RESEARCH ARTICLE

Juvenile Social Relationships Reflect Adult Patterns of Behavior in Wild Geladas

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Unlike many mammals, primates spend much of their lives as reproductively-immature juveniles. During the juvenile period, they develop social relationships and physical skills that both facilitate survival to adulthood and impact adult fitness. In this study, we use 2 years of observational data to examine the development of these skills across the juvenile period in a wild cercopithecine primate, the gelada (*Theropithecus gelada*). As adults, male and female geladas require different skills to be successful; we therefore expected sex differences in social behavior and partner choice during the juvenile period to already reflect these sex-specific trajectories. For example, males, who disperse at puberty and ultimately must challenge other adult males for access to mates, should invest in high-energy play-fighting with other males to develop fighting and rival assessment skills. In contrast, philopatric females, who remain with their close kin throughout their lives, should invest more in forming less-physical and more-social bonds with other females within their group. As predicted, sex differences that foreshadowed sex-specific adult roles were apparent in play rates, the average number of play partners per individual, grooming partner types and social partner preferences. Males played more and had more play partners than same-age females. Males also groomed more often with individuals from outside their natal group than females, although no sex difference was observed in either grooming rates or number of grooming partners per individual. Females stopped playing earlier than males, and instead invested in grooming relationships with close relatives. Additionally, we found that individual play and grooming rates were temporally consistent for both males and females (i.e., from one year to the next year), suggesting that individuals exhibit stable behavioral phenotypes. We conclude by discussing how early life in geladas may shape adult behavior and reproductive strategies. Am. J. Primatol. 77:1086–1096, 2015. © 2015 Wiley Periodicals, Inc.

Key words: juvenile social behavior; partner preference; play; sex-specific behavior; male dispersal

INTRODUCTION

A lengthy juvenile period distinguishes primates from other mammals. Young primates spend the time between weaning and sexual maturation developing species-specific and sex-specific behaviors, building relationships, and skills for adult life, and learning to negotiate their complex social and physical environments [Bekoff, 1984; Byers, 1998; Martin and Caro, 1985; Thompson, 1998]. Despite the demonstrated importance of this developmental period, primate research typically focuses on the adults of a species. Juveniles are notoriously challenging to study in the wild: their small body size makes them difficult to spot and individually identify, they move unpredictably, and they are constantly growing and changing. Yet, research on a diverse set of non-primate taxa has linked juvenile behavior and sociality to fitness-related skills such as territory establishment, successful reproduction,

and survival to adulthood [Atlantic salmon (*Salmo salar*): Fleming et al., 1997; bottlenose dolphins (*Tursiops* sp.): Stanton and Mann, 2012; song sparrows (*Melospiza melodia*): Templeton et al., 2012; feral horses (*Equus ferus*): Nuñez et al., 2015; though see Sharpe 2005a for an example to the contrary in meerkats (*Suricata suricatta*)]. In short, fitness is not based solely on skills acquired during adulthood.

Moreover, studies on adults, by definition, consider only those individuals that have successfully navigated and survived the challenges of the juvenile period. Yet, annual mortality rates of immature primates are often double those of adults of the same species [Ross and Jones, 1999]. Thus, to fully understand life histories, alternative reproductive strategies, and behavioral trajectories, we need to examine not only the adult endpoints of life, but also the early stages that precede them. Here, we examine sex and age differences in social behavior in the early stages of a long-lived primate, the gelada (*Theropithecus gelada*).

Geladas are a highly social, Old World monkey endemic to the Ethiopian highlands. The juvenile period may be particularly important for geladas because of their complex social system that allows juveniles from different groups to come together and interact. Geladas live in a large, multi-level society composed of two different types of core groups [Snyder-Mackler et al., 2012a]. The first core group is the reproductive unit, which contains one reproductively dominant "leader male", 1–12 related adult females [le Roux et al., 2010], and their dependent offspring [Dunbar and Dunbar, 1975]. Approximately 1/3 of reproductive units also include one or more subordinate "follower males" that are either unrelated adults or former unit leaders that participate in group defense and have few reproductive opportunities [Dunbar, 1984; Snyder-Mackler et al., 2012b]. Dozens of reproductive units travel and forage together in a band, and bands form large-scale aggregations (termed communities; Snyder-Mackler et al., 2012a) that can number up to 1200 individuals [Beehner et al., 2007; Kawai et al., 1983]. The second core group is the all-male group, or bachelor group, which is composed of 2–15 adult and subadult males that have dispersed from their natal units [Dunbar, 1993; Kawai et al., 1983; Pappano, 2013]. Bachelor groups generally remain at the periphery of bands but also are occasionally seen on their own [Kawai et al., 1983; Pappano, 2013; Snyder-Mackler et al., 2012b]. Female geladas are philopatric and (with a few exceptions) remain in their natal unit throughout their lives [le Roux et al., 2010]. Male geladas disperse at puberty either to bachelor groups [Dunbar and Dunbar, 1975] or directly into reproductive units [Barale et al., in prep.].

Despite geladas' large groups, the vast majority of affiliative adult interactions do not extend beyond the reproductive unit. By contrast, juvenile geladas are routinely observed playing and grooming with other juveniles from outside their natal unit. Two brief studies on juvenile geladas [Dunbar and Dunbar, 1975; Kawai, 1979] found that juveniles associated in "peer groups" (i.e., spatially discrete groups of non-adults; Dunbar and Dunbar, 1975). These studies reported that young juveniles (aged 6 months–2.5 years) played near their natal units in mixed-sex groups whose members were drawn from closely affiliated units [Kawai, 1979]. After age 2.5 years, females curtailed their participation in play, and males socialized primarily with other same-age males drawn from a wide variety of reproductive units [Dunbar and Dunbar, 1975; Kawai, 1979]. However, both studies were based on broad demographics rather than individually known animals, so our knowledge of this critical life stage remains limited. Regardless of whether or not juveniles are taking advantage of it, the unique nature of the gelada social system means that juveniles have the opportunity to interact with peers that may be males or females, kin or non-kin, strangers or familiar individuals, and the same age or a different age than themselves.

As adults, male, and female geladas rely on different sets of skills to be successful. Because females are philopatric, all adult females in gelada reproductive units are related. Adult females have a stable dominance hierarchy [le Roux et al., 2010], and form and maintain strong bonds with their female relatives through grooming interactions [Tinsley Johnson et al., 2013]. Females inherit their mothers' rank, and rank relationships are established at the end of the juvenile period through fighting and displacements within the unit [A. Lu, pers. comm.]. In contrast to females, males disperse from their natal units and join either all-male bachelor groups or reproductive units. At some point, males in bachelor groups leave and enter reproductive units, often by deposing an existing leader male through physical fighting and aggression [Dunbar and Dunbar, 1975]. Therefore, males rely on physical fighting abilities, stamina, and the ability to accurately assess competitors.

If juveniles are using the time before maturity to develop skills and relationships for adult life, then we expect sex differences to emerge during this time with respect to social behavior and social partner choice. For instance, as preparation for fighting and as a way to hone their assessment capabilities, males should invest in high-energy play-fighting with other juvenile males. By contrast, females should invest very little in play-fighting or any other social behavior with individuals from outside their natal unit. Rather, females should focus more on developing bonds with other females within their unit, either through grooming or through play. Therefore, we make the following predictions. (1) Juvenile males

will spend more time invested in play at all ages, will continue to have high rates of play at older ages, and will invest equally in relationships both within and outside their natal units. (2) Juvenile females will spend more time invested in grooming at all ages, will continue to have high rates of grooming at older ages, and will invest primarily in within-unit relationships with other females. (3) For all juveniles, we expect play rates to decline as juveniles mature. This ontogenetic decrease in play is common in a wide range of species [Fairbanks, 2000; Levy, 1979; Pusey, 1990], and several explanations have been proposed to explain it, including a replacement of play by truly aggressive behavior, dominance rank crystallization that makes play fighting unnecessary, and the onset of sexual maturation and a subsequent increase in sexually motivated behavior.

Although the gelada social system and adult behavior have been studied in depth (e.g., Dunbar and Dunbar, 1975; Kawai, 1979; le Roux et al., 2013; Pappano, 2013; Snyder-Mackler et al., 2012b), little is known about wild juvenile geladas' patterns of social behavior and partner preferences. Here, we use 2 years of detailed behavioral data collected on 74 wild juvenile geladas from the Simien Mountains National Park, Ethiopia, to examine how juveniles spend their social time across different ages. These data represent primarily cross-sectional data in combination with 2 years of longitudinal data on each subject. In particular, we investigated sex differences in social behavior, number and type of social partners, and partner preference to see if juvenile patterns imitate what we expect in adulthood.

METHODS
Study Area and Subjects

This research was conducted on 74 juvenile geladas ($N_{females} = 30$, $N_{males} = 44$; Table I) from 9 reproductive units in the Simien Mountains National Park, Ethiopia, and adhered to protocols approved by the Princeton Institutional Animal Care and Use Committee, the University of Michigan University Committee on Use and Care of Animals, the appropriate government offices in Ethiopia, and the ASP's Principles for the Ethical Treatment of Non Human Primates. All study subjects were individually recognized and fully habituated to human observers on foot. This specific gelada population has been under continuous study since January 2006 as part of the University of Michigan Gelada Research Project. Consequently, sex, exact birthdates (and thus ages), parentage, and unit membership were known for each individual. For males, we additionally recorded the date of dispersal, and for females we recorded the date of sexual maturation. The long-term project continually monitors all births, deaths, and disappearances as part of routine data collection.

Definition of a Juvenile

Although many studies define the lower bound of "juvenile" as the age at which weaning occurs, infant geladas begin to venture away from their mothers and interact with conspecifics before weaning (as early as 6 months of age). Therefore, we included all infant and juvenile geladas from 6 months of age until maturity (defined below).

Similar to other cercopithecines [Altmann et al., 1997, 1981], the end of the juvenile period and the onset of reproductive maturity for female geladas has been previously defined as the appearance of sexual swellings on the chest and neck [Roberts, 2012]. In this population, female maturity occurs at a median age of 4.19 ± 0.32 years [Roberts, 2012]. For males, an equivalent marker of reproductive maturity may be testicular enlargement [Beehner et al., 2009; Charpentier et al., 2008]. However, testicular enlargement has proved challenging to observe in gelada males (indeed, even in adults, testicles appear to remain inguinal and may never fully descend as in other cercopithecines [Altmann et al., 1977], Fig. 1). Consequently, we chose to define the end of the juvenile period in males using another important maturational milestone: dispersal from their natal reproductive unit [Beehner et al., 2009]. Although all juvenile male geladas eventually dispersed, age at dispersal was highly variable (median: 5.97 ± 1.01 years; range: 4.14–7.75 years; Fig. 2). Fully mature, but nulliparous, females (ages 4.2–7.0 years) were included in many of our analyses to allow us to compare behavioral data to same-age males who had not yet dispersed from their natal units.

Behavioral Data

We conducted repeated 15-min focal-animal observations [Altmann, 1974] on all study subjects. Observations occurred during daylight hours, 1–4 times/month per individual, from Sep 2011–Aug 2013. We collected an average of 11 hrs of observations/individual for a total of over 820 hrs of observations.

Specifically, we collected data on grooming interactions, types and durations of play behavior,
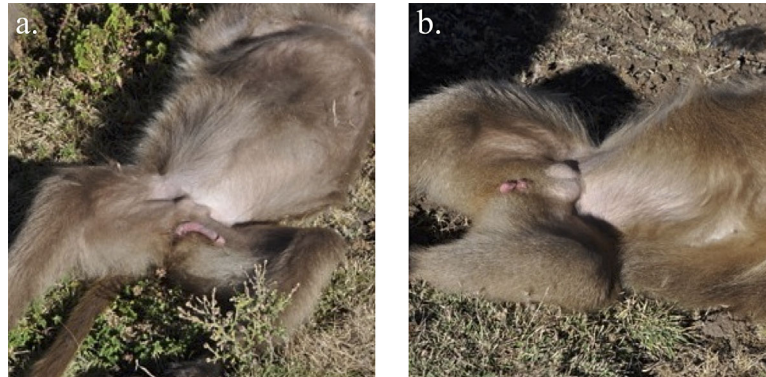
TABLE I. Number of Individuals in Each Age and Sex Category at the Start of the Study Period

Age (years)	0	1	2	3	4	5	6	7
females	3	4	5	4	4	5	3	2
males	3	6	7	7	10	6	3	2

Figure 1. Testes are inguinal in both subadult **(a)** and adult male geladas **(b)**. Thus, testicular descent is not a reliable marker of male maturity in this species, as testicles may never descend.

and play and grooming partner identity. In geladas, juvenile social play falls into two categories of semi-aggressive pseudo-fighting: *rough-and-tumble play* and *chasing*. Rough-and-tumble play is a full-contact, wrestling-style play that involves biting, grappling, mock charges, and acrobatics. Chasing involves one juvenile pursuing another while running. Chasing is often reciprocated, with the chasee becoming the chaser part way through the interaction, and usually occurs in conjunction with rough-and-tumble play. Males and females routinely exhibited both types of play behavior, with rough-and-tumble play occurring more frequently than chasing play for both males and females. For the sake of simplicity, and because the two types of play occurred together >90% of the time, we lumped both categories of play into a single "play" category for all analyses.

Both play rates and grooming rates were calculated by dividing the number of minutes observed in the behavior by the number of total minutes the animal was observed across the study period and converting this value into a "minutes/hour of observation" rate. We considered grooming partners to be any individual (i.e., juvenile or adult) that either groomed or was groomed by the focal animal.

We also recorded the unit size for each juvenile's natal unit. This number included all adults, juveniles, and infants. The number of individuals in a unit varied slightly over the course of our study as animals were born, died and dispersed. To deal with this variability, we recorded group size each month and then averaged over the study period to come up with a single value for each unit.

Pedigrees

Using observations to determine maternity and fecal DNA to determine paternity (for a full discussion of fecal extraction and analysis methods, see Snyder-Mackler et al., 2012b), we knew the identities of a juvenile's mother and father for 68 of our 74 study subjects (91.9%). Dyads that shared both parents were assigned r values of 0.50. Dyads that shared either a mother or father, but not both, (i.e., half-siblings) were assigned r values of 0.25. These two types of pairings were lumped together as *close kin*. Pairs whose mothers were related to one another but did not directly share parents were assigned r values between 0.10 and 0.24 (i.e., *distant kin*) depending on the relatedness of their mothers (relatedness of adult females was drawn from genetic work previously conducted on the population in two previous studies: Snyder-Mackler et al., 2012b; Tinsley Johnson et al., 2013). Dyads that were completely unrelated based on known parentage (and parentage relatedness) were assigned r values of 0 (i.e., *non-kin*). The 6 juveniles with one or more unknown parents were excluded from these analyses.
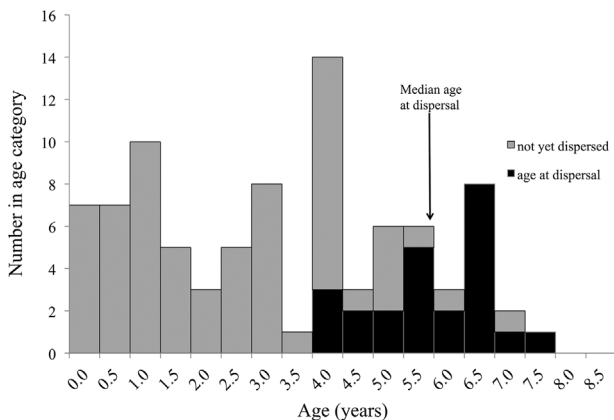

Figure 2. Number of juvenile males in study groups in each age category. Gray bars represent individuals that had not yet dispersed as of 12/31/14. Black bars represent individuals that dispersed during the study period, and indicate the age at which they dispersed. Median age at dispersal was 5.97 ± 1.01 years (range: 4.14–7.75 years).

Data Analysis

We calculated individual play and grooming rates from focal animal observations. Play and

grooming were recorded regardless of whether these behaviors were with other juveniles or with adults. Because most variables were non-normally distributed, we used non-parametric statistical tests for all analyses that did not require the use of multivariate statistics. Four analyses required a multivariate approach - (1) age/sex effects on play rates, (2) age/sex effects on the number of play partners, (3) age/sex effects on grooming rates, and (4) age/sex effects on grooming partners. Below, we describe how we handled each of these analyses.

First, we examined how age and sex contributed to rates of play and grooming. Play rates were non-normally distributed (one-sample Kolmogorov–Smirnov Test, $P < 0.05$), with many animals having no observations of play behavior across the entire study (i.e., many zeroes). Therefore, we divided the play data into a binary variable (i.e., those that had no play and those that had at least *some* play); and then we employed logistic regression to examine whether age and sex were significant predictor variables of whether animals played or not during the study period. We also added an additional variable, unit size (the total number of animals in the unit) to control for the possibility that individuals from larger units may have more social partners available than those from smaller units. Following this initial analysis, we removed all individuals with no play (i.e., the zeroes), we log-transformed play rates for the remaining individuals (achieving normality, one-sample Kolmogorov–Smirnov Test, $P > 0.05$), and we employed a linear model with the log-transformed play rates as the dependent variable, and age, sex, and unit size as predictor variables. Grooming rates, by contrast, were normally distributed, and thus we were able to directly employ a linear model for analyzing the effects of age, sex, and unit size.

Second, we examined how age, sex, and unit size contributed to the number of unique play and grooming partners. The number of play partners was heavily skewed towards 0, 1, and 2 partners. We thus employed a similar two-step procedure as described above. We reassigned the number of partners as a binary variable comprising "few" playmates (0–2 unique partners) and "many" playmates (3+ unique partners) and employed logistic regression to examine whether age, sex, and unit size were significant predictor variables. We then removed the individuals with "few social partners" and log-transformed the number of social partners for the remaining individuals (achieving normality, one-sample Kolmogorov–Smirnov Test, $P > 0.05$). For the number of grooming partners, we were able to achieve a normal distribution by simply taking the square root (one-sample Kolmogorov–Smirnov Test, $P > 0.05$). For both normalized dependent variables (number of play partners and number of grooming partners), we then employed a linear model with age, sex, and unit size as predictor variables.

Third, we investigated whether juveniles across different ages associated differently with individuals from three categories: their mother, another unit individual (juvenile or adult member of the same reproductive unit as the focal individual), or a non-unit individual (juvenile or adult from another reproductive unit). We compared males to females for each age and grooming partner category using a Mann–Whitney U test.

Fourth, to test for similarity in age between play and grooming partners, we used Moran's autocorrelation test. This test randomly permutes a matrix containing information about individual partner choices 10,000 times, and compares the results to a vector containing information about each individual's age. The matrices and vector are then tested for autocorrelation. Moran's I has a possible range from -1 (indicating perfect dispersion) to 1 (indicating perfect correlation), with scores near 0 representing a random distribution [Hanneman and Riddle, 2005; Valente, 2005]. To test whether play and grooming interactions were patterned by sex, we used a join-count autocorrelation test. Like Moran's autocorrelation test, the join-count test randomly permutes an actor-by-actor matrix 10,000 times. The number of entries within and between the two categories (in our case, male and female) are counted and compared for each permutation. Autocorrelation tests were conducted using UCINet v. 6 [Borgatti et al., 2002]. We then examined the fraction of all dyads that were close kin, distant kin, and non-kin (see definitions above) by assigning each pair observed playing or grooming together to the appropriate relatedness bin. We additionally divided dyads up as female–female, female–male, and male–male pairs and compared the fraction of individuals in each relatedness category to investigate sex-specific preferences for kin as social partners.

Finally, to examine individual consistency in play and grooming rates, we used a Spearman's rank-correlation test to compare individual play and grooming rates across the 2 years of the study. With the exception of the auto-correlation tests (performed in UCINet), all statistics were performed using SPSS v.21 [SPSS IBM, New York, 2009]. All statistical thresholds were set at $P = 0.05$.

RESULTS

Time Spent in Play Behavior

Play declined steadily with age for both males and females, although the decline was faster in females (Fig. 3). Age and sex were significant predictors of whether an animal played at all during the study period (logistic regression: $N = 163$, Cox and Snell $R^2 = 0.40$; age: Wald $= 30.15$, $P < 0.001$; sex: Wald $= 18.83$, $P < 0.001$), with older individuals and females being most likely to have never been
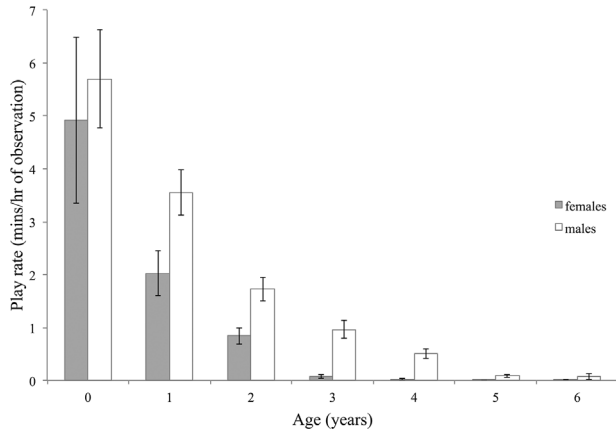
Figure 3. Age/sex differences in time spent playing. Play rate for males and females across the juvenile period. For ease of interpretation, the data represent the raw and not the transformed data. Gray bars indicate females; white bars are males. Age ($F = 272.47$, $P < 0.001$) and sex ($F = 39.80$, $P < 0.001$) were significant predictors of the rate of play for these animals.
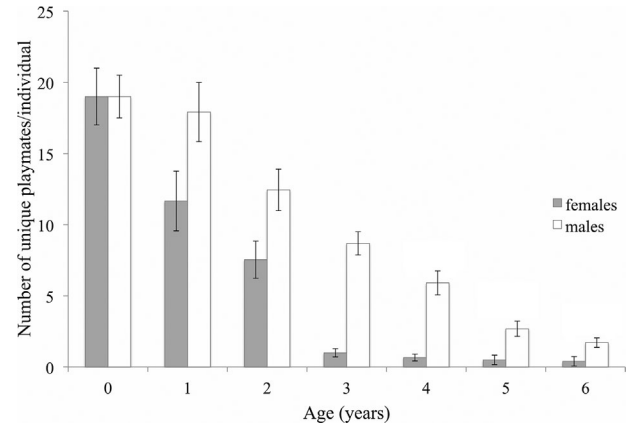

Figure 4. Age/sex patterns in number of playmates per individual. The number of unique playmates an individual had declined with age for both sexes. Gray bars indicate females; white bars are males. When controlling for observation time, age, sex, and unit size were all significant predictors of the number of playmates a juvenile interacted with (linear model: $N = 92$; observation time: $F = 23.64$, $P < 0.001$; age: $F = 84.86$, $P < 0.001$; sex: $F = 13.44$, $P < 0.001$; unit size: $F = 4.31$, $P = 0.041$).

observed playing. Unit size had no effect on whether an animal played or not ($P = 0.644$, Wald $= 0.21$). When we further analyzed only those animals that had *some* play observed during the study period, we found that age ($F = 272.47$, $P < 0.001$) and sex ($F = 39.80$, $P < 0.001$) were significant predictors of the rate of play for these animals (unit size, again, had no effect; $F = 2.25$, $P = 0.136$).

Number of Playmates

The number of unique playmates an individual interacted with also declined as juveniles aged, and this decline happened faster in females than in males (Fig. 4). Controlling for observation time, both age and sex were significant predictors of whether a juvenile had "few" (1–2) or "many" (3+) playmates, while unit size had no effect (logistic regression: $N = 157$, Cox and Snell $R^2 = 0.55$; observation time: Wald $= 4.24$, $P = 0.04$; age: Wald $= 34.02$, $P < 0.001$; sex: Wald $= 20.80$, $P < 0.001$; unit size: Wald $= 1.01$, $P = 0.316$). When we further analyzed only those individuals with 'many' playmates, we found that age, sex, and unit size were all significant predictors of the number of playmates a juvenile interacted with (linear model: $N = 92$; observation time: $F = 23.64$, $P < 0.001$; age: $F = 84.86$, $P < 0.001$; sex: $F = 13.44$, $P < 0.001$; unit size: $F = 4.31$, $P = 0.041$). Additionally, the number of playmates stabilized as individuals approached maturity (Fig. 4). For females, stabilization occurred at approximately 1 unique playmate/individual at age 3. For males, stabilization occurred at approximately 2 unique playmates/individual at age 5.

Age and Sex Preferences of Play Partners

Females did not display a preference for same-aged play partners (Moran's $I = 0.075$, $P = 0.18$) or

same-sex play partners (join-count test: female-female dyads: expected: 51 dyads, observed: 41 dyads, $P = 0.18$; female-male dyads: expected: 158 dyads, observed: 164 dyads, $P = 0.34$). By contrast, males were significantly more likely than expected to play with same-aged partners (Moran's $I = 0.233$, $P < 0.001$) and same-sex partners (join-count test: expected: 153 dyads, observed: 209 dyads, $P < 0.001$).

Relatedness of Play Partners

Females preferentially played with close kin, regardless of their partner's sex (Fig. 5). At least 60% of female–female and female–male play dyads were between individuals that were half-siblings (or closer) in relatedness. Males, on the other hand, did not prefer playing with close kin. Less than 30% of male–male dyads were between half-siblings or closer. Of the 209 male–male play dyads we observed, 43% were composed of non-kin, compared to less than 20% of both female–female and mixed-sex dyads.

Individual Consistency in Play Behavior

Because our analysis showed that play rates decreased predictably with age, we calculated a residual (age-corrected) play rate for each individual in each of the two 1-year time blocks to ascertain if juveniles that played more than expected for their age (i.e., had high residuals) in the first year, continued to do so a year later. We found that play rates were individually consistent and highly repeatable over time for both males and females (Spearman-rank correlation: males: $r_s = 0.56$, $t = 3.74$, $P < 0.001$; females: $r_s = 0.72$, $t = 3.90$, $P < 0.005$).
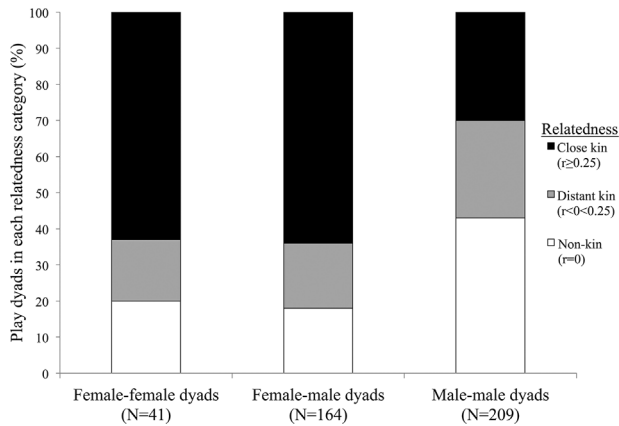
Figure 5. Play partners and relatedness. Percentage of play dyads in each of three relatedness categories (close kin: r ≥ 0.25, distant kin: 0<r<0.25, non-kin: r = 0). The majority of female–female and female–male dyads were between close kin, while less than 30% of male–male dyads were.

Time Spent in Grooming Behavior

Grooming rates increased as juveniles aged, and increased more for females than for males (Fig. 6). In a linear model, we found that age ($F = 4.55$, $P < 0.034$) and sex ($F = 8.61$, $P = 0.004$) were both significant predictors of grooming rate.

Number of Grooming Partners

Controlling for observation time, we found no sex differences in the number of grooming partners per individual at any age (linear model: $N = 92$; observation time: $F = 56.63$, $P < 0.001$; age: $F = 2.12$, $P = 0.149$; sex: $F = 0.79$, $P = 0.376$; unit size: $F = 0.31$, $P = 0.582$). All grooming relationships observed (100%) were reciprocal, with the partners involved changing roles (groomer vs. groomee) across grooming bouts and days. Additionally, the number
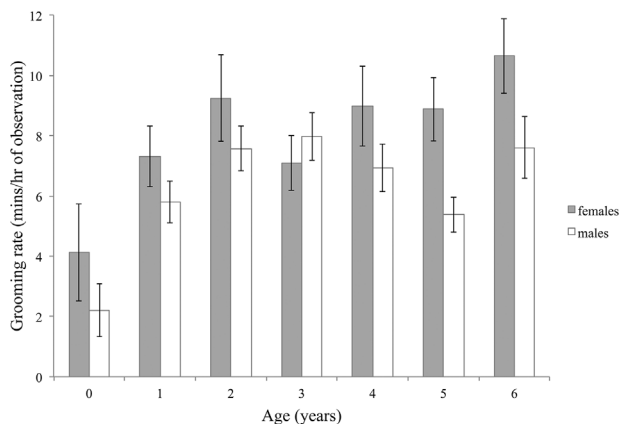

Figure 6. Age/sex differences in time spent grooming. Grooming rates for males and females across the juvenile period. For ease of interpretation, the data represent the raw and not the transformed data. Gray bars indicate females; white bars are males. Age ($F = 4.55$, $P = 0.034$) and sex ($F = 8.61$, $P = 0.004$) were both significant predictors of grooming rate.

of grooming partners per individual remained relatively constant across the juvenile period: from age 1 to 6, males had an average of 5.8 unique partners while females had an average of 5.4 grooming partners.

Age-Related Changes in Grooming Partner Preferences

Although the number of grooming partners/individual did not vary by age or sex groups, the *type* of grooming partner a juvenile associated with did change. During the first two years after birth, both males and females groomed almost exclusively with their mother (Fig. 7a). Grooming time with their mother declined steadily with increasing age. There was no sex difference in the percentage of time individuals groomed with their mothers at any age.

Not surprisingly, the opposite pattern was seen in the time juveniles spent grooming with other unit individuals (Fig. 7b). As individuals aged, the amount of time they groomed both adults and juveniles in their unit increased. Unit individuals were relatives of varying closeness. As was the case with mothers, no sex difference was seen in the percentage of grooming time juveniles spent with unit individuals.

A sex difference did exist in the percentage of total grooming time juveniles groomed individuals from outside their natal unit (Fig. 7c). Neither males nor females groomed with non-unit (unrelated) individuals before 1 year of age. From age 1 year onward, however, males groomed with non-unit individuals significantly more often than females did (Mann–Whitney U test: age 1: $U = 26.5$, $Z = 1.92$, $P < 0.03$; age 2: $U = 60$, $Z = 1.99$, $P < 0.05$; age 3: $U = 41$, $Z = 1.93$, $P < 0.03$; age 4: $U = 46$, $Z = 2.58$, $P < 0.005$; age 5: $U = 21$, $Z = 2.21$, $P < 0.01$; age 6: $U = 9$, $Z = 2.2$, $P < 0.01$). Moreover, males spent an increasing percentage of time grooming with non-unit partners as they matured (see Fig. 7c). These patterns were consistent across units of different size and sex composition.

Age and Sex Preferences of Juvenile Grooming Partners

Females preferred to groom juveniles that were outside their own age category (Moran's $I = -0.287$, $P < 0.0001$). Typically, these dyads involved a juvenile female grooming an infant from her natal unit. Males, in contrast, were significantly more likely than expected to groom with same-age juveniles (Moran's $I = 0.173$, $P < 0.01$). Additionally, males showed a preference for male grooming partners; male-male dyads occurred more frequently than expected (join-count test: expected: 174 dyads, observed: 229 dyads, $P < 0.005$). Female–female dyads occurred only as often as expected, and
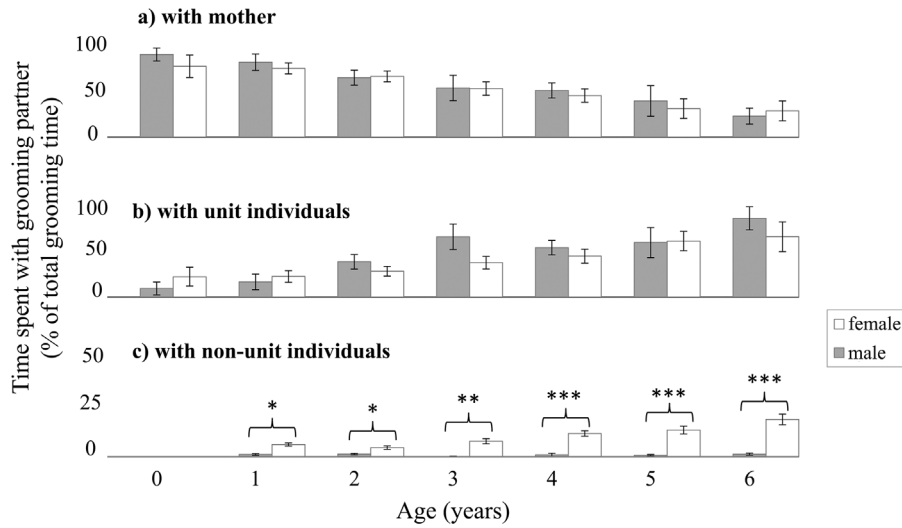
Figure 7. Age/sex differences in grooming partners. Age and sex patterns in grooming time spent with **a)** mothers, **b)** unit individuals (excluding mothers) and **c)** individuals outside the unit (as a percentage of total grooming time). The fraction of time spent grooming with mothers decreased with increasing age for both males and females. Simultaneously, the time juveniles spent grooming with other individuals in their units increased. Males (but not females) increasingly groomed with non-unit individuals as they got older.

mixed-sex dyads occurred significantly less often than expected (join-count test: female–female dyads: expected: 39 dyads, observed: 30 dyads, $P = 0.19$; female–male dyads: expected 183 dyads, observed: 164 dyads, $P < 0.04$).

Relatedness of Grooming Partners

Female-female grooming dyads existed primarily between close kin with 70% of female–female dyads occurring between females that were half or full sisters (close kin, Fig. 8). By contrast, only 41% of female–male dyads and 37% of male–male dyads were between half-siblings or more closely related individuals. Nevertheless, kinship was clearly important for all three types of dyads: non-kin grooming partners were present in only 23% of female–male and male–male dyads, and only 5% of female–female dyads (see Fig. 8).

Individual Consistency in Grooming Behavior

Grooming rates were individually consistent and repeatable over time for both juvenile females and juvenile males (Spearman-rank correlation: females: $r_s = 0.43$, $T = 2.26$, $P < 0.05$; males: $r_s = 0.41$, $T = 2.12$, $P < 0.05$).

DISCUSSION

Our results indicate that geladas exhibited very clear sex differences in social behavior from a young age. Males engaged in both play-fighting and grooming behavior throughout the juvenile period while females participated primarily in grooming. Moreover, sex differences in social behavior and

partner choice reflected sex-specific adult patterns in this species, suggesting that an important next step will be to link these divergent behaviors with adult fitness correlates.

Juvenile male geladas not only spent more time playing but also played with more unique individuals than did females of the same age. Not surprisingly, males' playmates were mostly same-age and same-sex partners, and relatedness did not affect partner choice. By contrast, females preferred kin as play partners, and showed no preference for age or sex in partner choice. A preference for same-age, same-sex partners among juvenile males has been noted in juvenile males of other cercopithecine primate
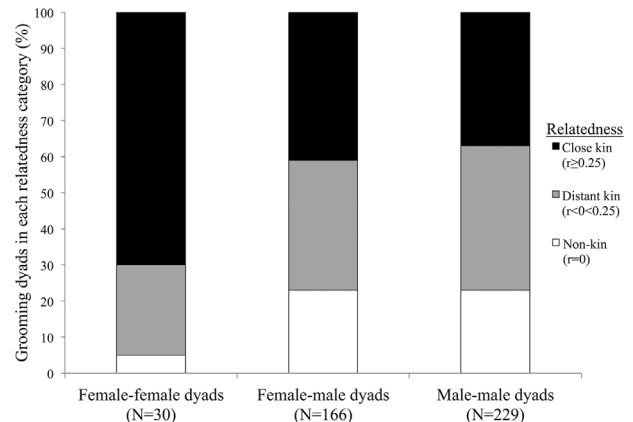

Figure 8. Grooming partners and relatedness. Percentage of grooming dyads in each of three relatedness categories (close kin: $r \geq 0.25$, distant kin: $0 < r < 0.25$, non-kin: $r = 0$). The majority of female–female and were between close female kin, while female–male and male–male dyads were more common between distant kin or non-kin. In all three types of dyads, close kin accounted for at least 77% of grooming partners.

species, including vervets [*Chlorocebus pygerythrus*, Fairbanks, 2002], hamadryas baboons [*Papio hamadryas*; Leresche, 1976], chacma baboons [*P. ursinus*; Cheney 1978a], and yellow baboons [*P. cynocephalus*; Pereira, 1984]. For example, Fairbanks [2002] in a study of 56 captive juvenile vervets, found that two-year-old males consistently selected male age-mates as play partners, and showed no preference for kin. Similarly, Cheney [1978a] found that juvenile male chacma baboons played most often with other male juveniles, although her study additionally found a preference for kin that was not apparent in Fairbanks' study or in ours. Similar patterns are seen in non-primate taxa as well (but see Sharpe 2005b for an example of no preference in meerkats). For example, in a study on Siberian ibex (*Capra ibex sibirica*), male kids played much more with other males than with females, and additionally showed a preference for same-age partners [Byers, 1980]. Similarly, a study on Belding's ground squirrels (*Spermophilus beldingi*) found that males preferentially selected male littermates as their primary play partner [Nunes et al., 2004].

Across species, juvenile males' preference for same-sex, same-age play partners is consistent with the hypothesis that juveniles select individuals that have particularly high value as playmates. Since play is hypothesized to assist with physical skills training and to provide individuals with the opportunity to assess potential competitors [Bekoff, 1984; Byers, 1998; Martin and Caro, 1985]—both skills that benefit dispersing males—a "high-value" play partner is one who is closely matched in size, strength, physical skill level, and motivation to play.

Relationships formed during the juvenile period may also help male geladas weather the dispersal transition (as is the case in Hanuman langurs (*Presbytis entellus*), Rajpurohit and Sommer, 2002), although additional research is needed to determine whether the bonds formed during the gelada juvenile period persist through dispersal and into adulthood, and if so, what effect they have on survival and reproductive success. Alternatively, specific bonds between individuals may not persist through dispersal and highly social males may instead benefit from time spent learning *how* to form relationships with peers. A recent study by Nuñez and colleagues [2015] on feral horses (*Equus caballus*) found that orphaned foals that had successfully built peer relationships before being orphaned were more likely to survive the loss of both parents and form new relationships than their less-social peers. A similar effect may exist in geladas, with males who are more social as juveniles surviving the dispersal transition more successfully not because of who specifically their social partners are, but because of their ability to build new bonds when needed.

We also found that juvenile males demonstrated a relatively late termination of play behavior compared to their female peers. Unlike females that curtailed play by age 3, juvenile males continued routine play behavior (with a variety of play partners) until age 5. Because adult males need to be adept at rival assessment and skilled at physical fighting to enable them to eventually challenge and defeat leader males [Dunbar and Dunbar, 1975], juvenile males may stand to benefit from continuing to play-fight with a variety of individuals across their growth and development (although it is also possible that gaining physical skills is not a primary purpose of play-fighting, as suggested by Sharpe 2005a). Because an adult female's relationships are entirely kin-mediated [le Roux et al., 2010], a female's social circle is not likely to change with age. Thus, female geladas have little evolutionary incentive to play and interact with unrelated individuals, and are likely to devote their time to social activities other than play-fighting (e.g. grooming, building alliances with female kin, practicing maternal behavior; Fairbanks, 2002) that will influence their fitness more directly.

Following this prediction, grooming partner preferences in juvenile geladas also reflected sex-specific adult trajectories. Females opted to build strong grooming relationships within their unit (particularly with close kin), and were rarely observed grooming with unrelated individuals. Similar patterns have been documented in other cercopithecine primate species (e.g., Cheney, 1978b; Silk et al., 1981, 1999). Male juveniles, by contrast, spent a significant and increasingly large fraction of their grooming time interacting with individuals from outside their unit as they aged.

Somewhat surprising was our finding that although juvenile females groomed preferentially with close kin, they did not show a preference for same-sex or same-age individuals as grooming partners. Because gelada females generally give birth to a single infant once every 2.37 years [Roberts et al., 2012], it is unlikely that juvenile females have closely related, same-age, female peers during much of the juvenile period. More often than not, we observed juvenile females selecting full- or half-sibling infants as their primary grooming partners, and, in many cases, combining grooming with practicing maternal behavior. This pattern is seen in a variety of other primates. For example, in a study of allomothering in juvenile female rhesus macaques, Small and Smith [1981] found that juveniles were more likely to "grab" their infant siblings for social interactions than half-siblings or non-relatives. Fairbanks [1990] also found that juvenile female vervets preferentially spent time caretaking, grooming, and carrying their infant siblings. Furthermore, Fairbanks found that this type of parenting practice paid off: females that practiced maternal behavior as juveniles were more likely than their peers to successfully rear their first live-born infant. It is also possible that a preference for close kin over

age-mates is an investment in valuable future grooming or alliance partners (e.g., Fairbanks, 2002; O'Brien and Robinson, 2002). This is likely in geladas: Tinsley Johnson and colleagues [2013] found that adult gelada females preferred relationships with females that had relatedness coefficients approaching the level of a mother and her offspring (or that of full siblings). Overall, our grooming results suggest that juvenile female geladas are opting to invest in social relationships that allow them to practice maternal behavior, to build ties with potential future allies, or both.

These differences in sex-specific play behavior and social partner preference highlight two divergent behavioral trajectories in geladas and suggest that geladas may be using their time as juveniles to build skills and form relationships that will help them succeed as adults. The multi-tiered gelada social system gives juveniles of both sexes the unique opportunity to engage in positive social interactions with individuals both within and outside their natal unit. These social interactions and bonds have the potential to impact adult fitness for both males and females (e.g., Fairbanks, 1990; O'Brien and Robinson, 2002; Rajpurohit and Sommer, 2002). However, our study was too short in duration to confirm that juvenile social interactions are actually beneficial in terms of lifetime reproductive success, or to uncover what precisely juveniles are gaining from them – social aptitude and physical skills? Long-term relationships with specific individuals? Something else entirely? The next step towards demonstrating that juvenile social behavior affects reproductive success would be to conduct longitudinal studies on these juveniles to explore whether play behavior affects adult success in males, and whether grooming and maternal practice impact adult success in females. To this end, we are continuing to follow the individuals in this study as they mature and reproduce.

Finally, this 2-year study revealed that individual play and grooming rates were consistent over a short period of time for both males and females. In short, individuals that played or groomed often for their age at 2 years old also played or groomed more than their peers at age 3. This individual consistency amidst the large age-sex class variation suggests that there may be some individually-stable behavioral phenotypes that are revealed by playing and grooming behavior—"social types" that have the potential to influence dispersal, reproduction, health, and longevity [e.g., Cote et al., 2010; Dingemanse et al., 2003; Kobasa, 1979; van Oers et al., 2008]. Quantifying stable social types in juvenile geladas and continuing to observe these specific individuals as they mature will add another dimension to our on-going research on the relationships between the juvenile period and adult skills and success.

REFERENCES

Altmann J 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Altmann J, Altmann SA, Hausfater G, McCuskey SA. 1977. Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. Primates 18:315–330.

Altmann J, Altmann SA, Hausfater G. 1981. Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. American Journal of Primatology 1:389–399.

Barale CL, Rubenstein DI, Beehner JC. 2015. In prep. Dispersal patterns of wild male geladas.

Beehner JC, Gebre B, Bergman TJ, McCann C. 2007. Population estimate for geladas (*Theropithecus gelada*) living in and around the Simien Mountains National Park, Ethiopia. SINET Ethiopian Journal of Science 30:149–154.

Beehner JC, Gesquiere L, Cheney DL, Seyfarth RM, Altmann J. 2009. Fecal testosterone related to age and life-history stages in male baboons and geladas. Hormones and Behavior 56:472–480.

Bekoff M 1984. Social play behavior. BioScience 34:228–233.

Borgatti SP, Everett MG, Freeman LC. 2002. Ucinet 6 for Windows: Software for social network analysis. Analytical Technologies, Harvard.

Byers JA 1980. Play partner preferences in Siberian ibex, Capra ibex sibirica. Zeitschrift für Tierpsychologie 53:23–40.

Byers JA 1998. Biological effects of locomotor play: getting into shape, or something more specific?. In: Bekoff M, Byers JA, editors. Animal Play: Evolutionary, Comparative, and Ecological Perspectives. New York: Cambridge University Press. p 205-220.

Charpentier MJE, Tung J, Altmann J, Alberts SC. 2008. Age at maturity in wild baboons: genetic, environmental and demographic influences. Molecular Ecology 17:2026–2040.

Cheney DL 1978a. The play partners of immature baboons. Animal Behaviour 26:1038–1050.

Cheney DL 1978b. Interactions of immature male and female baboons with adult females. Animal Behaviour 26:389–408.

Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). Proceedings of the Royal Society B: Biological Sciences 277:1571–1579.

Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ. 2003. Natal dispersal and personalities in great tits (*Parus major*). Proceedings of the Royal Society B: Biological Sciences 270:741–747.

Dunbar RIM 1984. Reproductive decisions: an economic analysis of gelada baboon social strategies. Princeton: Princeton University Press.p p. 276.

Dunbar RIM 1993. Social organization of the gelada. In: Jablonski NG, editor. Theropithecus: The Rise and Fall of a Genus. New York: Cambridge University Press. p 425-439.

Dunbar RIM, Dunbar P. 1975. Social Dynamics of Gelada Baboons. In: Szalay FS, editor. Contributions to Primatology. Basel: S. Karger. p -157.

Fairbanks LA 1990. Reciprocal benefits of allomothering for female vervets. Animal Behaviour 40:553–562.

Fairbanks LA 2000. The developmental timing of primate play: a neural selection model. In: Parker ST, Langer J, McKinney ML, editors. Biology, Brains and Behavior: the Evolution of Human Development. Santa Fe: School of American Research Press. p 131-158.

Fairbanks LA 2002. Juvenile vervet monkeys: establishing relationships and practicing skills for the future. In: Pereira ME, Fairbanks LA, editors. Juvenile Primates: Life History, Development, and Behavior. Chicago: University of Chicago Press. p 211-227.

Fleming IA, Lamberg A, Jonsson B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. Behavioral Ecology 8:470–480.

Hanneman RA, Riddle M. 2005. Introduction to Social Network Methods, Vol. 13. Oakland: University of California Press. p 121.

Kawai M 1979. Ecological and Sociological Studies of Gelada Baboons. In: Szalay FS, editor. Contributions to Primatology. Basel: S. Karger. p 344.

Kawai M, Ohsawa H, Mori U, Dunbar RIM. 1983. Social organization of gelada baboons: social units and definitions. Primates 24:13–24.

Kobasa SC 1979. Stressful life events, personality and health: an inquiry into hardiness. Journal of Personality and Social Psychology 37:1–11.

le Roux A, Beehner JC, Bergman TJ. 2010. Female philopatry and dominance patterns in wild geladas. American Journal of Primatology 71:1–9.

le Roux A, Snyder-Mackler N, Roberts EK, Beehner JC, Bergman TJ. 2013. Evidence for tactical concealment in a wild primate. Nature Communications 4:1462.

Leresche L 1976. Dyadic play in hamadryas baboons. Behaviour 57:3–4.

Levy J 1979. Play behavior and its decline during development in rhesus monkeys (Macaca mulatta) (Doctoral dissertation). Chicago: Univ. of Chicago.p 235.

Martin P, Caro TM. 1985. On the function of play and its role in behavioral development. In: Rosenblatt JS, Beer C, Busnel MC, editors. Advances in the Study of Animal Behavior. Orlando: Academic Press. p 59–103.

Nunes S, Muecke EM, Sanchez Z, Hoffmeier RR, Lancaster LT. 2004. Play behavior and motor development in juvenile Belding's ground squirrels (Spermophilus beldingi). Behavioral Ecology and Sociobiology 56:97–105.

Nuñez CMV, Adelman JS, Rubenstein DI. 2015. Sociality increases juvenile survival following a catastrophic event in the feral horse (Equus caballus). Behavioral Ecology 26:138–147.

O'Brien TG, Robinson JG. 2002. Stability of social relationships in female wedge-capped capuchin monkeys. In: Pereira ME, Fairbanks LA, editors. Juvenile Primates: Life History, Development, and Behavior. Chicago: University of Chicago Press. p 197-210.

Pappano DJ 2013. The reproductive trajectories of bachelor geladas (Doctoral dissertation). Ann Arbor: University of Michigan. p. 159.

Pereira ME 1984. Age changes and sex differences in the social behavior of juvenile yellow baboons (Papio cynocephalus) (Doctoral dissertation). Chicago: University of Chicago. p. 432.

Pusey AE 1990. Behavioral changes at adolescence in chimpanzees. Behaviour 115:203–246.

Rajpurohit LS, Sommer V. 2002. Juvenile male emigration from natal one-male troops in Hanuman langurs. In: Pereira ME, Fairbanks LA, editors. Juvenile Primates: Life History, Development, and Behavior. Chicago: University of Chicago Press. p p 86-103.

Roberts EK 2012. Behavioral endocrinology and reproductive strategies in wild female geladas (Theropithecus gelada) (Doctoral dissertation). Ann Arbor: University of Michigan. p. 160.

Roberts EK, Lu A, Bergman TJ, Beehner JC. 2012. A Bruce effect in wild geladas. Science 335:1222–1225.

Ross C, Jones KE. 1999. Socioecology and the evolution of primate reproductive rates. In: Lee PC, editor. Comparative Primate Socioecology. New York: Cambridge University Press. p 73-110.

Sharpe LL 2005a. Play fighting does not affect subsequent fighting success in wild meerkats. Animal Behaviour 69:1023–1029.

Sharpe LL 2005b. Frequency of social play does not affect dispersal partnerships in wild meerkats. Animal Behaviour 70:559–569.

Silk JB, Samuels A, Rodman PS. 1981. The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (Macaca radiata). Behaviour 78:111–137.

Silk JB, Seyfarth RM, Cheney DL. 1999. The structure of social relationships among female savanna baboons in Moremi Reserve. Botswana. Behaviour 136:679–703.

Small MF, Smith DG. 1981. Interactions with infants by full siblings, paternal half-siblings, and nonrelatives in a captive group of rhesus macaques (Macaca mulatta). American Journal of Primatology 1:91–94.

Snyder-Mackler N, Bergman TJ, Beehner JC. 2012a. Defining higher levels in the multilevel societies of geladas (Theropithecus gelada). International Journal of Primatology 33:1054–1068.

Snyder-Mackler N, Alberts SC, Bergman TJ. 2012b. Concessions of an alpha male? Cooperative defence and shared reproduction in multimale primate groups. Proceedings of the Royal Society B: Biological Sciences 279:3788–3795.

Stanton MA, Mann J. 2012. Early social networks predict survival in wild bottlenose dolphins. PLoS ONE 7.

Templeton CN, Reed VA, Campbell SE, Beecher MD. 2012. Spatial movements and social networks in juvenile male song sparrows. Behavioral Ecology 23:141–152.

Thompson KV 1998. Self assessment in juvenile play. In: Bekoff M, Byers JA, editors. Animal Play: Evolutionary, Comparative, and Ecological Perspectives. New York: Cambridge University Press. p 183-204.

Tinsley Johnson E, Snyder-Mackler N, Beehner JC, Bergman TJ. 2013. Kinship and dominance rank influence the strength of social bonds in female geladas. International Journal of Primatology 35:288–304.

Valente TW 2005. Network models and methods for studying the diffusion of innovations. In: Carrington PJ, Scott J, Wasserman S, editors. Models and Methods in Social Network Analysis. New York: Cambridge University Press. p 101.

van Oers K, Drent P, Dingemanse NJ, Kempenaers B. 2008. Personality is associated with extrapair paternity in great tits, Parus major. Animal Behaviour 76:555–563.