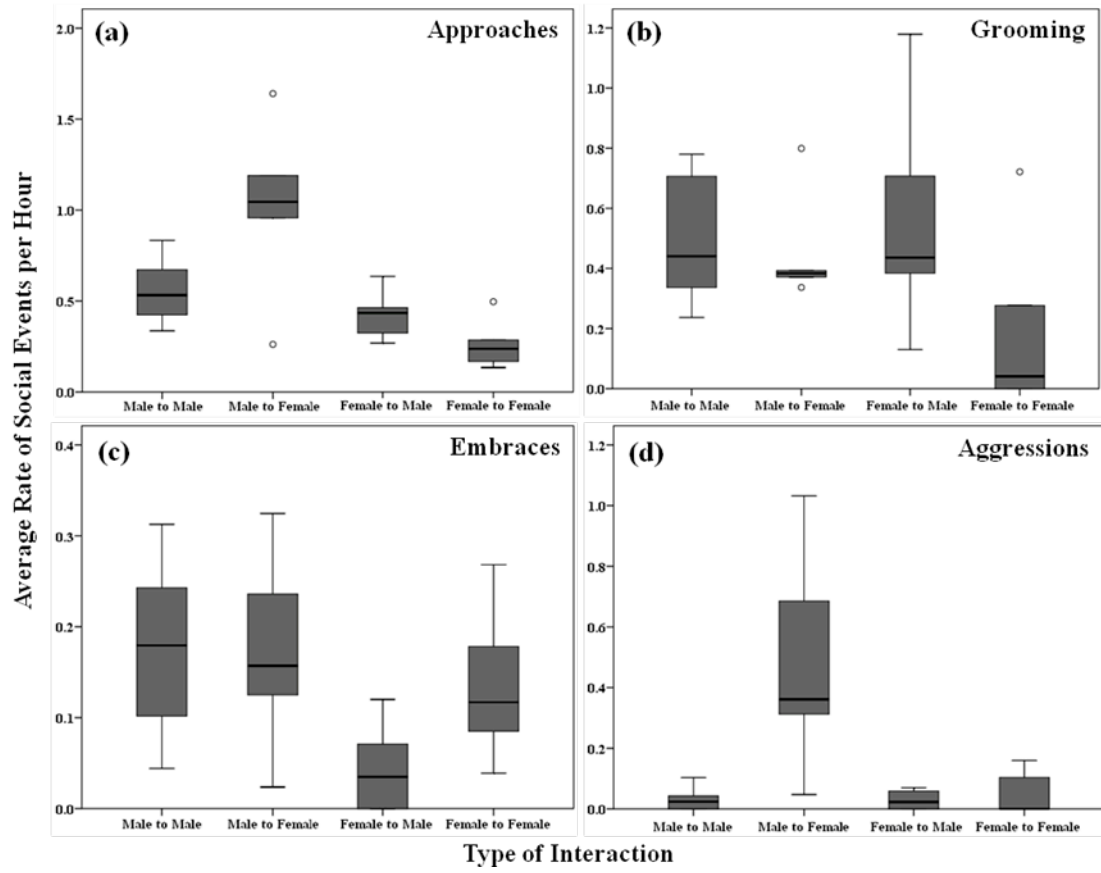


Fig. 4. Average percentage of Observation Time spent in (a) Proximity and (b) Grooming per Hour.

