RESEARCH ARTICLE

Female Philopatry and Dominance Patterns in Wild Geladas

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Cercopithecines have a highly conserved social structure with strong female bonds and stable, maternally inherited linear dominance hierarchies. This system has been ascribed to the pervasiveness of female philopatry within the typical multi-male, multi-female social groups. We examined the relationship between female philopatry, dominance hierarchies, and reproduction in geladas (*Theropithecus gelada*), a species with an unusual multi-leveled society. During a 4-year field study on a wild population in the Simien Mountains National Park, Ethiopia, we observed 14 units across two bands of geladas that underwent a number of events, such as male takeovers and female deaths, which could potentially disrupt female relationships and unit structure. First, we corroborate earlier reports that gelada females are natally philopatric: we observed no interunit migrations, and the female mortality rate was comparable to that of philopatric baboons (suggesting all female disappearances were indeed deaths). Second, contrary to previous reports, data from this long-term study show that geladas exhibit the linear and stable dominance hierarchies typical of other Cercopithecines. Moreover, female ranks appear to be maternally inherited. Third, we found no evidence that alpha females aggressively target the lowest ranking individuals, nor did rank confer clear reproductive advantages to dominant females within our 4-year observation period. As such, geladas fit the allostatic load model [Goymann & Wingfield, Animal Behaviour 67:591–602, 2004]. Our study confirms the importance of female philopatry in the kin-based Cercopithecine dominance system. Am. J. Primatol. 73:422–430, 2011.   © 2010 Wiley-Liss, Inc.

INTRODUCTION

Primates have remarkably diverse social systems—even closely related species can exhibit highly divergent systems (e.g. capuchins, *Cebus* spp. [Matthews, 2009]). In contrast with most primates, however, Cercopithecines exhibit a highly conserved social system [Di Fiore & Rendall, 1994] comprising multi-male, multi-female groups with female dominance ranks that are stable, linear [e.g. Isbell & Young, 1993; Range & Noë, 2002], and maternally inherited [Kapsalis, 2004]. Such ranks are maintained via strong intrasexual grooming relationships and coalitions [Silk, 1993]. This predominant structure across Cercopithecines has been ascribed to the prevalence of female philopatry [Silk, 1987]. Because females remain in their natal groups with close kin, long-term bonds are established along matrilineal lines, sustaining and reinforcing stable dominance structures [e.g. Bernstein & Ehardt, 1985; Cheney, 1977; Horrocks & Hunte, 1983]. However, because the Cercopithecine pattern is highly conserved, there are very few exceptions for testing the importance of female philopatry to the overall Cercopithecine social structure (i.e. pattern of social interactions

[cf. Hinde, 1976; Kappeler & van Schaik, 2002]). A notable exception is the hamadryas baboon (*Papio hamadryas*). This species supports the correlation between female philopatry and relationship patterns as hamadryas females are nonphilopatric, have no clear or consistent dominance ranks, and generally—though not always [Swedell, 2000, 2002]—exhibit weak female bonds [Kummer, 1968; Swedell, 2006]. However, hamadryas baboons have a different social organization (i.e. societal composition [Kappeler & van Schaik, 2002]) from other Cercopithecines.

Rather than the typical multi-male, multi-female organization, they have a multi-level (or "modular") society based on one-male units [reviewed by Grüter & Zinner, 2004; Kummer, 1968]. Thus, although this species attests to the relationship between philopatry and stable dominance hierarchies [Bernstein & Ehardt, 1985; Silk, 1993], their unusual social system may be a confounding variable.

Only one other Cercopithecine exhibits multi-level societies based on one-male units—the gelada (*Theropithecus gelada*). Gelada one-male units aggregate in fission–fusion bands of up to 1,000 members [Dunbar, 1980a; Kawai et al., 1983; Mori, 1979]. Each one-male unit has a number of adult females and one leader male that has exclusive reproductive access to unit females. Females within one-male units are reported to have close female bonds [Dunbar, 1979] and are also thought to be philopatric with respect to the unit [Dunbar, 1983c]. Gelada units and bands are relatively stable in composition in the northern ranges of their habitat [Ohsawa & Dunbar, 1984], although this stability may break down in more extreme environments [Mori et al., 1999]. Thus, geladas present an ideal example for examining the relationship between a multi-leveled society, female philopatry, and other aspects of the conserved Cercopithecine social system.

Previous studies have suggested that geladas may contradict the general Cercopithecine pattern: although females are philopatric; female dominance ranks are reportedly not an inherited system based on matrilines but rather a product of female age, aggression, and coalition partnerships [Dunbar, 1983c, 1986, 1993]. Based on such a system, Dunbar predicted that the strongest, prime age females with strong coalitionary support would (temporarily) occupy the top ranks. However, this fluid structure is contradicted by observations of long-term rank stability in captive groups [Bernstein, 1975]. These contradictions may have arisen because most of the extant research on gelada social behavior has been conducted in captivity or as part of short-term (6–9 month) field studies. Therefore, our primary objective is to describe female dominance relationships using long-term data from one population of wild geladas.

Geladas are also useful for exploring the nature and consequences of dominance in Old World monkeys. More often than not, it is unclear what the benefits of high rank position are. Although some Cercopithecine females show a positive correlation between food-based condition and rank [Mori, 1979; Whitten, 1983], such a relationship is not always present [Fairbanks & McGuire, 1984; Post, 1981], and it may not translate into long-term reproductive success [e.g. Smuts & Nicolson, 1989]. In captive Cercopithecines, higher ranking females often have improved reproductive success [Garcia et al., 2006; Zumpe & Michael, 1996], but this relationship may attenuate in wild populations due to external factors

such as infanticide and predation [Cheney et al., 2004]. Recently, the allostatic load model [Goymann & Wingfield, 2004] has been proposed to compare the physiological costs of dominant and subordinate rank positions. This model ascribes a specific allostatic load to an individual's rank position, assigning one score to *attaining* a rank position and another score to *maintaining* it. For example, a dominant's total allostatic score will be higher for a rank system maintained by aggression than a rank system based on inherited ranks [Goymann & Wingfield, 2004]. The relative allostatic scores then predict the costs and benefits associated with differential ranks. Importantly, the allostatic load model implies that high rank does not necessarily accord physiological benefits to dominants, unless low ranks come with significant costs [see also Abbott et al., 2003]. In geladas, Dunbar [1983c, 1993] reports a positive relationship between female rank and reproductive success—an inequality thought to be acquired and maintained by high-ranking individuals harassing low-ranking individuals. Supporting this mechanism, a study of captive geladas found that dominant females harassed subordinates resulting in lengthened ovarian cycles and reproductive failure [McCann, 1995]. However, if geladas conform to the Cercopithecine social structure and rank positions are inherited and maintained without much aggression, then a positive relationship between rank and reproductive success contradicts the predictions of the allostatic load model.

In this study, we use 4 years of data from a population of wild geladas to: (1) confirm female philopatry and to answer the following questions about female dominance relationships within units: (2) Is the dominance hierarchy linear? (3) Are dominance ranks stable over time? (4) Are female dominance ranks maternally inherited? (5) Is there a relationship between female rank and aggression? and (6) Do high-ranking females have higher reproductive success (as measured by interbirth intervals and fertility rates) than low-ranking females?

METHODS

Behavioral Sampling

The data from this study come from two bands of wild geladas living in the Sankaber area of the Simien Mountains National Park, Ethiopia. These bands have been under continuous observation since January 2006, and the demographic data for this study span more than 4 years (January 2006–March 2010). Note that all research herein adhered to the American Society of Primatologists' principles for the ethical treatment of primates. We use these demographic data for all analyses that require known birth dates (i.e. determining female philo-

patry, using known mother–daughter relationships, and calculating interbirth intervals and fertility rates). For analyses related to aggression, rank relationships and grooming dyads, we use data from a 2-year period of intensive behavioral observations (March 2008–2010; 1,542 observation days). During this period, we conducted: (1) repeated 15-min focal observations of all target females during which all social interactions were timed and described (381.3 focal observation hours in total, 3.8 ± 0.4 hr per female), and (2) ad libitum observations of adult females, focusing on dominance interactions within units (163.3 ± 23.5 observation hours per unit).

Philopatry

We have demographic and life-history data from a total of 61 adult and 62 juvenile females across 14 one-male units. We had 27 adult females with data from all the four observation years and three or more years of data for 39 of these females. Because the majority of adult females (i.e. females that have reached menarche) were born before the start of the study, we broadly classify adult females into three age categories (young, prime, and old; see Table I). A few of these adult females ($N = 9$) were born during the first year of the study, and thus exact ages were known. All other females are referred to as "juveniles" until they reach menarche.

With respect to female philopatry for one-male units, we make the following classifications:

- Female *philopatry*—when females remain in their natal one-male unit throughout life. No females emigrate from or immigrate into one-male units (i.e. no female dispersal).
- Unit *fission*—when an existing unit splits into two or more smaller units, each with their own leader male.
- Female *disappearance*—when a female disappears and is not observed in a neighboring unit or band. Note: we assume these disappearances are deaths (see below).

To calculate "female observation years," we determined the number of observation years for all

TABLE I. Adult Female Age Classes Used in This Study, Based on Kawai et al. [1979] and Dunbar [1980a]

Age category	Physical description	Age (years)
Young	Nulliparous female that has reached menarche with cyclical sexual swelling	3.5–5.0
Prime	Primiparous to multiparous, no signs of coat or tooth wear	5.0–8.5
Old	Multiparous, clear signs of coat and tooth wear	8.5+

adult females. For young females, we did not count observation time until 1 year after menarche to compensate for the period of adolescent sterility typical of most Cercopithecines [e.g. see Anderson & Bielert, 1994].

Stability of Ranks

For each unit, we constructed dominance hierarchies based on win–loss matrices using the following data: (1) all dyadic dominance acts noted during ad lib observations (including all aggression, submission, supplants, visual threats, and vocal threats), and (2) all supplants from focal observations. Supplants were noted when a female approached another female and usurped her immediate foraging spot (or, more rarely, her grooming interaction). To investigate dominance changes across time, we constructed each unit's dominance matrix four times—once every 6 months across the 2-year observation period.

Linearity of the Hierarchy

The linearity of the resulting hierarchies was calculated after Strayer and Strayer's [1976] index of linearity:

$$\text{index} = 100 \times \left(\frac{\text{dyads}_{\text{total}} - \text{reversals}_{\text{total}}}{\text{dyads}_{\text{total}}} \right)$$

where dyads$_{\text{total}}$ is the number of dyadic dominance interactions within a unit; and reversals$_{\text{total}}$ is the number of acts that violate the hierarchy. In this index, a value of 100% would indicate a completely linear hierarchy.

Maternal Inheritance of Ranks

We had demographic records for nine adult females since birth and thus knew who their mother was. Kin relations among other adult females were inferred from close grooming partnerships. Specific grooming data used to establish putative kin relationships are presented elsewhere [le Roux et al., in preparation], but, in brief, grooming rates (calculated from focal observations) were used to identify strongly preferred grooming partners, who were then tentatively designated as "kin" [cf. Dunbar, 1984; Silk et al., 1999]. Although we understand that this method for assigning kin relationships is less than ideal (and, genetic data are forthcoming), we are merely looking for patterns consistent (or not consistent) with the hypothesis that daughters inherit ranks just below those of their mothers (i.e. close grooming partners are also adjacent in rank, with the much-younger female of the dyad ranked just below the older female). Observations of close grooming relationships in our known mother–daughter dyads (whether the daughter was adult or juvenile) corroborate this approach.

Dominance Rank and Aggression

For calculations of aggression rates (initiated and received), we used data only from focal samples and only from females that had more than 1 hr of data. As physical acts of aggression are rarely captured in focal animal samples, we included all visual and vocal threats as well as actual aggressive acts directed toward or received from any other individual (including juveniles and individuals in other units). Note that the data used to calculate rates of aggression are *not* the same as the data used to calculate the dominance matrices (see Stability of Ranks section).

Dominance Rank and Reproductive Success

As our proxies for reproductive success, we first calculated the interbirth intervals (IBIs) for all females with more than one infant born during the 4-year observation period. Second, we determined each adult female's fertility rate across the same period. Fertility rates were calculated by dividing the number of offspring for each female (born during the observation period) by her observation years (see "Philopatry" section for how this was calculated). Although rank positions were determined from data collected during the 2-year period of intensive observations, we have confirmed herein that ranks are stable across time, and therefore we make the assumption that older females maintained their ranks across the entire 4-year period.

Statistical Analyses

All statistical tests were performed using R Statistics [2009], and results are presented as mean $\pm$ SEM. To compare females from different ranks across units of varying sizes, we assigned each female a relative rank within her unit, ranging from 0 (lowest rank) to 1 (highest rank), calculated as follows:

$$\text{relative rank} = \frac{N - \text{ord rank}}{N - 1}$$

where N is the number of adult females in the unit and ord rank is the female's ordinal rank position in the hierarchy.

For all rank analyses, we used both relative ranks and ordinal ranks to confirm the outcomes. Results remained the same whether we used relative or ordinal ranks. For simplicity (and for comparisons across different sized units), we present only the results based on relative ranks.

RESULTS

Philopatry

In 242.5 adult female years and 130.5 juvenile female years, we found no evidence that females disperse from their natal unit. We never observed new/unknown females entering any of our target units, nor did we observe "unattached" females without a leader male. When units fissioned ($N = 3$, see below), the newly formed units contained subsets of all the original females and remained within the original band.

Sixty-two females were born into our target units during the 4-year observation period. Of these, the nine females that reached menarche did so within their natal unit. The disappearance/death rate of infants and juveniles was consistent with mortality data published elsewhere for this population [Beehner & Bergman, 2008], and we never observed the dispersal of juvenile females from their natal units.

A total of 21 adult females disappeared across the study period. Of these, 15 were old females and four were prime females with obvious health problems shortly before their disappearance (parasitic swellings identified as *Coenurus* that are known to infect geladas, see p 38 in Ohsawa [1979]). Only two were healthy young females who disappeared without any clear cause. Importantly, none of these females was later observed in neighboring units in either band. Assuming all disappearances were due to female mortality, the annual mortality rate for adult females in this population is 0.07 ± 0.02 (range: 0.02–0.15). Excluding the disappearances of the two healthy young females has a negligible effect on this annual mortality rate.

Stability of Ranks

We recorded 805 dominance interactions for 59 individuals (two females from our original 61 females disappeared before the more intensive focal data collection period) from 14 one-male units across the 2-year period. All results suggest that gelada females have stable, linear dominance hierarchies. We found no reversals in rank position (for any female in any unit) when we compared the matrices across the four periods. Correspondingly, when assessing linearity based on the rank positions in the initial time period, there was no change in linearity when data from subsequent time periods were added (recall that changes in rank positions should cause linearity to decrease over time, Fig. 1; ANOVA: $F_{3,44} = 0.034$; $P = 0.992$). Furthermore, the dominance matrices were unaffected by deaths and births or disruptive events such as unit takeovers and fissions. Nine females, across seven different units, died during the 2-year period. These females occupied all rank positions. In neither case did these deaths cause a change in the dominance hierarchy (except that, by definition, those ranking below the dead female moved up one position). Births ($N = 56$ across 2 years) did not have any effect on females' rank positions. Nine unit takeovers were recorded during our observational period, and in none of these did the change in male leadership lead to fluctuations in
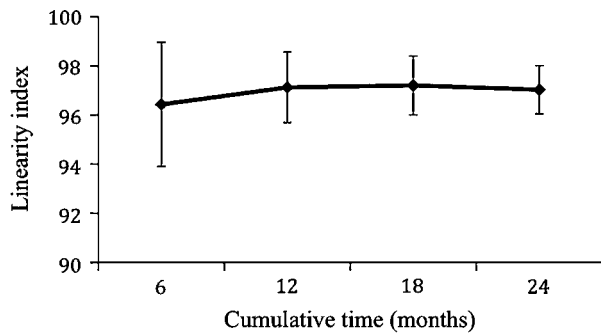
Fig. 1. The average linearity index ($\pm$SEM) of 14 gelada one-male units across blocks of time ranging from 6 months to 2 years. Pooling data from longer periods of time did not change the linearity of these units' dominance hierarchies (see text for data), indicating stable hierarchies.

female hierarchies. We observed three fissions where large units ($N > 9$ adult females) split into smaller units following a unit takeover. In all the three cases, females' rank positions were maintained in relation to one another after the split. Furthermore, ranks did not differ by age category ($F_{2,65} = 0.557$, $P = 0.576$).

Linearity of the Hierarchy

The average index of linearity across the 14 units was 97.0% (range: 87.5–100.0%). Of all 805 rank interactions, only 24 (3.0%) violated the established hierarchy. None of these temporary "reversals" resulted in lasting changes in rank position.

Maternal Inheritance of Ranks

Results suggest that a daughter inherits a dominance rank directly below that of her mother. The nine females whom we knew from infancy to adulthood all ranked just below their mothers. In one case, a young female was the daughter of an alpha female who died shortly after the daughter reached adulthood. This daughter immediately became the new alpha female despite being younger and smaller than all the other females in the unit. Three of these known daughters established strong, mutually preferred grooming relationships with their mothers (the other known daughters matured later and we did not obtain sufficient grooming data to confirm their grooming preferences). Corroborating these data from known mother–daughter pairs, we observed seven additional stable grooming dyads consisting of females born before our observation period. In five of these dyads, the younger female in the dyad (i.e. the putative daughter) always ranked just below the older female. In the other two of these pairs, the females appeared close together in age (estimated 2–3 years apart) and may have been siblings; in both of these units, a much older female had recently died and it is possible that both females were the offspring of the older female. Currently, we are unable to address sister rank relations and
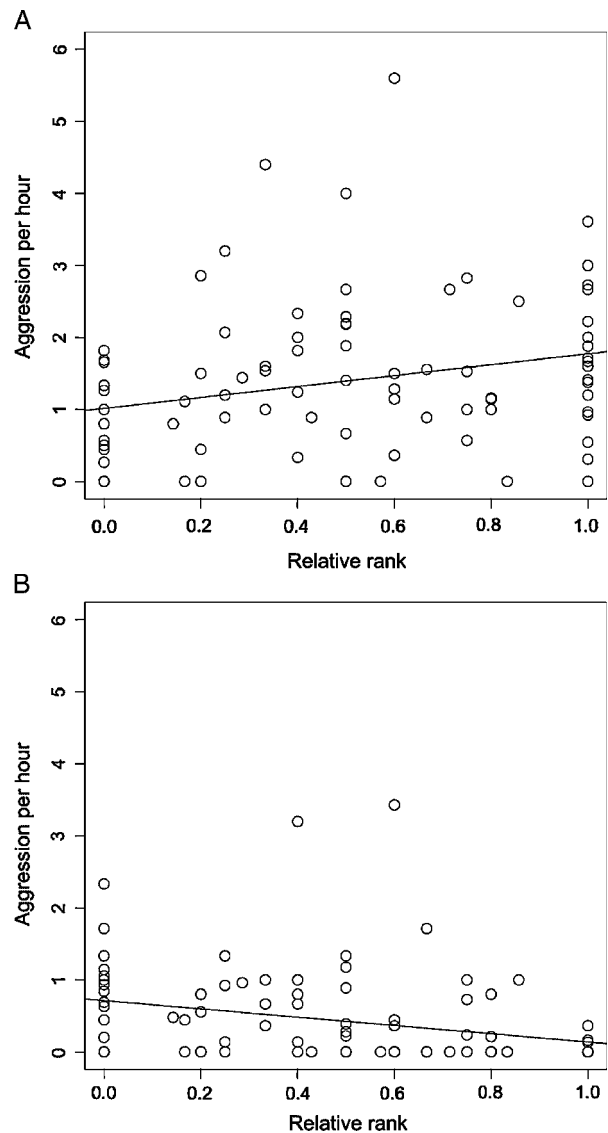

Fig. 2. The hourly rates of aggression (**A**) initiated and (**B**) received, by adult female geladas of different ranks (ranging from lowest rank, 0, to highest rank, 1). There is a weak, but significant, relationship between aggression initiated and rank, as well as aggression received and rank.

whether younger sisters always outrank older sisters ("youngest ascendancy" rule [Datta, 1988]). Genetic analyses are being conducted to confirm the nature of these relationships.

Dominance Rank and Aggression

With the exception of the lowest ranking female, all females within a unit were equally aggressive. Although a relationship emerged between dominance rank and aggressiveness with higher ranking females exhibiting more aggression (Fig. 2A, adjusted $R^2 = 0.057$; $P = 0.014$), this relationship disappeared when the lowest ranking female in each unit was removed from the analysis (adjusted $R^2 = -0.012$;

$P = 0.660$). Additionally, there was no sign of targeted aggression by alpha females. A paired t-test comparing aggression directed by alpha females toward the females adjacent to them in the hierarchy vs. the lowest ranking females, revealed no differences in rates of aggression ($t_{20.18} = -0.026$, $P = 0.980$). There was a correlation between dominance rank and aggression received (Fig. 2B, adjusted $R^2 = 0.091$; $P = 0.002$), but this relationship became nonsignificant when we excluded the alpha females in each unit (adjusted $R^2 = 0.012$; $P = 0.172$). Therefore, regardless of rank, all females initiated and received the same amount of aggression with two exceptions: the alpha females (who received very little aggression) and the lowest ranking females (who initiated very little aggression). In summary, with respect to aggression, there are similar costs to being both high and low ranking.

Dominance Rank and Reproductive Success

Across 191.5 female observation years on 61 females of known rank (mean = 3.14 ± 0.16 years per female; $N = 43$ females with 2.5 or more observation years), we found no relationship between dominance rank and reproductive success. First, we examined whether higher ranking females had shorter IBIs. For females that gave birth more than once ($N = 39$), the average IBI was 2.26 ± 0.08 years (range: 0.99–3.12 years). There was no relationship between rank and IBI (adjusted $R^2 = -0.023$; $P = 0.693$). Alpha females (IBI: 2.49 ± 0.11 years) did not have shorter IBIs than all females of other ranks combined (IBI: 2.26 ± 0.10 years; $t_{27.45} = -1.548$, $P = 0.133$), nor did the lowest ranking females have longer IBIs (2.53 ± 0.28 years) than all females of other ranks combined (IBI: 2.28 ± 0.08 years; $t_{5.91} = 0.841$, $P = 0.433$). However, our inability to detect a relationship between rank and IBI may be due to our small sample of females with complete IBIs. Therefore, we also examined the relationship between rank and fertility, which allowed us to include females with less than two births. Each of the 61 adult females gave birth to an average of 0.45 ± 0.03 infants per year (range: 0–3 infants per female). With this expanded data set, we still found no relationship between dominance rank and fertility rate (adjusted $R^2 = -0.013$; $P = 0.593$). Moreover, alpha females did not have significantly higher fertility rates (mean: 0.43 ± 0.07) compared with females of other ranks combined (mean: 0.46 ± 0.43; $t_{20.86} = -0.393$, $P = 0.698$), nor did the lowest ranked females in each unit have significantly lower fertility rates (0.45 ± 0.07) compared with females of other ranks combined (mean: 0.45 ± 0.03; $t_{18.39} = -0.019$, $P = 0.985$).

DISCUSSION

Data from this ongoing, long-term field study of geladas strengthen the evidence of the highly conserved nature of the Cercopithecine social system: the typical maternally inherited dominance structure [Altmann, 1980; Bernstein et al., 1993; Cheney & Seyfarth, 1985] is evident even in the exceptional case of geladas' multi-level society, and unusual habitat. Furthermore, the link between female philopatry and a stable dominance structure among females [di Fiore & Rendall, 1994; Silk, 1993] is also supported. We found no evidence of female dispersal. Although we could not unambiguously confirm any deaths, the mortality/disappearance rate of females in our study population (0.02–0.15 deaths/female/year) is comparable to the mortality rate of other Papionin baboons, such as chacma baboons, *P. ursinus* (0.04–0.16 deaths/female/year [Cheney et al., 2004]). All but two of the missing females were either severely ill or old enough to die of old age. We observed no migration of adult or juvenile females between units or bands, confirming earlier reports that very few females transfer between units [Dunbar, 1979; Dunbar & Dunbar, 1975; Ohsawa, 1979]. Although genetic data will be necessary to confirm gelada female philopatry (and maternally inherited dominance ranks), our observations of known mother–daughter pairs remaining together in the same unit, even after a fission, suggest that female geladas are philopatric.

Gelada females have a linear, maternally inherited dominance hierarchy typical of Cercopithecines, exhibiting a rank system that is stable across time and disruptive events, such as unit takeovers and fissions. Young females appear to inherit the rank just below that of their mothers, and contrary to Dunbar [1993], there is no age-based distribution of dominance in our study population—females of all ages occupy top, middle, and bottom ranks. The proportion of dominance acts that violated the hierarchy (3.0%) was higher in our gelada population than in other Cercopithecines (2.0% in vervet monkeys, *Chlorocebus aethiops* [Cheney et al., 1981]; 0.8% in olive baboons, *Papio anubis* [Smuts, 1985]; 1.2% in rhesus macaques, *Macaca mulatta* [Missakian, 1972]). These differences may simply result from different data collection procedures (and/or standard errors in such estimates) but they may also suggest that gelada hierarchies, although stable and linear, are less strict than those of other Old World monkeys. This could be a reflection of their food source—primarily, but not exclusively [Fashing et al., 2010], grass [Dunbar & Bose, 1991; Iwamoto, 1979]—which is evenly distributed and not defensible by any single, dominant female. If food competition is low, dominance hierarchies in geladas may be more tolerant than in other Cercopithecines [Garber, 1987].

In gelada society, characterized by low levels of aggression and maternally inherited ranks, the costs and benefits of high vs. low rank positions appear to be relatively equal. We found no signs of targeted harassment of low-ranking females, as previously

reported by Dunbar [1980b] for this population. Further, in contrast to earlier reports from the same population [Dunbar, 1980b], our results thus far suggest that females of all dominance ranks have equal reproductive success, at least in terms of IBI and fertility over a short period (4 years). Although our data set is admittedly limited at this time, it is nevertheless much larger than another data set that did find such a relationship [Dunbar, 1980b]. Although it is not unusual to find a weak or nonexistent relationship between reproductive success and female dominance rank in primates [Cheney et al., 2004; Silk, 1993], short-term relationships [e.g. Johnson, 2003] can often be outweighed by longer-term patterns [e.g. Cheney et al., 2004]. It is possible, therefore, that high rank can confer long-term reproductive advantages to females, such as allowing them to reach an earlier menarche, or have a longer reproductive tenure [e.g. Altmann et al., 1988]. Additionally, in geladas the arrival of a new leader male may have profound consequences for female reproduction. New leader males often kill the unweaned infants of unit females to hasten their return to fertility [Beehner & Bergman, 2008; Mori et al., 1997]. Since sexually selected infanticide is the leading cause of death for gelada infants [Beehner & Bergman, 2008], females with successful counter-strategies to infanticide are sure to gain a reproductive advantage. Across the nine takeovers described here, five suspected cases of infanticide occurred [Beehner & Bergman, unpublished data], but we have not yet found any rank-related advantage.

Our demographic and behavioral data suggest that gelada females fall within the general Cercopithecine pattern in terms of female philopatry and dominance relationships. These results, of course, raise the question of why geladas should maintain a dominance hierarchy at all—a hierarchy that holds few clear reproductive benefits for high-ranking females, at least in the short term. One possible explanation might be found in the geladas' recent natural history. Predators, such as spotted hyenas, leopards, and caracal, have declined greatly in number throughout Ethiopia and specifically the Simien Mountains [Hürni & Stiefel, 2003], and are therefore not a strong factor in current gelada mortality at this site [Dunbar, 1977, 1986]. However, historically predation may have been a much stronger shaping force in gelada socioecology [Dunbar, 1986; Jolly, 1972, cited in Iwamoto, 1993]; and in an extant gelada population living in a more predator-rich and harsh environment, males are known to attack predators [Iwamoto et al., 1996]. In other primate populations where predation is a strong selective agent, high female rank may confer advantages [e.g. van Noordwijk & van Schaik, 1999]. If dominant gelada females have privileged access to the leader male (as suggested by Dunbar [1983b, 1993], but questioned elsewhere [Dunbar, 1983a]),

they may therefore be better protected than more peripheral females. As our long-term data collection continues, we will continue to explore possible short-term (e.g. hormonal) and long-term (e.g. components of reproductive success) consequences of dominance rank in female geladas.

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