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The Development of Sex Differences in Play in Wild White-Faced Capuchins

A thesis submitted in partial satisfaction of the

requirements for the degree of Masters of Arts

in Anthropology

by

Sasha Lutz Winkler

2020

ABSTRACT OF THE THESIS


The Development of Sex Differences in Play in Wild White-Faced Capuchins


by


Sasha Lutz Winkler

Masters of Arts in Anthropology

University of California, Los Angeles, 2020

Professor Erica A. Cartmill, Chair


Many mammalian species display sex differences in the frequency of play behavior, particularly in the domain of social play. Yet the animal literature largely lacks longitudinal studies on developmental patterns of play over the lifespan, which are important for understanding the timing of sex differences and the evolutionary functions of this ubiquitous behavior. I analyzed sex-specific patterning of social play, solitary play, and grooming using an 18-year dataset on a cohort of 38 wild white-faced capuchin monkeys (*Cebus capucinus*) followed since infancy. Rates of each behavior were measured as the proportion of point samples taken during focal follows in which the individual was engaging in social play, solitary play, or grooming. To determine sex differences in the rates of these behaviors, I ran three Poisson generalized linear mixed models with a random effect for each individual. Results for social play and solitary play showed significant fixed effects for age, such that rates of both types of play decreased with age. Results for social play showed significant fixed effects for sex and the interaction between sex

and age, such that males had higher overall rates of social play than females and had a slower decline in the rate of social play with age compared to females. Solitary play did not show a significant fixed effect for sex; however, rates of solitary play decreased more quickly over time for females than for males. Females had significantly higher overall rates of grooming than males, and the interaction between sex and age was significant such that rates of grooming increased more quickly over time for females than males; in fact, the proportion of time spent grooming increased over the lifespan for females but decreased over the lifespan for males. My results suggest that males allocate more time overall toward social play than females, particularly throughout the juvenile period, but that females may compensate for lower bonding opportunities in social play through increases in time spent grooming. Results were consistent with two functional hypotheses of play, the practice and bonding hypotheses. This longitudinal study demonstrates that play behavior may be critical for the development of sex-specific social strategies and emphasizes the importance of lifespan perspectives on behaviors such as play and grooming.

The thesis of Sasha Lutz Winkler is approved.


Susan Emily Perry

Harold Clark Barrett

Erica A. Cartmill, Committee Chair


University of California, Los Angeles

2020

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# Introduction

Play is both an important and enigmatic behavior in evolutionary science. Play occurs in nearly all young mammals, as well as in other taxa, and is costly with regard to time and energy expenditure (Burghardt, 2005). As a potential locus of exploration and learning in development, play may have an important role in influencing or predicting adult behavior (Bateson & Martin, 2013; Gopnik et al., 2017). Play is also a domain where sex differences in adult behavior become apparent at a young age in humans and other mammalian species (Meaney et al., 1985). While the developmental patterns of play are fairly well studied in humans (Pellegrini & Smith, 1998; Power, 2000), the animal literature largely lacks longitudinal data on developmental patterns of play over the lifespan, which are important for understanding the evolutionary forces driving patterns of play across age and sex. The current study investigates such developmental patterns of play in a unique dataset that tracked individuals from several groups of wild white-faced capuchin monkeys (*Cebus capucinus*) for 18 years.

In most mammals, play tends to be more frequent early in life and become less frequent with age (Bateson & Martin, 2013). While some species, like humans, continue to play into adulthood, there are other species in which play is rare or nonexistent among adults (Byers & Walker, 1995). Generally, more precocial species tend to have lower rates of play and a shorter developmental period during which play occurs (Ortega & Bekoff, 1987). This emphasizes the potential role of play in learning. Sexual maturity may mark an important developmental milestone for play in many species; as sexually mature animals increase the time devoted to behaviors that more directly improve reproductive success, like mating and parental care, play

appears to decrease in frequency. Even in species that continue to play as adults, rates of play are almost invariably higher in immature animals.

The evolutionary function of play behavior has long puzzled biologists, as the fitness benefits of play are difficult to detect and measure. For example, in his book on play in rhesus macaques, Donald Symons detailed a non-exhaustive list of eighteen different functional hypotheses for the existence of play (Symons, 1978). While some of these hypotheses posit immediate, primarily physical benefits of play, many propose that play in the juvenile period translates to delayed fitness benefits in adulthood. One such hypothesis is the ***practice hypothesis***. According to the practice hypothesis, play provides practice for skills needed in adulthood; for example, social rough-and-tumble play (i.e., "play fighting") is seen as practice for skills needed during real fights in adulthood, such as physical agility and tactical skills (Martin & Caro, 1985; Symons, 1978). Another hypothesis for the function of play, particularly for social primates, is the ***bonding hypothesis***. The bonding hypothesis argues that playing with others allows animals to form, test, and learn about social bonds (Poirier & Smith, 1974; West, 1974). These hypotheses are not mutually exclusive and are difficult to disentangle empirically, as acknowledged by many scholars (e.g., Bateson & Martin, 2013).

It is also possible that different types of play might have evolved for different reasons (Smaldino et al., 2019). Play is often split into two categories: ***social play***, such as rough-and-tumble play, and ***solitary play***, which includes non-social object and locomotor play (Pellegrini & Smith, 2005). Simple locomotor play might confer primarily physical benefits ("motor training hypothesis;" Byers & Walker, 1995), while complex social play might confer benefits in social skills, aggressive tactics, or bond formation and strengthening. Object play may help animals learn about the physical affordances of objects in their environments (Bjorklund &

Gardiner, 2010). The proportion of time and energy devoted to these different types of play varies across species (Cordoni et al., 2018; Fry, 2005; Palagi, 2006). Within a given species, the frequency of different types of play may vary across developmental stages and across the sexes. Together, these sources of variation suggest that different types of play may confer subtly different evolutionary benefits for males and females, animals of different ages, or according to the specific socioecology of each species. A better understanding of sex and age differences in play may therefore help to shed further light on the evolutionary functions of play, especially when contextualized within the species' socioecology.

**Sex Differences in Play**

The presence of sex differences in the development of play could support either or both of the primary functional hypotheses discussed: the practice and bonding hypotheses. The ***practice hypothesis*** predicts that the sex that has greater need for physical agility and tactical skills in adulthood will have higher rates of social rough-and-tumble play, which consists of modified aggressive behaviors like gentle biting, wrestling, and chasing. Similarly, the practice hypothesis predicts that the sex with a greater need for extractive foraging or other fitness-relevant object manipulation in adulthood will have higher rates of solitary object play as juveniles. Predictions for the developmental timing of sex differences in play are a bit more obscure. On the one hand, one sex might maximize lifetime play by continuing to play over a longer period of development; alternatively, those animals might play more earlier in life in order to reach proficiency at that skill more quickly, after which they might stop playing or play at reduced rates, having already gained the needed benefits from play.

In contrast, the ***bonding hypothesis*** predicts higher rates of social play in the sex which gains a greater fitness advantage from having strong social bonds. This may decrease over development if the social bonds (and bond-formation skills) become solidified and further play has diminishing returns; however, if play helps to maintain bonds in adulthood that are important for fitness, one would expect social play to continue throughout the lifespan. The bonding hypothesis provides no specific predictions for solitary play. Regardless, both the practice and bonding theories suggest that sex differences in play should mirror adult sex-specific behavioral strategies for reproduction and survival.

Sex differences in social play are common in cross-sectional research. Studies have found higher rates of social play among males than females in a broad range of mammal species, from rats to humans (Auger & Olesen, 2009; Fry, 2005; Poole & Fish, 1976). This sex difference has been observed in many Old World monkeys and apes (e.g., gorillas: Maestripieri & Ross, 2004; orangutans: Rijksen, 1978; rhesus macaques: Brown & Dixson, 2000; vervet monkeys: Raleigh et al., 1979), and some New World monkeys (e.g., spider monkeys: Rodrigues, 2014). However, this pattern of higher rates of social play in males is by no means ubiquitous, even among primates. For example, studies have found no sex differences in play in common marmosets (Stevenson & Poole, 1982), coppery titi monkeys (Chau et al., 2008), wolves (Cordoni, 2009), or meerkats (Sharpe, 2005). The socioecology and mating system of a species likely has an effect on the development of sex differences in play. For example, there is preliminary evidence that monogamous mating systems are correlated with similar rates of play between males and females, for both social and solitary play (Chau et al., 2008). It is possible that in species that are monogamous (e.g., titi monkeys) or polyandrous (e.g., marmosets), reduced male-male

competition may explain the reduced selection pressure for higher rates of rough-and-tumble play in males.

Other studies have indicated that sex differences in play can vary over the course of development. Research on spider monkeys found that males had higher rates of social play than females as juveniles (Rodrigues, 2014), but another study found the opposite pattern for social play in adulthood, such that females played at higher rates than males (Fedigan & Baxter, 1984). Rodrigues (2014) suggested that female spider monkeys may need to continue playing into adulthood because they are the dispersing sex and thus have a continuing need for the bonding benefits of social play compared to males. In hyenas, a species in which females are dominant to males and display many male-typical behaviors and hormonal profiles, one study found that immature females had higher rates of social play than immature males, but there was no difference in rates of solitary object play (Pedersen et al., 1990). However, a longitudinal study in hyenas from infancy to adulthood found only sex differences in the interaction of sex and age on the rate of social play, although that study analyzed rates of initiating social play, rather than rates of the overall time spent in social play (Grebe et al., 2019). The authors found that rates of play initiation decreased with age for both sexes, and the rate of decrease with age was steeper for females than males. Studies like these highlight the need for more research that investigates sex differences in play while accounting for important differences between social and solitary play, and for changes over the course of development. Longitudinal data from wild white-faced capuchins in Costa Rica collected by Perry and colleagues (Perry et al., 2012) provides the rare opportunity to analyze such developmental patterns over decades of research.

**Play in White-Face Capuchins**

White-faced capuchins (*Cebus capucinus*) are an excellent species for research on play because they have long juvenile periods, engage in both social and solitary play, and their social behavior is well-studied (Perry et al., 2012). Despite their social behavior being well-studied, to my knowledge no research has been published on the presence or absence of sex differences in play for this species, or about patterns of play over the lifespan. Evidence of sex differences in play is minimal among other capuchin species (subfamily Cebinae). In a small sample of nine captive juvenile tufted capuchins (*Sapajus apella)*, Paukner and Soumi (2008) found sex differences in social play, such that males had higher rates of social play than females, but there was no sex difference in the rates of solitary play. This study was cross-sectional, with data collected over a four-month period, and did not investigate any changes in the sex difference over development. The current study addresses some of these limitations by analyzing rates of social and solitary play in 38 subjects for up to 18 years of life. Additionally, because the current study concerns wild populations, the results may provide a more ecologically valid perspective on the expression and evolution of play behavior. Rates of play are typically higher in captive animal populations, potentially obscuring sex differences that might occur in the wild (Baldwin & Baldwin, 1974; Himmler et al., 2013).

Because the socioecology of a species might affect developmental patterns of play across the sexes, play research in white-faced capuchins benefits from an understanding of their sex-specific behaviors and reproductive strategies. White-faced capuchins live in multi-male, multi-female groups of approximately 5-40 members, although adult males may spend short periods of their lives in all-male bachelor groups (Perry, 2012). They have unusually long juvenile periods and lifespans for small New World primates, living up to 37 years in the wild and up to 55 years

in captivity (Hakeem et al., 1996; Perry, 2012). Females reach sexual maturity around ages 5.5-7.5 years, with mean age of first reproduction 6.22 years, while the minimum age of first reproduction for males is around 7.5 years old (Perry, 2012; Perry et al., 2012). The extended juvenile period appears to be an important time for developing skills such as extractive foraging techniques (Perry, 2009), some of which may be achieved through object play.

In white-faced capuchins, females are philopatric and males disperse from their natal groups (Perry et al., 2012). At the Lomas Barbudal field site in Costa Rica, where the data for the current study were collected, the average age of first male migration was 7.6 years, while the average age was 4.5 years among white-faced capuchins in another long-term study at Santa Rosa National Park in Costa Rica (Fedigan & Jack, 2012; Perry et al., 2012). As a result of female philopatry, females generally spend their entire lives with kin (related females) while males do not, although males often co-emigrate with their brothers or other related males (Perry, 2012). Males often migrate to different social groups multiple times throughout their lives (Perry, 2012). Males may thus have a greater need to develop social skills for forming bonds with unrelated monkeys in new groups; skills which, according to the bonding hypothesis, could be developed through social play. Play in the juvenile period could be especially important for males if it allows them to form and test strong bonds with other males before co-emigrating, while still in the relatively safe environment of their natal groups. Despite this, Perry and colleagues (2017) found no effect of the rate of social play in male white-faced capuchins on the age of emigration or the time to obtaining their first alpha position. This provides no support for the idea that higher rates of play earlier in development might speed up the timing of important developmental milestones for male capuchin fitness.

Another factor potentially influencing rates of social play is white-faced capuchins' high degree of male reproductive skew. Alpha males monopolize mating opportunities and sire about 96% of the infants born to females that are not their daughters or granddaughters (Godoy et al., 2016; Muniz, 2008). Subordinate males provide important support to the alpha male and females by helping defend the group from predators and out-group males, but they usually do not have access to mating opportunities themselves unless they overthrow the alpha (Perry & Manson, 2008). Due to the high reproductive skew, increasing indirect fitness by supporting related males to achieve alpha status may be an adaptive strategy for some subordinate males. Thus, male reproductive success is generally dependent on the ability to form aggressive alliances with other males (kin or non-kin) and take over new groups of unrelated females by (collaboratively) defeating resident males, in order to gain access to mating opportunities (Perry 2012). In contrast, female reproductive success is less skewed and is likely dependent on competition over access to food resources (Perry et al., 2012; Silk, 1993).

The high reproductive skew in males compared to females is important as it likely puts greater selection pressure on males (1) to develop fighting skills and (2) to create strong social bonds with other males, which form the basis of aggressive alliances. Both of these factors suggest that males should have a greater need for social play during the juvenile period compared to females, whether the benefit is increased fighting skills (i.e., the practice hypothesis) or forming bonds with other males (i.e., the bonding hypothesis).

In addition to improving rank, and thus mating opportunities, fighting skill is known to have a greater impact on mortality for male white-faced capuchins than for females (Perry, 2012). While female white-faced capuchins form aggressive coalitions, they generally are less physically injurious and do not have a substantial impact on their mating opportunities (Gros-

Louis et al., 2003; Perry, 1996). Therefore, under the practice hypothesis, males of this species should have higher rates of social rough-and-tumble play in order to practice those skills.

Nevertheless, sex differences in white-faced capuchins' social play could also be compatible with the bonding hypothesis (although they cannot be explained solely by the bonding hypothesis). While social bonds are crucial for male reproductive success, they are also important for female reproductive success; for example, bonded females may help one another through alloparenting and coalitionary aid (Perry, 2012). Perry (2009) found no sex differences in the amount of time immature males and females spent alone or in proximity to their mothers, suggesting that they spend similar amounts of time socializing overall.

Instead of using social play to build social bonds, females may instead use grooming. Grooming is known to be an important method of forming social bonds in white-faced capuchins, especially between females (Manson et al., 1999). In adulthood, female-female grooming bouts are much more frequent than male-female and male-male grooming (Perry, 1996). Additional research suggests that males and females in this species may establish, maintain, and strengthen social bonds through different means as adults. Adult females tend to bond with one another by grooming and engaging in relaxed affiliative interactions, while adult males tend to maintain bonds through lower levels of these behaviors, as well as resting in contact, social play, and participating in other types of unusual affiliative behaviors (e.g., social "games" and dyadic bonding rituals; Perry, 1996, 1998; Perry et al., 2003). A similar pattern may emerge early in development, with juvenile females already allocating more time toward grooming and juvenile males engaging in more social play.

In sum, close dyadic bonds are beneficial for both males and females, but because males have the added challenges of integrating into new social groups, forming high-stakes aggressive

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alliances, and overcoming the odds stacked against them by a high reproductive skew, one could argue that social bonds are likely to provide more direct fitness benefits for males than females. Alternatively, female white-faced capuchins may rely more heavily on behaviors such as grooming to form bonds; by replacing social play with grooming, they may continue to gain social bonding benefits but not the fighting benefits associated with social play. Studying sex differences in both play and grooming may thus help to elucidate sex differences in the means by which social bonds are formed and maintained throughout the lifespan.

In contrast to social play, solitary (e.g., object and locomotor) play is likely to fulfill the same function for male and female white-faced capuchins. If it is true that different types of play can serve different evolutionary functions, one would expect no sex difference in rates of solitary play when males and females have similar needs for the development of foraging and basic locomotor skills. This may depend on the species' diet and socioecology. Female reproductive success across primates is generally more dependent on food availability than male reproductive success (Silk 1993), and there is some evidence that adult female white-faced capuchins spend more time foraging than adult males (Rose, 1994). However, there is no evidence of sex differences in basic locomotion, other than differences in the need for fighting skills, as discussed previously. Additionally, the closely-related tufted capuchins (*Sapajus apella*), which have similar socioecologies and extractive foraging niches, do not show sex differences in rates of solitary play (Paukner & Suomi, 2008). Thus, it is possible but unlikely that white-faced capuchins will display sex differences in solitary play.

**Research Questions and Predictions**

The current study analyzes the patterning of play behavior in white-faced capuchins over the lifespan, and seeks to answer the following research questions: are there sex differences in the rates of social and solitary play, and how do these sex differences change over development? Additionally, I investigated whether there might be evidence for a trade-off in the activity budget of males and females between grooming and play. In other words, if social play provides important bond-formation benefits, and females play less often than males, might females compensate for the lack of bonding opportunities by increasing rates of other bond-formation behaviors like grooming? Finally, I was interested in whether the observational evidence provides support for any of the functional hypotheses about play—what, if anything, can sex differences in play tell us about play's ultimate evolutionary functions?

Based on the patterns of development, dispersal, and play in other primate species and the social system in white-faced capuchins, I predicted (1) that rates of both social and solitary play would decrease with age, (2) that males would have higher rates of social play when compared to females throughout the lifespan, and (3) that there would be no sex difference in rates of solitary play.

Most research studies on play in animals are cross-sectional, having a study design that compares static age groups or sex differences. However, it is critical to conduct longitudinal studies to understand the timing and emergence of sex- and age-specific patterns in play. I examined sex differences in play in a cohort of wild white-faced capuchins that were observed over 18 years (Perry et al., 2012), to see when sex differences emerged and whether sex differences in play were consistent with known sex-specific reproductive strategies.

# Methods

## Field Site and Subjects

The data for this study were collected from 2002 to 2019, as part of the Lomas Barbudal Monkey Project, a longitudinal study of wild white-faced capuchin monkeys led by Dr. Susan Perry that began in 1990. The field site includes the Reserva Biológica Lomas Barbudal in the Guanacaste province of Costa Rica and surrounding private areas. Subjects (N= 38) included 18 males and 20 females. Subjects were born between August 2000 and April 2005, and were regularly monitored with ongoing behavioral observations beginning in 2002 (or at birth for those born after 2002).

The 38 subjects were born into one of three habituated social groups (group names AA, FF, RR). Over the course of the study, the three original groups fissioned, producing seven additional multi-male, multi-female social groups (FL, MK, CU, CE, DI, RF, SP), and one long-term all-male group (LB)[1]. As described in the introduction, male capuchins generally disperse from their natal groups and may switch groups several times throughout their lives, including spending periods in all-male groups. Some of the males in this study migrated from their natal group to groups that were observed as part of the Lomas Barbudal Monkey Project, while others migrated to unmonitored groups and were thus lost to the research team, aside from rare glimpses when unhabituated groups were encountered. Thus, throughout the course of this study, subjects were in a total of 11 monitored social groups (those named above), the unmonitored group BD, several small male-only groups, and other unmonitored, unhabituated social groups.

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[1] AA's fission products include AA, FL, and CE. FF's fission products include FF and RF. RR's fission products include RR, MK, DI, SP, and LB. MK later fissioned into MK and CU. The original name was kept by the larger group after each fission event.

Twenty out of 38 subjects were lost to observation before the end of the study. Of the 20 original females, 10 were presumed to have died, with mean age of death 10.12 years (SD = 5.17 years). Of the 18 original males, only one was observed throughout the entire study period, four were known to have emigrated from the study groups, two likely emigrated from the study groups, nine likely died, and two disappeared for unknown reasons. If males disappeared when they were young and were the only group member to disappear at that time, they were presumed to be dead. If older males disappeared simultaneously with another male from their group, they were presumed to have emigrated outside the study area. The average age of disappearance or death for males was 4.36 years (SD = 3.31 years).

**Data Collection**

Rates of social play, solitary play, and grooming were calculated using data from point samples taken during focal follows of each subject. During the focal follows, instantaneous point samples were taken every 2.5 minutes, recording the individual's state activity and proximity to other monkeys. For example, if the focal individual was engaged in social play at the 2.5 minute mark, "social play" would be recorded for that point sample (although the name of the play partner was not recorded). Only one subject was followed at a time, ensuring that each play instance was only recorded once. Data were collected by one observer who watched and narrated the behaviors, while a second observer input data on a handheld Psion or Android device and assisted observations when necessary (e.g., to confirm the identity of non-focal individuals for the proximity data; Perry et al., 2012). Focal follows were at least 10 minutes in duration, with some longer depending on the year of the study.

While the length of the focal follows varied, the protocol for data collection was otherwise uniform throughout the study period. Consistency between observers was ensured by interobserver reliability tests. Before contributing data, all observers had to pass tests requiring 100% accuracy on monkey identifications, 100% accuracy in the coding scheme, 97% accuracy in speed typing, and 97% accuracy in matching their recorded observations to those of other trained observers in the field during focal follows. Interobserver reliability tests were repeated monthly to ensure lack of drift, and samples for which the observer team (typist and spotter) disagreed regarding monkey identifications or behaviors were discarded.

Observers rotated between the different habituated groups in teams of two or more such that one to three groups were followed simultaneously on a given day, depending on the size of the observation team at the time. The number of days that each group was followed also depended on the size of the observation team, although effort was made to observe each habituated group at least once a month. There was high variability in the number of point samples for each subject per year, ranging from 3 to 2561 point samples for years in which data could be collected on each subject (mean = 870.5 samples per monkey/per year, SD = 651.5).

For the purposes of this study, ***social play*** was defined as any of a number of specific play behaviors performed with at least one social partner (Play Bite, Play Chase, Play Flee, Play Hit, Play Invite/Play Face, Play Bounce/Jump, Chicken Fight, Play Pull, Play Overlord, Play Push, Play Lunge, Play Threat, Play Pounce On, Play Wrestle; see Appendix Table 1). These behaviors were identified as playful, rather than aggressive, by the presence of play-specific signals (e.g., play-specific facial expressions), absence of audible vocalizations, modified forms (e.g., slow, exaggerated movement, bouncy gait, or gentle versions of aggressive behaviors), or by their co-occurrence with other behaviors that clearly fit those criteria. ***Solitary play*** ("solo

play" in ethogram) was defined as "engaging in object manipulations for no obvious foraging purpose, or engaging in extraneous, sometimes exaggerated body movements that seem to serve no obvious purpose for locomotion, foraging, care of the body (comfort or hygiene), or social interaction." ***Grooming*** was defined as "one monkey picks through the hair of another monkey with the hands and/or mouth; the recipient of this behavior is generally in a reclining posture."

**Statistical Analysis**

To determine sex differences in the rates of each behavior, I ran a series of three Poisson generalized linear mixed models, with social play, solitary play, and grooming as the outcome variables. Each model included sex, age, and the interaction between sex and age as predictor variables, with a random effect for individual to account for repeated sampling for each individual over time. This random effect allowed the intercepts to vary by individual but not the regression coefficients (i.e., the main effects of sex, age, or sex*age were not allowed to vary by individual).

For each model (social play, solitary play, and grooming), the outcome variable was the proportion of the total point samples per year in which the given behavior occurred. To achieve this, the point sample data were aggregated for each individual by each year of age. Thus, for each year, an individual had a count of total point samples, and a count of point samples for each behavior (e.g., for the given year, how many point samples was individual X observed in social play, solitary play, and grooming). The total number of point samples was included as the exposure variable in the Poisson model in order to model the outcome variable as a rate and to control for variation in the number of times each individual was observed.

Each model assumes that the number of observations of the outcome behavior has a Poisson distribution (an appropriate maximum entropy distribution for rare count variables; McElreath, 2020). For example, using the log link function, the model formula for the average number of social play observations per monkey per year is given by:

$$\log(\lambda_{ij}) = \beta_0 + U_{0j} + \beta_1 \text{sex}_{ij} + \beta_2 \text{age}_{ij} + \beta_3 * \text{sex}_{ij} * \text{age}_{ij}$$

where $\lambda$ is the rate or the average number of social play observations per monkey per year, $i$ is the count of social play observations per monkey per year, $j$ is the individual monkey, and $U_{0j}$ is the random intercept effect for individual. The solitary play and grooming models used a similar model formula, but with $\lambda$ representing the rate of solitary play or grooming per monkey per year, respectively.

All statistical analyses were conducted in the R programming environment (R Core Team, 2019). Regression models were fit using the *glmer* function within the *lme4* package (Bates et al., 2015). 95% confidence intervals for all figures were calculated using the *bootMer* function in the *lme4* package.

## Results

### Do rates of social play vary by sex and age?

The social play model showed a significant fixed effect for sex, such that males had higher rates of social play than females ($\beta_{\text{sex}}=0.322$, P=0.002). There was a significant effect of age, such that rates of play for both sexes decreased with age ($\beta_{\text{age}}=-0.215$, P<0.001). The interaction between sex and age was also significant, such that the decline of the rate of play with

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age was faster for females than males ($\beta_{sex*age}$=0.103, P<0.001). This interaction was likely driven by males, but not females, increasing rates of social play over time in the early juvenile period (see Figure 1).
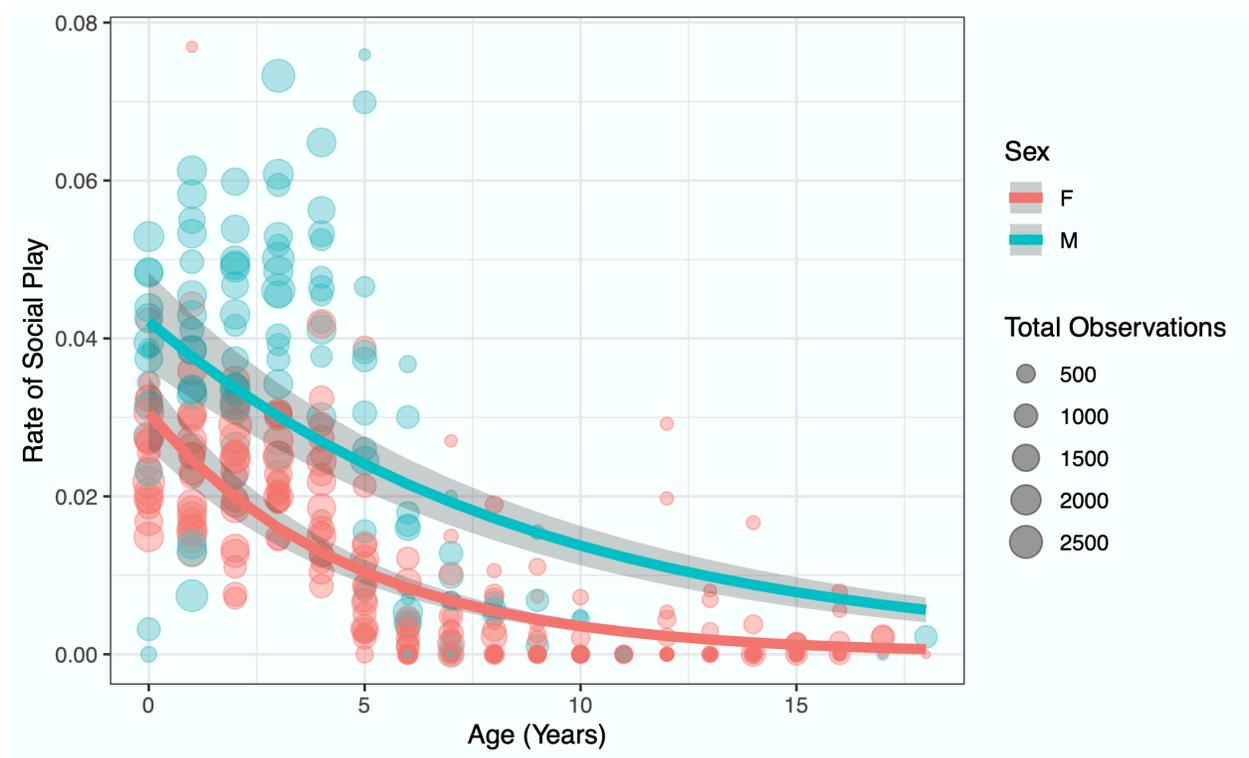


**Figure 1: Social Play Model Predictions.** Rates of social play (as a proportion of the total point samples per year) are plotted against age in years. The first year of life is coded as 0. Circles represent the proportion of point samples in which an individual monkey was engaging in social play in a given year, with the size of the circle representing the total number of point samples for the individual in the same year. Lines represent predictions from the Poisson mixed model. Shaded areas represent bootstrapped 95% confidence intervals of the predictions.

**Do rates of solitary play vary by sex and age?**

The solitary play model did not have a significant fixed effect for sex ($\beta_{sex}$=-0.107, P=0.624) suggesting there was no significant difference between male and female rates of solitary play. The effect of age was significant, such that older monkeys had lower rates of solitary play ($\beta_{age}$=-0.488, P <0 .001). There was also a significant interaction of age and sex,

such that females reduced rates of solitary play over time more quickly than males

($\beta_{sex*age}$=0.090, P = 0.014). However, as can be seen in Figure 2, this effect size was fairly small

as there was negligible difference in the predicted rate of solitary play between the sexes at any

age.

The solitary play data had one extreme outlier, a six-year-old male (RU) who was

observed to have an unusually high rate of solitary play (rate of solitary play = 0.2, Z-score

among all six-year-olds = 5.1, see Figure 3). However, this extreme value was likely an artifact

of the small number of observations for that individual in his sixth year: there were only five

point samples for him that year, one of which was solitary play. Because the solitary play

regression model accounted for the total number of point samples as the exposure variable, this

outlier is not likely to have had an outsized effect on the model overall. In fact, rerunning the

model with the outlier removed had no substantive effect on any of the coefficient estimates or

inferences ($\beta_{sex}$=-0.104, P=0.633, $\beta_{age}$=-0.487, P<0.001, $\beta_{sex*age}$=0.086, P=0.018). Thus, the

outlier was kept in the dataset when fitting the model but removed from Figure 2 for

visualization purposes.

**Figure 2: Solitary Play Model Predictions.** Rates of solitary play (as a proportion of the total point samples per year) are plotted against age in years. The first year of life is coded as 0. Circles represent the proportion of point samples in which an individual monkey was engaging in solitary play in a given year, with the size of the circle representing the total number of point samples for the individual in the same year. Lines represent predictions from the Poisson mixed model. Shaded areas represent bootstrapped 95% confidence intervals of the predictions. Note that the outlier from Figure 3 is not visible in this figure.
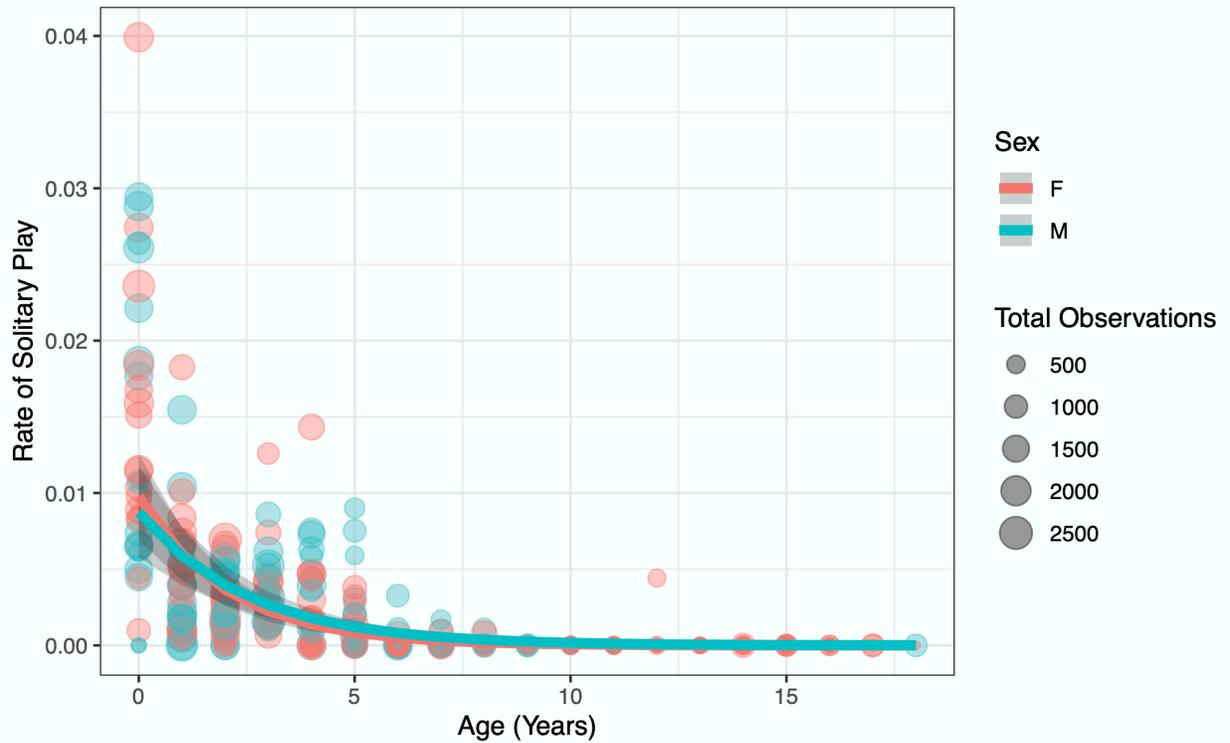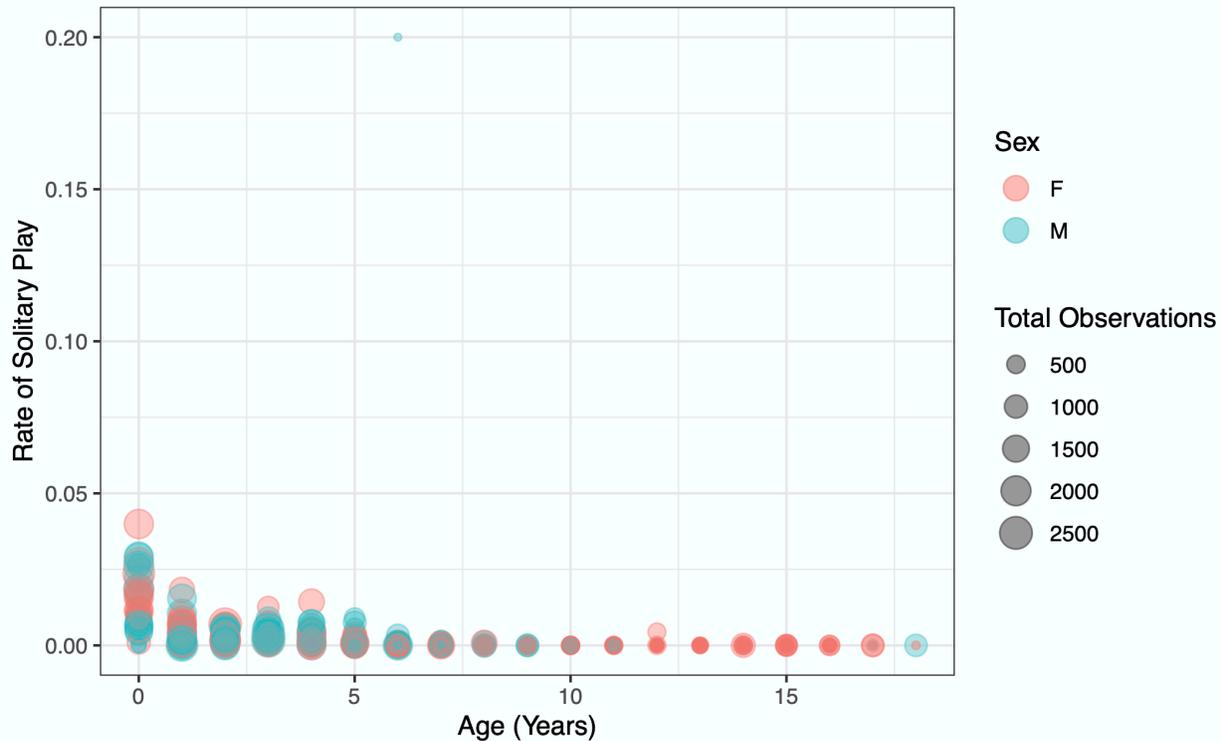
**Figure 3: Solitary Play Rates with Outlier.** Rates of solitary play (as a proportion of the total point samples per year) are plotted against age in years. The first year of life is coded as 0. Circles represent the proportion of point samples in which an individual monkey was engaging in solitary play in a given year, with the size of the circle representing the total number of point samples for the individual in the same year. In this figure, the outlier (male with solitary play in 1 of 5 point samples taken at age 6) can be clearly seen. The outlier was included in the model but removed from Figure 2 in order to better visualize the model predictions.

**Do rates of grooming vary by sex and age?**

The grooming model had a significant fixed effect for sex, such that females had higher rates of grooming than males ($\beta_{sex}$=-0.225, P=0.048). The effect of age was also significant, such that rates of grooming increased with age overall ($\beta_{age}$= 0.073, P<0.001). Finally, the interaction of age and sex was significant such that female grooming rates increased with age, while male grooming rates decreased with age ($\beta_{sex*age}$= -0.139, P<0.001); the rate of grooming increases by 7.5% for each additional year of age for females and decreases by 6.3% for each additional year of age for males (see Figure 4).
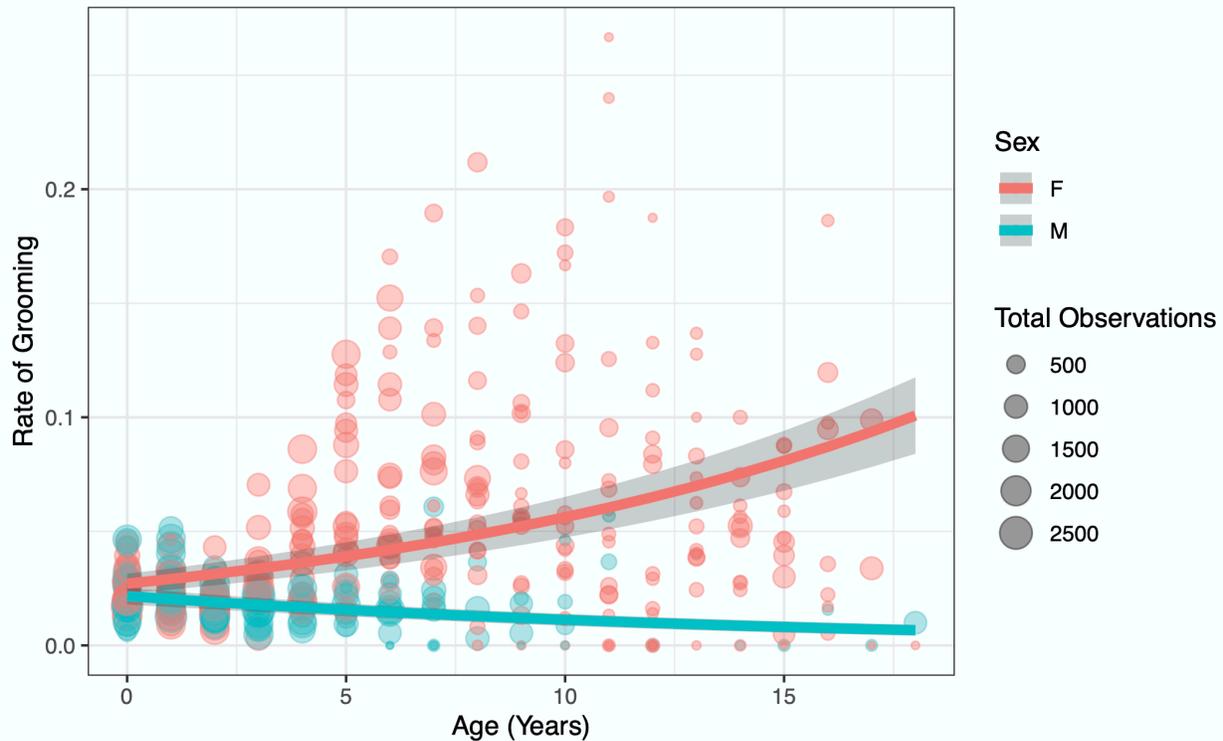
**Figure 4: Grooming Model Predictions.** Rates of grooming (as a proportion of the total point samples per year) are plotted against age in years. The first year of life is coded as 0. Circles represent the proportion of point samples in which an individual monkey was engaging in grooming in a given year, with the size of the circle representing the total number of point samples for the individual in the same year. Lines represent predictions from the Poisson mixed model. Shaded areas represent bootstrapped 95% confidence intervals of the predictions.

## Discussion

Consistent with the general mammalian trend, rates of play in white-faced capuchins were greatest early in life and declined with age, for both social and solitary play and for both males and females. There were sex differences in the rates of social play in this species, such that the average rate was higher in males than females. Additionally, while both males and females had declining rates of social play as age increased, the decline was steeper for females compared to males. However, my analysis of solitary play found no sex difference in the average rate of solitary play and a negligible (albeit statistically significant) interaction effect between sex and

age in which females had a slightly steeper decline of solitary play with age, compared to males. Finally, I investigated the possibility of time budget tradeoffs between social play and grooming, a known bond-formation behavior. Older animals groomed at higher rates on average than younger animals, and females groomed at higher rates than males. The effect of age on grooming interacted with sex such that the rate of grooming tended to increase with age for females but not for males. These patterns of grooming were consistent with previous studies on grooming in white-faced capuchins (Manson et al., 1999; Perry, 1996, 1998).

Together, these results suggest that white-faced capuchin males allocate more time toward social play than females throughout both the juvenile period and adulthood.  I propose that females may compensate for lower opportunities to form social bonds via play through increases in their rates of grooming. This sex difference in development may simply reflect that females and males allocate social effort in different ways, or it may reflect that males and females have different needs for developing the particular kinds of tactical skills that can be practiced in rough-and-tumble social play. Interestingly, the interaction of sex and age on social play rate appears in Figure 1 to be at least partially driven by males (but not females) increasing rates of social play over time during the early juvenile period, with male social play peaking around ages 3 to 4. This suggests that males maximize social play at the time right around or before the average age of dispersal out of the natal group. This may indicate that social play has particular benefits for male survival or reproductive success during that uncertain period.

Under the practice hypothesis, playing provides benefits for the development of sex-specific behaviors. The finding of higher rates of social play, but not solitary play, in juvenile male white-faced capuchins compared to females could reflect important differences in the types of social behaviors that are most crucial for each sex's reproductive success in adulthood.

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Fighting skills are important for male reproductive success as they allow males to enter and take over groups of females. Males that are unable to achieve alpha status in new social groups might never gain access to reproductive opportunities. Fighting requires not just physical agility, as might be developed through solitary play, but also tactical maneuvers and social skills, which likely require practice with partners. Social play may also help to develop a greater understanding of the social affordances of physical maneuvers—for example, assessing one's own physical power relative to others, predicting the loyalty of allies, or learning how to avoid conflict escalation. In contrast, physical fighting skills are not as critical for female reproductive success. If social play allows white-faced capuchins to explore and hone specific skills that are needed in adulthood, my finding that males partake in higher rates of social (primarily rough-and tumble) play are consistent with the practice hypothesis.

The results are also consistent with the bonding hypothesis for the function of play, which is not necessarily mutually exclusive from the practice hypothesis. While social play may function to form social bonds, females may preferentially form social bonds through grooming. However, the relationship between social play and grooming is purely correlational, and more research would be needed to substantiate this exploratory link. Future comparisons between species may give us clues into the potential bonding functions of play. For example, social bonds may be particularly important for capuchins, resulting in both physical and bonding benefits of play, whereas in species where there is less reproductive skew or where reproductive success is less dependent on bonds and alliances, play (even social play) may primarily confer physical benefits.

While the current study findings are consistent with several functional hypotheses regarding play, it is important to remember that sex differences in play are not *necessarily*

meaningful in terms of adult behavior. For example, a study in meerkats found no correlation between the frequency of play-fighting in early life and subsequent fighting success in adulthood, for either sex (Sharpe, 2005). Cords and colleagues (2010) have argued that sex differences in juvenile behavior can anticipate adult behavior in some cases, but researchers should not overlook the immediate consequences of a behavior in favor of delayed ones (Cords et al., 2010). Additionally, Pellegrini and Smith (2005) argued that although it is possible that males and females in many species evolved different play styles to develop different skills needed in adulthood, it is also possible that sex differences in juvenile play could simply be due to size dimorphisms or to sex-specific nutritional or energetic demands at different points in development (Pellegrini & Smith, 2005).

The current analysis was limited in several ways by the information available in the longitudinal dataset. The first limitation is that although there was a distinction between social and solitary play, the dataset did not make distinctions between subtypes of these categories. For example, the social play category included all rough-and-tumble play behaviors, and distinctions were not made between specific behaviors within that category (e.g., play bouncing versus play biting; see ethogram in Appendix Table 1). The solitary play category included both object and locomotor play. An additional challenge with recording solitary, object play was that a conservative definition was used during data collection that excluded handling of leaves, sticks, or other food items, in the absence of any obvious repetition, modification, or exaggeration from functional food handling. Thus, handling of food items was generally categorized as foraging in the dataset, even though theoretically a monkey could play with those items. Most definitions of play in the animal literature exclude behaviors that could be interpreted as foraging, so the exclusion of these behaviors is not unique to the current study (Burghardt, 2005). However, it is

important to recognize that studies of play in wild animals probably underestimate the rate of object play by disregarding play that may occur with food items, particularly for omnivorous animals like capuchins (in which case even inedible objects like sticks or rocks are commonly handled to eat insects off of them).

A final limitation is that the point samples analyzed in this study did not contain information on the partners or direction of social behaviors. For example, whether grooming was given or received at the time of the point sample was not specified. Previous studies have shown that adult female white-faced capuchins are most likely to groom with other females or the alpha male (Perry 1996). Adult males rarely groom one another, and when they do participate in grooming interactions it is often when they receive grooming from females. In fact, it is likely that a large portion of the grooming time attributed to adult males in this study was due to males (particularly alpha males) receiving grooming from females.

This study raises several questions that should be explored in future work. Previous research suggests that preferences for social play partners may depend on sex in some primate species (e.g., Lutz et al., 2019). Future analyses should address the extent to which the sex differences in rates of social play in white-faced capuchins may be driven by partner preferences, for example if males and/or females preferentially initiate play with male partners. The rate of play might also depend on the number of siblings or the total number of juveniles in each group that are available as playmates at any given time. Other future directions include exploring the relationship of play to social bonding. For example, if male white-faced capuchins that play together as juveniles are more likely to co-emigrate together, that could indicate that play provides important opportunities for young males to strengthen and test these fitness-relevant relationships, while in the protected space of their natal group. While Perry and colleagues

(2017) found no relationship between rates of social play and time to emigration or time to first alpha male status, that paper used a broader sample of individuals with lower sampling rates, and did not consider the identity of play or co-emigration partners. The bonding hypothesis might also be supported if females that play together as juveniles are more likely to support each other in aggressive coalitions, or to be grooming partners in adulthood. Finally, longitudinal datasets such as the one used in this study provide excellent opportunities to investigate whether play in early life is associated with any concrete fitness benefits in adulthood. With longitudinal data, it may be possible to assess delayed fitness benefits in variables like rank acquisition, number of offspring, or outcomes linked to fighting skills such as fighting success or wounding frequency.

Lifespan perspectives on behaviors such as play and grooming allow us a better understanding of the developmental patterns of these behaviors and how they have evolved both within and across species. The current study demonstrates that playing with one another may help prepare young white-faced capuchins for navigating the rich social world of adult life, and provides a promising area for future research.

## Ethics Statement

This research was approved by the Animal Research Committee at the University of California, Los Angeles (ARC 1996-122, 2005-084, 2016-022, and associated renewals) and was conducted in accordance with United States and Costa Rica federal and international laws.

# Appendix

**Table 1: Ethogram of Behaviors.**

| Behavior | Specific examples | Ethogram Definition |
|---|---|---|
| *Social Play* | Play Bite | One monkey gently mouths another monkey, generally in the context of play wrestling. |
| | Play Chase | One monkey gallops in pursuit of another monkey, generally with a bouncy gait, and with no accompanying vocalizations. Play chases are often invited by running away and looking over the shoulder at the other monkey. |
| | Play Flee | In the context of other play behaviors, one monkey runs away from another monkey, who is typically chasing him/her. |
| | Play Hit | A monkey slaps another monkey with a slow, exaggerated motion, generally in the context of play wrestling. |
| | Play Invite/Play Face | The monkey's mouth is open, and the teeth do not show, with the exception of the tips of the canines. |
| | Play Bounce/Jump | In the context of other play behaviors, the monkey bounces up and down, either on a branch or on the ground. |
| | Chicken Fight | Two monkeys hang by their tails, swatting at and grappling with one another. |
| | Play Pull | In the context of other play behaviors, one monkey grabs some body part (usually a limb) of another monkey and pulls on it. |
| | Play Overlord | In the context of other play behaviors, one monkey gets on the back of another monkey and clasps his/her hands around the bottom monkey's chest so that their heads are stacked on top of one another. |
| | Play Push | In the context of other play behaviors, one monkey shoves another monkey. |

| | | |
|---|---|---|
| | Play Lunge | A play lunge is identical to an aggressive lunge, except that it is always performed in silence and in the context of other play behaviors. |
| | Play Threat | In the context of other play behaviors, the monkey opens the mouth so that the teeth are visible, lays the ears back, and stares at another monkey. |
| | Play Pounce On | Leap on top of another monkey in a play bout. |
| | Play Wrestle | Two or more monkeys grapple in slow motion with their arms, legs, and sometimes tail, in silence. |
| *Solitary Play* *[Solo Play]* | | A monkey engages in object manipulations for no obvious foraging purpose, or engages in extraneous, sometimes exaggerated body movements that seem to serve no obvious purpose for locomotion, foraging, care of the body (comfort or hygiene), or social interaction. |
| *Grooming* | | One monkey picks through the hair of another monkey with the hands and/or mouth; the recipient of this behavior is generally in a reclining posture. |

# References

Auger, A. P., & Olesen, K. M. (2009). Brain Sex Differences and the Organisation of Juvenile Social Play Behaviour. *Journal of Neuroendocrinology*, *21*(6), 519–525. https://doi.org/10.1111/j.1365-2826.2009.01871.x

Baldwin, J. D., & Baldwin, J. I. (1974). Exploration and Social Play in Squirrel Monkeys (*Saimiri*). *American Zoologist*, *14*(1), 303–315. https://doi.org/10.1093/icb/14.1.303

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bateson, P., & Martin, P. (2013). *Play, Playfulness, Creativity, and Innovation*. Cambridge University Press.

Bjorklund, D. F., & Gardiner, A. K. (2010). *Object Play and Tool Use: Developmental and Evolutionary Perspectives* (P. Nathan & A. D. Pellegrini, Eds.). Oxford Handbooks Online. https://doi.org/10.1093/oxfordhb/9780195393002.013.0013

Brown, G. R., & Dixson, A. F. (2000). The development of behavioural sex differences in infant rhesus macaques (*Macaca mulatta*). *Primates*, *41*(1), 63–77. https://doi.org/10.1007/BF02557462

Burghardt, G. (2005). *The Genesis of Animal Play*. Massachusetts Institute of Technology.

Byers, J. A., & Walker, C. (1995). Refining the Motor Training Hypothesis for the Evolution of Play. *The American Naturalist*, *146*(1), 25–40. https://doi.org/10.1086/285785

Chau, M. J., Stone, A. I., Mendoza, S. P., & Bales, K. L. (2008). Is Play Behavior Sexually Dimorphic in Monogamous Species? *Ethology*, *114*(10), 989–998. https://doi.org/10.1111/j.1439-0310.2008.01543.x

Cordoni, G. (2009). Social play in captive wolves (*Canis lupus*): Not only an immature affair.

　　*Behaviour*, *146*(10), 1363–1385. https://doi.org/10.1163/156853909X427722

Cordoni, G., Norscia, I., Bobbio, M., & Palagi, E. (2018). Differences in play can illuminate

　　differences in affiliation: A comparative study on chimpanzees and gorillas. *PLOS ONE*,

　　*13*(3), e0193096. https://doi.org/10.1371/journal.pone.0193096

Cords, M., Sheehan, M. J., & Ekernas, L. S. (2010). Sex and age differences in juvenile social

　　priorities in female philopatric, nondespotic blue monkeys. *American Journal of*

　　*Primatology*, *72*(3), 193–205. https://doi.org/10.1002/ajp.20768

Fedigan, L. M., & Baxter, M. J. (1984). Sex differences and social organization in free-ranging

　　spider monkeys (*Ateles geoffroyi*). *Primates*, *25*(3), 279–294.

　　https://doi.org/10.1007/BF02382267

Fedigan, L. M., & Jack, K. M. (2012). Tracking Neotropical Monkeys in Santa Rosa: Lessons

　　from a Regenerating Costa Rican Dry Forest. In P. M. Kappeler & D. P. Watts (Eds.),

　　*Long-Term Field Studies of Primates* (pp. 165–184). Springer Berlin Heidelberg.

　　https://doi.org/10.1007/978-3-642-22514-7_8

Fry, D. P. (2005). Rough-and-Tumble Social Play in Humans. In A. D. Pellegrini & P. K. Smith

　　(Eds.), *Play in Great Apes and Humans* (pp. 54–88). The Guilford Press.

Godoy, I., Vigilant, L., & Perry, S. E. (2016). Inbreeding risk, avoidance and costs in a group-

　　living primate, *Cebus capucinus*. *Behavioral Ecology and Sociobiology*, *70*(9), 1601–

　　1611. https://doi.org/10.1007/s00265-016-2168-1

Gopnik, A., O'Grady, S., Lucas, C. G., Griffiths, T. L., Wente, A., Bridgers, S., Aboody, R.,

　　Fung, H., & Dahl, R. E. (2017). Changes in cognitive flexibility and hypothesis search

　　across human life history from childhood to adolescence to adulthood. *Proceedings of the*

National Academy of Sciences, *114*(30), 7892–7899.

https://doi.org/10.1073/pnas.1700811114

Grebe, N. M., Fitzpatrick, C., Sharrock, K., Starling, A., & Drea, C. M. (2019). Organizational

and activational androgens, lemur social play, and the ontogeny of female dominance.

*Hormones and Behavior*, *115*, 104554. https://doi.org/10.1016/j.yhbeh.2019.07.002

Gros-Louis, J., Perry, S., & Manson, J. H. (2003). Violent coalitionary attacks and intraspecific

killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates*, *44*(4), 341–

346. https://doi.org/10.1007/s10329-003-0050-z

Hakeem, A., Sandoval, G. R., Jones, M., & Allman, J. (1996). Brain and Life Span in Primates.

In J. E. Birren, K. W. Schaie, R. P. Abeles, M. Gatz, & T. A. Salthouse (Eds.), *Handbook*

*of the Psychology of Aging* (4th ed., pp. 78–104). Academic Press, Inc.

Himmler, B. T., Stryjek, R., Modlinska, K., Derksen, S. M., Pisula, W., & Pellis, S. M. (2013).

How domestication modulates play behavior: A comparative analysis between wild rats

and a laboratory strain of Rattus norvegicus. *Journal of Comparative Psychology*

*(Washington, D.C.: 1983)*, *127*(4), 453–464. https://doi.org/10.1037/a0032187

Lutz, M. C., Ratsimbazafy, J., & Judge, P. G. (2019). Use of social network models to

understand play partner choice strategies in three primate species. *Primates*, *60*(3), 247–

260. https://doi.org/10.1007/s10329-018-00708-7

Maestripieri, D., & Ross, S. R. (2004). Sex differences in play among western lowland gorilla

(*Gorilla gorilla gorilla*) infants: Implications for adult behavior and social structure.

*American Journal of Physical Anthropology*, *123*(1), 52–61.

https://doi.org/10.1002/ajpa.10295

Manson, J. H., Rose, L. M., Perry, S., & Gros-Louis, J. (1999). Dynamics of Female–Female Relationships in Wild *Cebus capucinus*: Data from Two Costa Rican Sites. *International Journal of Primatology*, *20*(5), 679–706. https://doi.org/10.1023/A:1020700718458

Martin, P., & Caro, T. M. (1985). On the Functions of Play and Its Role in Behavioral Development. In J. S. Rosenblatt, C. Beer, M.-C. Busnel, & P. J. B. Slater (Eds.), *Advances in the Study of Behavior* (Vol. 15, pp. 59–103). Academic Press. https://doi.org/10.1016/S0065-3454(08)60487-8

McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and Stan* (2nd ed.). Taylor and Francis, CRC Press.

Meaney, M. J., Stewart, J., & Beatty, W. W. (1985). Sex Differences in Social Play: The Socialization of Sex Roles. In J. S. Rosenblatt, C. Beer, M.-C. Busnel, & P. J. B. Slater (Eds.), *Advances in the Study of Behavior* (Vol. 15, pp. 1–58). Academic Press. https://doi.org/10.1016/S0065-3454(08)60486-6

Muniz, L. (2008). *Genetic Analyses of Wild White-Faced Capuchins (Cebus capucinus)* [Ph.D. Thesis]. Universität Leipzig.

Ortega, J. C., & Bekoff, M. (1987). Avian Play: Comparative Evolutionary and Developmental Trends. *The Auk*, *104*(2), 338–341. JSTOR.

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implicationsfor natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, *129*(3), 418–426. https://doi.org/10.1002/ajpa.20289

Paukner, A., & Suomi, S. J. (2008). Sex differences in play behavior in juvenile tufted capuchin monkeys (*Cebus apella*). *Primates; Journal of Primatology*, *49*(4), 288–291. https://doi.org/10.1007/s10329-008-0095-0

Pedersen, J. M., Glickman, S. E., Frank, L. G., & Beach, F. A. (1990). Sex differences in the

    play behavior of immature spotted hyenas, *Crocuta crocuta*. *Hormones and Behavior*,

    *24*(3), 403–420. https://doi.org/10.1016/0018-506X(90)90018-S

Pellegrini, A. D., & Smith, P. K. (1998). The Development of Play During Childhood: Forms

    and Possible Functions. *Child Psychology and Psychiatry Review*, *3*(2), 51–57.

    https://doi.org/10.1111/1475-3588.00212

Pellegrini, A. D., & Smith, P. K. (2005). Play in great apes and humans. In *The Nature of Play:*

    *Great Apes and Humans* (pp. 285–298). The Guilford Press.

Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys,

    *Cebus capucinus*. *American Journal of Primatology*, *40*(2), 167–182.

Perry, S. (1998). Male-Male Social Relationships in Wild White-Faced Capuchins, *Cebus*

    *capucinus*. *Behaviour*, *135*(2), 139–172. JSTOR.

Perry, S. (2009). Conformism in the food processing techniques of white-faced capuchin

    monkeys (*Cebus capucinus*). *Animal Cognition*, *12*(5), 705–716.

    https://doi.org/10.1007/s10071-009-0230-3

Perry, S. (2012). Chapter 4 - The Behavior of Wild White-Faced Capuchins: Demography, Life

    History, Social Relationships, and Communication. In H. J. Brockmann, T. J. Roper, M.

    Naguib, J. C. Mitani, & L. W. Simmons (Eds.), *Advances in the Study of Behavior* (Vol.

    44, pp. 135–181). Academic Press. https://doi.org/10.1016/B978-0-12-394288-3.00004-6

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H.,

    Panger, M., Pyle, K., & Rose, L. (2003). Social Conventions in Wild White-faced

    Capuchin Monkeys: Evidence for Traditions in a Neotropical Primate. *Current*

    *Anthropology*, *44*(2), 241–268. https://doi.org/10.1086/345825

Perry, S., Godoy, I., & Lammers, W. (2012). The Lomas Barbudal Monkey Project: Two

    Decades of Research on *Cebus capucinus*. In P. M. Kappeler & D. P. Watts (Eds.), *Long-*

    *Term Field Studies of Primates* (pp. 141–163). Springer Berlin Heidelberg.

    https://doi.org/10.1007/978-3-642-22514-7_7

Perry, S., & Manson, J. H. (2008). *Manipulative Monkeys: The Capuchins of Lomas Barbudal*.

    Harvard University Press.

Poirier, F. E., & Smith, E. O. (1974). Socializing Functions of Primate Play. *American Zoologist*,

    *14*(1), 275–287. https://doi.org/10.1093/icb/14.1.275

Poole, T. B., & Fish, J. (1976). An investigation of individual, age and sexual differences in the

    play of Rattus norvegicus (Mammalia: Rodentia). *Journal of Zoology*, *179*(2), 249–259.

    https://doi.org/10.1111/j.1469-7998.1976.tb02294.x

Power, T. G. (2000). *Play and Exploration in Children and Animals*. Lawrence Erlbaum

    Associates.

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. R Foundation

    for Statistical Computing. https://www.R-project.org/

Raleigh, M. J., Flannery, J. W., & Ervin, F. R. (1979). Sex differences in behavior among

    juvenile vervet monkeys (*Cercopithecus aethiops sabaeus*). *Behavioral and Neural*

    *Biology*, *26*(4), 455–465. https://doi.org/10.1016/S0163-1047(79)91482-1

Rijksen, H. D. (1978). *A field study on Sumatran orang utans (Pongo pygmaeus abelii Lesson*

    *1827): Ecology, behaviour and conservation* [Phd, Veenman].

    https://library.wur.nl/WebQuery/wurpubs/71969

Rodrigues, M. A. (2014). Emergence of Sex-Segregated Behavior and Association Patterns in

Juvenile Spider Monkeys. *Neotropical Primates*, *21*(2), 183–188.

https://doi.org/10.1896/044.021.0204

Rose, L. M. (1994). Sex differences in diet and foraging behavior in white-faced capuchins

(*Cebus capucinus*). *International Journal of Primatology*, *15*(1), 95–114.

https://doi.org/10.1007/BF02735236

Sharpe, L. L. (2005). Play fighting does not affect subsequent fighting success in wild meerkats.

*Animal Behaviour*, *69*(5), 1023–1029. https://doi.org/10.1016/j.anbehav.2004.07.013

Silk, J. B. (1993). The evolution of social conflict among female primates. In W. A. Mason & S.

P. Mendoza (Eds.), *Primate Social Conflict* (pp. 49–83). State University of New York

Press.

Smaldino, P. E., Palagi, E., Burghardt, G. M., & Pellis, S. M. (2019). The evolution of two types

of play. *Behavioral Ecology*, *30*(5), 1388–1397. https://doi.org/10.1093/beheco/arz090

Stevenson, M. F., & Poole, T. B. (1982). Playful interactions in family groups of the common

marmoset (*Callithrix jacchus jacchus*). *Animal Behaviour*, *30*(3), 886–900.

https://doi.org/10.1016/S0003-3472(82)80163-2

Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. Columbia University Press.

West, M. (1974). Social Play in the Domestic Cat. *American Zoologist*, *14*(1), 427–436.

https://doi.org/10.1093/icb/14.1.427