

O brother, where art thou? The varying influence of older siblings in rank acquisition by female baboons

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Received: 9 March 2009 / Revised: 16 June 2009 / Accepted: 28 June 2009 / Published online: 25 July 2009
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Abstract Males in sexually dimorphic species like baboons appear to have surprisingly little influence on the reproduction and dominance ranks of their female kin, even though they could potentially increase their fitness by helping their relatives improve their ranks. Male baboons are able to dominate females several years before they emigrate, but their presence has no effect on relatives' dominance ranks, at least when female kin are present. As a result, females usually acquire ranks within their matriline, above their older sisters. We describe the process of rank acquisition among orphaned and non-orphaned juvenile and adolescent females in a group of free-ranging baboons. Orphaned females were significantly more likely than non-orphaned females to acquire unexpected ranks. Orphaned females with older sisters often acquired ranks within the matriline, but below their older sisters'. Orphaned females with older brothers were likely to rise in rank above their matriline. Females' interventions on behalf of younger sisters always supported the existing female dominance hierarchy, while males' interventions tended to act against it. Similarly, in playback experiments, females appeared to be willing to support their younger sister only in disputes

with lower-ranking females. In contrast, males appeared to be willing to support their sister even in disputes with higher-ranking females. Fraternal support enables females to improve their dominance ranks, but only if their mothers have died. It remains a puzzle why males have so little influence on their female relatives' ranks when female kin are present, and so much when they are absent.

Keywords Baboon · Rank acquisition · Brothers · Sisters · Orphans · Male investment in kin

Introduction

Cooperation among male genetic relatives occurs in a large variety of animal mating systems, including lekking species (e.g., peacocks, *Pavo cristatus*: Petrie et al. 1999; turkeys, *Meleagris gallopavo*: Krakauer 2005), cooperatively breeding species (e.g., golden lion tamarins, *Leontopithecus rosalia*: Bales et al. 2006; wild dogs, *Lycaon pictus*: Girman et al. 1997), and some polygynandrous species (e.g., lions, *Panthera leo*: Packer et al. 1991; cheetah, *Acinonyx jubatus*: Caro 1994; rhesus macaques, *Macaca mulatta*: Meikle and Vessey 1981; chimpanzees, *Pan troglodytes*: Langergraber et al. 2007). In contrast, there is very little evidence that males ever enhance the fitness of female kin. This may occur in part because sex-biased dispersal usually provides males with little opportunity to interact with female kin after adolescence. It remains puzzling, however, that males appear not to exert an influence on their mothers' or sisters' reproductive success prior to dispersal. This is especially true of highly dimorphic primate species like baboons (*Papio hamadryas* spp.), where males begin to outrank females several years before they emigrate.

Communicated by S. Alberts

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Female cercopithecine primates live in very conservative societies in which daughters “inherit” dominance ranks similar to their mothers’, largely as a result of interventions from both kin and non-kin that support the existing dominance hierarchy (e.g., Japanese macaques, *M. fuscata*: Chapais et al. 1991; vervet monkeys, *Chlorocebus aethiops*: Cheney and Seyfarth 1990; baboons: Walters 1980, Pereira 1988, 1989; Silk et al. 1999, 2006a, b; reviewed by Walters and Seyfarth 1987; Chapais 1992; Silk 2002). As a rule, daughters attain ranks above all adult females whom their mothers dominate and below all females who dominate their mothers; within the family, younger sisters usually outrank older sisters (e.g., Japanese macaques: Kawai 1958; Kawamura 1958; Koyama 1967; Hill and Okayasu 1996; rhesus macaques: Datta 1988). This creates a system in which each matriline can be ranked relative to others, and individual ranks within a matriline are based on birth order. Rank changes across matriline are aggressively resisted by higher-ranking females, with the result that females rarely acquire ranks that are not contiguous with the rest of their matriline (e.g., baboons: Samuels et al. 1987; Cheney and Seyfarth 2007). This resistance may be related to the fitness benefits associated with high dominance rank. Although reproductive skew is relatively low, high-ranking females typically enjoy some reproductive advantages over lower-ranking ones (e.g., Japanese macaques: Sugiyama and Ohsawa 1982; baboons: Barton and Whiten 1993; Altmann et al. 1988; Altmann and Alberts 2003; Wasser et al. 2004; reviewed by Silk 2002; Cheney et al. 2004).

The regularity of maternal rank acquisition suggests that males play little role in the process. This is somewhat surprising because males could have an important impact on the outcome of contests among females, particularly in the case of baboons. Regardless of their mother’s status, male baboons outrank females by around 5 years of age, several years before they emigrate (Pereira 1988; Cheney et al. 2004; Cheney and Seyfarth unpublished). Young males therefore have the opportunity to support their female kin in disputes involving the members of higher-ranking matriline. The negligible role played by males in female rank acquisition is puzzling because it would seem to be in the interests of a male’s inclusive fitness that his female kin attain higher ranks.

A related question is what happens to a female’s rank when kin support is absent entirely or when her only close relatives are males. Experimental and observational studies of Japanese macaques (Chapais 1988a, b), vervet monkeys (Cheney and Seyfarth 1990), and baboons (Johnson 1987) indicate that females often fall in rank to previously subordinate matriline when they are deprived of the support of female kin, but this is not always the case (rhesus macaques: Sade 1972; Japanese macaques: Mori et al. 1989; Kutsukake 2000).

In this paper, we examine the influence of male kin, female kin, and the absence of kin on the acquisition of female rank in a group of wild chacma baboons (*Papio hamadryas ursinus*). We first examine whether orphans are less likely than non-orphans to acquire their expected ranks and describe how the presence of mothers, sisters, and brothers affects rank acquisition within and between matriline. We next appraise the type and rate of interventions received by young females in the process of attaining their ranks. Finally, we compare the behavior of male and female siblings in playback experiments in which we simulated attacks on their younger sister.

Methods

Study site and subjects

The behavioral study was conducted in the Moremi Game Reserve, in the Okavango Delta of Botswana during 2003 and 2004, supplemented by long-term demographic data from 1992 to 2007 (for a description, see Cheney et al. 2004; Cheney and Seyfarth 2007). The study group contained approximately 70 individuals, including an average of nine adult males, 23 adult females, and 17 juvenile and adolescent females (ten non-orphans and seven orphans). All animals were fully habituated to human observers on foot, and maternal relatedness for all natal animals was known. For ease of discussion, “brothers” and “sisters” refer to maternal siblings.

Female baboons at this site reach menarche at around 5 years of age and give birth at a mean of 6.8 years (Cheney et al. 2004). They begin to establish their adult ranks as juveniles and usually have fully established ranks by the time they first give birth (Hausfater et al. 1982; Pereira 1989; Cheney and Seyfarth unpublished data). Males begin to outrank most females by around 5 years of age and enter the adult male hierarchy at around 8 years (Altmann and Alberts 1987, 2005; Kitchen et al. 2003; Beehner et al. 2006; Cheney and Seyfarth unpublished). Most males disperse between 9 and 11 years (Alberts and Altmann 1995; Cheney et al. 2004), though a small number remain in their natal groups throughout their lives. Adult male baboons are approximately twice as heavy as females (Altmann and Alberts 2003).

Calculating expected rank

Dominance ranks were determined by the direction of approach–retreat interactions (Silk et al. 1999). Forty females born between January 1989 and December 2002 achieved a rank within the adult female hierarchy. A female gained her expected rank if by age 6 she had: (1) attained a

rank immediately above any older sisters; (2) or, if she had no sisters, attained a rank adjacent to that of her mother; (3) or, if her mother was dead, attained her mother's former position. This method is conservative in that it counts each unexpected rank only once. For example, the youngest sister in the alpha matriline failed to outrank one of her older sisters. Although her older sister "incorrectly" inherited the alpha position, we considered only the younger sister as having failed to attain her expected rank since the elder sister had successfully outranked her older sister at age 6.

We divided all females who did not attain their expected ranks into two categories. Females in the *within*-matriline category acquired ranks within their matriline but failed to outrank their older sisters. Females in the *outside-of*-matriline category acquired ranks above or below their matriline's rank, not contiguous with the ranks of any female kin. Several females changed ranks well after they had established their adult ranks (Engh et al. 2006). We do not consider these late rank changes here.

Logistic regression

To assess which characteristics were most important in determining whether a female attained her expected rank, we used three predictors in a stepwise logistic regression: orphan status (orphaned before 4 years of age, yes/no), presence of brothers (yes/no), and presence of sisters (yes/no). Older brothers and sisters were counted as present if they lived in the group at any time when the female was between 4 and 6 years of age. This age range was chosen because previous research has indicated that all females have begun to establish their adult ranks by the age of 4 (although many do so before this age; Hausfater et al. 1982); adult ranks have usually stabilized by the time females give birth between 6 and 7 years of age (Cheney and Seyfarth unpublished data). We selected our final model using SPSS's (v. 16.0) backward selection procedure based on the likelihood statistic with p to remove set at 0.10. Because rank acquisition appeared to be fundamentally different for females who gained unexpected ranks outside of their matrilines as opposed to within their matrilines, we tested the model using each as a dependent variable.

Interventions

Interventions occurred when an individual supported a juvenile or adolescent female who was involved in an aggressive interaction by threatening the female's opponent. Threats included eye threats, head bobs, lunges, chases, and bites. Interventions in which the coalition partner helped the female to threaten a member of a lower-ranking matriline were scored as ones that supported the female dominance

hierarchy. Interventions in which the coalition partner defended the female against aggression from a member of a higher-ranking matriline were scored as acting against the dominance hierarchy.

Intervention rates were calculated from focal animal observations (Altmann 1974). To increase sample size for our analysis of intervention patterns, we supplemented focal data with ad libitum observations.

Playback experiments

To test whether older brothers and sisters responded differently when their younger sister was threatened, we designed a playback experiment in which an adult female appeared to be giving threat-grunts to the younger sister while the younger sister screamed. In paired trials, each older sibling heard one of two call sequences: one in which the younger sister's screams were combined with the threat-grunts of a female from a higher-ranking matriline, to mimic a dispute that supported the dominance hierarchy, and one in which her screams were combined with the threat-grunts of a female from a lower-ranking matriline, to mimic a dispute that acted against the hierarchy. After each playback, the older sibling was observed for 10 min to determine whether she/he subsequently approached the speaker. Subjects included all of the older siblings of female juveniles in the group: six brothers and six sisters.

All threat-grunts and screams used as stimuli had been recorded within the previous year using Sennheiser ME88 microphones and Sony Walkman Pro cassette recorders. Calls were digitized and analyzed using Cool Edit software (Syntrillium, Phoenix, AZ, USA) to ensure that all were of similar duration (3 to 4 s) and had similar call bout characteristics, including call rate and intercall intervals. Each sequence was designed to mimic naturally occurring bouts of threat-grunts and screams and consisted of one threat-grunt followed by one scream, then two threat-grunts followed by two screams. Playback sequences were similar in amplitude, matching the amplitude of naturally occurring calls. To avoid the possibility that some screams might be more salient or of greater intensity than others, the same scream sequence was played to a given subject in each of the two conditions, creating a matched-pair experimental design. In each pair of trials, the rank distance between each threatening female and the screaming sister was similar. All younger sisters present in the group appeared as "screamers" (age range 23 to 63 months).

Call sequences were played from a Bose Roommate II speaker concealed in vegetation approximately 5 m from the subject. Trials were initiated when the older sibling was out of sight of the individuals whose calls were being played and either sitting or feeding with its face oriented at a 90–135° angle from the speaker. We used a Sony DCR-

Table 1 Dominance rank attainment by females orphaned before 48 months

	No siblings	Sister	Brother	Both
Achieve expected rank	3	1	0	1
Achieve unexpected outside matriline	2 (below)	0	3 (above)	1 (above)
Achieve unexpected within matriline	NA	2 (below)	0	1 (below)

TRV25 digital video camera to record subjects' orientation responses relative to the speaker immediately before and after the playback. Films were analyzed using Ulead 5.0 (Ulead Systems) software. No individual was the subject of more than one playback per week, and a maximum of one playback occurred each day.

Two dependent variables were scored in the video analysis: duration of looking toward the speaker in the first 10 s after call onset and latency to move more than 2 m toward the speaker. The former variable was assumed to measure a subject's interest in a dispute, the latter variable its willingness to intervene. We considered subjects to be looking toward the speaker as soon as they moved their heads in the direction of the speaker ($\pm 30^\circ$).

Results

Demographic data

Females who were orphaned before the age of 4 were significantly less likely to achieve their expected ranks than were non-orphaned (Fisher's exact test: $N=40$, two-tailed, $p=0.003551$). Nine (64%) of the 14 females orphaned before the age of 48 months attained unexpected ranks (Table 1). Six of these nine females acquired a rank outside of their matriline—two below their matriline and four above their matriline. The two orphans who fell below their matriline had no siblings. All of the four orphans who rose in rank above their matriline had older brothers.

In contrast, only three (12%) of the 26 females whose mothers were still alive at 48 months achieved unexpected ranks, and in all cases these unexpected ranks were within their own matrilines (Table 2).

Because the processes underlying rank changes within and outside of matrilines appeared to be fundamentally different, we modeled these two types of rank changes separately, using the presence of brothers, the presence of sisters, and orphan

status as predictor variables (outside matrilines: 80% correct, $\chi^2=19.133$, $df=2$, $p<0.001$, Nagelkerke $R^2=0.507$; within matrilines: 65% correct, $\chi^2=8.733$, $df=2$, $p<0.013$, Nagelkerke $R^2=0.262$).

In the stepwise regression predicting rank changes outside of the matriline, orphan status (Wald=11.218, $df=1$, $p=0.001$) and the presence of older brothers (Wald = 3.238, $df=1$, $p=0.072$) were included in the final model. The odds ratios indicate that females who were orphaned when young were 20 times more likely to acquire unexpected ranks outside of their matriline than non-orphaned females. Orphaned females with an older brother were five times more likely to attain unexpected ranks than females without a brother; in all cases, these females attained higher than expected ranks (Table 1). Orphans who had brothers but no sisters were more likely to acquire higher than expected ranks than orphans who had both brothers and sisters. All four orphans with brothers only acquired higher than expected ranks outside of the matriline. Of the three orphans with both brothers and sisters, one acquired a higher than expected rank outside of the matriline; one acquired a lower than expected rank within her matriline, and one acquired her expected rank.

In the model predicting rank changes within the matriline, both orphan status and presence of older sisters were included. Consistent with the overall pattern, females who were orphaned before 4 years of age were five times less likely to attain their expected ranks (Wald = 4.452, $df=1$, $p=0.035$). The effect of sisters on rank changes within the matriline was similar to the effect of brothers on rank changes outside the matriline. An orphaned female was five times more likely to attain an unexpected rank within the matriline if she had an older sister (Wald = 4.452, $df=1$, $p=0.035$). Females with more sisters were more likely than those with fewer sisters to acquire unexpected ranks ($R_s^2=-0.579$, $N=40$, $p<0.001$). This was true even if we excluded females with no sisters ($R_s^2=-0.617$, $N=20$, $p=0.004$). There was some indication that females who were

Table 2 Dominance rank attainment by non-orphaned females

	No siblings	Sister	Brother	Both
Achieve expected rank	8	5	4	6
Achieve unexpected outside	0	0	0	0
Achieve unexpected within	0	1 (above) 2 (below)	0	0

orphaned when they were very young were less likely to acquire their expected ranks than females who were orphaned when they were older. The mean orphaned age of the three females who failed to acquire their within-matriline expected rank was 26 months (range 15–33). In contrast, the mean orphaned age of the two females who did acquire their expected ranks was 46 months (range 44–47). The presence of brothers had no effect on rank acquisition within the matriline.

In sum, there was a strong pattern for orphaned females to attain unexpected ranks. If the orphan had older sisters, these sisters could outrank her within the matriline. In contrast, if she had an older brother, she was likely to acquire an adult rank outside of her matriline that was substantially higher than expected. Finally, if the orphan had neither sisters nor brothers, she was more likely to fall in rank below her matriline.

Orphaned females who acquired an unexpected rank outside of their matriline typically rose above or fell below at least two matriline. One female rose above four previously higher-ranking matriline. All females who rose in rank above their matriline retained their new ranks even after their brother emigrated from the group.

Interventions

Because orphaned females with older brothers tended to rise above their expected rank outside of the matriline and orphans with older sisters often fell below their expected ranks within the matriline, it seemed possible that brothers and sisters might intervene in their siblings' disputes in different ways. Results suggest that patterns of intervention did differ for males and females. Mothers and older sisters intervened on behalf of juvenile and adolescent females only when these individuals were threatening an individual belonging to a lower-ranking matriline (Table 3). In contrast, brothers' interventions usually occurred when

Table 3 Patterns of intervention by mothers, sisters, brothers, and non-kin in support of orphaned and non-orphaned juvenile and adolescent females

Who intervenes?	Orphans		Nonorphans	
	Mean intervention, (rate/h; SD)	% against hierarchy	Mean intervention rate/h (SD)	% against hierarchy
Mother	NA	NA	0.18 (± 0.16)	0
Older sister	0	0	0.04 (± 0.04)	0
Female non-kin	0.20 (± 0.13)	14	0.20 (± 0.16)	0
Older brother	0.33 (± 0.22)	62	0.66 (± 0.61)	100
Male non-kin	0.04 (± 0.02)	75	0.01 (± 0.01)	100

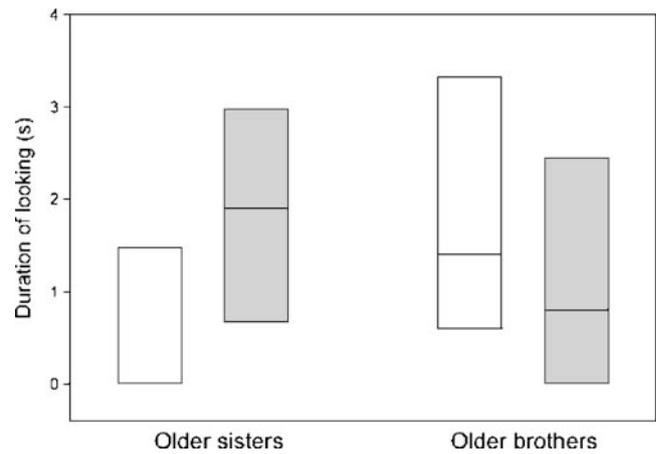


Fig. 1 The duration that brothers and sisters looked in the direction of the speaker when their younger sister appeared to be being threatened by a female from a higher-ranking matriline (open box plots) or a female from a lower-ranking matriline (gray box plots). Box plots indicate median values and second and third quartiles

their sister was being threatened by the member of a higher-ranking matriline (Table 3). Thus, while mothers' and sisters' interventions supported the existing dominance hierarchy, brothers' interventions more often contravened it.

Orphaned females' rank ascendancy was not the result of higher rates of support from brothers. In fact, brothers whose mothers had died intervened on behalf of their sisters at lower rates than did brothers whose mothers were still alive (Table 3).

Finally, there was little indication that orphaned females had stronger bonds with their brothers than nonorphans did, at least as measured by grooming interactions, because brothers and sisters were rarely observed to groom each other.

Playback experiments

Given the pattern of naturally occurring interventions, we predicted that older sisters would respond more strongly to a call sequence suggesting that their younger sister was being threatened by a lower-ranking female than to a sequence suggesting that she was being threatened by a higher-ranking female. Conversely, we predicted that males would be indifferent to the rank of their younger sister's opponent and respond equally strongly in both trial types.

Although sample sizes were necessarily small, results indicated substantial differences in the way that brothers and sisters reacted to threats to their younger sister. Older sisters responded significantly more strongly when their sister appeared to be being threatened by a lower-ranking female than when she appeared to be being threatened by a high-ranking female (Figs. 1 and 2). When their sister's screams were paired with the threat-grunts of lower-ranking females, older sisters looked toward the speaker for a longer

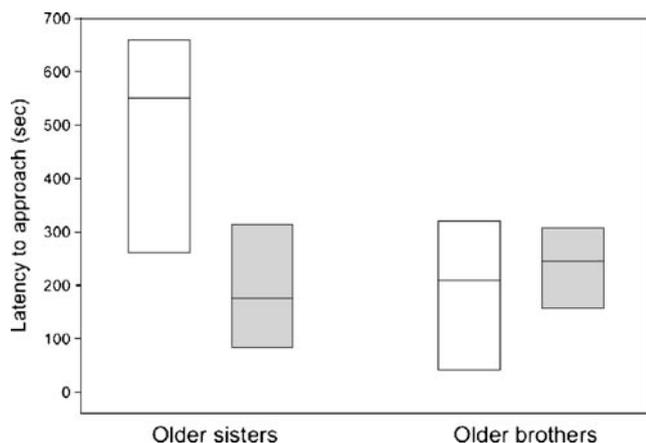


Fig. 2 The latency with which brothers and sisters approached the speaker when their younger sister appeared to be being threatened by a female from a higher-ranking matriline (*open box plots*) or a female from a lower-ranking matriline (*gray box plots*). Legend as in Fig. 1

time, and they approached the speaker sooner (duration of looking: $Z=-2.032$, $N=6$ (one tie), $p=0.042$; latency to approach: $Z=-1.992$, $N=6$, $p=0.046$).

In contrast, older brothers' responses to their sister's screams did not differ according to the rank of the apparent opponent (Figs. 1 and 2). There was no difference between call sequence types in brothers' duration of looking or latency to approach the speaker (duration of looking: $Z=-0.405$, $N=6$ (one tie), $p=0.686$; latency to approach: $Z=-1.363$, $N=6$, $p=0.173$).

When their sister appeared to be receiving aggression from a lower-ranking female, brothers' and sisters' responses were similar (Figs. 1 and 2; duration of looking: $U=-0.969$, $N_1=6$, $N_2=6$, $p=0.332$; latency to approach: $U=-0.801$, $N_1=6$, $N_2=6$, $p=0.423$). However, when their sister appeared to be receiving aggression from a higher-ranking female, older brothers approached the speaker more quickly than older sisters (Fig. 2; Mann–Whitney $U=-1.925$, $N_1=6$, $N_2=6$, $p=0.054$).

There was no indication that siblings whose mothers had died responded more strongly to their sisters' screams than did siblings whose mothers were still alive.

Discussion

These results demonstrate that rank acquisition in female baboons is strongly influenced by the presence or absence of mothers, sisters, and brothers. Older siblings had little impact on rank acquisition when mothers were still alive; non-orphaned females attained their expected ranks within the matriline, almost always above their older sisters. The presence and sex of older siblings had important effects, however, for orphaned females. Orphaned females with

older sisters often achieved lower than expected ranks within the matriline. In contrast, orphaned females with older brothers were likely to achieve higher than expected ranks outside of their matriline. Finally, orphaned females without siblings were likely to fall below their matriline's rank.

Given these outcomes, it was not surprising to find that, in both our observations and our playback experiments, males and females responded very differently to threats to their younger sister. Older sisters' interventions on behalf of their younger sister reinforced the existing female dominance hierarchy, while the majority of older brothers' interventions acted against it. Similarly, in playback experiments, older sisters responded weakly to call sequences suggesting that their sister was being threatened by a higher-ranking female, but much more strongly if it appeared that she was being threatened by a lower-ranking female. In contrast, older brothers responded equally strongly to apparent threats from both higher- and lower-ranking females. Males appeared to treat all threats to their sister as equivalent, whereas females were acutely aware of the rank of their sister's opponents and avoided disputes involving the members of higher-ranking matrilines.

It is possible that brothers' intervention patterns simply reflected their ignorance of the female dominance hierarchy. This seems unlikely for two reasons. First, males' patterns of intervention were not random but almost always acted against the dominance hierarchy. Second, other playback experiments have shown that males recognize each other's dominance ranks (Kitchen et al. 2005) and monitor the status of consortships (Crockford et al. 2007), indicating that they are attentive to other individuals' relationships in at least some contexts.

It seems more likely that males do recognize females' relative dominance ranks but are willing to support their sister in conflicts with members of higher-ranking matrilines because such interventions involve little risk and some potential benefit. Because males outrank all females, the only risk to an older brother is that posed by other males who may be relatives or close associates of the higher-ranking female. Given that high rank can confer reproductive benefits to females, males may gain inclusive fitness benefits by helping their sister secure higher-ranking positions.

The situation is quite different for older sisters. Although both sisters would benefit by improving their matriline's rank, the conservatism of the matrilineal dominance hierarchy limits females' mobility. Because females cannot defeat members of higher-ranking matrilines, they can provide little help to their younger sister in contests against more dominant females. Furthermore, while it is in the interests of females to ensure that their younger sister does

not fall below the matriline's rank, they derive little benefit if they allow her to rise in rank within it. Thus, in the absence of maternal support, females often assume ranks below their older sisters (see also Chapais et al. 1994 for similar data on Japanese macaques).

The observation that brothers can enhance their orphaned sister's rank begs several obvious questions. First, why does not the presence of brothers always cause their sister's rank to rise, even when mothers are still alive? Similarly, why do not all females exploit the power of their adolescent sons and brothers? Studies of captive macaques suggest that adult natal males do occasionally play a role in the ascendance of their matriline's rank (Ehardt and Bernstein 1986; Gygax et al. 1997). However, there is no evidence from any cercopithecine monkeys that adolescent males routinely help their sisters or mothers to rise in rank. Similarly, although the support of unrelated males has been observed to destabilize the female dominance hierarchy in captive Japanese macaques (Chapais and Lecompte 1995), the strong support of adult male "friends" (e.g., Palombit et al. 1997) has never resulted in female rank upheavals in this population of baboons (Cheney and Seyfarth unpublished). Indeed, the lack of sway exerted by unrelated high-ranking adult males on female dominance rank makes the comparatively greater influence of adolescent natal males all the more puzzling. One explanation is that interventions by mothers and sisters act to reify existing rank relations, thereby reinforcing the status quo and diminishing the influence of brothers. When these individuals are removed, however, the support of brothers against the members of higher-ranking matrilines constitutes the primary form of support that females receive. Somewhat surprisingly, the effect of brothers on their sister's rank seems to be somewhat independent of intervention rate because orphaned females did not receive higher rates of support from their brothers than did non-orphans.

Second, why do other females continue to accept an orphan's elevated status after her brother has emigrated and is no longer available to provide support? It seems possible that the absence of matrilineal kin frees orphaned females to establish relationships with the members of higher-ranking matrilines, which help to solidify their acquired positions. This strategy, however, is presumably also open to low-ranking female whose kin are still alive, yet females with kin almost never acquire high ranks outside their matrilines. It seems more likely that orphaned females benefit from the conservative pattern of rank maintenance that prevails among female cercopithecine primates. High-ranking allies may be necessary to induce rare rank reversals, but once a female has acquired her new position, she becomes an integral part of a system in which most alliances support the status quo. Similar stability following rank upheaval has been observed in this group of baboons

(Engh et al. 2006), as well as in Japanese macaques (Chapais and Larose 1988; Chapais et al. 2001) and vervet monkeys (Cheney and Seyfarth 1990).

In sum, a mother's absence appears to transform a virtually certain outcome—in which the adolescent female assumes a rank within her matriline above her older sisters—into an uncertain one. Whether the female acquires a dominance rank within or outside of her matriline that is higher or lower than expected depends on the presence or absence of brothers, sisters, or both. The support of female kin acts to reinforce existing rank relations, while the support of male kin acts to violate them, but only if the mother is absent. It remains a puzzle why the support of brothers has so little influence on female rank acquisition when female kin are present but so much influence when they are absent.

Acknowledgments We are grateful to the Office of the President of the Republic of Botswana and the Botswana Department of Wildlife and National Parks for permission to conduct research in the Moremi Reserve. We thank A. Mokopi, M. Mokopi, and K. Seyfarth for their help with data collection and B. Chapais, J. Silk, and J. Walters for comments on earlier versions of this paper. Research was supported by NIH grant MH62249 and was approved by the Animal Care and Use Committee of the University of Pennsylvania (Protocol #19001).

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