RESEARCH ARTICLE

Infant Mortality Following Male Takeovers in Wild Geladas

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Since Sugiyama's [1965] first observations of infanticide, empirical evidence from a multitude of primate species has supported the sexual selection hypothesis—the idea that males enhance their reproductive success by killing nonrelated, unweaned infants to hasten the mothers' return to fertility. Like other primates that live in social groups where paternity certainty is high, the social structure of geladas [Theropithecus gelada] suggests that infanticide by males could enhance their reproductive success. Nevertheless, empirical evidence for infanticide in this species is limited to anecdotal accounts. Using the timing of infant mortality and female reproductive and behavioral data collected across 26 months from a population of geladas living in the Simien Mountains National Park, Ethiopia, we test whether sexually selected infanticide occurs in this species. We also examine two additional hypotheses [noninfanticide hypothesis and generalized aggression hypothesis] for this population. Results suggest that sexually selected infanticide in geladas may, indeed, be a threat to females with dependent infants. First, male takeovers—the most likely time for infanticide—were associated with subsequently elevated rates of infant death [a 32-fold increase] comprising nearly 60% of all infant mortality. Second, females who lost infants during this period returned to fertility more quickly than if infants had lived [IBIs were 50% shorter], and third, all of these females were observed to mate with the new male. We found little to no support for other hypotheses. Finally, these results raise the possibility that anecdotal reports [from previous studies and this study] of pregnancy termination, accelerated weaning, and deceptive sexual swellings may represent female counterstrategies to male infanticide in geladas. Am. J. Primatol. 70:1152–1159, 2008. © 2008 Wiley-Liss, Inc.

INTRODUCTION

Following repeated observations of males killing infants in Hanuman langurs [Presbytis entellus], Sugiyama [1965] was the first to postulate a functional explanation for infanticide in primates. He proposed that males kill nonrelated, unweaned infants in order to hasten their mother's return to fertility. This idea, now known as sexually selected infanticide [Hrdy, 1974], has since been modeled into a formal hypothesis [the sexual selection hypothesis] with the following critical components: (1) infanticide is an evolved strategy that is not the result of atypical conditions or pathology, (2) the mother can be fertilized more quickly than if the infant had lived, (3) the male perpetrator is likely to sire subsequent infants with the mother, and (4) the male perpetrator is not related to the victim [reviewed in Hausfater & Hrdy, 1984; Hrdy, 1979]. Since Sugiyama's first account, empirical evidence from a multitude of primate species has offered support to this hypothesis [see Table 2.1 in van Schaik, 2000], fueling a theoretical debate that has continued since the sexual selection hypothesis was first conceptualized [reviewed in Sommer, 2000].

Additional explanations for infanticide have also been proposed and have received some support [reviewed in van Schaik, 2000]. Indeed, the most well-supported of these was proposed by Mohnot [1971], the second person after Sugiyama to report infant killing in primates. Mohnot proposes a mechanistic [rather than adaptive] explanation by

hypothesizing that infanticide is the result of redirected aggression exhibited by males in the context of male–male competition. A more recent version of this hypothesis, called the generalized aggression hypothesis [Bartlett et al., 1993], suggests that infanticide is merely a by-product of the elevated rates of aggression that usually accompany instability in the male dominance hierarchy or the arrival of a new male in the group. Under this hypothesis, male aggression should be directed at the mothers as much as the infants. It is important to point out, however, that owing to their different levels of explanation [proximate vs. ultimate], the sexual selection and generalized aggression hypotheses are not mutually exclusive hypotheses.

Receiving little support from wild populations, and related to the generalized aggression hypothesis, is the social pathology hypothesis [summarized in Boggess, 1979; Dolhinow, 1977], which proposes that infant killing results from atypical conditions that provoke pathological behavior such as overcrowding, captivity, or provisioning. Under this hypothesis, males [or females] kill infants because they are pathological, and as such, infanticide occurring under such circumstances has no functional explanation.

For any species where infant killing is observed, it is important for researchers to test different explanations for such behavior. An explanation for infanticide is necessary for understanding not only possible reproductive strategies of males, but also those of females. For example, in species where sexually selected infanticide occurs, we might expect females to exhibit adaptive counterstrategies, either to spare their infant from an infanticidal attack [e.g. Colmenares & Gomendio, 1988; accelerated weaning, Rowell, 1978; ''deceptive'' sexual swellings, Zinner & Deschner, 2000], or to off-set the costs of an inevitable infanticide [e.g. induced abortion, Bruce, 1960; Stehn & Richmond, 1975]. In the following study, we examine data from a population of wild geladas [*Theropithecus gelada*], a primate for which both infanticide and female counterstrategies have been reported to occur, but only anecdotally.

The reproductive unit of geladas [the one-male unit] comprises a single reproductive male [leader male], several adult females, their offspring, and possibly one or more follower males [generally former unit leaders or young adult males, but without reproductive access to females; Dunbar 1984]. Often many one-male units will travel and forage together throughout the day in a cohesive group [the band]. Threats to a leader male's reproductive tenure come from young ''bachelor'' males who roam around together in all-male groups. Following a successful challenge, a bachelor male takes over the unit, and thus gains sole reproductive access to females within the unit [hereafter, ''takeover'']. Thus, geladas resemble many other primates that live in social groups where paternity certainty is

high [reviewed in Janson & van Schaik, 2000; Pradhan & van Schaik, 2008], suggesting that infanticide by males could enhance reproductive success. Furthermore, like baboons, geladas are nonseasonal breeders, and the period between the birth of one infant and the next conception is prolonged compared to *Papio* baboons [approximately 2 years, $N = 25$; Beehner & Bergman, unpublished data]. Moreover, this period is substantially reduced if a female loses her infant prior to weaning [Dunbar, 1980; Mori & Dunbar, 1985; and see data below]. Therefore, if a new leader male's reproductive success is contingent upon unit females returning to a fertile state, a male taking over a unit with nonrelated, dependent infants could benefit from infanticide.

However, empirical evidence for the occurrence of infanticide in geladas is limited. Most data on wild geladas derive from a population in the Simien Mountains National Park. Across several study periods between 1971–1976, Mori and Dunbar [1985] did not observe a single case of suspected or confirmed infanticide for geladas living in the Gich and Sankaber areas of the park. Mori and Dunbar [1985] proposed that infanticide may not benefit new leader males because most lactating females [with the exception of early lactation] resume cycling immediately following male takeovers [e.g. Rowell, 1972, 1978], effectively removing the main functional explanation for infanticide [Dunbar, 1984]. By contrast, anecdotal evidence from several captive and one wild population in the Arsi region of Ethiopia [Angst & Thommen, 1977; Moos et al., 1985; Mori et al., 1997, 2003] indicates that adult males do occasionally injure or kill infants in the context of unit takeovers. Although infant deaths occurring in the context of unit takeovers suggest a sexually selected strategy, any or all of these deaths could also be explained by the social pathology or generalized aggression hypotheses. The captive infanticides [$N = 4$; Angst & Thommen, 1977; Moos et al., 1985] might have been the by-product of captive [and possibly pathological] behavior, and the cases observed in the wild might have resulted from the aggression following a recent takeover where leadership had not yet been established [$N = 1$; Mori et al., 1997] or from human provisioning and capture [$N = 2$; Mori et al., 2003].

Here we report additional infant mortality data from wild geladas collected across more than 2 years from the same population studied by Dunbar [1984]. We test the following hypotheses regarding the pattern and timing of infant mortality: (1) Non-infanticide hypothesis—if infant mortality is unrelated to a male reproductive strategy, then we predict that infant deaths will occur at random with respect to male takeovers. (2) Generalized aggression hypothesis—if infant mortality is merely a by-product of excess male aggression, then we expect

that infant deaths will be disproportionately associated with takeovers [when aggression is high] and that infants will die/disappear at the time of the takeover. We also expect to see injuries to other animals [particularly females] at this time. (3) Sexual selection hypothesis—if infant mortality is the result of an adaptive male reproductive strategy, then we predict that (a) the new male will not be related to infants that die/disappear, (b) elevated rates of infant mortality will primarily occur *after* a successful takeover by the new male, (c) females whose infants die/disappear will resume estrus cycling more quickly than they would otherwise, and (d) the new male will sire subsequent infants with these females. Hypotheses 1 and 3 are mutually exclusive, whereas hypotheses 2 and 3 could represent a proximate and ultimate explanation for the same phenomenon. Therefore, distinguishing between these two hypotheses depends primarily on the timing of the infant deaths/disappearances and whether most of them occur at the time of the takeover or afterwards.

METHODS

Study Site and Subjects

The data for this study come from a population of wild geladas living in the Michiby and Chilquanit areas of the Simien Mountains National Park, Ethiopia. Data analyzed for this study comprise a 26-month period from January 2006 to March 2008. We selected 18 one-male units across two different bands as target units for this study. Target units in one band [$N = 15$] were observed almost every day, and target units in the other band [$N = 3$] were observed at least once every 5 days. Subjects included 28 leader males, 13 follower males, 117 mature females [i.e. exhibiting sexual swellings], and 130 infants. Data collection relevant for this study included (1) a census of all target animals, (2) the identity of the leader male, (3) the reproductive status of all mature females [cycling, pregnant, or lactating], (4) observed copulations, (5) the presence or absence of dependent infants, and (6) births of new infants. This research was approved by the University Committee on Use and Care of Animals [UCUCA] at the University of Michigan and adhered to the laws and guidelines of Ethiopia.

Infant Ages and Interbirth Intervals

Of the 130 dependent infants in this study, 70 were born after the study began and thus have a known date of birth [DOB]. The other 60 infants were born earlier to the start of the study and, thus, have estimated DOBs. DOBs for infants were estimated based on a combination of photographs of gelada infants with known ages in this population and published descriptions of known ages of gelada

infants [Dunbar & Dunbar, 1975]. Characteristics used to estimate infant ages include coat and muzzle color, overall size, and overall physical development and coordination. Estimated ages are more easily assigned to younger infants and likely to be more accurate. Thus, for three very young infants we were able to estimate the DOB to within 1 month; for five infants we were able to estimate the DOB to within 2 months; and for nine infants we were able to estimate the DOB to within 3 months. For the rest of the infants [$N = 43$] we estimated DOBs to within 6 months. Two sets of age determinations [by each author] were made independently based on the same criteria, and both sets were in agreement. Ten dependent infants were removed from the data set because they were considered too old to be at risk of infanticide [see Results]. Thus, the sample size for analyses was 120 infants.

For interbirth interval [IBI] analyses, our subjects comprised 30 females that gave birth during the study period. Of these, 25 IBIs were used to calculate the mean IBI for this population [including all successfully weaned infants and all nontakeover related infant deaths, cf. Bartlett et al., 1993]. Five IBIs were used to calculate the mean IBI for females with takeover-related infant deaths. For comparison, we also calculated the mean IBI for this population excluding [$N = 24$] and including [$n = 30$] all infant deaths. The mid-point of the estimated DOB range was used to calculate IBIs.

Unit Takeovers

Successful unit takeovers can take up to several days from start to finish, and generally we were able to observe part or all of each unit takeover. At the time of takeover, we noted any associated injuries or deaths. We continued to monitor the unit closely [daily, if possible] during the weeks and months afterwards to note any infant deaths/disappearances. Based on our demographic records, we are confident that we were able to record all infant deaths/ disappearances. As dependent [or recently weaned] infants are unlikely to survive outside their natal unit, we will subsequently refer to all infant disappearances as "deaths."

Data Analysis

Because a female's IBI increases as the age of infant death increases, there is an age beyond which IBIs are no longer accelerated by infant death. Therefore, first we determined which infants in our data set were vulnerable to sexually selected infanticide [as per Crockett & Sekulic, 1984; van Schaik, 2000]. Following this analysis, we conservatively modified our infant sample size to $N = 120$.

Second, we compared overall infant mortality rates for this population with infant mortality rates during the period following a unit takeovers.

Research in other primate species has indicated that the risk of infanticide is highest within a few months of male status changes [Beehner et al., 2005; Crockett & Sekulic, 1984; Sommer, 1994]. Therefore, we define the period within which we would expect elevated rates of infanticide [provided infant ages did not exceed the threshold age] as the 4 months following a successful takeover. Using a binomial test, we calculated whether rates of infant mortality were higher than expected by chance during this period.

Third, we used a Mann–Whitney U test to compare whether the IBIs for females with takeover-related infant deaths were shorter than the IBI's for all other females. All statistical tests were conducted using SPSS [16.0] and the statistical threshold was set at $P = 0.05$.

RESULTS

Observed Infanticide

One infanticide was directly observed during the study period. The infant was not a member of a target unit [and thus not included in the 14 infant deaths reported below]. However, because the event was recorded as part of a separate study on bachelor males, we were able to identify the aggressor. During an attempted takeover, one author [J.C.B.] observed the bachelor male grab a very young infant in his mouth, shake it briefly, and drop it as he ran away. The infant was dead by the time the mother and leader male arrived. Although this case of infanticide was not included in any of the analyses below, it nevertheless confirms that males do kill infants in this population.

Determining Infants at Risk for Infanticide

IBI length was a function of infant survival, such that the younger an infant died, the shorter the subsequent IBI [Fig. 1; $R^2 = 0.89$, $N = 7$, $P < 0.05$; $y = 0.07\,x + 0.92$]. Based on this regression line and the mean IBI for this population [2.49 y, see below], the age at which infanticide would no longer be adaptive is 1.86 y. To account for potential error introduced by the large percentage of estimated ages among older infants, we conservatively reduced this estimate [by 6 mos] to the age of 1.26 y. Thus, only infants under this age were considered "vulnerable" to infanticide and included in subsequent analyses.

Unit Takeovers

Across the study period, we recorded 11 successful unit takeovers, for a breeding male replacement rate of 0.30 replacements/male/year [see Janson & van Schaik, 2000, p. 478, for how this rate is calculated]. Of these takeovers, three occurred in units with no dependent infants. Of the eight unit
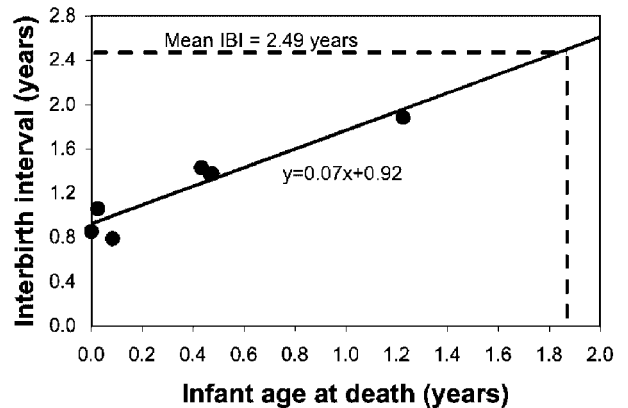

Fig. 1. Linear regression between infant age at death and the subsequent interbirth interval of its mother. Each point represents one female interbirth interval.

TABLE I. One Male Units With Takeovers and Subsequent Infant Deaths

Unit taken over	Infants in unit at takeover	Dead infants after takeover	Possible infanticide?
SAW	0	N/A	N/A
USA	0	N/A	N/A
WAY	0	N/A	N/A
LEB	1	0	no
FUJ	5	0	no
YAH	1	1	yes
ROY	1	1	yes
FRA	1	1	yes
IRA	1	1	yes
NIK	3	2	yes
ZEU	3	2	yes

takeovers with dependent infants present, two takeovers were associated with no infant deaths, and six takeovers were associated with at least one infant death [Table I]. Of the total number of infants in units following takeovers [$N = 16$], eight of them died during the 4 months following the takeover. For takeovers associated with more than one infant death [$N = 2$], both deaths occurred in the same week [Table II].

We did not observe any of the following associated with a takeover-related infant death: (1) cannibalism of the dead infant by the male, (2) injuries to the new leader male after the infant's death, (3) injuries to the mother of the dead infant [or any other females, follower males, or juveniles].

Infant Mortality

Of 120 total infants, we recorded 14 infant deaths across the study [infant mortality = 5.4% per y]. Six of these deaths occurred outside the context of a unit takeover: five with the disappearance [and

TABLE II. All Infant Deaths in Target Units Across 26 months

Infant's mother	Infant age at death (mos)	Time from takeover to death (mos)	Cause of death
WIL	0.3	0.10	Possible infanticide
HOP	1.0	0.13	Possible infanticide
HES	1.7	0.49	Possible infanticide
HER	1.8	0.49	Possible infanticide
AXU	4.1	3.00	Possible infanticide
ZAY	5.6	0.26	Possible infanticide
ZIO	5.7	0.26	Possible infanticide
BRY	7.2	2.80	Possible infanticide
APP	0.9	N/A	Mother's disappearance
LIP	6.2	N/A	Mother's disappearance
ALI	9.4	N/A	Mother's disappearance
LIM	14.7	N/A	Mother's disappearance
CEL	15.1	N/A	Mother's disappearance
PEN	15.2	N/A	Unknown

likely death, see Discussion] of the mother. The other cause of death remains unknown.

Eight of the 14 infant deaths [57.17%] occurred during the period after a successful unit takeover [Table II]. Infants were 32 times more likely to die following unit takeovers than they were at other times. Based on the rate of infant mortality during nontakeover periods, this rate is significantly higher than expected by chance [Binomial Test: $P < 0.01$].

We recorded one stillbirth across the study period. Notably, the stillbirth occurred 1 week after a successful takeover. Close observation of the dead infant indicated that it was not fully developed. Based on records of this female's previous sexual swellings, we estimate that the infant was born 2 months prematurely. Nevertheless, because the death occurred during the period of gestation [i.e., a miscarriage and not an infanticide], we do not include it in any of our analyses.

Subsequent Mating

In all eight cases of infant death following takeovers, the females resumed cycling within 1 month, and the new leader male was observed to copulate with the female whose infant died.

Interbirth Intervals

Interbirth intervals were significantly shorter for females whose infants died following takeovers as compared with the mean IBI for the population [Mann–Whitney U Test: $Z = -3.47$, $P < 0.001$, Fig. 2]. The population mean IBI [excluding only takeover-related deaths] was 2.40 y [$N = 25$, range 1.6–3.0 y], whereas the mean IBI for females that had their previous infant die following a takeover was 1.20 y [$N = 5$], a reduction of 50%. For comparison, the population mean IBI excluding all infant deaths was 2.47 y [$N = 24$] and including all infant deaths was 2.22 y [$N = 30$].
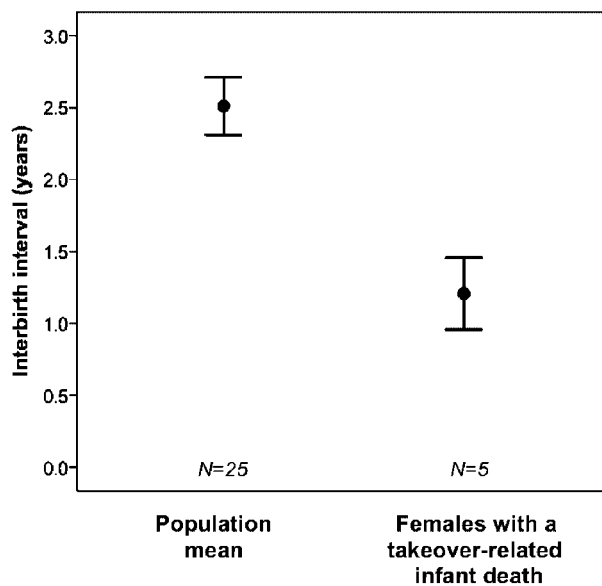

Fig. 2. Mean interbirth interval ($\pm$SEM) for all females in the population (including females with nontakeover related deaths) compared with the mean interbirth interval for females with takeover-related infant deaths (possible infanticides).

DISCUSSION

Noninfanticide Hypothesis

In this gelada population, infant mortality, extremely low across most of the year, was significantly higher than expected by chance during the 4 months after a new male took possession of a one-male unit. The nonrandom distribution of infant deaths indicates that infant mortality occurred disproportionately in conjunction with male takeovers; and therefore, the noninfanticide hypothesis is an unlikely explanation for these infant deaths.

Generalized Aggression Hypothesis

We observed one case of infanticide *during* an attempted takeover. The infanticidal male killed the

infant during his [failed] attempt at gaining control over the unit. Because this male was not successful at taking over the unit, he did not mate with the female afterwards. This observation offers some support to the generalized aggression hypothesis, in that an infant was killed during the aggression surrounding the takeover itself, but the male was not able to secure any reproductive advantage as a result. However, this explanation does not necessarily run contrary to the sexual selection hypothesis. Had the male successfully taken over the unit, he would, indeed, have mated with the mother of the dead infant. This difference underscores the importance of distinguishing between different levels of explanation [Tinbergen, 1963]. In other words, though generalized aggression associated with takeovers might be a mechanism for infant killing, this does not preclude sexually selected infanticide as an ultimate explanation.

Moreover, other results from this study are incompatible with the generalized aggression hypothesis. In all other cases of takeover-related infant mortality [$N = 8$], deaths occurred at least a few days after the takeover when levels of aggression were low. Additionally, the nontakeover infant deaths [$N = 6$] were unlikely to have resulted from unobserved "failed" takeovers, because five of these infant deaths were in conjunction with the mother's death. Prior to these females' deaths, they all had clear signs of an infection resulting from a ruptured parasitic growth [probably *Multiceps serialis*; see Ohsawa, 1979, p. 38 for details on this parasite]. The other case of infant death was recorded at the time of weaning, with no other signs of an attempted takeover [e.g. injuries to the leader male] in this unit. Consequently, the aggression associated with takeovers is probably not a major source of infant mortality in this population.

Sexual Selection Hypothesis

The majority of infant mortality in this population was consistent with the sexual selection hypothesis. First, infant mortality was significantly higher than expected by chance during the 4 months following a takeover. Although unit takeovers themselves can take several days to occur, the end of the takeover period is clearly marked by the end of regular contact-aggression between the males. The former leader male relinquishes sexual access to sexually receptive unit females, and the new leader male assumes reproductive control. All subsequent aggression between the former and current leader male is characterized by clear submissive behaviors by the former leader [e.g. screaming, pulled back lip, crouching] and is generally in the context of defending lactating females and their offspring [Beehner & Bergman, unpublished data]. Indeed, the role of the follower male as infant protector [or

female "friend," Palombit et al., 1997] has yet to be systematically studied in geladas, and previous studies on this population report that old follower males are extremely protective of infants and "are prepared to take on quite extraordinary odds in their defense" [Dunbar, 1984, p. 208].

Second, females whose infants died following takeovers, had significantly shorter IBIs than the mean IBI for the population. Indeed, the death of an infant halved the time until a female's next infant. This is consistent with many primate studies where IBIs were calculated for females who lost infants to infanticide compared with the population mean [e.g. Borries, 1997; Crockett & Sekulic, 1984; Sommer, 1994; Struhsaker & Leland, 1985]. Currently, we do not have data on IBIs for females whose offspring died at an age above the threshold expected under the sexual selection hypothesis [all infants who fit this profile were not members of units with takeovers]. Therefore, we currently cannot address the question of whether there are instances in which infant deaths do not accelerate a female's return to fertility. However, we can say that all infants that *did* die during the post-takeover period were well below this threshold age.

Third, in all cases, the new leader males were the only males later observed to mate with the mothers following the death of their infant. All females resumed cycling within a month and were sexually receptive to the new leader male. Given the relatively closed reproductive unit, it is highly probable that the new leader sired (or will sire) these females' subsequent offspring. Although at this time we are not able to confirm paternity with genetic data, extra-unit paternity [or follower-male paternity] in geladas is thought to be extremely low [Mori, 1979].

Finally, although we currently do not have genetic data on relatedness, we think it highly unlikely that new leader males were closely related to any of the infants that died. The conserved pattern among Old World monkeys is for males to disperse from their natal group to join individuals unrelated to themselves [di Fiore & Rendall, 1994]. It would be extremely surprising if a bachelor male took over a one-male unit containing his close relatives—particularly given the thousands of animals he has to choose from. Even if mechanisms promoting kin recognition were discounted, statistically this outcome is unlikely to occur. Nevertheless, we acknowledge that at the present time, we cannot reject this possibility.

In sum, sexually selected infanticide appears to be an adaptive strategy for new leader males in this population. However, new leader males of larger units might have more to gain from infanticide than males of smaller units—mainly because these males generally have shorter reproductive tenures. For example, our largest one-male unit [with 12 adult

females] was taken over three times across the study period for an average reproductive tenure of 1.02 y/male [this tenure length is *not* thought to be representative for this population, only for this unusually large unit]. The observation that larger units have higher rates of takeover than smaller units was also reported by Dunbar [1984] for this same population [see also Crockett & Janson, 2000]. We are continuing to collect data to examine alternative male reproductive strategies and how infanticide might relate to male tenure length, as well as additional variables such as the number of females in the unit and the ratio of cycling to noncycling females.

Our results conflict with observations by Mori and Dunbar [1985] on this same population. Across several observation periods between 1973 and 1976, Mori and Dunbar observed no cases of infanticide. They did, however, find that females with infants between 6–24 months of age returned to a fertile state much sooner than expected after a takeover. Furthermore, they recorded the occurrence of spontaneous abortions following takeovers [we also observed at least one miscarriage following a takeover], and these females subsequently resumed cycling and mated with the new male. Thus, although no infanticides occurred during their study period, they report incidences of behavior consistent with two counterstrategies to infanticide: the accelerated weaning of offspring [Colmenares & Gomendio, 1988; see also Rowell, 1978;], and spontaneous abortion following the arrival of a new male [Colmenares & Gomendio, 1988; see also Pereira 1983]. Despite accounts of spontaneous abortions in the wake of recent takeovers for baboons and geladas, spontaneous abortion is generally thought to be rare among female primates [van Schaik et al., 1999], owing to the high cost to females. Although we lack data on the fitness costs and benefits to individual females, we nevertheless hypothesize that accelerated weaning and spontaneous abortion could be important counterstrategies to male infanticide under certain conditions.

Combined with data from this study, sexually selected infanticide is likely a threat to females with dependent infants in this population. In fact, our preliminary data on possible gelada infanticide [comprising nearly 60% of infant mortality in our target units] is comparable to data from other species where sexually selected infanticide has been reported to occur [e.g. Cheney et al., 2004]. Based on previous reports in geladas [as well as observational data from this study], we suspect that female geladas have additional counterstrategies to infanticide, including the formation of defensive alliances [e.g. Smuts & Smuts, 1993] the development of deceptive sexual swellings [Zinner & Deschner, 2000], and the display of false sexual receptivity [Cords, 1984; Hrdy, 1974, 1977]. Recall that Mori and Dunbar [1985] reported

that lactating females often developed sexual swellings following a takeover. However, without simultaneous hormonal data, it is difficult to ascertain whether these sexual swellings represent a true return to fertility or rather a false fertility as reported for hamadryas baboons [Zinner & Deschner, 2000] and long-tailed macaques [Engelhardt et al., 2007]. We have recently initiated the collection of behavioral and hormonal data from females to address these possible counterstrategies to infanticide.

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