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EMERGENCE OF SEX-SEGREGATED BEHAVIOR AND ASSOCIATION PATTERNS IN JUVENILE SPIDER MONKEYS

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Abstract

Sex-segregation occurs in a number of mammals, and is typically attributed to differences in body size, reproductive energetics, or social roles. Although most primates remain in cohesive groups, spider monkeys exhibit fission-fusion dynamics and sex-segregated association patterns. Here, I present results on sex differences in behavior and subgrouping in juvenile spider monkeys. I found that the monkeys exhibit several aspects of sex-differentiated behavioral and grouping patterns that emerge despite the fact that both sexes ranged with their mothers. I conclude that juvenile spider monkeys exhibit sex-segregated behavior and association patterns earlier than previously reported for this species. Because the hypotheses regarding body size dimorphism and reproductive energetics do not apply to these juveniles, I attribute these differences to social roles.

Key Words: *Ateles,* juveniles, fission-fusion, social behavior, social play, sex-segregation

Resumen

La segregación por sexo ocurre en un número de mamíferos y es típicamente atribuida a diferencias en tamaño corporal, aspectos energéticos de la reproducción, o roles sociales. Aunque la mayoría de primates permanecen en grupos cohesivos, los monos araña exhiben dinámicas de fisión-fusión y patrones de asociación por segregación de sexos. Aquí presento resultados de diferencias de comportamiento por sexos y formación de subgrupos en monos araña juveniles. Encontré que los monos araña exhiben varios aspectos comportamentales y patrones de agrupamiento diferenciados por sexo que emergen a pesar del hecho de que ambos sexos se desplazaban con sus madres. Concluyo que los monos araña juveniles exhiben un comportamiento segregado por el sexo y patrones de asociación más tempranos que los previamente reportados para esta especie. Debido a que la hipótesis del dimorfismo por tamaño corporal y la energética de la reproducción no aplica a estos juveniles, atribuyo estas diferencias a los roles sociales.

Palabras Clave: *Ateles***,** juveniles**,** fisión-fusión, comportamiento social, juego social, segregación por sexo

Introduction

Sex segregation occurs in a number of vertebrates, and is associated with divergence in body size, social roles, reproductive energetics, or dispersal patterns (Conradt, 1999; Main, Weckerly, & Bleich, 1996; Sterck, Watts, & van Schaik, 1997). Unlike other mammals, sex segregation is rare in primates (Aureli et al., 2008; Chapman, Chapman, & Wrangham, 1995; Watts, 2005). Patterns of sexual segregation in spider monkeys are attributed to a combination of social and energetic factors. Males engage in social behaviors that optimize access to mating opportunities, including coalition building, achieving dominance, and territorial behavior, whereas females increased foraging efforts while remaining in core areas to protect offspring and reduce travel costs (Wrangham, 1980; Chapman et al., 1995; Watts, 2005).

The divergent spatial structure of spider monkey populations may pose several cognitive and social challenges to individual animals (Aureli et al., 2008; Barrett, 2003), which are likely intensified for immatures. Whereas juveniles in cohesive groups may have several opportunities to interact, in dispersed groups they may be constrained by maternal behavior (i.e., ranging and grouping patterns). Given that males and females face different social challenges as adults (Trivers, 1972; Wrangham, 1980), preparation for these challenges during the juvenile period may be important, especially if early preparation increases adult fitness. Preparation may include sex segregation during this life stage. In chimpanzees, immature males socialize with a wider variety of conspecifics, whereas immature females concentrate social interactions with their mothers,

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and develop social and foraging patterns that reflect these associations (Pusey, 1983, 1990). Vick (2008) reports similar social patterns for immature spider monkeys. However, these trends are significant only when including subadults, or when specifically comparing the oldest juveniles and subadults (ages 42-60 months). Thus, it is unclear whether differences remain when only considering juveniles (ages 15-50 months –[age criteria following Van Roosmalen and Klein, 1988]).

In this study I describe the juvenile social structure of a wild population of black-handed spider monkeys (*Ateles geoffroyi*) in Costa Rican lowland rainforest. Because adults face differential energetic and social constraints, I predict female juveniles will spend more time foraging to gain ecological competence, whereas males will spend more time socializing to gain social skills. Based on the hypothesis that juvenile social behavior prepares for adult social roles, I predict that juveniles will exhibit the sex-typical patterns of social behavior reported for adults, but exhibit similar subgrouping patterns.

Methods

I conducted behavioral observations from 23 December 2005 - 5 January 2006, and from 12 May 2006 - 2 August 2006 at El Zota Biological Field Station in Costa Rica. El Zota is situated in the northeast of the country at 10°57.6 N, 83°75.9'W (Lindshield & Rodrigues, 2009; Pruetz & LaDuke, 2001). This area receives approximately 4000 mm of rainfall annually and exhibits mild seasonality. Research was conducted on the Pilón group, the best-habituated of two *A. geoffroyi* populations at El Zota (Rodrigues, 2007). This population (n = 30) ranges through the southeastern portion of the property, in an area composed of secondary and swamp forest, gallery forest, and plantation (Lindshield, 2006).

Observations were made on eight juveniles, defined as individuals approximately 15-50 months old who travel independently of the mother but remain in close contact and range with her (Van Roosmalen and Klein, 1988). There were two J-1 females, two J-1 males, one J-2 female, two J-2 males, and one J-3 female. The sex of juveniles is easily distinguished by the pendulous clitoris of the females, and age was assessed visually based on Roosmalen and Klein's (1988) criteria. Focal subjects were individually identified on the basis of external characteristics, including body size, sex, facial features, and pelage.

Data collection

Two-minute instantaneous focal sampling was used to collect data on focal individuals (Altmann, 1974). Due to loss of contact with focal subjects, focal observation length varied (48.8 ±52.0 min). All individuals were observed between 0530 and 1,830 h, with 53.9% of focal data collected in the morning and 48.1% collected in the afternoon. The following data were collected from each individual: 1) identity and activity of focal animal, 2) identity of all visible party members, 3) initiator/recipients of social interaction, and 4) type of social interaction. Activities included travel, rest, feed/forage, social interactions, and "other" behaviors (object manipulation, tool use, solitary play). Social interactions were classified into affiliative behaviors (huddle, embrace, touch, groom, play, whinny, nurse, cling, or bridge) and agonistic behaviors (avoid, displace, chase, harass, display, fight, weaning rejection, or distress vocalization). Following Ramos-Fernández (2005), party was defined as a group of individuals which associated with each other and remained within 30 meters of one another. Party sizes were calculated using individually locomoting individuals (ILI), in which dependent infants are not counted as separate individuals (Weghorst, 2007).

Data Analysis

A total of 74.5 hours of instantaneous focal data were collected (males: 36.3 hours; females: 38.20; mean±SE: 8.06±2.48 hours) and I collected all-occurrence data of focal social behavior during each focal sample (Altmann, 1974). Behaviors that were typically brief, including maternal care (nurse, cling, bridge), agonism, and whinny are reported as events/hour, and behavioral states that occurred for variable durations of time, including groom, huddle, and play, are reported as minutes/hour. Although maternal care behaviors such as nurse and cling were occasionally longer in duration and could be considered states, they were typically brief and thus treated as events. Time spent in play (min/hr) between same- and opposite-sex play partners was corrected for time spent in parties with potential partners and analyzed using Wilcoxon signed-rank tests. Activity budgets were compared using chi-square tests. All other behavioral data were compared using Mann-Whitney U tests, and statistics were run in SPSS statistical software (SPSS Inc., Chicago, IL, USA). Significance threshold was set at $\alpha = 0.05$. All test results are reported as mean ± SE, with N=8 and two-tailed p-values. Following the suggestions of Nakagawa (2004), effect size *(r)* and 95% confidence intervals (C.I.) are presented for the Mann-Whitney and Wilcoxon tests. All activity variables are presented as percentage of total behavior (mean ±SE).

Results

Activity budgets

Male and female engaged in comparable amounts of each activity category (χ^2=8.0, p=0.333, df=7, for all activity categories).

Social behaviors

Social behavior consisted predominantly of play, grooming, huddling, and whinnying (Fig. 1). Male and female juveniles did not differ in grooming (females: 2.34±0.49 min/hr; males: 1.01±0.63 min/hr; U=3.00, p=0.146,

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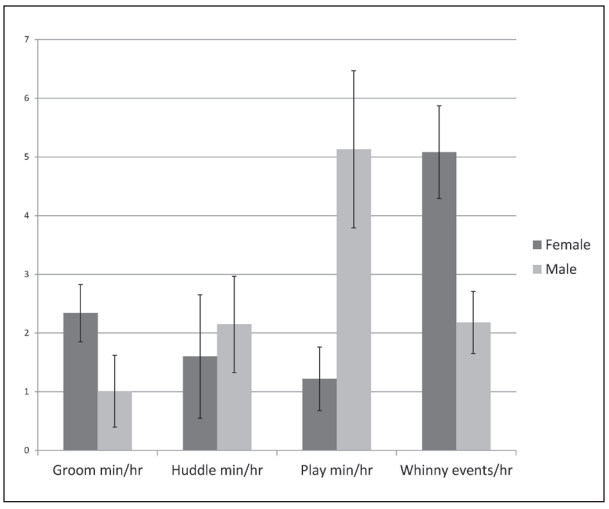


Figure 1. Sex differences in social behaviors for female and male juvenile spider monkeys.

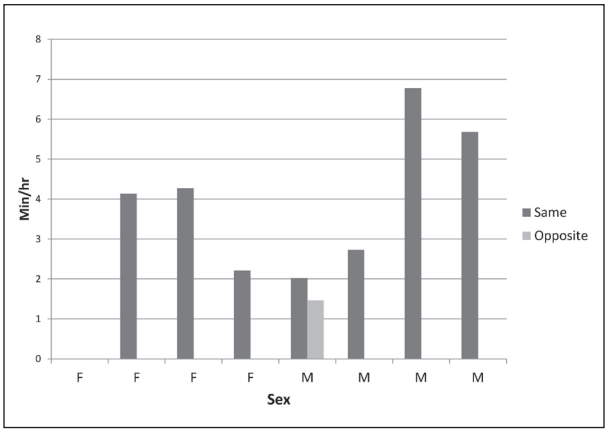


Figure 2. Same vs. opposite sex play partners for female (F) and male (M) juvenile spider monkeys.

r=-0.182, C.I.= -0.786 ± 0.600) or huddling (females: 1.60±1.05 min/hr; males: 2.15±0.82; U=12.00, p=0.248, *r*=0.144, C.I.= -0.624±0.770) rates. Males however tended to play more often than females (females: 1.22±0.54 min/hr; males: 5.13±1.34 min/hr; U=14.00, p=0.083, *r*=0.217, C.I.= -0.576± 0.799). Females whinnied more than males (females: 5.08±0.79 events/hr, males: 2.18±0.53 events/hr), and this difference was significant (U=-0.00, p=0.026, *r*=0.289, C.I.= -0.522± 0.825).

Juvenile males and females did not differ in their total amount of grooming. However, only the juvenile females groomed other conspecifics (females: 0.22±0.11 min/hr; males: 0.00±0.00), and this difference was significant (U=2.00, p=0.047, *r*=-0.2.48, C.I.=-0.811± 0.553). Juvenile females received more grooming than juvenile males, but this difference was not significant (females: 1.04±0.19 min/hr; males: 0.50±0.31; U=4.00, p=0.245, *r*=0.109, -0.6453± 0.756). Focal subjects played with juveniles of the same sex significantly more than juveniles of the opposite sex (W=0.00, p=0.018, *r*=-0.300, C.I.= -0.829± 0.513; Fig. 2).

Maternal Care

No difference in maternal care was observed (females: 1.54±0.75 events/hr; males=2.31±1.69 events/hr; U=-9.00, p=0.773; *r*=0.036, C.I.= -0.686± 0.7224). Younger juveniles (J-1: 3.46±1.39) received more maternal care than older juveniles (J-2 and J-3: 0.38±0.10), and this difference was significant (U=0.00, p=0.021, *r*=-0.289, C.I.= -0.522± 0.825).

Party Size and Composition

Juvenile males were in larger parties than juvenile females (females: 2.70± 0.43 ILI; males: 3.83±0.97 ILI; U=16.00, p=0.021, *r*=0.288, C.I.= -0.522± 0.825). Individuals of both sexes spent the majority of their time in parties with their mother (females=100.00±0.00%; males=98.25±01.75%). Moreover, juvenile males exhibited a non-significant trend spending more time in parties containing adult males (females=4.03±2.57%; males=26.47±9.44%; U=14.000, p=0.083; *r*=0.212, C.I.= -0.573± 0.801).

Discussion

My findings suggest that juvenile spider monkeys exhibit sex-segregation in some, but not all behavioral patterns. Juvenile males and females did not differ in activity patterns. Males tend to play more, whereas females whinnied more frequently. Although juvenile males and females engaged in comparable amounts of overall grooming, only females reciprocated this behavior. Both males and females played predominantly with same-sex play partners. Although juvenile individuals of both sexes spent most of their time in parties with their mother, juvenile males were in larger parties, and tended to be in parties with adult males more frequently. Together, these patterns suggest that sex-segregated patterns of behavior and association are initiated during the juvenile stage, despite any ranging limitations imposed upon by their mothers.

My findings provide additional support for Vick's (2008) conclusions that sex differences in spider monkey behavior emerge during juvenility. However, in Vick's (2008) study, some differences only appeared after 42 months of age. Given that all male juveniles in my study were under 36 months, these results suggest that some sex differences may emerge at earlier ages than previously documented. Patterns observed in both studies suggest that juvenile females have limited social opportunities compared to juvenile males, as is reported for other male-philopatric, fission-fusion species, including other Atelines (Stevenson, 1998; Strier, 2002), as well as chimpanzees (Pusey, 1983, 1990), and bottlenose dolphins (Gibson & Mann, 2008).

The sex differences observed here are in line with the findings of other studies of primate behavior (e.g. squirrel monkeys: Biben, 1986; rhesus macaques: Hassett, Rupp,

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& Wallen, 2010; stump-tailed macaques: Lee, Mayagoitia, Mondragón-Ceballos, & Chiappa, 2010; long-tailed macaques: van Noordwijk, Hemelrijk, Herremans, & Sterck, 2002; chimpanzees: Lonsdorf et al., 2014; Murray et al., 2014; Pusey, 1983; humans: Pellegrini, 2004). For example, in my study, only juvenile females ever groomed other conspecifics, and these females had stronger grooming relationships with their mothers than juvenile males did. Grooming is the predominant form of affiliative social behavior within the primate order (Henzi & Barrett, 1999; Seyfarth, 1977), and in the majority of species females groom more frequently than males (Mitchell & Tokunaga, 1976). Additionally, in stump-tailed macaque, juveniles females groom mothers at an early age than males (Lee et al., 2010), and in chimpanzees, juvenile females maintain stronger spatial relationships with mothers than males (Pusey, 1983). Similar to the juveniles in this study, adult females spider monkeys typically use whinny vocalizations more often than males (Fedigan and Baxter, 1984). Finally, sex segregation in play is one of the most common patterns in juvenile mammals (Roney & Maestripieri, 2003). Both sexes in this study concentrated their play patterns predominantly with same-sex peers. This is consistent with the sex-segregated play patterns in other primates, including humans, macaques, and squirrel monkeys (Biben, 1986; Hassett et al., 2010; Pellegrini, 2004; van Noordwijk et al., 2002).

In dispersed social structures, proximity and subgrouping patterns can provide valuable insight into social dynamics. Although sex differences in subgrouping patterns are explained through ecological and social factors (Chapman et al., 1995; Fedigan & Baxter, 1984; Wrangham, 1980), most of these factors should affect juvenile males and females similarly. Juvenile A. geoffroyi of both sexes have similar body sizes and growth rates (Corner & Richtsmeier, 1993). Thus an energetics-based explanation cannot account for the observed differences in juvenile behaviors. The availability of playmates (Lehmann & Boesch, 2005), and greater social opportunities (Otali & Gilchrist, 2005) for offspring, may entice mothers with juveniles to range in larger subgroups when ecological conditions permit. For male-philopatric species, these benefits are likely greater for male offspring who will remain in the community and maintain those relationships throughout life. Several mechanisms may account for the larger subgroup size of juvenile males and higher rates of grouping with adult males: 1) mothers may make subgrouping decisions to provide their male offspring with greater social opportunities, 2) other conspecifics, particularly adult males, may be more attracted to parties with juvenile males, or 3) juvenile males themselves may influence maternal subgrouping choices (e.g., Pusey 1983). More research is necessary to evaluate the relevance of these mechanisms for explaining the complex social dynamics of spider monkey populations.

The results of my study support van Noordwijk's (2002) assertion that the emergence of sex-typical behaviors occurs before these differences can be explained by immediate social or nutritional needs. While juvenile males' choice of play partners may the beginning of forming life-long bonds, juvenile females' engagement with female peers is more difficult to explain in the context of female dispersal. In spider monkeys communities, it is possible that young females may emigrate as a cohort, or encounter émigrés from their natal community after dispersal. While this phenomenon has not been documented in spider monkeys, immigration with a close peer or sibling has been reported in species characterized by male dispersal, such as squirrel monkeys (Mitchell, 1994), lemurs (Sussman, 1991), and macaques (Meikle & Vessey, 1981). Furthermore, play interactions as a juvenile may be important for learning how to negotiate amiable relationships with other females while integrating into a new social group. This may be one explanation for why female spider monkeys continue to engage in play during adulthood (Fedigan & Baxter, 1984; Pellis & Iwaniuk, 2000).

Overall, these patterns indicate that juvenile spider monkeys begin certain aspects of sex-segregated behavior earlier than previously reported. Given that they maintain equivalent body sizes through juvenility and forage at similar rates, these differences are best attributed to preparation for social roles in adulthood. However, further study is needed to determine if there are any sex differences in diet or foraging strategies, and more research is need on immigration and play patterns in adult females.

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