

Is Play Behavior Sexually Dimorphic in Monogamous Species?

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Abstract

Monogamy is a relatively rare social system in mammals, occurring only in about 3% of mammalian species. Monogamous species are characterized by the formation of pair-bonds, biparental care, and a very low level of sexual dimorphism. Whereas in most polygynous species males engage in more rough-and-tumble play than females, we predicted that males and females of monogamous species would have similar, or monomorphic, play behavior. In this study, we focused on two monogamous species: coppery titi monkeys (*Callicebus cupreus*) and prairie voles (*Microtus ochrogaster*). We documented the development of play behavior in both species, and quantified different types of play behavior. We did not find any sex differences in either species in the frequencies and types of play. However, we did find sex differences in the choice of play partner in titi monkeys: female offspring spent a higher proportion of time playing with their father, while male offspring played equally with their mother and father. It is possible that rough-and-tumble play behavior is monomorphic in many monogamous mammals, perhaps reflecting differences from polygynous species in the effects of exposure to early androgens or in the estrogen receptor distribution. However, more subtle differences in monomorphic play behavior, such as choice of partner, may still exist.

Introduction

Play behavior involves both risks and benefits. It demands energy and exposes the animal to risks such as injuries, falls and greater susceptibility to predators (Fagen 1981). Sharpe et al. (2002) demonstrated that meerkats with less food availability could not afford the cost of play because they were either conserving their energy or looking for food. Furthermore, not only is play risky for the individual, sometimes the individual's supervising parents are at risk as well (Fagen 1981; Nunes et al. 1999). However risky it may be, animals may benefit by practicing and preparing for future situations through play. For example, the animal may hone its locomotor and motor skills when play-fighting or chasing (Spinka

et al. 2001; Nunes et al. 2004; Burghardt 2005), increase its reproductive fitness by engaging in sexual play (Mitchell 1979), maintain friendships or test dominance relationships (Pellis & Pellis 1998). If we are to assume that play is adaptive, species have presumably compromised between costs and benefits in a way in which the benefits outweigh the costs (Burghardt 2005).

Polygynous species commonly exhibit sex differences in play (Poirier & Smith 1974; Mitchell 1979; Meaney et al. 1985; Nunes et al. 1999, 2004; Power 2000). In general, males of polygynous or promiscuous species (such as rats) demonstrate more rough-and-tumble play (Pellis et al. 1997). This relationship holds true across taxa; squirrel monkey (*Saimiri sciureus*) males play rougher, more often and for longer

periods than females (Biben 1998). In an evolutionary framework, the ultimate cause of differences in play between males and females may be due to the differential impact that fighting has on reproductive success, while proximate causes may include the different motivation each sex has for the different types of play (Pellis et al. 1997). Males may engage in more rough play because it prepares them for the challenges they face in seeking mates outside the natal group (Fagen 1981). Male rhesus macaques (*Macaca mulatta*) disperse from the natal group, and also exhibit more rough-and-tumble play compared with females, which are philopatric. Similarly, female Belding's squirrels do not play as much as their male peers, perhaps because they do not leave their natal sites to compete for mates, whereas males do (Nunes et al. 2004). Other aspects of play may also differ between the sexes; for instance, males may play more with other males (Burghardt 2005). Whereas male rats tend to engage more in play-fighting, females may engage more in 'maternal play' (Pellis et al. 1997).

On a proximate level, these sex differences in play of polygynous animals are strongly determined by the actions of perinatal androgens on the amygdala (Meaney & McEwen 1986; Field et al. 2006, 2006). Meaney and McEwen showed that female rats whose amygdala were exposed to testosterone neonatally had increased amounts of play-fighting compared with controls (Meaney & McEwen 1986; Hines 2003). The amygdala contains androgen receptors which respond to neonatal hormones to sexually differentiate the central nervous system and shape play dimorphism (Meaney & McEwen 1986; De Vries & Simerly 2002). Neonatal castration reduces masculinization of male play behavior in rats (Smith et al. 1998). Human females, who are exposed to high androgen levels prenatally because of a genetic disorder known as congenital adrenal hyperplasia (CAH) exhibit an increase in male-typical play behaviors such as rough-and-tumble play and playing more with 'masculine' toys (Hines 2003). These genetic females also exhibit a decrease in female-typical play (while controlling for cultural differences) (Hines 2003). However, female spotted hyenas, which display masculinized genitalia, display few differences in play behavior (litters with male cubs tend to play-bite their mother more than litters with all-female cubs) (Drea et al. 1996).

Androgens exert their effects on sexual differentiation via aromatization to estrogens, and there is also evidence that altered levels of neonatal estrogens

can masculinize play behavior (Field et al. 2006; Ferrey et al. 1993; Pellis 2002; Field et al. 2006; Dessì-Fulgheri et al. 2002). In rats, these sex differences in play are primarily apparent post-puberty, thus suggesting both organizational and activational effects of androgens (Pellis 2002). However, in humans and non-human primates these sex differences already exist much earlier in development (Goldberg & Lewis 1969; Mitchell 1979; Meaney 1988).

In contrast, monogamous species display less physical and behavioral sexual dimorphism, presumably because there has been less selection on males to evolve traits that would help them fight or attract mates (Kleiman 1977; Abbott & Hearn 1978, 1978; Plavcan & van Schaik 1997). There is relatively little published data on play behavior in monogamous mammals (Power 2000). The available data suggest that monogamous species such as the bush dog (*Speothos venaticus*), maned-wolf (*Chrysocyon brachyurus*) and the crab-eating fox (*Cerdocyon thous*) show neither physical sexual dimorphism nor dimorphism in play behavior (Biben 1983). Monogamous grasshopper mice (*Onychomys leucogaster*) (Davies & Kemble 1983; Pellis et al. 2000), common marmosets (Stevenson & Poole 1982) and cotton-top tamarins (*Saguinus oedipus*) (Cleveland & Snowdon 1984) also did not show any sex differences in play behavior. Very little is known about naturally occurring levels of neonatal androgens in any monogamous species. However, studies in prairie voles (*Microtus ochrogaster*) suggest that regulation of sexual differentiation may occur differently in this monogamous species than in laboratory rats or mice (Roberts et al. 1997; Lonstein et al. 2005). Neonatal castration does not feminize sexual behavior, and neonatal administration of testosterone does not increase mounting in females (Roberts et al. 1997). We, like previous authors (Smith 1982; Power 2000), hypothesized that because monogamous species exhibit monomorphism in many other behaviors such as biparental care, males and females would also exhibit similar amounts of rough-and-tumble play. We tested this hypothesis in two monogamous species, coppery titi monkeys (*Callicebus cupreus*) and prairie voles (*Microtus ochrogaster*).

The coppery titi monkey is a monogamous, arboreal New World primate species that demonstrates a strong pair-bond and extensive male participation in infant carrying (Mendoza & Mason 1986). Males and females exhibit no physical sexual dimorphism, and infants have a strong, preferential attachment to their father (Hoffman et al. 1995). Prairie voles are

microtine rodents native to the American Midwest, and demonstrate a pair-bond both in the field and the laboratory (Getz et al. 1981; McGuire et al. 2003). Prairie voles demonstrate high levels of infant care by both parents and also by older offspring (Thomas & Birney 1979), with fairly few differences in frequencies or durations of parenting behavior between mothers and fathers (Lonstein & De Vries 1999). Play behavior in titi monkeys has been described in three infants by (Fragaszy et al. 1982), but the sample size in this study was too small to permit comparison of sex differences. Preliminary observations of three female prairie voles also suggested that patterns of play were similar to those described for male siblings (Pierce et al. 1991). Here we document the development of play behavior in both species, then test for the existence of dimorphism in play and examine the choice of play partners. We predicted a lack of sexual dimorphism in rough-and-tumble play, also known as contact play. We also predicted a preference for the father over the mother as a play partner in young titi monkeys, because of their preferential emotional attachment to their fathers (Hoffman et al. 1995).

Materials and Methods

Subjects

Titi monkeys (Callicebus cupreus)

Subjects for this study were 10 juvenile titi monkeys (five males and five females). All were laboratory-born at the California National Primate Research Center. These subjects were housed in 10 different family groups (see Table 1 for the basic demographics of each group). Each family group was housed in a 1.2 m × 1.2 m × 2.1 m stainless steel cage with four horizontal perches arranged in a stepwise fash-

ion across the width of the cage, and one U-shaped perch on the door of the cage. Twice a day, groups were fed a diet consisting of monkey chow soaked in orange juice, apples, bananas, baby carrots, cottage cheese, and vitamin powder. Diet, husbandry, and training have been described elsewhere (Mendoza & Mason 1986; Tardif et al. 2006).

Six of the 10 fathers were previously used in an experiment in which they received a lesion of the prefrontal cortex (in the area near the arcuate dimple, which receives projections from the somatosensory cortex). These males are identified in Table 1. Post-lesion, these males did display changes in behavior towards their mates, including being less likely to break contact and spending more time grooming (Mendoza et al. 2006). The offspring of the lesioned males were evenly divided between males (three) and females (three). We first statistically compared offspring of lesioned and non-lesioned males for any differences that may have been associated with the lesions (sample sizes were six offspring of lesioned fathers, four offspring of non-lesioned fathers). All behaviors recorded in this study were compared between offspring of lesioned and those of non-lesioned males by repeated-measures ANOVA as described in the *Data Analysis* section; in addition, we ran analyses using non-parametric tests because of the small sample size. There were no differences in any behavior between offspring of lesioned fathers and offspring of non-lesioned fathers, and we therefore combined the groups. Results of the ANOVAs were as follows: solitary play ($F_1 = 0.05$, $p = 0.837$); contact play ($F_1 = 0.29$, $p = 0.617$); pulling/hanging ($F_1 = 0.14$, $p = 0.726$); chasing ($F_1 = 0.02$, $p = 0.901$); total play ($F_1 = 0.01$, $p = 0.906$). Obviously, use of offspring of these males was not ideal and should be kept in mind when interpreting the results.

Table 1: Titi monkey family group compositions and parental ages

Family cage number	Sex of infant	Age of father when juvenile was born	Father has lesion?	Age of mother when juvenile was born	Number of older brothers	Number of older sisters
2	F	14 yr 11 mo 8 d	No	2 yr 11 mo 18 d	1	0
3	M	9 yr 3 mo 13 d	Yes	6 yr 9 mo 15 d	1	1
4	M	6 yr 7 mo 12 d	No	9 yr 3 mo 10 d	1	0
6	M	9 yr 12 d	Yes	8 yr 6 mo 9 d	2	0
8	M	8 yr 9 mo 3 d	Yes	7 yr 2 mo 1 d	0	1
11	F	3 yr 2 mo 3 d	No	3 yr 1 mo 6 d	0	0
12	F	9 yr 5 mo 20 d	Yes	8 yr 12 d	1	0
14	F	7 yr 1 mo 19 d	Yes	8 yr 28 d	1	1
16	F	8 yr 5 mo 24 d	Yes	7 yr 10 mo 28 d	1	1
21	M	4 yr 10 mo 25 d	No	2 yr 9 mo 5 d	0	0

Prairie voles (Microtus ochrogaster)

We observed the behavior of 40 juvenile prairie voles (20 males and 20 females). The voles used in the study were descendants of a wild stock originally caught near Champaign, Illinois. The stock was systematically outbred. Animals were maintained on a 14 h light : 10 h dark cycle and allowed high-fiber Purina rabbit chow and water ad libitum. Each family group contained three to four juveniles. Families were housed in two large polycarbonate cages (44 × 22 × 16 cm) connected via a polycarbonate tube and provided with cotton for nesting material.

At 20 d, juveniles were weighed and received color-coded aluminum ear tags (National Band model 1005-1; National Band and Tag Company, Newport, KY) for individual identification. Four randomly selected juveniles (two males and two females) from each litter were kept with parents. Any remaining juveniles (i.e. litters greater than four juveniles) were removed from the cage.

Behavior Quantification*Titi monkeys*

The titi monkeys were filmed three times a week from birth to 3 mo of age, then once a week from 3 to 6 mo of age, using a Sony Handycam camcorder (Sony, Tokyo, Japan) fixed on a tripod but operated by an observer (model HDR- HC1 HDV 1080i). Sessions were 1 h long and balanced across morning and afternoon hours. Observers were familiar to the subjects and subjects did not respond to observer presence after the camera was set up. The sessions were then quantified using Behavior Tracker 1.5 with video module (<http://www.behaviortracker.com>). The total time observed per monkey from 0 to 3 mo was 36.6 ± 0.82 h (mean \pm SE), within the range of 33 to 41 h. The total time observed per monkey from 3 to 6 mo of age was 14 ± 0.23 h within the range of 13 to 15 h. Five different types of play behaviors were scored: chasing, solitary play, contact play, and pulling or hanging onto another monkey's tail (see Table 2 for definitions). We also recorded whether the play occurred with the mother, father, or an older sibling.

Prairie voles

Real-time behavioral observations were conducted for 20-min sessions on juveniles using Behavior Tracker 1.5. For each litter, one observation session was conducted per day on one male and another on

Table 2: Behavioral categories used in observations of titi monkey play

Chasing	Juvenile chasing another monkey
Contact play	Juvenile and another family member wrestling, jumping on the other or 'chicken-fighting'
Hanging or pulling another's tail	Juvenile yanking, pulling or hanging from another family member's tail
Solitary play	Juvenile bouncing or climbing around the parent, hanging upside down from the cage bars or doing any type of exploring either with their mouths or with their hands (also known as object play when exploring an object such as another's nametag, or cage's locks)

Table 3: Behavioral definitions used in descriptions of prairie vole play

Wrestling	Facing another animal, often in a ventrum-to-ventrum embrace, and biting the other animal's body without inflicting wounds
Tackling	Jumping or pouncing on another animal
Boxing	Standing on hind legs and batting at another animal with forepaws. Other animal usually reciprocates
Other Play	Other forms of play, such as biting another animal's ear, or chasing another animal when the chase leads to one of the behaviors described above

one female. Observations were conducted on each pair of juveniles during 2 d in each age range of 20 to 30, 30 to 40 and 40 to 50 d of age. Observations were conducted during morning hours (08:00 and 12:00 hours) or afternoons (13:00 and 17:00 hours). The total time observed per individual vole was 66.7 ± 14.6 min. Each juvenile was observed for play displays of any type of play (see Table 3 for play categories). We also recorded whether play occurred with an adult, another juvenile or with an infant sibling.

Data Analysis

For titi monkeys, we examined sex differences in play during two time periods: 0–3 and 3–6 mo. These periods were chosen because the rates and types of play changed dramatically as infants became more independent. We present our results here in two different ways. A repeated-measures ANOVA was performed across the full time period of data collection. The Shapiro–Wilks and Kolgomorov–Smirnov tests were used to assess normality of the residuals. Only solitary play and total play displayed a normal distribution for the residuals; however, the results for all the analyses are presented here, with the caveat that their p-values may not be exact.

The two time periods were also analyzed separately (rather than through repeated-measures ANOVA) because of the failure of the repeated-measures ANOVA to meet normality assumptions or to allow transformation to normality for some behaviors. Durations of play behavior for titi monkeys were analyzed by ANOVA, with sex as an independent variable and number of siblings as a covariate. Choice of adult play partner was analyzed as the ratio of time spent playing with the father divided by total time spent playing with the father and the mother. Correlations between the choice of adult play partner and the time spent being carried as an infant by the father and mother were carried out by Pearson's correlation. All tests were checked for assumptions of ANOVA, *p*-values were set at 0.05 and all tests were two-tailed.

For prairie voles, we examined sex differences in play during three time periods: 20–30, 30–40 and 40–50 d, using a repeated-measures ANOVA. The number of play bouts observed in a 20-min period was square-root-transformed because of non-normality of the data. All tests were checked for assumptions of ANOVA, *p*-values were set at 0.05 and all tests were two-tailed.

Results

Titi monkeys

Social play behaviors of the titi monkeys emerged within the first 4 mo of life. Juveniles started

demonstrating solitary play at an average of 35.2 ± 2.6 d of age (mean \pm SE). Pulling and hanging on tails was first observed at an average of 63.9 ± 5.24 d of age. Contact and chase behaviors were first observed at similar ages, an average of 81.6 ± 5.71 and 89.5 ± 6.53 d of age, respectively.

In a repeated-measure analysis of play behavior with number of siblings as a covariate, we found no effect of sex on solitary play ($F_1 = 3.86$, $p = 0.12$), contact play ($F_1 = 0.81$, $p = 0.42$), chasing ($F_1 = 0.14$, $p = 0.73$), pulling and hanging on tails ($F_1 = 0.02$, $p = 0.90$), or total play ($F_1 = 3.31$, $p = 0.14$). In a separate analysis of the ages of 0–3 mo, we found marginally significant differences in total duration of play behavior between males and females, with the number of siblings as a covariate (Fig. 2; $F_1 = 4.76$, $p = 0.07$), as well as in solitary play ($F_1 = 4.58$, $p = 0.07$). There were no sex differences in contact play ($F_1 = 0.22$, $p = 0.65$), chasing ($F_1 = 0.00$, $p = 0.98$) or pulling and hanging on others' tails ($F_1 = 0.10$, $p = 0.76$; Fig. 1).

Similarly, we found no significant differences during the ages of 3–6 mo in total duration of play behavior between males and females, with the number of siblings as a covariate (Fig. 1) ($F_1 = 0.09$, $p = 0.78$). There were no sex differences in contact play ($F_1 = 0.52$, $p = 0.49$), solitary play ($F_1 = 2.10$, $p = 0.19$), chasing ($F_1 = 1.21$, $p = 0.31$) nor pulling or hanging on others' tails ($F_1 = 2.01$, $p = 0.20$). At

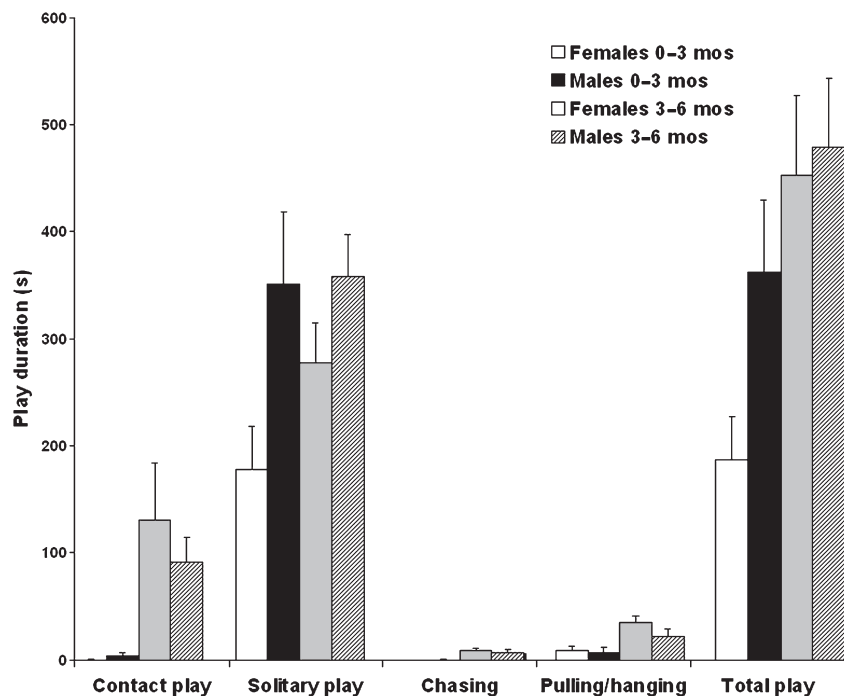


Fig. 1: Mean durations of play categories in titi monkeys comparing males and females during two age periods: 0–3 and 3–6 mo. There were no significant sex differences in any play category. Some mean and standard error values for contact play and chasing in months 0–3 are too small to be visualized in this graph. The mean for female contact play is 0.42 ± 0.28 . The mean for female chasing is 0.04 ± 0.03 and male chasing 0.38 ± 0.38 .

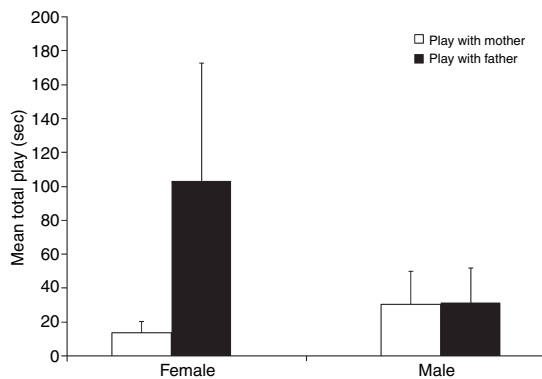


Fig. 2: Sex differences in parental play partners 3–6 mo of age for titi monkeys. There were significant sex differences in the choice of adult play partner ($F_1 = 11.07$, $p = 0.01$). While males had no preference for either mother or father, females preferred their father to their mother.

3–6 mo of age, the number of siblings had a significant effect only on the duration of time spent chasing; fewer siblings were associated with more chasing ($F_1 = 20.57$, $p < 0.01$). Average time spent chasing per hour (means and standard errors) as follows: with 0 siblings, 16.23 ± 2.92 s/h; with one sibling, 8.28 ± 1.62 s/h; with two siblings, 3.13 ± 1.76 s/h.

At 0–3 mo of age, there were no significant differences in proportion of time spent with each adult play partner ($F_1 = 1.45$, $p = 0.27$). However, at 3–6 mo of age, the proportion of time that females spent playing with their father vs. their mother was significantly different than the proportion of time males spent playing with their fathers vs. their mothers ($F_1 = 11.07$, $p = 0.01$; Fig. 2). The amount of time that infants were carried by their father during weeks 2–4 did not correlate with the time spent playing with the father ($r = 0.17$, $p = 0.63$). However, the amount of time that infants were carried by their father was positively correlated with time spent playing with the mother ($r = 0.64$, $p < 0.05$); i.e. infants whose fathers carried them more spent more time playing with their mothers.

Prairie voles

Prairie voles began playing as infants as early as 14 d, with play rates increasing after day 20. Nonetheless, play rates remained low throughout (Fig. 3). Most play took place between 20 and 30 d, and occurred either between juveniles or between juveniles and their father. No play bouts with mothers were ever observed. Because play frequencies were low, we combined all play categories observed (Table 3) for statistical analyses.

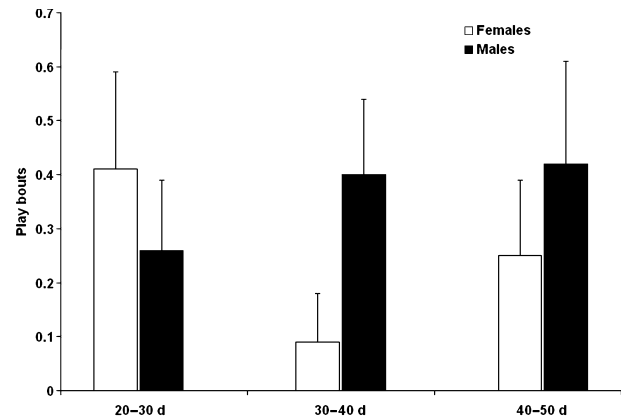


Fig. 3: Mean number of prairie vole play bouts observed in a 20-min session (mean \pm standard error). Total play rates were not significantly affected by sex ($F_{1,43} = 0.96$, $p = 0.33$) nor age ($F_{2,43} = 0.56$, $p = 0.57$). Neither was there an interaction between sex and age ($F_{1,2} = 2.52$, $p = 0.09$).

Mean rates of play for the entire period were 0.26 ± 0.09 play bouts per observation for males and 0.35 ± 0.09 play bouts per observation for females. Proportions of males and females observed playing did not differ significantly, with nine of 20 males demonstrating play behavior during the observations and 10 of 20 females playing.

Total play rates were not significantly affected by sex ($F_{1,43} = 0.96$, $p = 0.33$) or age ($F_{2,43} = 0.56$, $p = 0.57$). There was no interaction between sex and age ($F_{1,2} = 2.52$, $p = 0.09$). We also examined play bouts with fathers, and found no significant effects of sex ($F_{1,43} = 0.88$, $p = 0.77$) or age ($F_{2,43} = 1.48$, $p = 0.23$). There was no interaction between sex and age ($F_{1,2} = 2.21$, $p = 0.12$). Finally, no significant effects were found for play solely between juveniles. This was true for sex ($F_{1,43} = 1.11$, $p = 0.61$), age ($F_{1,43} = 0.22$, $p = 0.82$) and the interaction between sex and age ($F_{1,43} = 2.76$, $p = 0.08$).

Discussion

Our results support the hypothesis that monogamous mammals show little sexual dimorphism in contact play behavior. This relationship was consistent across time, even past the age where male prairie voles are sexually mature (Mateo et al. 1994). Interestingly, although overall rates of contact play were not sexually dimorphic, the proportion of time spent playing with one parent vs. the other was sexually dimorphic in titi monkeys; juvenile females spent a higher proportion of time in play with their fathers, while juvenile males played equally with their mothers

and fathers. While prairie vole juveniles did not show this differential preference, it could be partially because prairie vole mothers did not engage in play behavior at all. Titi monkeys under the age of 3 mo also demonstrated a marginal sex difference in solitary play, as well as a marginal sex difference in total play. However, the sample of monkeys for this study was very small, and a larger sample size might well show a sex difference in solitary play.

Processes of sexual differentiation during development are likely responsible for the patterns of play behavior we observed. Neonatal androgens and estrogens have both been implicated in the development of play behavior, although as detailed above, these processes may differ in sexually monomorphic species. This is not to say that all monogamous species will have evolved the same mechanisms for sexual differentiation, or that they will not be responsive to neonatal steroid hormone manipulation. When marmosets were given more testosterone than normal during their critical period for masculinization, they exhibited more rough-and-tumble play (Abbott & Hearn 1978). In prairie voles, neonatal castration did affect later alloparental care, although it did not feminize sexual behavior (Roberts et al. 1997; Lonstein et al. 2002). Because of their appearance in diverse taxonomic groups, multiple cases of independent evolution, and probable descent from polygynous ancestors (Kleiman 1977), it is quite possible that proximate mechanisms for behavior in monogamous species have evolved differently in different species (Wynne-Edwards & Timonin 2007).

While there were no statistically significant sex differences observed in this study, there were several interesting non-significant trends in the data. For instance, for titi monkeys aged 0–3 mo, male infants tended to display more solitary play behavior than female infants (and this difference in solitary play is also reflected in total play). It is possible that the very small sample size of monkeys for this study affected our statistical power, and that we would have found a sex difference given a larger sample. However, it is also possible that composition of the groups involved, rather than a real sex difference, played a role in this result; the infant male with the highest level of solitary play (over 500 s per hour-long observation) had a particularly 'teasing' older sibling that he appeared to avoid rather than seek out for play. A second, non-significant but interesting pattern was the drop in female prairie vole play at 30–40 d (not seen in males). Prairie voles have a post-partum estrus (Carter et al. 1989) with a 21-d

gestation period; therefore, 30–40 d old siblings might very well be engaged in alloparental care. Although juvenile males are often alloparental than juvenile females in laboratory tests (Roberts et al. 1998), the animals from this study, as well as additional litters were also observed for naturally expressed alloparental behavior in their natal group. Females spent significantly more time in the nest with pups than males did ($F_{1,44} = 4.49$, $p = 0.03$; Stone, A. I.; Mathieu, D.; Griffin, L.; Bales, K. L. unpublished data). It is possible that the drop in play is explained by a rise in this competing behavior.

Because titi monkeys display an unusual infant-rearing system in which fathers are the primary caregivers and attachment figures (Mendoza & Mason 1986), we also examined which of the parents' infants were more likely to engage in play, and whether or not this differed by sex of the infant. Juvenile female titi monkeys spent a higher proportion of time playing with their father than with their mother; this contrasts with males which did not appear to differentiate between their parents (Fig. 4). Although males carry both male and female infants for the majority of the time (Mendoza & Mason 1986), it is possible that other types of parental behaviors such as licking or grooming are unequally distributed between males and females. In rats, mothers anogenitally lick male pups more than female pups (Moore & Morelli 1979). It is possible that if fathers preferentially direct some aspect of infant care such as licking towards female infants, it later increases the motivation of the female juveniles to interact with their father (Kaplan & Rogers 1999). It is also possible that the motivation for playing comes primarily from the parent rather than the juvenile, and that fathers are either more motivated to play with daughters or less motivated to play with sons.

It is also especially interesting that infants whose fathers carried them at higher rates actually played more with their mothers. It is possible that the tendency of the father to seek proximity to its pair-mate brings those infants whose fathers carry them more into contact with their mother more frequently. Finally, we found that fewer siblings in a family group leads to increased time spent in chasing behavior by the juvenile. Perhaps those juveniles with fewer siblings available for play spend more time in chasing as an attempt to entice their parents into play behavior.

The evolution of monogamy has involved suites of variables including certain characteristics of temperament, high social motivation with an attraction to

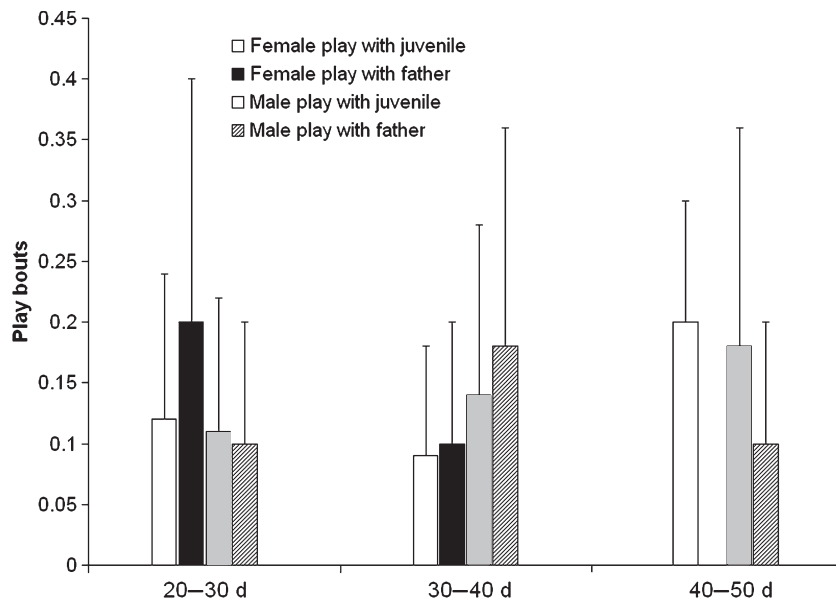


Fig. 4: Play partners for juvenile prairie voles. The amount of play with their father was neither affected by sex ($F_{1,43} = 0.88$, $p = 0.77$) nor age ($F_{2,43} = 1.48$, $p = 0.23$). There was no interaction between sex and age ($F_{1,2} = 2.21$, $p = 0.12$). No significant effects were found for play between juveniles: this was true for sex ($F_{1,43} = 1.11$, $p = 0.61$), age ($F_{1,43} = 0.22$, $p = 0.82$) and the interaction between sex and age ($F_{1,43} = 2.76$, $p = 0.08$).

the partner, responsiveness to infant stimuli, biparental care and paternal tolerance among others (Mendoza et al. 2002). As a consequence of increased parental tolerance, juveniles may have a lengthy period of dependence (Kleiman 1977) and an extended period for behaviors such as play. Both dynamics of monogamous family groups, and further investigation into processes of sexual differentiation in monogamous species, should prove fruitful in our understanding of this social system.

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