

# The relationship between social play and developmental milestones in wild chimpanzees (*Pan troglodytes schweinfurthii*)

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Social play is common among many group-living animals, but the benefits are not well understood. Proposed benefits include increased muscle coordination as the result of increased locomotor versatility and development, and strengthened social bonds through interactions with like-aged individuals. In this study, we used 33 years of long-term behavioral data on infant chimpanzees in Gombe National Park, Tanzania, to examine these potential benefits of social play, specifically how the percentage of time engaged in social play relates to motor and social developmental milestones. We predicted that infants who engaged in more social play would achieve motor and social milestones at younger ages. We found that individuals that spent more time engaging in social play achieved the motor milestones of riding dorsally and traveling independently at earlier ages. Additionally, we found that the amount of play was correlated with earlier ages for reaching the social milestones of spatial independence from mother, first grooming of non-maternal kin, and first observed mating attempt. This is the first study in great apes to demonstrate a relationship between play behavior and developmental milestones, supporting the hypotheses that play provides motor, and social benefits.

## KEYWORDS

chimpanzees, developmental milestones, play benefits, social play

## 1 | INTRODUCTION

Play behavior is contextually defined and can be identified as being (i) non-adaptive in context; (ii) voluntary, pleasurable, or self-rewarding; (iii) structurally or temporally different from related “serious” behavior systems; (iv) expressed repeatedly, usually during development; and (v) initiated in a relatively relaxed setting (Burghardt, 2005). Play types include locomotor play, object play, and social play, which may involve wrestling, grappling, sparring, slapping, mouthing and biting, and other exaggerated and nonaggressive behaviors with one or more individuals (Fagen, 1981). As such, play behavior likely carries costs to the participants. It is energetically demanding (Nunes, Muecke, Anthony, & Batterbee, 1999; Sharpe, Clutton-Brock, Brotherton, Cameron, & Cherry, 2002),

and has been linked to an increased risk of disease transmission (Kuehl, Elzner, Moebius, Boesch, & Walsh, 2008), injury (Foerster, 2008; Goodall, 1968), and even mortality (Harcourt, 1991). Given these costs, for play behavior to be adaptive, it should be associated with some benefit(s). Play behavior is suggested to be important in development and related to various short-term and long-term benefits (Bekoff, 1988; Burghardt, 2005; Fagen, 1981). We refer to short-term benefits as those that occur during the developmental period but may translate into downstream effects on dominance rank and fitness. Social play is the most studied play style and the primary focus for adaptive hypotheses and benefits (Graham & Burghardt, 2010).

To date, much of the research on nonhuman play behavior has focused on long-term benefits, including establishing dominance

(yellow-bellied marmots, *Marmota flaviventris*; chimpanzees, *Pan troglodytes*) (Blumstein, Chung, & Smith, 2013; Paquette, 1994), reproductive success (Belding's ground squirrel, *Urocitellus beldingi*) (Nunes, Muecke, Lancaster, et al., 2004), and survival (horses, *Equus caballus*; brown bears, *Ursus arctos*; mountain goats, *Oreamnos americanus*) (Cameron, Linklater, Stafford, & Minot, 2008; Fagen & Fagen, 2009; Théoret-Gosselin, Hamel, & Côté, 2015). However, not all play behavior is associated with demonstrated long-term benefits: meerkat (*Suricata suricatta*) play is not associated with any enhanced cohesion, reduced aggression, dispersal partnership or fighting success (Sharpe, 2005a, 2005b, 2005c; Sharpe & Cherry, 2003). Social play may derive different benefits both between species (Pellis & Pellis, 2017) and within a species (Marks, Vizconde, Gibson, Rodriguez, & Nunes, 2017). Understanding the proximate benefits of play will create a more complete picture of the mechanisms by which the ultimate benefits are achieved. Martin and Caro (1985) suggest that play can accelerate development and lead to motor and social benefits. Subsequently, faster achievement of developmental milestones could have strong social and reproductive benefits. For example, among rhesus macaques, early rearing conditions and foot-clasp mounting behavior as a juvenile were strong determinants of adult mating success (Goy & Wallen, 1979).

The following adaptive functional hypotheses for play are not mutually exclusive and may be more relevant at different points during development.

### 1.1 | Motor benefits

Play has been hypothesized to be involved with motor learning and development (Bekoff, 1988; Byers & Walker, 1995), given that play is most frequent among immature individuals (Fagen, 1981) and coincides with neuromuscular development. For example, the frequency and intensity of locomotor play was related to earlier achievement of motor skills in immature male Assamese macaques (*Macaca assamensis*) (Berghanel, Schulke, & Ostner, 2015). Also, the amount of social play and number of play partners, especially in males, was related to improved motor skills in Belding's ground squirrels (Nunes, Muecke, Sanchez, Hoffmeier, & Lancaster, 2004). Additionally, children (Fantuzzo, Sekino, & Cohen, 2004; Pellegrini & Smith, 1998) and marmosets (*Callithrix jacchus jacchus*) (Chalmers & Locke-Haydon, 1984) that engaged in more social play had better movement and coordination skills.

#### 1.1.1 | Social benefits

Social play behavior is also associated with various social benefits including social competence, establishing dominance, and reproductive success (Graham & Burghardt, 2010; Poirier & Smith, 1974). Rats (*Rattus norvegicus*) (reviewed in Pellis & Pellis, 2009) and rhesus monkeys (Deutsch & Larsson, 1974; Kempes, Gulickx, van Daalen, Louwerse, & Sterck, 2008) raised in isolation (or with limited social interaction during development) as juveniles were overly aggressive during social interactions with conspecifics as adults. Findings

regarding the role of play and social dominance have been mixed; in captive adolescent chimpanzees (Paquette, 1994) and yellow-bellied marmots (Blumstein et al., 2013), there was a relationship between social play winners and dominance formation, while in meerkats, play fighting did not predict later fighting success (Sharpe, 2005c). In terms of reproductive success, Nunes, Muecke, Lancaster, et al. (2004) demonstrated that female Belding's ground squirrels that played more were more likely to successfully reproduce as yearlings. However, assessing long-term social benefits such as reproductive success becomes exceedingly difficult to measure in long-lived animals, including social primates.

### 1.2 | Training for the unexpected

The training for the unexpected hypothesis posits that a predominant ancestral function of play is to rehearse behavioral sequences under safe conditions in which animals will purposefully lose control of the situation (Spinka, Newberry, & Bekoff, 2001). Animals learn how to improvise their behavior to recover quickly from atypical body positions and movements. The training for the unexpected hypothesis makes motor and social predictions; most notably that play: (i) results in an increased versatility of movements used to recover from losing balance or control and (ii) enhances the ability of animals to cope with unexpected situations, including a less pronounced physiological response to a stressor (Spinka et al., 2001). Numerous examples are seen across species and play contexts, for example, object play drop and catch behavior in herring gulls (*Larus argentatus*) (Gamble & Cristol, 2002); disorienting movements of headshaking during both solitary and social play in Hanuman langurs (*Semnopithecus entellus*) (Petru, Spinka, Lhota, & Sipek, 2008), and self-handicapping behavior during social play in dogs (*Canis familiaris*) (Bekoff, 1995); rats (Pellis, Pellis, & Bell, 2010); squirrel monkeys (*Samiri*) (Baldwin & Baldwin, 1974); baboons (*Papio anubis*) (Owens, 1975); and chimpanzees (Goodall, 1986; Hayaki, 1985; Mendoza-Granados & Sommer, 1995). Practice during play could potentially lead to more proficient motor and social skills with the ability to most appropriately respond to variable and unpredictable situations (Spinka et al., 2001).

### 1.3 | Chimpanzee play

In primates, play is one of the first behaviors that occurs in infants beyond interaction with mother (Poirier & Smith, 1974). Chimpanzee infants primarily engage in social play with their mothers during the first months of life (Goodall, 1968). Then, within a few months, infant chimpanzees break contact with their mothers and begin to engage in solitary and social play, with about half of all dyadic play being with other infants (Heintz, 2013). Social play varies during development with infants engaging in more rough and tumble play and juveniles engaging in more complex and innovative social play (Cordoni & Palagi, 2011). Primates have an extended juvenile period, which is associated with critical social and environmental learning (Joffe, 1997). In particular, social play is positively associated with brain size in primates, indicating an important role in cognition and development

(Lewis, 2000). Bonobos (*Pan paniscus*), which have an extended developmental period compared to chimpanzees (Wobber, Wrangham, & Hare, 2010), receive numerous immediate and delayed benefits from their play (Palagi & Cordoni, 2012). These patterns of the complexity of play being positively correlated with the length of the juvenile period are also observed in rodents (Pellis & Iwaniuk, 2000). Additionally, social play is associated with social behavioral flexibility in primates (Montgomery, 2014).

Here, we examine the relationship between social play and developmental milestones in wild chimpanzees using a detailed long-term dataset of mother-infant behavior from the Kasekela community in Gombe National Park, Tanzania. We predicted that higher rates of social play would be associated with earlier achievement of social and motor developmental milestones for infant chimpanzees.

Chimpanzees live in fission-fusion social systems enabling individuals to interact with a wide variety of social partners in different contexts. Males are characterized by a linear dominance hierarchy that correlates with reproductive success (Boesch, Kohou, Néné, & Vigilant, 2006; Newton-Fisher, Thompson, Reynolds, Boesch, & Vigilant, 2010; Wroblewski et al., 2009). Adult and adolescent eastern chimpanzee males are more social than females and usually travel and forage with other males, while adult females travel in small groups with dependent offspring (Wrangham & Smuts, 1980). Infants remain in relatively constant contact with their mothers until around 6 months of age and are partially nutritionally dependent on their mother throughout infancy until weaning between 3–5 years of age (Goodall, 1986). After weaning, juveniles continue to associate with their mothers almost exclusively (Pusey, 1983, 1990). Time spent in association with the mother drastically declines upon onset of adolescence (8–12 years of age), coinciding with the onset of sexual cycling in females and puberty in males around 8–9 years of age (Pusey, 1983, 1990). In adulthood, males form stronger intrasexual alliances and social bonds than females do (Gilby & Wrangham, 2008; Mitani, 2009), aiding in the acquisition and maintenance of social dominance. Nevertheless, some related and unrelated females also develop strong social bonds (Foerster et al., 2015), which may be critical to successful integration into a new community. Therefore, for both sexes, there is potential adaptive value in developing early social skills.

We examined developmental milestones related to motor development, including riding dorsally on the mother and independent traveling. We also examined developmental milestones related to social development, including spatial independence from the mother, first grooming an individual beyond the immediate family, and the emergence of male mating behavior.

## 2 | METHODS

### 2.1 | Study site

Gombe National Park is approximately 35 km<sup>2</sup> and is located on the western border of Tanzania. The Park currently contains three chimpanzee communities: the central Kasekela community, the northern Mitumba community, and the southern Kalande community.

Studies on the wild chimpanzees inhabiting this area began in 1960, and observational research continues to the present (Goodall, 1986; Wilson, 2012). The Kasekela community was the focus for the analyses reported here. The average community size was 54 individuals (range 41–69) with 13 infants (0–5 years; range 9–18), 4 juveniles (5–8 years; range 2–9), 6 adolescents (8–12 years; range 2–11), and 30 late adolescents and adults (>12 years; range 21–40).

### 2.2 | Behavioral data collection

This study includes long-term behavioral data that have been collected on chimpanzee mothers and dependent offspring in Kasekela from 1978 to 2011. Briefly, this standardized dataset includes instantaneous scan sampling (Altmann, 1974) at 1-min intervals on the mother, infant, and next oldest sibling (when present). On each scan, researchers record each individual's behavior and the distances of the individuals from one another. Scans were recorded as a "bad observation" if a focal animal was out of view or if the behavior was uncertain. Average daily observation time on focal individuals during the study period was 3.7 hr (range 1–11.5 hr). For analyses presented here, we used behavioral definitions from the Gombe chimpanzee glossary (the Jane Goodall Institute, unpublished records, Lonsdorf et al., 2014) that are similar to other chimpanzee ethograms (Nishida, Kano, Goodall, McGrew, & Nakamura, 1999). We focused on social play because we were interested in the possible effects of play on both physical and social development milestones. We focused on the following behaviors that have been consistently recorded in the long-term dataset:

1. Social play—Non-aggressive interaction between two or more individuals that includes one or more of the following: tickling, wrestling, chasing, kicking, rubbing, thrusting, biting, or pulling. May incorporate an object (e.g., tugging of sticks back and forth).
2. Riding dorsally—The infant is transported as it lies or sits on the mother's back.
3. Travel—Continuous movement from one point to another.
4. Social groom—Parting of another individual's hair with hands, fingers and/or lips and removal of debris or ectoparasites.
5. Mating attempt—Infant or juvenile male tries to mount a fully tumescent late adolescent or adult female (>12 years).

Additionally, all individuals present in the group were identified to determine party composition every 5 min. A party is defined as a subgroup of individuals that travels, forages, and/or rests together. Play data were examined for individuals ranging from 1 to 3 years of age, when social play peaks (Heintz, 2013). In total, we included behavioral data on 31 infant chimpanzees, although sample size varied based on analyses (described below).

In addition to the mother-infant behavioral dataset, we used data from all-day focal follows to identify a male's first mating attempt with a maximally-tumescent adult female. Field assistants follow one chimpanzee each day, usually from night nest to night nest and collect continuous data that includes all occurrence mating behavior (Goodall, 1986; Wilson, 2012). The research team has the goal of collecting one

follow on each focal chimpanzee per month. This study was approved by the Research Committee at the Lincoln Park Zoo (Chicago, IL) and is in accordance with the American Society of Primatologists principles for the ethical treatment of primates.

### 2.3 | Behavioral metrics

We calculated percentage of time engaged in social play by dividing the total minutes of social play by the total observation minutes (excluding the minutes recorded as bad observation) in a period of interest, multiplied by 100. We then investigated the relationship between percentage of time engaged in social play and the first observed occurrence of indicators of either motor or social development (Lonsdorf et al., 2014). To limit any error that could result from uneven sampling in determining milestone attainment, we implemented strict inclusion criteria based on observations prior to the first occurrence of a behavior, as described below.

Riding dorsally on the mother's back during travel requires core strength and balance and is the main method of riding on the mother (as opposed to clinging ventrally) once this milestone is achieved. Although riding dorsally for the first time can be observed as early as 17 weeks (Goodall, 1968, 1969), the average age infants begin dorsally riding was reported to be between 5–7 months of age (Goodall, 1968). Since dorsal riding occurs much earlier than the other milestones, we limited analyses of dorsal riding data to individuals that were observed for at least 20 hr from 0 to 1 years of age and also were observed for at least 5 hr within 3 months prior to the milestone. As such, we compared achievement of this milestone to percent of play during the first year only.

All subsequent developmental milestones (independent travel, spatial independence, grooming, and first mating attempt) occurred in the 1–3 year age range, when social play was most frequent. Infant chimpanzees first begin to walk as early as 17 weeks of age (Goodall, 1968). As infants develop, they walk intermittently during play, eating, or other behaviors. However, consistent and sustained traveling (when mother is also traveling) occurs later in infancy and is a useful and appropriate metric to assess motor development with infant chimpanzees. Independent traveling has been defined as "individuals traveling extensively by themselves" (Greengrass, 2005) and occurs in chimpanzees as early as 2.25 years but riding remains a frequent mode of travel until after 5 years of age (Doran, 1997; Lonsdorf et al., 2014) or when the next sibling is born.

Over the course of development, infants progressively increase the distance and time spent away from their mother (Plooij, 1984). As primate infants grow, they increasingly initiate the majority of making and breaking contact and proximity to their mother (Deng & Zhao, 1991; Forster & Cords, 2002; Rijt-Plooij & Plooij, 1987). Chimpanzee infants are initially entirely dependent on their mother (Bloomsmith et al., 2003) and do not break contact until between 12–24 weeks of age (Goodall, 1968; Rijt-Plooij & Plooij, 1987). Therefore, distance from the mother can be considered a social milestone because it indicates social independence and exploration.

We examined when an infant first groomed another individual excluding the mother and maternal kin, as a measure for social

development. Grooming behavior is an important social tool in most primates for establishing and maintaining social bonds (reviewed in Lehmann, Korstjens, & Dunbar, 2007). During development, infant chimpanzees are groomed primarily by their mothers and first begin grooming their mother approximately between 25 and 30 weeks of age (Goodall, 1968). Grooming frequency increases later in infancy (Lonsdorf et al., 2014) and becomes more important during the juvenile and adolescent life stages (Pusey, 1990).

Infant male chimpanzees also develop some sociosexual behavior by the age of 1 year (Goodall, 1968; Pusey, 1990). While these males are not reproductively mature, this early experience may be important for developing proper mating technique and behavior, as has been found in rhesus monkeys (*Macaca mulatta*) (Goy & Wallen, 1979). Females generally do not mate until adolescence, which corresponds to the timing of female-biased dispersal (Pusey, 1990).

We calculated play metrics over the entire 1–3 year age range to maximize the number of focal observations used to calculate play frequency; previous studies have demonstrated that play frequency does not vary by age in this time period (Heintz, 2013). For these milestones, we only included individuals that were observed for at least 50 hr across the 1–3 year age range, observed at least once every 6 months, and observed for at least 5 hr within 3 months prior to the milestone. We defined these milestones as follows:

1. Independent traveling: The first observed occurrence of the infant traveling for a continuous 3-min bout while the mother was also traveling. This milestone accurately represents a sustained traveler because it would require developed motor skills, strength, and stamina.
2. Spatial independence: The first observed occurrence of the infant exceeding a distance of 5 m from its mother. This milestone is associated with social development because it is a measure of when the infant is comfortable being at a significant distance from its mother. We took care to ensure that these instances were not spurious (e.g., the result of brief social excitement) by confirming that the infant was engaged in play, eating or travel, was not showing distress, and its separation from the mother was not related to aggression.
3. Social grooming: The first observed occurrence of the infant grooming an individual other than the mother or a maternal sibling.
4. Mating: The first observed mating attempt by males toward fully tumescent females (>12 years) that were not maternal relatives. We extracted mating data from both long-term datasets described above, each of which record mating-related behaviors opportunistically.

### 2.4 | Statistical analyses

We used Spearman rank correlations to compare age of achievement of developmental milestones to social play percentage due to non-normally distributed data. All non-parametric analyses were analyzed using Systat version 11 (Systat Software, Inc., Chicago,

IL). During preliminary analyses, we used GLMMs to examine whether inclusion of multiple offspring from the same mothers impacted our results; it did not. The explanatory power of those models was less than that of the simpler correlation approach as described above.

### 3 | RESULTS

Each milestone has sample sizes specific to the analysis based on individuals that met our sampling criteria during the period of achieving the milestone. We list the average age and range of milestones in Table 1.

#### 3.1 | Physical development milestones

The dorsal riding milestone was negatively correlated with social play between 0 and 1 years (Figure 1;  $p = -0.436$ ,  $n = 21$ ,  $p = 0.047$ ). Similarly, the independent traveling milestone was negatively correlated with social play across the 1–3 year age range (Figure 2;  $p = -0.558$ ,  $n = 21$ ,  $p = 0.009$ ). (We also examined traveling bouts of 2 and 4 min. We found a similar pattern of correlation between independent traveling and social play for each choice of traveling bout durations that we examined).

#### 3.2 | Social development milestones

The spatial independence milestone was negatively correlated with social play across the 1–3 year age range (Figure 3;  $p = -0.582$ ,  $n = 13$ ,  $p = 0.035$ ). We found a negative trend (Figure 4,  $p = -0.507$ ,  $n = 15$ ,  $p = 0.052$ ) between the grooming milestone and social play across the 1–3 year age range. First mating attempt was only assessed for males because we did not have the necessary sample size to examine it in females given that females typically disperse around the time of sexual maturity. Males achieved this milestone at a younger age when they played more across the 1–3 year age range (Figure 5;  $p = -0.762$ ,  $n = 8$ ,  $p = 0.021$ ).

### 4 | DISCUSSION

We found that percent of time spent in social play in wild chimpanzees correlated with both motor and social developmental milestones. In fact, infants that engaged in more social play achieved these milestones at an earlier age. These findings are the first study in non-human apes to demonstrate a relationship between play behavior

and developmental milestones that may have downstream effects on fitness.

Our results demonstrated that social play was related to two measures of physical development, namely, riding dorsally and independent travel. The average age at which infant chimpanzees began to ride dorsally was approximately 6 months. This milestone was negatively associated with social play percentage between 0 and 1 years of age, suggesting that individuals that played more frequently during early infancy begin riding dorsally at a younger age. Play behavior could contribute to the development of necessary strength and coordination to begin riding dorsally. Similarly, social play was negatively correlated with traveling independently across the 1–3 year age range.

We found that infant chimpanzees that engaged in more social play also became spatially independent from their mothers at an earlier age. Potentially, the unexpected nature of social play (Spinka et al., 2001) might serve as training to enable infants to adjust their behavior and emotions flexibly and adaptably to the challenges of varied and unpredictable social situations or to practice generating creative solutions to challenges (Bateson & Martin, 2013). Problems of such high physical-cognitive complexity almost surely require creative thinking, and encounters of this general type may well be riskier when the infant is spatially farther from their mother.

While the negative relationship between social play and the grooming developmental milestone was limited to a trend, grooming is an important social tool for establishing and maintaining social bonds (Cords, 2002; Silk, Altmann, & Alberts, 2006). Non-maternal social bonds in chimpanzees can last for more than 10 years (Mitani, 2009), so social bonds established during infancy through social play or grooming could potentially persist into adulthood and provide critical alliances as males climb the social hierarchy. Additionally, the development of social bonds and social skills is important for females as they prepare for emigration (Foerster et al., 2015). Future studies should consider the long-term utility of play relationships.

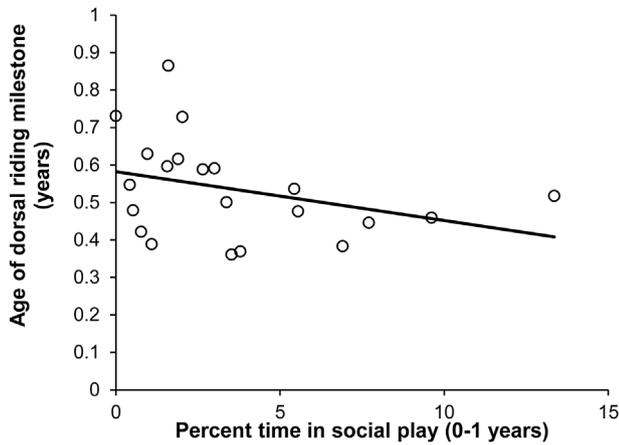
Finally, we found that social play in male infant chimpanzees was correlated with earlier mating attempts. This early practice could be very important for developing reproductive skills and strategies that may have downstream effects on adult male fitness. For example, in rhesus monkeys, early mounting experience in juveniles is a strong determinant of mating success as adults (Goy & Wallen, 1979).

We cannot establish the direction of causality linking play with motor or social development. It is equally possible that stronger or bolder infants play more or that playing enhances physical or social development. To distinguish between these main effects and to investigate their possible interaction, future studies could assess

**TABLE 1** Age at which each developmental milestone was achieved

	Dorsal riding	Travel independence	Spatial independence	Grooming	Mating attempt (male only)
Infant age	0.54 ± 0.03 SE (0.36–0.87; $n = 21$ )	2.26 ± 0.13 SE (1.37–3.61; $n = 21$ )	1.66 ± 0.11 SE (0.94–2.28; $n = 13$ )	1.79 ± 0.20 SE (0.30–2.93; $n = 15$ )	2.84 ± 0.62 SE (1.10–5.75; $n = 8$ )

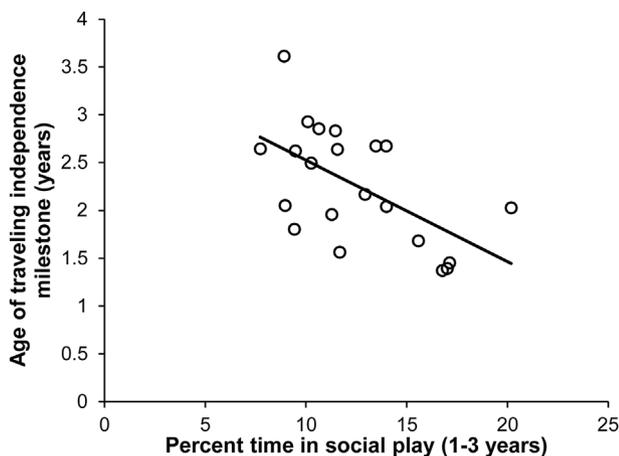
Values given are averages ages in years with standard error, range, and sample size.



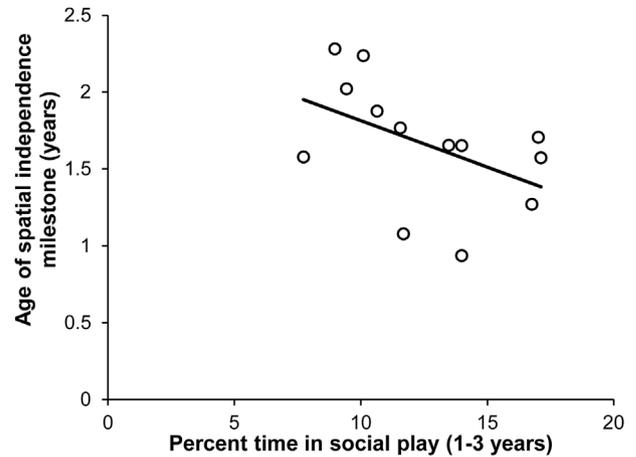
**FIGURE 1** Relationship between percent time in social play and age of first dorsal riding. Each data point represents one individual. Best-fit lines are least squares regressions

baseline physical measures before the onset of play behavior, but this approach would be most feasible in a captive setting that offered a higher degree of control and access to animals (Berghanel et al., 2015). In rats, it has been demonstrated that lack of play opportunities negatively impacts social competence and related neural systems (Burluson et al., 2016; Schneider et al., 2016). These findings provide some support for a causal process between the correlations found between social play and the achievement of motor and social milestones in chimpanzees.

Overall, our results suggest that there is an important relationship between social play and development milestones for infant chimpanzees. In particular, these results provide support for both the motor development (Byers, 1998; Byers & Walker, 1995), and social development (Poirier & Smith, 1974) hypotheses. While our analysis was cross-sectional in nature, ongoing research is examining within-individual correlations between these and other milestones. Individuals that learn and develop faster as infants may

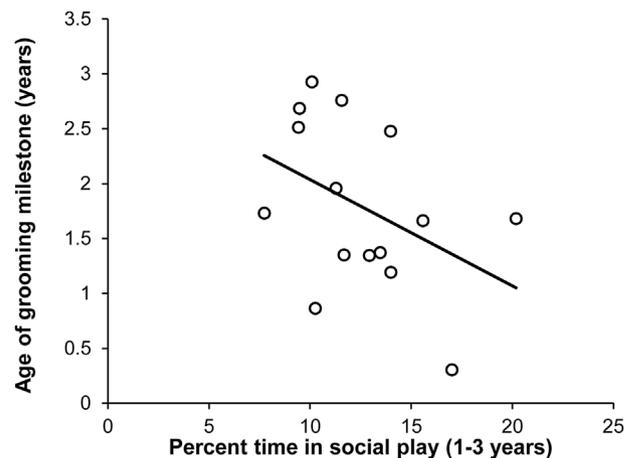


**FIGURE 2** Relationship between percent time in social play and age of first 3 min travel bout. Each data point represents one individual. Best-fit lines are least squares regressions

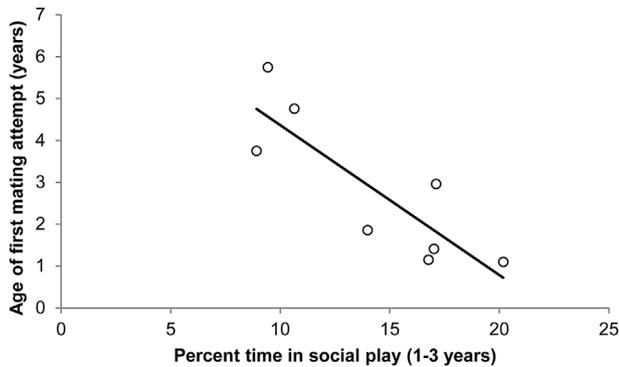


**FIGURE 3** Relationship between percent time in social play and age of first occurrence of infant exceeding distance of 5 m from mother. Each data point represents one individual. Best-fit lines are least squares regressions

potentially also be more successful later on and better equipped to handle unexpected situations (Spinka et al., 2001). Measuring unexpected situations in the field is challenging but our measure for spatial independence may be a good proxy. Previous hypotheses have suggested that play behavior has long-term benefits, such as increased reproductive success (Ahloy Dallaire & Mason, 2017; Nunes, Muecke, Lancaster, et al., 2004) and increased survival (Cameron et al., 2008; Fagen & Fagen, 2009; Théoret-Gosselin et al., 2015). However, the benefits of play may also be shorter-term and occur earlier in development (Berghanel et al., 2015; Martin & Caro, 1985). For the current study, we combined all social play, however, it is likely that specific types of play can benefit age/sex classes differently such as play parenting in female lowland gorillas (*Gorilla gorilla gorilla*) (Meder, 1990) or rough-and-tumble play in rhesus macaques (Brown & Dixson, 2000).



**FIGURE 4** Relationship between percent time in social play and age of first occurrence of grooming a non-maternal individual. Each data point represents one individual. Best-fit lines are least squares regressions



**FIGURE 5** Relationship between male social play percentage and age of first mating attempt with an adult female. Each data point represents one individual. Best-fit lines are least squares regressions

Together, our results demonstrate the importance of social play during chimpanzee development. Primates have an extended juvenile period and use this time to learn and develop skills needed to navigate through their complex and dynamic social environment (Joffe, 1997). Social play can provide a safe platform to develop and evaluate motor skills and social relationships. These short-term benefits of play can help accelerate normal development and give individuals a social head start that could ultimately impact dominance (Blumstein et al., 2013) and reproductive success (Nunes, Muecke, Lancaster, et al., 2004). Indeed, a study in Assamese macaques found that both play frequency and intensity predicted motor development (Berghanel et al., 2015). Play is just one type of behavioral category that is intermixed with other behaviors during development (Caro, 1988). Nevertheless, there is accumulating evidence that play has both short-term and potentially long-term motor and social benefits (Palagi, 2011; Pellis & Pellis, 2016).

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## REFERENCES

- Ahloy Dallaire, J., & Mason, G. J. (2017). Juvenile rough-and-tumble play predicts adult sexual behaviour in American mink. *Animal Behaviour*, 123, 81–89.
- Altmann, J. (1974). Observational study of behavior—sampling methods. *Behaviour*, 49(3–4), 227–267.
- Baldwin J. D., & Baldwin J. I. 1974. Exploration and social play in squirrel monkeys (*Saimiri*). *American Zoologist*, 14(1), 303–315.
- Bateson P., & Martin P. (2013). *Play, playfulness, creativity and innovation*. Cambridge, United Kingdom: Cambridge University Press.
- Bekoff, M. (1988). Motor training and physical fitness: Possible short- and long-term influences on the development of individual differences in behavior. *Developmental Psychobiology*, 21(6), 601–612.
- Bekoff, M. (1995). Play signals as punctuation—the structure of social play in canids. *Behaviour*, 132, 419–429.
- Berghanel, A., Schulke, O., & Ostner, J. (2015). Locomotor play drives motor skill acquisition at the expense of growth: A life history trade-off. *Science Advances*, 1(7), e1500451.
- Bloomsmith, M. A., Kuhar, C., Baker, K., Lambeth, S., Brent, L., Ross, S. R., & Fritz, J. (2003). Primiparous chimpanzee mothers: Behavior and success in a short-term assessment of infant rearing. *Applied Animal Behaviour Science*, 84(3), 235–250.
- Blumstein, D. T., Chung, L. K., & Smith, J. E. (2013). Early play may predict later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). *Proceedings of the Royal Society B-Biological Sciences*, 280(1759), 20130485. <https://doi.org/10.1098/rspb.2013.0485>
- Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, 130(1), 103–115.
- Brown, G. R., & Dixson, A. F. (2000). The development of behavioural sex differences in infant rhesus macaques (*Macaca mulatta*). *Primates*, 41(1), 63–77.
- Burghardt G. M. (2005). *The genesis of animal play: Testing the limits*. Cambridge: The MIT Press.
- Burleson, C. A., Pedersen, R. W., Seddighi, S., DeBusk, L. E., Burghardt, G. M., & Cooper, M. A. (2016). Social play in juvenile hamsters alters dendritic morphology in the medial prefrontal cortex and attenuates effects of social stress in adulthood. *Behavioral Neuroscience*, 130(4), 437.
- Byers J. A. (1998). Biological effects of locomotor play: Getting into shape, or something more specific? In M. Bekoff, & J. A. Byers, (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 205–220). Cambridge: Cambridge University Press.
- Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *American Naturalist*, 146(1), 25–40.
- Cameron, E. Z., Linklater, W. L., Stafford, K. J., & Minot, E. O. (2008). Maternal investment results in better foal condition through increased play behaviour in horses. *Animal Behaviour*, 76(5), 1511–1518.
- Caro, T. M. (1988). Adaptive significance of play: Are we getting closer? *Trends in Ecology & Evolution*, 3(2), 50–54.
- Chalmers, N. R., & Locke-Haydon, J. (1984). Correlations among measures of playfulness and skillfulness in captive common marmosets (*Callithrix jacchus jacchus*). *Developmental Psychobiology*, 17(2), 191–208.
- Cordoni, G., & Palagi, E. (2011). Ontogenetic trajectories of chimpanzee social play: Similarities with humans. *PLoS ONE*, 6(11), e27344. <https://doi.org/10.1371/journal.pone.0027344>
- Cords, M. (2002). Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour*, 139, 291–314.

- Deng, Z. Y., & Zhao, Q. K. (1991). Early mother-infant relationships of *Macaca thibetana* at Mt. emei China. *Primates*, 32(2), 197–205.
- Deutsch, J., & Larsson, K. (1974). Model-oriented sexual behavior in surrogate-reared rhesus monkeys. *Brain Behavior and Evolution*, 9(3), 157–164.
- Doran, D. M. (1997). Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal of Human Evolution*, 32(4), 323–344.
- Fagen R. (1981). *Animal play behavior*. New York, New York: Oxford University Press.
- Fagen, R., & Fagen, J. (2009). Play behaviour and multi-year juvenile survival in free-ranging brown bears, *Ursus arctos*. *Evolutionary Ecology Research*, 11(7), 1053–1067.
- Fantuzzo, J., Sekino, Y., & Cohen, H. L. (2004). An examination of the contributions of interactive peer play to salient classroom competencies for urban Head Start Children. *Psychology in the Schools*, 41(3), 323–336.
- Foerster, S. (2008). Two incidents of venomous snakebite on juvenile blue and Sykes monkeys (*Cercopithecus mitis stuhlmanni* and *C.m. albogularis*). *Primates*, 49(4), 300–303.
- Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour*, 105, 139–152.
- Forster S., & Cords M., (2002). Development of mother-infant relationships and infant behavior in Wild Blue Monkeys (*Cercopithecus mitis stuhlmanni*). In M. E. Glenn, & M. Cords, (Eds.), *The guenons: Diversity and adaptation in african monkeys*. New York: Kluwer Academic/Plenum Publishers.
- Gamble, J. R., & Cristol, D. A. (2002). Drop-catch behaviour is play in herring gulls, *Larus argentatus*. *Animal Behaviour*, 63(2), 339–345.
- Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, 62(11), 1831–1842.
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, 1, 161–311.
- Goodall J., (1969). Mother-offspring relationships in free-ranging chimpanzees. In D. Morris, (Ed.), *Primate ethology* (pp. 287–346). Chicago: Aldine.
- Goodall J. (1986). *The chimpanzees of Gombe: Patterns of behaviour*. Cambridge, MA: Belknap Press.
- Goy, R. W., & Wallen, K. (1979). Experimental variables influencing play, foot-clasp mounting and adult sexual competence in male rhesus monkeys. *Psychoneuroendocrinology*, 4(1), 1–12.
- Graham, K. L., & Burghardt, G. M. (2010). Current perspectives on the biological study of play: Signs of progress. *Quarterly Review of Biology*, 85(4), 393–418.
- Greengrass E. (2005). Aggression and play in wild chimpanzees. Bristol: Bristol University (unpublished doctoral dissertation).
- Harcourt, R. (1991). Survivorship costs of play in the South American fur seal. *Animal Behaviour*, 42(3), 509–511.
- Hayaki, H. (1985). Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates*, 26(4), 343–360.
- Heintz MR. (2013). The immediate and long-term benefits of social play in wild chimpanzees (*Pan troglodytes*). Chicago: University of Chicago (unpublished doctoral dissertation).
- Joffe, T. H. (1997). Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution*, 32(6), 593–605.
- Kempes, M. M., Gulickx, M. M. C., van Daalen, H. J. C., Louwse, A. L., & Sterck, E. H. M. (2008). Social competence is reduced in socially deprived rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 122(1), 62–67.
- Kuehl, H. S., Elzner, C., Moebius, Y., Boesch, C., & Walsh, P. D. (2008). The price of play: Self-organized infant mortality cycles in chimpanzees. *PLoS ONE*, 3(6), e2440.
- Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, 74, 1617–1629.
- Lewis, K. P. (2000). A comparative study of primate play behaviour: Implications for the study of cognition. *Folia Primatologica*, 71(6), 417–421.
- Lonsdorf, E. V., Markham, A. C., Heintz, M. R., Anderson, K. E., Ciuk, D. J., Goodall, J., & Murray, C. M. (2014). Sex differences in wild chimpanzee behavior emerge during infancy. *PLoS ONE*, 9(6), 9.
- Marks, K. A., Vizconde, D. L., Gibson, E. S., Rodriguez, J. R., & Nunes, S. (2017). Play behavior and responses to novel situations in juvenile ground squirrels. *Journal of Mammalogy*, 98(4), 1202–1210.
- Martin, P., & Caro, T. M. (1985). On the functions of play and its role in behavioral-development. *Advances in the Study of Behavior*, 15, 59–103.
- Meder, A. (1990). Sex differences in the behaviour of immature captive lowland gorillas. *Primates*, 31(1), 51–63.
- Mendoza-Granados, D., & Sommer, V. (1995). Play in chimpanzees of the Arnhem Zoo- self-serving compromises. *Primates*, 36(1), 57–68.
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633–640.
- Montgomery, S. H. (2014). The relationship between play, brain growth and behavioural flexibility in primates. *Animal Behaviour*, 90, 281–286.
- Newton-Fisher, N. E., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, 142(3), 417–428.
- Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, 107(2), 141–188.
- Nunes, S., Muecke, E. M., Anthony, J. A., & Batterbee, A. S. (1999). Endocrine and energetic mediation of play behavior in free-living Belding's ground squirrels. *Hormones and Behavior*, 36(2), 153–165.
- Nunes, S., Muecke, E. M., Lancaster, L. T., Miller, N. A., Mueller, M. A., Muelhaus, J., & Castro, L. (2004). Functions and consequences of play behaviour in juvenile Belding's ground squirrels. *Animal Behaviour*, 68(1), 27–37.
- Nunes, S., Muecke, E. M., Sanchez, Z., Hoffmeier, R. R., & Lancaster, L. T. (2004). Play behavior and motor development in juvenile Belding's ground squirrels (*Spermophilus beldingi*). *Behavioral Ecology and Sociobiology*, 56(2), 97–105.
- Owens, N. W. (1975). Social play behavior in free-living baboons, *Papio anubis*. *Animal Behaviour*, 23, 387–408.
- Palagi E. (2011). *Playing at every age: Modalities and potential functions in non-human primates* (pp. 70–82). Oxford, UK: Oxford University Press.
- Palagi, E., & Cordoni, G. (2012). The right time to happen: Play developmental divergence in the two pan species. *PLoS ONE*, 7(12), e52767.
- Paquette, D. (1994). Fighting and playfighting in captive adolescent chimpanzees. *Aggressive Behavior*, 20(1), 49–65.
- Pellegrini, A. D., & Smith, P. K. (1998). Physical activity play: The nature and function of a neglected aspect of play. *Child Development*, 69(3), 577–598.
- Pellis, S. M., & Iwaniuk, A. N. (2000). Comparative analyses of the role of postnatal development on the expression of play fighting. *Developmental Psychobiology*, 36(2), 136–147.
- Pellis S. M., & Pellis V. C. (2009). *The playful brain*. Oxford: Oneworld Publications.
- Pellis S. M., & Pellis V. C. (2016). *Play and cognition: The final frontier* (pp. 201–230). Hauppauge, NY: Nova Science Publishers.
- Pellis, S. M., & Pellis, V. C. (2017). What is play fighting and what is it good for? *Learning & Behavior*. <https://doi.org/10.3758/s13420-017-0264-3>
- Pellis, S. M., Pellis, V. C., & Bell, H. C. (2010). The function of play in the development of the social brain. *American Journal of Play*, 2(3), 278–296.

- Petru, M., Spinka, M., Lhota, S., & Sipek, P. (2008). Head rotations in the play of Hanuman langurs (*Semnopithecus entellus*): Description and analysis of function. *Journal of Comparative Psychology*, 122(1), 9–18.
- Plooij F. X. 1984. The Behavioral development of free-living chimpanzee babies and infants. *Monographs on Infancy*, 207.
- Poirier, F. E., & Smith, E. O. (1974). Socializing functions of primate play. *American Zoologist*, 14(1), 275–287.
- Pusey, A. E. (1983). Mother offspring relationships in chimpanzees after weaning. *Animal Behaviour*, 31, 363–377.
- Pusey, A. E. (1990). Behavioral changes at adolescence in chimpanzees. *Behaviour*, 115, 203–246.
- Rijt-Plooij, H. H. C., & Plooij, F. X. (1987). Growing independence, conflict and learning in mother-infant relations in free-ranging chimpanzees. *Behaviour*, 101, 1–86.
- Schneider, P., Bindila, L., Schmahl, C., Bohus, M., Meyer-Lindenberg, A., Lutz, B., ... Schneider, M. (2016). Adverse social experiences in adolescent rats result in enduring effects on social competence, pain sensitivity and endocannabinoid signaling. *Frontiers in Behavioral Neuroscience*, 10. Article 203. <https://doi.org/10.3389/fnbeh.2016.00203>
- Sharpe, L. L., Clutton-Brock, T. H., Brotherton, P. N. M., Cameron, E. Z., & Cherry, M. I. (2002). Experimental provisioning increases play in free-ranging meerkats. *Animal Behaviour*, 64, 113–121.
- Sharpe, L. L. (2005a). Frequency of social play does not affect dispersal partnerships in wild meerkats. *Animal Behaviour*, 70(3), 559–569.
- Sharpe, L. L. (2005b). Play does not enhance social cohesion in a cooperative mammal. *Animal Behaviour*, 70(3), 551–558.
- Sharpe, L. L. (2005c). Play fighting does not affect subsequent fighting success in wild meerkats. *Animal Behaviour*, 69(5), 1023–1029.
- Sharpe, L. L., & Cherry, M. I. (2003). Social play does not reduce aggression in wild meerkats. *Animal Behaviour*, 66(5), 989–997.
- Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61(2), 183–195.
- Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: Training for the unexpected. *Quarterly Review of Biology*, 76(2), 141–168.
- Théoret-Gosselin, R., Hamel, S., & Côté, S. D. (2015). The role of maternal behavior and offspring development in the survival of mountain goat kids. *Oecologia*, 178(1), 175–186.
- Wilson M. L., (2012). Long-term studies of the chimpanzees of gombe national park, Tanzania. In P. M. Kappeler, & D. P. Watts, (Eds.), *Long-term field studies of primates* (pp. 357–384). Heidelberg: Springer.
- Wobber, V., Wrangham, R., & Hare, B. (2010). Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, 20(3), 226–230.
- Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility Supplement*, 13–31.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, 77(4), 873–885.

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