



Complex sources of variance in female dominance rank in a nepotistic society



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Many mammalian societies are structured by dominance hierarchies, and an individual's position within this hierarchy can influence reproduction, behaviour, physiology and health. In nepotistic hierarchies, which are common in cercopithecine primates and also seen in spotted hyaenas, *Crocuta crocuta*, adult daughters are expected to rank immediately below their mother, and in reverse age order (a phenomenon known as 'youngest ascendancy'). This pattern is well described, but few studies have systematically examined the frequency or causes of departures from the expected pattern. Using a longitudinal data set from a natural population of yellow baboons, *Papio cynocephalus*, we measured the influence of maternal kin, paternal kin and group size on female rank positions at two life history milestones, menarche and first live birth. At menarche, most females (73%) ranked adjacent to their family members (i.e. the female held an ordinal rank in consecutive order with other members of her maternal family); however, only 33% of females showed youngest ascendancy within their matriline at menarche. By the time they experienced their first live birth, many females had improved their dominance rank: 78% ranked adjacent to their family members and 49% showed youngest ascendancy within their matriline. The presence of mothers and maternal sisters exerted a powerful influence on rank outcomes. However, the presence of fathers, brothers and paternal siblings did not produce a clear effect on female dominance rank in our analyses, perhaps because females in our data set co-resided with variable numbers and types of paternal and male relatives. Our results also raise the possibility that female body size or competitive ability may influence dominance rank, even in this classically nepotistic species. In total, our analyses reveal that the predictors of dominance rank in nepotistic rank systems are much more complex than previously thought.

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Dominance hierarchies have repeatedly evolved in group-living mammals (e.g. primates: Kawai, 1958; Hausfater, 1974; carnivores: Holekamp & Smale, 1991; rodents: Berdoy & Drickamer, 2007; ungulates: Clutton-Brock, Guinness, & Albon, 1982; Fairbanks, 1994; elephants: Moss & Poole, 1983; Archie, Morrison, Foley, Moss, & Alberts, 2006; pinnipeds: Cassinin, 1999). Dominance hierarchies are characterized by asymmetric relationships between individuals, in which higher-ranking animals consistently defeat lower-ranking animals in agonistic encounters. These asymmetric relationships among group members are thought to evolve when within-group competition is high and resources can be defended by

one or a few individuals (Clutton-Brock & Huchard, 2013; Isbell & Young, 2002; van Schaik, 1989; Wrangham, 1980). Consequently, in rank based societies, high-ranking animals have priority of access to critical resources such as food, mates, or high-quality habitat (reviewed in Dunbar, 1988; van Schaik, 1983). Furthermore, high-ranking animals often experience fitness benefits such as enhanced reproductive success or higher offspring survival (e.g. red deer, *Cervus elaphus*: Clutton-Brock, Albon, & Guinness, 1988; yellow baboons, *Papio cynocephalus*: Alberts & Altmann, 2003; Altmann et al., 1996; wild dogs, *Lycaon pictus*: Creel, Creel, Mils, & Monfort, 1997; spotted hyaenas, *Crocuta crocuta*: Holekamp, Smale, & Szykman, 1996; chimpanzees, *Pan troglodytes*: Pusey, Williams, & Goodall, 1997). Given the widespread impact of dominance rank on fitness-related traits, understanding the predictors of dominance rank is an important goal in behavioural ecology.

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Two main types of dominance hierarchies have evolved in mammals. One type is based on individual competitive ability, and the main predictors of rank are thus age, strength and/or body size (e.g. mantled howler monkeys, *Alouatta palliata*: Jones, 1980; male baboons: Alberts, Watts, & Altmann, 2003; male red deer: Clutton-Brock et al., 1982; female African elephants, *Loxodonta africana*: Archie et al., 2006). The second type is the 'nepotistic' dominance hierarchy, in which individuals acquire dominance ranks similar to those of their kin (typically because relatives support one another in agonistic encounters; Langergraber, 2012). In some cases, both nepotistic and size/strength-based hierarchies can result in despotism, where reproductive success is entirely or largely skewed towards dominant individuals (e.g. in cooperatively breeding species such as meerkats, *Suricata suricatta*: Griffin et al., 2003; and wolves, *Canis lupus*: Packard, 2003). Alternatively, both types of hierarchies can result in egalitarian societies, in which all members have the opportunity to reproduce (e.g. female African elephants: Archie et al., 2006; female mountain gorillas, *Gorilla beringei beringei*: Robbins, Robbins, Gerald-Steklis, & Steklis, 2007). However, even in egalitarian systems, reproductive success is often positively correlated with dominance rank (i.e. high-ranking individuals outperform low-ranking individuals; Alberts & Altmann, 2003; Altmann et al., 1996; Pusey et al., 1997; Robbins et al., 2007).

Nepotistic dominance hierarchies, the focus of this study, are thought to evolve when individuals benefit from assisting their relatives in agonistic encounters (van Schaik, 1989; Wrangham, 1980); thus, nepotistic hierarchies are commonly observed among females in group-living matrilineal species, where female kin reside together throughout their lives (e.g. female Japanese macaques, *Macaca fuscata*: Kawai, 1958; Kawamura, 1958; female baboons: Hausfater, 1974; female spotted hyaenas: Holekamp & Smale, 1991; female geladas, *Theropithecus gelada*: Le Roux, Beehner, & Bergman, 2011). Notably, the majority of nepotistic dominance hierarchies described thus far (among noncooperative breeders) occur in primates. A prominent exception is the spotted hyaena, in which nepotistic rank hierarchies have independently evolved. Spotted hyaenas live in matrilineal societies in which competition for food can be intense (Frank, 1976). The shared societal features of spotted hyaenas and nepotistic primate societies (i.e. female matrilineality, male dispersal and within-group feeding competition) are thus strongly implicated as selective forces in the evolution of nepotistic dominance hierarchies.

In systems that form nepotistic dominance hierarchies, dominance ranks are assumed to be highly predictable and stable, because they are determined by family relationships (Kawamura, 1958; Langergraber, 2012; Sade, 1967; Walters & Seyfarth, 1987). Typically, a mother and her daughters occupy adjacent rank positions (by 'adjacent rank positions' we mean ranks that are next to each other in ordinal position; for instance, a mother and daughter occupying ordinal rank positions 3 and 4, respectively, would be considered 'adjacently ranked'). In addition, in nepotistic rank systems studied thus far, maturing females typically rank above their older sisters but below their mothers, a system known as 'youngest ascendancy' (reviewed in Horrocks & Hunte, 1983 for primates; see also Holekamp & Smale, 1991 for spotted hyaenas).

These patterns are assumed to be fixed within and across generations, but several case studies have documented unexpected rank outcomes in nepotistic systems. For example, case studies of pigtailed monkeys, *Macaca nemestrina*, olive baboons, *Papio anubis*, and bonnet macaques, *Macaca radiata*, have all revealed situations in which individuals occasionally hold ranks far above or below the ranks of their female kin, rather than adjacent to them (Bernstein, 1969; Johnson, 1987; Silk, Samuels, & Rodman, 1981). Furthermore, studies of olive baboons and several macaque species have observed rank reversals (i.e. an exchange of ordinal rank positions)

between mothers and daughters, as well as violations of the youngest ascendancy pattern (Chikazawa, Gordon, & Bean, 1979; Combes & Altmann, 2001; Hill & Okayasu, 1995; Silk et al., 1981). While these case studies have provided glimpses into individual variability in rank outcomes, they have not been followed up with systematic analyses of sources of variance in dominance rank. Consequently, our understanding of the factors that determine dominance rank position in nepotistic societies, and that, in turn, affect fitness, remains incomplete.

Our goal here was to address this gap, by systematically examining the frequency and causes of unexpected rank outcomes in a species that forms nepotistic dominance hierarchies. Specifically, we used a large, longitudinal data set from a natural population of female yellow baboons (Alberts & Altmann, 2012), in which dominance hierarchies are well described (Hausfater, 1974; Hausfater, Altmann, & Altmann, 1982; Samuels, Silk, & Altmann, 1987) and the fitness benefits of high dominance rank are well understood (Altmann & Alberts, 2003; Altmann, Hausfater, & Altmann, 1988). Thus, a female should strive to attain or exceed her expected position within the group hierarchy, but what determines her success or failure? Here, we examine the effects of demography and maternal and paternal kin on a female's likelihood of violating expected, traditional nepotistic rank patterns. Specifically, we asked in what circumstances does a female (1) fail to occupy a rank adjacent to other members of her matriline, (2) fail to occupy a rank higher than her older sisters, in violation of the youngest ascendancy rule and (3) outrank her mother? By addressing these questions, we hoped to gain insight into the kin relationships that are critical sources of support, or competition, for females in nepotistic societies. In addition, we aimed to understand the demographic conditions or family circumstances that result in dominance ranks that are higher or lower than expected, as these outcomes likely carry fitness consequences.

We chose to examine these rank outcomes at two life history milestones: menarche (i.e. maturation) and first live birth. With the help of her kin (in the form of aggressive coalitions and interventions in agonistic encounters), a female baboon spends her juvenile years challenging and defeating females that belong to lower-ranking matrilineal lines (reviewed in: Holekamp & Smale, 1991; Silk, 2002; Walters & Seyfarth, 1987). By menarche, the female is expected to hold a rank adjacent to members of her own matriline (Charpentier, Tung, Altmann, & Alberts, 2008; Walters, 1980; Walters & Seyfarth, 1987). This rank is thought to reflect her stable, lifelong position in the group hierarchy, and, consequently, many studies have examined dominance rank at this milestone (Chikazawa et al., 1979; Combes & Altmann, 2001; Samuels et al., 1987). However, females at menarche vary in the extent to which they successfully dominate females from lower-ranking matrilineal lines (Hausfater et al., 1982; Walters, 1980), yet no studies have systematically examined rank changes following menarche. Therefore, to present a more complete picture of adult female rank dynamics, we also examined female rank outcomes at first life birth. This life history milestone signifies the first time that a female becomes a mother, which is the next major behavioural transition after puberty. Below, we present hypotheses regarding each of the rank outcomes we examined, at both menarche and first life birth.

When Does a Female Fail to Rank Adjacent to Other Members of Her Matriline?

Studies have repeatedly demonstrated (all in cercopithecine primates) that a female co-residing with her mother and maternal sisters is more likely to occupy a rank adjacent to members of her matriline (Bernstein, 1969; Engh, Hoffmeier, Seyfarth, & Cheney,

2009; Hausfater et al., 1982; Samuels et al., 1987). For example, a female chacma baboon, *Papio ursinus*, co-residing with her mother is more likely to rank with her matriline than an orphaned female; however, an orphaned female with older sisters is more likely to rank with her matriline than a female without any maternal kin (Engh et al., 2009). Furthermore, recent evidence from chacma baboons highlights maternal brothers as an additional source of kin support for females: orphaned females co-residing with their older maternal brothers often ranked above their matriline at age 6 years (although this effect did not extend to nonorphans; Engh et al., 2009). Taken together, this evidence suggests that the availability of kin support is a key predictor of dominance rank outcomes, probably because mothers, fathers and maternal siblings intervene to assist their kin in agonistic encounters (Buchan, Alberts, Silk, & Altmann, 2003; Engh et al., 2009; Horrocks & Hunte, 1983), and this support appears to be a crucial mechanism by which females attain dominance rank (reviewed in Langergraber, 2012). Therefore, we predicted that the presence of close female kin (mothers and maternal sisters) and close male kin (fathers and maternal brothers) would increase a female's likelihood of ranking with, or above, her matriline.

When Does a Female Fail to Show Youngest Ascendancy?

Theory predicts that mothers should support their offspring in reverse age order, because reproductive value is inversely correlated with age (in nondeclining populations, such as the Amboseli baboon population; Schulman & Chapais, 1980). The system of youngest ascendancy in nepotistic societies is thought to reflect this preference: mothers provide preferential support to their youngest daughters, and thus younger daughters come to rank above their older sisters. Therefore, we predicted that the presence and support of the mother would be a key predictor of youngest ascendancy (Datta, 1988; Missakian, 1972). Specifically, we predicted that a female would be most likely to show youngest ascendancy if her mother was co-resident with her and still the highest-ranking member of her matriline. However, in the absence of a dominant mother to enforce youngest ascendancy, we

Table 1
Sample sizes of female yellow baboons used in all described analyses

Analysis	At menarche	At first live birth
Females with known dates for each maturational milestone	206	176
Females excluded from analyses because of incomplete evidence to support their rank (for details see Methods)	12	10
Females included in analyses of rank position relative to other matriline members		
Full data set	194	166
Focal's mother and sisters occupied nonadjacent rank positions	8	6
Focal was the only living adult female member of her matriline	27	0
Reduced data set with known paternity	142	118
Females included in analyses of youngest ascendancy within the matriline		
Full data set (including only females with adult maternal sisters)	85	64
Reduced data set with known paternity	67	48

predicted that competition among maternal sisters, especially in large matriline, would often prevent the youngest daughter from showing youngest ascendancy.

When Does a Female Outrank Her Mother?

Most analyses of nepotistic dominance hierarchies focus on a female's position within a family that is dominated by her mother, but females do sometimes outrank their mothers. The position of the daughter vis-à-vis the mother is of interest because maternal support is often key in determining whether females attain their expected dominance rank (reviewed in Langergraber, 2012). When daughters outrank their mothers, a potential conflict of interest occurs for the mother, because by allowing her daughter to outrank her, she herself loses potential fitness benefits. Two main hypotheses have emerged to explain why females in nepotistic rank

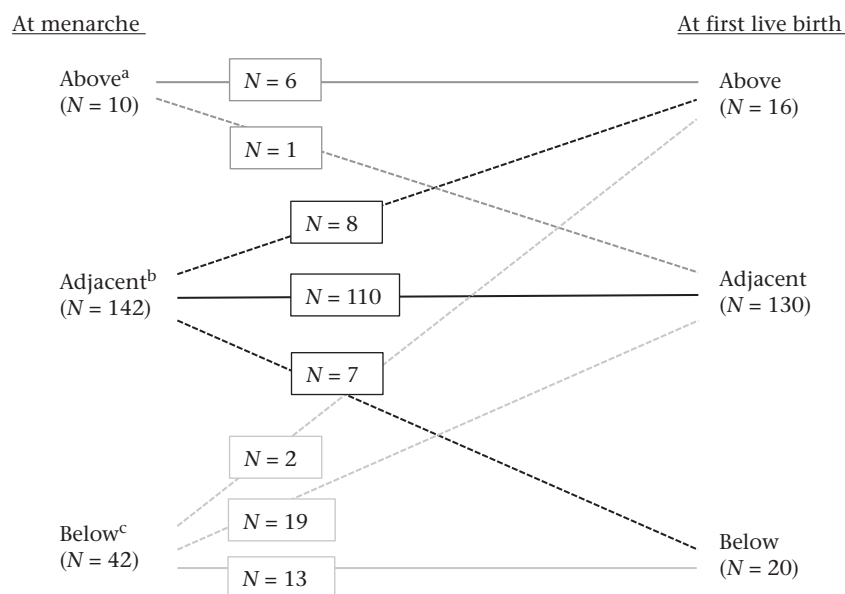


Figure 1. Dynamic nature of rank attainment in yellow baboons. The number of females that ranked adjacently to, above or below other members of their matriline at menarche and at first live birth are shown (see text for definitions of 'adjacent', 'above' and 'below'). We also depict the number of females, from each category, that retained or changed their position between menarche and first live birth. Some individuals died or were censored (i.e. did not produce a live offspring) between menarche and first live birth: ^a $N = 3$; ^b $N = 17$; ^c $N = 8$.

systems occasionally outrank their mothers (as observed by: Chikazawa et al., 1979; Combes & Altmann, 2001; Fedigan, 1976; Koyama, 1970; Missakian, 1972). First, competitive ability may generally decline with age, and thus mothers may fall in rank when they are old and weak (Hrdy & Hrdy, 1976). Alternatively, ageing mothers may engage in 'consensual' rank reversals with their daughters, which have higher reproductive value; consequently, mothers gain inclusive fitness benefits by raising the rank of their more fertile close kin (Chapais & Schulman, 1980; Combes & Altmann, 2001). Previous research in Amboseli has generally supported this model of mother–daughter rank reversals: most (>80%) mothers are outranked by at least one mature daughter before death, but females of comparable age without mature daughters rarely experience rank reversals. In addition, the likelihood of a rank reversal between a mother and her mature daughter increases with maternal age (although this pattern does not apply to alpha-ranked mothers, which never relinquish their position to a mature daughter; Combes & Altmann, 2001). Here, we provide a follow-up to these analyses (which examined data from 1977 to 2000) using an additional decade of data (2000–2010), and again test the hypothesis that the probability of a mother–daughter rank reversal will generally increase with maternal age. This follow-up is important to the current study, which is concerned with understanding how kin relationships and family circumstances influence individual dominance rank outcomes.

METHODS

Study Population and Study Subjects

The data reported here were recorded as part of an ongoing, long-term study of wild baboons in and around Amboseli National Park, Kenya (from 1971 to present). The Amboseli Baboon Research Project (ABRP) records group membership, mating and social behaviour on a near-daily basis in this population (see Alberts & Altmann, 2011 for details of data collection). In addition, the ABRP routinely records major demographic and life history events, including age at maturation (menarche for females and testicular enlargement for males; Charpentier et al., 2008). Female baboons are philopatric or 'matrilocal', remaining in their group of birth throughout their lives. Consequently, maternal identities, as well as maternal relatives, are known for all Amboseli females, with the exception of those few who were already adult when the study began. These females (i.e. those with unknown mothers and maternal kin) were excluded from our analyses.

Females experience their first agonistic win over an adult female at a median age of 2.24 years in Amboseli (Charpentier et al., 2008), but this milestone may be followed by a long period of slow rank ascendancy (reviewed in: Holekamp & Smale, 1991; Silk, 2002; Walters & Seyfarth, 1987). Here we focus not on this developmental process, but on predictors of the rank position that a female has attained by the time she reaches maturity. Only females with known mothers and with known age at menarche ($N = 206$, mean age at menarche \pm SD = 4.52 ± 0.41 years) or age at first live birth ($N = 176$, mean age at first live birth \pm SD = 6.17 ± 0.67 years) were included in our data sets. The data sets at these two time points were not identical: some individuals were dead or censored before they experienced their first live birth (i.e. had not produced a live offspring during the study period), and some individuals were excluded because insufficient data were available to support their rank positions (see Table 1, Fig. 1). Our data set spanned several decades (1977–2010) and social groups ($N = 9$ social groups), including one social group that experienced a brief period of rank instability (as described by Samuels et al., 1987). Paternity was determined through microsatellite genotyping (Alberts, Buchan, &

Altmann, 2006; Buchan et al., 2003) and was available for two-thirds of the females in each data set (menarche: $N = 142$ of 206; first live birth: $N = 118$ of 176; Table 1).

Female Dominance Rank

Female dominance rank was assigned using ad libitum observations of dyadic agonistic encounters in each social group. Win/loss records were compiled into a pairwise interaction matrix on a monthly basis, and rank orderings were then chosen to minimize entries below the diagonal (Hausfater, 1974). This method of rank assignment has been consistently used for decades by the ABRP, as well as other research groups (Archie et al., 2006; Silk et al., 1981; Whitten, 1983), and has been extensively described (Hausfater et al., 1982; Onyango, Gesquiere, Wango, Alberts, & Altmann, 2008; Samuels et al., 1987; Silk, Altmann, & Albert, 2006). During a few periods of sparse observation, fewer interactions per adult female dyad were recorded and linear dominance hierarchies were difficult to assess; we excluded females from our data set when incomplete evidence was available to support their dominance rank at menarche or first live birth (see Table 1 for sample sizes).

Variance in Female Dominance Rank: Kinship and Demographic Variables

To understand how a female's mother influenced her likelihood of ranking adjacent to her maternal family members, we created a continuous measure of maternal presence. This measure reflected the availability of maternal support throughout development and the juvenile period, which we believed would be important to measure because rank attainment is a process that can last months or years. Specifically, we created a variable equal to the proportion of the female's life spent co-residing (living in the same social group) with her mother; co-residence ended if the mother died or if the mother–daughter pair permanently resided in different social groups following a group fission.

To understand how a female's mother influenced her likelihood of showing youngest ascendancy, we created a categorical variable describing both the presence of the mother as well as her position within the matriline. We believed that both the support of the mother, as well as her degree of 'control' over the matriline, would influence the focal female's likelihood of showing youngest ascendancy. Specifically, we noted the status of the mother as (1) having retained her expected position as the highest-ranking member of the matriline, (2) having lost this position to a mature daughter or (3) no longer co-residing with the focal female.

We measured the presence of sisters as the number of mature (i.e. postmenarcheal) maternal sisters present at the focal female's menarche or first live birth. In contrast, mature (i.e. post testicular enlargement) maternal brothers had often dispersed by the time a sister matured or gave birth to a live offspring (male's median age at dispersal = 7.47 years; Charpentier et al., 2008); nevertheless, we hypothesized that their support during the year leading up to these events might be influential (as suggested by Engh et al., 2009). We therefore measured the presence of maternal brothers as the proportion of days spent in co-residency with the focal female, but only over the year preceding menarche or first live birth. We measured the presence of brothers in several other ways as well: (1) as the proportion of days spent in co-residency with the focal female, from birth to menarche, and (2) as a binary variable noting whether the focal female had any mature maternal brothers at menarche. All methods produced similar results (see Supplementary Tables S1, S2).

For each variable addressing the influence of siblings, we used identical methods to measure the presence of maternal and

paternal siblings. Because paternal identity was not available for all individuals, we performed initial analyses using the full data set, focusing on maternal relatives only. We then repeated all analyses with a restricted data set composed of individuals with known paternity (see [Table 1](#) for sample sizes). These analyses included all previously described variables, as well as paternal presence (measured similarly to maternal presence, as described above) and presence of mature paternal brothers and mature paternal sisters. To our knowledge, this is the first attempt to understand how paternal relatives influence female dominance rank in any social system.

Finally, we included demographic variability, specifically the number of adult females in the social group, in our analyses because females in larger groups will typically face more opponents in their attempt to rise from the ranks of juveniles into the adult hierarchy.

When Does a Female Fail to Rank Adjacent to Other Members of Her Matriline?

We examined the rank positions of 194 females at menarche and 166 females at first reproduction that met our criteria for analysis ([Table 1](#)). These are highly overlapping but not identical data sets. Each female was scored as occupying one of three mutually exclusive types of rank position: (1) ranking adjacently to living members of her matriline (as expected); (2) ranking below her matriline (with at least one nonmatriline member between the focal female and her mother or mature maternal sisters); or (3) ranking above her matriline (with at least one nonmatriline member between the focal female and her maternal sisters or mother). In 14 cases (8 at menarche, 6 at first live birth), the focal female had a living mother and one mature sister, which occupied rank positions that were not adjacent to each other; in these cases, we asked whether the focal female ranked adjacently to her mother. If she did so, we considered the focal female to be ranked adjacently to her matriline, but not if otherwise. Some females (27 at menarche, 29 at first live birth) were the only living adult female members of their respective matriline; for these females, we determined dominance rank outcomes with respect to the mother's last recorded rank. Each orphaned female was classified as 'ranked above her matriline' if she outranked individuals dominant to her mother, or as 'ranked below her matriline' if she failed to outrank her mother's subordinates.

We used multinomial logistic regression to model the three possible dominance rank outcomes (female ranked with her matriline, ranked above, or ranked below). Multinomial logistic regression conducts binary comparisons between categorical outcome variables, to examine the effect of predictors on the probability of one outcome versus a second outcome ([Hosmer & Lemeshow, 2000](#)). We therefore report the influence of each predictor variable on a female's probability of ranking above her matriline versus occupying an adjacent rank, as well as her probability of ranking below her matriline versus occupying an adjacent rank.

Models were selected using an information-theoretic approach. This method offers a valuable alternative to model selection based on null hypothesis testing, especially when trying to determine the relative importance of a set of predictors that might influence a response variable ([Burnham & Anderson, 1998](#); [Symonds & Moussalli, 2010](#)). However, a key feature of the information-theoretic approach is that comparisons must be made between models using identical data sets. We therefore began by fitting models to the full data set (focusing on maternal relatives only, as described above). We then repeated the model selection procedure using the restricted paternal data set and the additional paternal

relative variables, also described above. We performed these analyses at the two selected time points: menarche and first live birth. In total, we therefore fitted four sets of models (full data set at menarche, full data set at first live birth, restricted paternal data set at menarche, restricted paternal data set at first live birth).

We evaluated candidate models based on their Akaike Information Criterion (AIC) values, and more specifically, on their AIC_c values. AIC_c is derived from AIC, but imposes a stronger penalty for extra parameters; this penalty is highly recommended for small sample sizes to prevent overfitting ([Burnham & Anderson, 1998](#)). AIC and AIC_c converge as sample size increases, and it is therefore conservative to select models using AIC_c values. We ultimately selected the best, most parsimonious model as that with the lowest AIC_c value. When two or more models had an AIC_c difference of <2 , we considered these models as equally parsimonious ([Burnham & Anderson, 1998](#)). All analyses were conducted in R (version 2.15.0, R Foundation for Statistical Computing, Vienna, Austria).

When Does a Female Fail to Show Youngest Ascendancy?

Here, we focused on females at menarche (who were by definition the youngest adult members of their respective matriline), and asked whether each focal female showed youngest ascendancy within her matriline. Females with no adult maternal sisters at the time of menarche were excluded from this analysis. We conducted a parallel analysis of youngest ascendancy at first live birth, focusing on females that were still the youngest mature member of their respective matriline at this time point (see [Table 1](#) for sample sizes).

We modelled rank outcomes within matriline as a function of current maternal status (mother present and still highest ranking, mother present but not highest ranking, mother absent), presence of maternal brothers (measured as the proportion of time that an older brother was present during the year prior to menarche or first birth), and presence (number) of maternal sisters at menarche or first birth. Again, we used logistic regression and the model selection procedures described above. As with our first question, parallel analyses were conducted with the full data set at the two time points of interest, and then with the reduced data set (focusing on females with known paternity; [Table 1](#)) to incorporate paternal presence and paternal siblings. All analyses were conducted in R (version 2.15.0).

When Does a Female Outrank Her Mother?

To assess unexpected rank outcomes within matriline further, we tracked the ranks of every mother–daughter pair from January 2000 to December 2010 and determined whether and when the daughter outranked her mother (following [Combes & Altmann, 2001](#)). Only mature females co-residing with their mothers ($N = 90$ pairs, 55 unique mothers) were included in the data set. Mother–daughter pairs were classified either as 'reversing pairs' (if the daughter occupied a rank above her mother), or as 'non-reversing pairs' (if the daughter occupied a rank below her mother). Reversing pairs were further classified as first or second reversals, indicating whether the mother had previously ranked below another daughter. Nonreversing pairs included cases in which mother and daughter were still alive at the end of 2010 but had not reversed (termed right-censored pairs), as well as cases in which the mother or daughter died during the study period without reversing.

To account for the censored nature of the data, we used survival analysis (also known as failure time analysis; [Lee, 1980](#)) to model the proportion of mothers that ranked above their daughters as a function of maternal age (following [Combes & Altmann, 2001](#)).

Table 2
Summary of rank positions of female yellow baboons at menarche and first live birth, relative to those of their matriline

	At menarche		At first live birth	
	N	Proportion of total	N	Proportion of total
Ranked above matriline	11	0.05	16	0.10
Ranked adjacent to other matriline members	142	0.73	130	0.78
Ranked below matriline	42	0.22	20	0.12
Total	195		166	

Interestingly, as in Combes and Altmann (2001), the highest-ranking females in our data set (the ‘alpha’ females) never engaged in rank reversals with their daughters. Consequently, we excluded these five alpha females (i.e. the ‘alpha’ females from five distinct social groups), from our survival analysis. Mantel–Cox log-rank tests were used to compare failure time curves for first versus second reversing cases. Failure time analyses were conducted in SPSS (version 20, IBM, Armonk, NY, U.S.A.) and R (version 2.15.0).

RESULTS

When Does a Female Fail to Rank Adjacent to Other Members of Her Matriline?

At menarche, 73% of females occupied a rank adjacent to their immediate female kin; 5% of females ranked above their matriline and 22% ranked below their matriline (Table 2). By first live birth, many females that previously ranked below their matriline had

‘corrected’ their position and ranked with their matriline; in total, 78% of the females in our data set ranked with their matriline at first live birth. Interestingly, a few females ‘overcorrected’, increasing the small fraction of total females that ranked above their matriline (10%). Finally, 12% of females ranked below their matriline at first live birth; this category included females that had also ranked below their matriline at menarche ($N = 13$), as well as females that fell in rank between menarche and first live birth ($N = 7$; see Table 2, Fig. 1).

At menarche, the model with the lowest AIC_c value included maternal presence, number of maternal sisters and group size (Table 3). At first live birth, the best model included the number of maternal sisters and group size alone, with maternal presence no longer contributing to the most parsimonious model; however, maternal presence was included in the third most parsimonious model (delta AIC_c = 2.09). A model including number of sisters alone (rather than number of sisters and group size) also fitted the data well (delta AIC_c = 0.85). Parameter estimates from models with the lowest AIC_c values, and in a few cases, from other models of interest, are reported below.

A female that co-resided with her mother for shorter periods was more likely to rank below ($\beta \pm \text{SE} = -2.40 \pm 0.77$) and, surprisingly, above ($\beta = -2.56 \pm 1.27$) her matriline at menarche, compared to a female that co-resided with her mother for most of her immature period (Fig. 2). A female with fewer mature maternal sisters was more likely to rank below her matriline than a female with large numbers of kin (at menarche: $\beta = -0.52 \pm 0.25$; at first live birth: $\beta = -1.86 \pm 0.65$). A female from a large group was more likely to rank below her matriline than a female from a small group (at menarche: $\beta = 0.12 \pm 0.04$; at first live birth: $\beta = 0.12 \pm 0.06$), although this demographic effect was small.

Table 3
Influence of maternal relatives on whether a female yellow baboon occupied a rank adjacent to other members of her matriline (at menarche and first live birth)

	Fixed effects	K	AIC	AIC _c	Delta AIC _c	Akaike weight
At menarche N=194	Mother+Sisters+Group size	3	272.38	272.45	0.00	0.61
	Mother+Group size	2	274.90	274.95	2.50	0.17
	Mother+Sisters+Brothers+Group size	4	275.72	275.82	3.37	0.11
	Mother+Brothers+Group size	3	278.15	278.22	5.77	0.03
	Group size	1	278.62	278.65	6.20	0.03
	Sisters+Group size	2	279.69	279.74	7.29	0.02
	Mother	1	280.68	280.71	8.26	0.01
	Mother+Sisters	2	281.85	281.90	9.45	0.01
	Intercept only	0	282.86	282.87	10.42	0.00
	Sisters+Brothers+Group size	3	282.95	283.03	10.57	0.00
	Mother+Brothers	2	284.65	284.70	12.24	0.00
	Sisters	1	285.41	285.44	12.99	0.00
	Mother+Sisters+Brothers	3	285.84	285.92	13.46	0.00
	Brothers	1	286.86	286.89	14.44	0.00
	Sisters+Brothers	2	289.41	289.46	17.01	0.00
At first live birth N=166	Sisters+Group size	2	146.70	146.76	0.00	0.38
	Sisters	1	147.58	147.61	0.85	0.25
	Mother+Sisters+Group size	3	148.76	148.85	2.09	0.13
	Sisters+Brothers+Group size	3	149.92	150.01	3.25	0.08
	Mother+Sisters	2	149.99	150.05	3.29	0.07
	Sisters+Brothers	2	150.78	150.84	4.08	0.05
	Mother+Sisters+Brothers+Group size	4	152.11	152.22	5.46	0.02
	Mother+Sisters+Brothers	3	153.29	153.37	6.61	0.01
	Intercept only	0	227.07	227.08	80.32	0.00
	Group size	1	229.37	229.40	82.64	0.00
	Brothers	1	229.76	229.80	83.04	0.00
	Mother	1	230.47	230.50	83.74	0.00
	Mother+Group size	2	232.62	232.68	85.92	0.00
	Mother+Brothers	2	233.25	233.31	86.55	0.00
	Mother+Brothers+Group size	3	235.04	235.13	88.37	0.00

Fixed effects, number of variables included (K), Akaike information criteria (AIC), AIC_c, delta AIC_c and Akaike weights (Burnham & Anderson, 1998) are provided for each candidate model. Delta AIC_c was calculated as the difference between a given model and the best model. Akaike weights reflect the probability that a given model was the best model in the candidate model set. Models are sorted in order of their Akaike weights and those with a delta AIC_c < 2 are in bold. Here, the variables ‘sisters’ and ‘brothers’ refer to maternal siblings only.

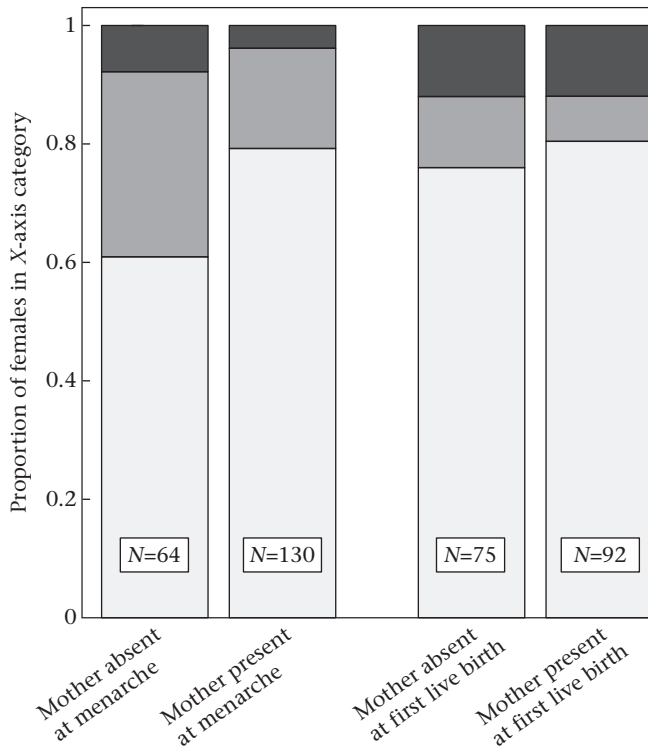


Figure 2. Influence of maternal presence on a female yellow baboon's rank at menarche and at first live birth. Proportion of females that ranked adjacent to (open bars), above (dark grey bars) or below (light grey bars) members of their matriline, at both time points, for females whose mothers were present (i.e. mother co-resided with the focal female) versus absent (mother did not co-reside with the focal female at menarche). For ease of visualization, maternal presence is given as a dichotomous variable here, although it was analysed as a continuous variable; see text for definitions of 'adjacent', 'above' and 'below'.

Our analyses of the influence of fathers and paternal siblings did not reveal any strong effects, although models including these variables were often equally parsimonious to models without them (Table 4). At menarche, the best model fitted to the restricted paternal data set included the same predictors identified as important in analyses using the full data set; paternal kin variables were not included in the best model. At first live birth, the model with the lowest AIC_c included paternal sisters (as well as maternal presence, number of maternal sisters and group size), but this model was not distinguishable from a model that did not include paternal sisters ($\Delta AIC_c = 0.73$). Where fathers, paternal sisters and paternal brothers were included in a likely model, paternal kin moderately increased a female's chance of ranking with or above her matriline (range of β estimates = -0.09 to 0.04). This was true both at menarche (see models ranked 2 through 6, all with $\Delta AIC_c < 2$) and at first live birth (see top-ranking models; Table 4).

When Does a Female Fail to Show Youngest Ascendancy?

By menarche, only 33% ($N = 28/85$) of females showed youngest ascendancy. Although this percentage increased to 49% ($N = 33/68$) by first live birth, it was still much lower than the expectation of traditional models. At both time points, a female's chance of showing youngest ascendancy was heavily dependent on the status of her mother (Fig. 3): at menarche and at first live birth, the most parsimonious models all included an effect of maternal status/position. Specifically, a female whose mother was present and was the highest-ranking member of the matriline was more likely to show

youngest ascendancy than a female whose mother was absent or outranked by another daughter; this was true at both menarche ($\beta = 1.75 \pm 0.63$) and first live birth ($\beta = 2.94 \pm 1.15$). At menarche, an individual whose mother was present, but was not the highest-ranking member of the matriline, was more likely to show youngest ascendancy than an individual whose mother was absent ($\beta = -2.42 \pm 1.13$); however, at first live birth, both of these types of females were equally likely to show youngest ascendancy.

A female's chance of showing youngest ascendancy was also dependent on the number of mature maternal sisters with which she co-resided with (Table 5). Specifically, as the number of maternal sisters increased, the chance of showing youngest ascendancy decreased, although the effect was moderate (at menarche: $\beta = -0.63 \pm 0.43$; at first live birth: $\beta = -0.91 \pm 0.52$).

We could not reject the hypothesis that the presence of a maternal brother increased a female's chance of showing youngest ascendancy: at both menarche and first live birth, a model including the presence of an older maternal brother (in addition to the number of maternal sisters and the status of mother) had a $\Delta AIC_c < 2$. However, the direction of this effect was inconsistent: a female that experienced more time with an older brother in the year prior to first live birth appeared more likely to show youngest ascendancy ($\beta = 1.38 \pm 1.15$), while more time with an older brother in the year prior to menarche appeared to decrease a female's chance of showing youngest ascendancy ($\beta = -0.33 \pm 0.78$). Furthermore, at both time points, models including maternal brother presence had low Akaike weights relative to the top-ranking models, indicating a relatively low probability that these were among the best models.

In addition, we could not reject the hypothesis that fathers and paternal siblings exerted some influence on dominance rank outcomes within matriline: at both menarche and first live birth, the best model included maternal status and the number of maternal sisters, but adding father or paternal sibling presence produced nearly equally parsimonious models ($\Delta AIC_c < 2$; Table 6). Again, however, the putative effects were small and inconsistent. At menarche, paternal siblings decreased a female's chance of showing youngest ascendancy, but these effects were apparently reversed at first live birth.

When Does a Female Outrank Her Mother?

In 34% ($N = 31$ of 90) of the mother–daughter pairs we examined, daughters occupied rank positions above their mothers at some point during adulthood. As noted in Methods, we did not observe reversals involving the five 'alpha' (highest-ranking) females in this data set, suggesting that alpha females may never cede rank (see also Combes & Altmann, 2001). Daughters that outranked their mothers did so at a mean age \pm SD of 6.73 ± 2.48 years, and their mothers were, on average, 17.34 ± 4.27 years when these reversals occurred. These 31 reversing mother–daughter pairs included 20 instances of first reversals and 11 instances of second reversals. Daughters of second reversing pairs were significantly younger at the time of reversal than daughters of first reversing pairs (mean \pm SD: second reversing pairs = 5.59 ± 1.88 years; first reversing pairs: 7.36 ± 2.59 years; Student's t test: $t_{30} = -2.00$, $P = 0.05$). Furthermore, survival curves describing the probability of reversal as a function of age significantly differed between second reversing and first reversing pairs (log-rank test: $\chi^2_{30} = 24.32$, $P < 0.01$; Fig. 4). In general, older mothers were more likely to experience a second reversal at any given age. Forty-four per cent ($N = 24$ of 59) of nonreversing pairs were considered right censored, while the remaining cases ($N = 35$ of 59) never experienced reversals before the mother or the daughter died.

Table 4
Influence of maternal and paternal relatives on whether a female yellow baboon occupied a rank adjacent to other members of her matriline (at menarche and first live birth)

Fixed effects		K	AIC	AIC _c	Delta AIC _c	Akaike weight
At menarche N=142	Mother+Maternal sisters+Group Size	3	178.40	178.47	0.00	0.20
	Mother+Maternal sisters+Group size+Paternal brothers	4	178.56	178.66	0.18	0.18
	Mother+Maternal sisters+Group size+Paternal sisters	4	178.66	178.75	0.28	0.17
	Mother+Maternal sisters+Group size+Father	4	179.87	179.97	1.49	0.09
	Mother+Maternal sisters+Group size+Father+Paternal brothers	5	180.17	180.29	1.82	0.08
	Mother+Maternal sisters+Group size+Paternal sisters+Paternal brothers	5	180.24	180.36	1.89	0.08
	Mother+Maternal sisters+Group size+Father+Paternal sisters	5	180.78	180.90	2.42	0.06
	Mother+Maternal sisters+Group size+Maternal brothers	4	182.28	182.38	3.90	0.03
	Mother+Maternal sisters+Group size+Maternal brothers+Paternal brothers	5	182.45	182.57	4.09	0.03
	Mother+Maternal sisters+Group size+Father+Paternal sisters+Paternal brothers	6	182.53	182.67	4.19	0.02
	Mother+Maternal sisters+Group size+Maternal brothers+Paternal sisters	5	182.59	182.71	4.23	0.02
	Mother+Maternal sisters+Group size+Maternal brothers+Father	5	183.78	183.90	5.42	0.01
	Mother+Maternal sisters+Group size+Maternal brothers+Paternal sisters+Paternal brothers	6	184.14	184.28	5.81	0.01
	Mother+Maternal sisters+Group size+Maternal brothers+Father+Paternal brothers	6	184.16	184.30	5.82	0.01
	Mother+Maternal sisters+Group size+Maternal brothers+Father+Paternal sisters	6	184.72	184.86	6.39	0.01
	Mother+Maternal sisters+Group size+Maternal brothers+Father+Paternal sisters+Paternal brothers	7	186.48	186.64	8.17	0.00
	Paternal sisters	1	192.93	192.96	14.48	0.00
	Intercept only	0	193.91	193.92	15.45	0.00
	Paternal brothers	1	194.31	194.33	15.86	0.00
Father	1	194.37	194.40	15.93	0.00	
At first live birth N=118	Mother+Maternal sisters+Group Size+Paternal sisters	4	92.63	92.75	0.00	0.33
	Mother+Maternal sisters+Group Size	3	93.39	93.48	0.73	0.23
	Mother+Maternal sisters+Group Size+Father	4	96.12	96.23	3.48	0.06
	Maternal sisters+Group Size+Paternal sisters	3	96.35	96.44	3.69	0.05
	Mother+Maternal sisters+Group size+Maternal brothers+Paternal sisters	5	96.39	96.53	3.78	0.05
	Mother+Maternal sisters+Group size+Paternal sisters+Paternal brothers	5	96.46	96.61	3.86	0.05
	Mother+Maternal sisters+Group Size+Paternal brothers	4	96.53	96.64	3.89	0.05
	Maternal sisters+Group Size	2	96.76	96.82	4.07	0.04
	Mother+Maternal sisters+Group size+Father+Paternal sisters	5	96.76	96.90	4.15	0.04
	Mother+Maternal sisters+Group Size+Brothers	4	96.85	96.97	4.22	0.04
	Mother+Maternal sisters+Group size+Maternal Brothers+Father+Paternal sisters	6	98.96	99.13	6.38	0.01
	Mother+Maternal sisters+Group size+Father+Paternal sisters+Paternal brothers	6	99.11	99.28	6.53	0.01
	Mother+Maternal sisters+Group size+Father+Paternal brothers	5	99.28	99.43	6.68	0.01
	Mother+Maternal sisters+Group size+Maternal Brothers+Father	5	99.51	99.66	6.91	0.01
	Mother+Maternal sisters+Group size+Maternal Brothers+Paternal brothers	5	99.71	99.86	7.11	0.01
	Mother+Maternal sisters+Group size+Maternal Brothers+Paternal sisters+Paternal brothers	6	100.15	100.32	7.57	0.01
	Mother+Maternal sisters+Group size+Maternal Brothers+Father+Paternal brothers	6	102.45	102.62	9.87	0.00
	Mother+Maternal sisters+Group size+Maternal Brothers+Father+Paternal sisters+Paternal brothers	7	102.76	102.96	10.21	0.00
	Paternal sisters	1	156.07	156.11	63.36	0.00
	Intercept only	0	158.74	158.75	66.00	0.00
	Paternal brothers	1	160.94	160.98	68.23	0.00
	Father	1	161.45	161.48	68.73	0.00

These analyses used the reduced data set of females for whom paternity analyses were complete (see text). Columns as in Table 3.

DISCUSSION

Our analyses present a striking picture of female rank as both dynamic across early adulthood and contingent on the social and family environment. Traditional models accurately describe the default structure of nepotistic rank systems, but we have found much more variance around these expected rankings than we anticipated. Specifically, our results highlight the overwhelming influence of maternal presence and position on female dominance rank in our study system, as well as the impact of matriline size and group size. Furthermore, we could not rule out the possibility that father, brothers or paternal siblings affected female rank, although the evidence for such effects was weak in our data set. Taken together, these results emphasize that kin support and competition contribute greatly to female rank and, consequently, to fitness, even in nepotistic rank systems where dominance rank has historically been thought of as predetermined.

Influence of Maternal Presence on Female Dominance Rank Outcomes

Maternal effects were profound in our data set, especially early in adulthood. A female that spent little time co-residing with her

mother was unlikely to occupy a rank adjacent to members of her matriline by menarche. Surprisingly, these orphaned females were more likely to rank below and above their respective matriline compared to nonorphans. Although this effect seems unexpected, our results corroborate previous findings from chacma baboons in the Okavango Delta of Botswana, where orphans similarly tend to rank above their matriline (Engh et al., 2009). It appears that the absence of maternal support and influence may, in some circumstances, free the maturing female from a determined outcome (in which she assumes a rank within her matriline). The mechanism for this ‘freeing’ of maternal influence is unknown; one possibility is that orphaned females become more reliant on their own individual fighting ability, and thus orphaned females that are physically strong may rise higher in rank than expected. Note, however, that female primates are much more likely to suffer from a lack of maternal support than to benefit from it, not only in terms of rank outcomes (Fig. 2), but also in terms of behavioural and social development (Botero, MacDonald, & Miller, 2013; Clay & de Waal, 2013; Missakian et al., 1972), as well as mortality risk (Hasegawa & Hiraiwa, 1980).

While maternal presence strongly influenced a female's likelihood of ranking adjacent to members of her matriline at menarche, group size and matriline size were the most consistent predictors of

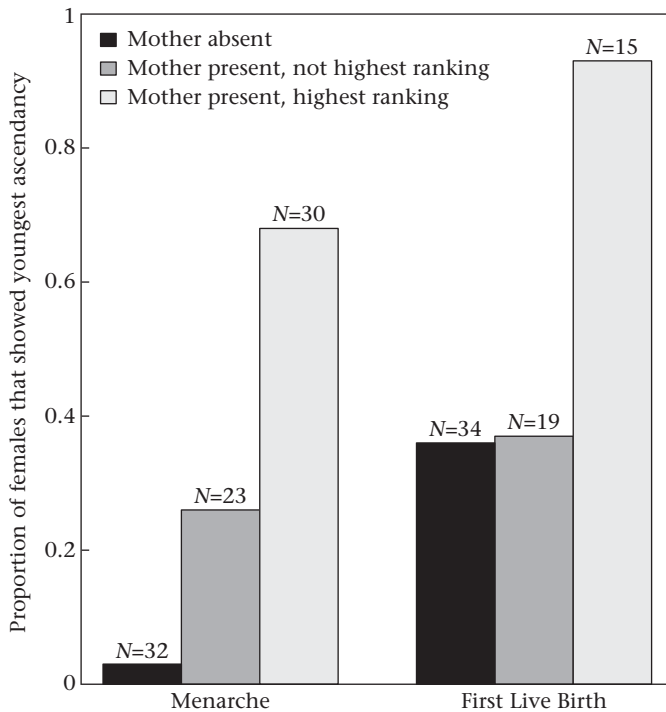


Figure 3. Influence of maternal status on youngest ascendency at menarche and at first live birth in yellow baboons. Proportion of females showing youngest ascendency, at both time points, stratified by maternal status. 'Mother absent': the mother died or no longer resided in the group; 'Mother present, not highest ranking' and 'Mother present, highest ranking': the position of mothers present within their respective matriline.

whether a female ranked with her matriline at first live birth. Maternal presence contributed to a well-fitted, although not equally parsimonious, model ($\Delta AIC_c = 2.09$), suggesting that the influence of maternal presence on female rank outcomes diminished across early adulthood. This conclusion is also supported by our analyses of youngest ascendency: maternal presence predicted youngest ascendency for females at menarche, but not at first live birth. The diminishing effect of maternal presence is somewhat puzzling, as cercopithecine mothers spend considerable time with their adult daughters and may even support them in agonistic encounters (Fairbanks & McGuire, 1986; Kurland, 1977). Three possible mechanisms for this diminishing maternal effect may act independently or in concert. First, by the time a female reaches her first live birth, her mother may have younger adult daughters, on which she would preferentially focus her attention (Nakamichi, 1991). Second, a female may have lost her mother around the time of her first live birth, as the average age at maternal loss in our data set occurred around this time (at 6.71 ± 4.23 years, compared to 6.17 ± 0.67 years for live birth). Finally, young adult females continue to grow for several years after menarche (Altmann, Gesquiere, Galbany, Onyango, & Alberts, 2010) and may thus gain significant strength and fighting ability between menarche and first birth; such a gain in individual physical competence may contribute to a waning of maternal influence.

Maternal presence also influenced a female's likelihood of showing youngest ascendency, as did maternal position within the matriline. Orphaned females rarely outranked their older sisters at menarche, although they sometimes did so at first live birth. At both time points, a daughter whose mother was still the highest-ranked member of the matriline was more likely to show youngest ascendency than a female whose mother ranked below one of her daughters. Theory suggests that, in nondecreasing populations,

mothers should support the youngest daughter in sister/sister disputes because of her high reproductive value (Schulman & Chapais, 1980), but this adaptive explanation for reverse age-ordered rank among sisters is disputed (see Horrocks & Hunte, 1983). It appears, then, that when mothers were 'in control', a maturing female was more likely to occupy a position beneficial to her mother, rather than being outranked by her older sisters. Furthermore, our failure time analysis of mother–daughter rank reversals indicates that mothers that lost their position at the top of their respective matriline were disproportionately older mothers, indicating that a daughter's chance of attaining youngest ascendency will generally decline as her mother ages.

Our failure time analysis also highlights the increasing probability that a mature daughter will outrank her mother as a function of age. Furthermore, the line on Fig. 4 indicating second reversals closely parallels the line indicating first reversals, in spite of the small sample size of second reversals. This indicates that these two processes happened at essentially the same rate, with a simple difference in timing; the second daughter does not disproportionately benefit from the rank reversal between her older sister and her mother (i.e. the first loss to a daughter did not somehow trigger a rapid decline in maternal rank, but rather that maternal rank declined in a simple stepwise, age-dependent manner).

Influence of Maternal and Paternal Siblings on Female Dominance Rank Outcomes

The presence of maternal sisters increased a female's chances of ranking adjacent to her matriline, presumably because maternal sisters provide critical support in agonistic encounters with unrelated females (Chapais, 1988; Johnson, 1987). However, it appears that sisters competed with each other within matriline, and females that matured in large matriline were less likely to show youngest ascendency than those that matured in smaller matriline. In other words, older sisters appeared to support their kin's ascent over members of unrelated, lower-ranking matriline, but did not readily cede their own rank to a younger sibling. These patterns are expected if dominance rank is positively correlated with reproductive success: females may gain inclusive benefits by raising the social status (and consequently the fitness) of their close relatives, but they should not compromise their own direct fitness by doing so (Chapais & Schulman, 1980; Hamilton, 1963).

Table 5

Influence of maternal relatives on youngest ascendency within matriline of yellow baboons (at menarche and first live birth)

	Fixed effects	K	AIC	AIC _c	Delta AIC _c	Akaike weight
<i>At menarche</i> N=85	Mother+Sisters	2	77.59	77.67	0.00	0.39
	Mother	1	77.95	78.00	0.33	0.33
	Mother+Sisters+Brothers	3	79.41	79.53	1.86	0.15
	Mother+Brothers	2	79.93	80.01	2.34	0.12
	Sisters	1	105.19	105.24	27.56	0.00
	Sisters+Brothers	2	106.90	106.99	29.31	0.00
	Intercept only	0	109.74	109.75	32.08	0.00
	Brothers	1	111.72	111.77	34.09	0.00
<i>At first live birth</i> N=67	Mother+Sisters	2	80.16	80.27	0.00	0.41
	Mother+Sisters+Brothers	3	80.76	80.92	0.65	0.29
	Mother	1	81.62	81.68	1.41	0.20
	Mother+Brothers	2	83.04	83.15	2.88	0.10
	Sisters+Brothers	2	90.54	90.65	10.38	0.00
	Sisters	1	90.70	90.76	10.49	0.00
	Intercept only	0	94.87	94.88	14.61	0.00
	Brothers	1	95.61	95.67	15.40	0.00

Columns as in Table 3.

Table 6
Influence of maternal and paternal relatives on youngest ascendancy within matriline of yellow baboons (at menarche and first live birth)

	Fixed effects	K	AIC	AIC _c	Delta AIC _c	Akaike weights
At menarche N=64	Mothers+Maternal sisters	2	64.69	64.80	0.00	0.25
	Mother+Maternal sisters+Paternal brothers	3	66.13	66.29	1.49	0.12
	Mother+Maternal sisters+Father	3	66.28	66.45	1.64	0.11
	Mother+Maternal sisters+Paternal sisters	3	66.51	66.68	1.88	0.10
	Mother+Maternal sisters+Maternal brother	3	66.67	66.83	2.03	0.09
	Mother+Maternal sisters+Father+Paternal brothers	4	67.77	67.99	3.19	0.05
	Mother+Maternal sisters+Paternal sisters+Paternal brothers	4	68.06	68.28	3.47	0.04
	Mother+Maternal sisters+Maternal Brothers+Paternal brothers	4	68.07	68.29	3.49	0.04
	Mother+Maternal sisters+Father+Paternal sisters	4	68.11	68.33	3.53	0.04
	Mother+Maternal sisters+Maternal Brothers+Father	4	68.28	68.50	3.70	0.04
	Mother+Maternal sisters+Maternal Brothers+Paternal sisters	4	68.50	68.72	3.92	0.04
	Mother+Maternal sisters+Father+Paternal sisters+Paternal brothers	5	69.70	69.98	5.18	0.02
	Mother+Maternal sisters+Maternal Brothers+Father+Paternal brothers	5	69.76	70.04	5.24	0.02
	Mother+Maternal sisters+Maternal Brothers+Paternal sisters+Paternal brothers	5	70.01	70.29	5.49	0.02
	Mother+Maternal sisters+Maternal Brothers+Father+Paternal sisters	5	70.11	70.39	5.59	0.02
	Mother+Maternal sisters+Maternal Brothers+Father+Paternal sisters+Paternal brothers	6	71.70	72.03	7.23	0.01
	Intercept only	0	83.00	83.85	19.05	0.00
	Paternal sisters	1	84.93	83.90	19.10	0.00
	Father	1	84.57	84.64	19.83	0.00
	Paternal brothers	1	83.84	85.00	20.19	0.00
At first live birth N=48	Mothers+Sisters	2	59.32	59.48	0.00	0.26
	Mother+Maternal sisters+Maternal brother	3	60.39	60.61	1.14	0.15
	Mother+Maternal sisters+Paternal brother	3	60.55	60.77	1.30	0.13
	Mother+Maternal sisters+Paternal sisters	3	60.77	61.00	1.52	0.12
	Mother+Maternal sisters+Father	3	60.81	61.04	1.56	0.12
	Mother+Maternal sisters+Maternal brothers+Paternal sisters	4	61.78	62.09	2.61	0.07
	Mother+Maternal sisters+Paternal sisters+Paternal brothers	4	61.86	62.16	2.68	0.07
	Mother+Maternal sisters+Maternal brothers+Paternal brothers	4	62.04	62.35	2.87	0.06
	Mother+Maternal sisters+Maternal brothers+Father	4	62.11	62.41	2.93	0.06
	Mother+Maternal sisters+Father+Paternal brothers	4	62.16	62.46	2.99	0.06
	Mother+Maternal sisters+Father+Paternal sisters	4	62.53	62.83	3.35	0.05
	Mother+Maternal sisters+Maternal brothers+Paternal sisters+Paternal brothers	5	63.34	63.72	4.24	0.03
	Mother+Maternal sisters+Maternal brothers+Father+Paternal sisters	5	63.71	64.09	4.61	0.03
	Mother+Maternal sisters+Father+Paternal sisters+Paternal brothers	5	63.73	64.11	4.63	0.03
	Mother+Maternal sisters+Maternal brothers+Father+Paternal brothers	5	63.79	64.17	4.70	0.02
	Mother+Maternal sisters+Maternal brothers+Father+Paternal sisters+Paternal brothers	6	65.29	65.75	6.27	0.01
	Intercept only	0	68.46	68.48	9.00	0.00
	Paternal brothers	1	70.14	70.23	10.75	0.00
	Paternal sisters	1	70.39	70.48	11.00	0.00
	Father	1	70.46	70.54	11.07	0.00

These analyses used the reduced data set of females for whom paternity analyses were complete (see text). Columns as in Table 3.

Similarly, we expected paternal sisters to assist females in attaining, or exceeding, their expected dominance ranks, because paternal sisters would gain inclusive fitness benefits by enhancing the reproductive success of a close relative.

Female baboons differentiate their paternal kin from nonkin and even bias their social behaviour towards paternal sisters (Alberts, 1999; Smith, Alberts, & Altmann, 2003; see also Widdig, Nurnberg, Krawczak, Streich, & Bercovitch, 2001 for similar data in rhesus macaques, *Macaca mulatta*). However, our analyses indicate that paternal sisters had minimal, inconsistent influences on female rank, possibly because paternal sisters were often spread across the group hierarchy, and in particular were sometimes low ranking and hence unable to provide meaningful support. We present a summary of the paternal sister scenarios encountered by females in our data set in Supplementary Fig. S1; this figure highlights the relative rarity of any one type of family structure in our data set and the consequent reduction in our power to detect systematic effects of paternal sisters.

Influence of Male Kin on Female Dominance Rank Outcomes

We did not find strong or conclusive effects of fathers, maternal brothers or paternal brothers on female rank outcomes, although the presence of these male kin types were included in some likely (AIC_c < 2) models. It may be that our sample set was not

adequately powered to detect what are probably small effects, or it may be that male kin truly did not exert much influence on female rank. Given that fathers (Buchan et al., 2003) and brothers (Engh et al., 2009) do intervene in agonistic encounters, often support their female kin against higher-ranking individuals and would gain inclusive fitness benefits by enhancing this fitness-related trait in a close relative (Hamilton, 1963; see discussion in Engh et al., 2009), it is surprising that the effects of male kin appear to be negligible in our data set. If males can and do intervene in female agonistic interactions, why is the evidence for male kin effects on female rank so weak?

The lack of detectable male kin effects may result from the great variety of social situations that males encounter, rendering an effect of male support difficult to detect in the aggregate. For example, kin selection theory predicts that maternal brothers should support their sisters in disputes with members of unrelated matriline, yet it is less clear how they should allocate support amongst their maternal sisters (to whom they are equally related). Similarly, fathers and paternal brothers are often related to females spread across the group's hierarchy and must decide which relatives to support and under what circumstances. Supplementary Fig. S2 summarizes all possible combinations of paternal and maternal female relatives that a male may co-reside with, highlighting the variety of ways in which males are predicted to partition their support as a result of social group composition. We think that a

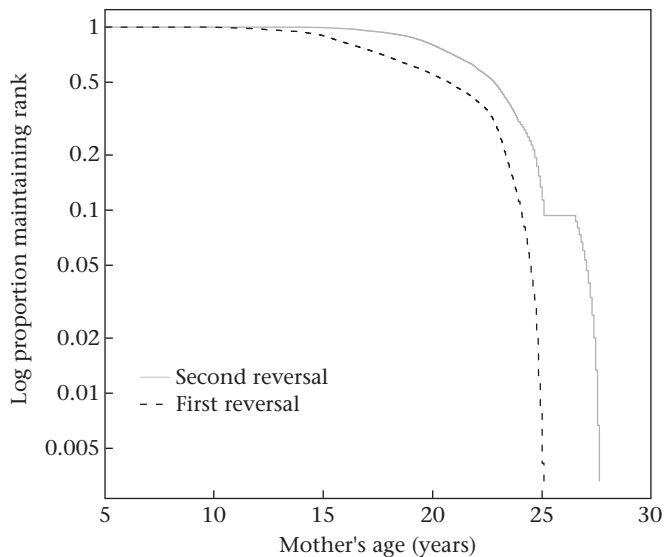


Figure 4. Influence of maternal age and history on probability of mother–daughter rank reversal in yellow baboons. Failure time plots depicting the proportion of mothers that maintained their expected rank (i.e. did not rank below a mature daughter) as a function of age. Results are stratified by maternal reversal history: ‘first reversal’ means that the mother had not previously ceded rank to a mature daughter; ‘second reversal’ means that the mother had previously ceded rank to a mature daughter.

general effect of male kin is difficult to detect in our data set because of this variation.

Nepotistic versus Size/Strength-based Hierarchies

In societies where intragroup competition for resources is high, we expect that dominance hierarchies will evolve (Isbell & Young, 2002; van Schaik, 1989; Wrangham, 1980). These hierarchies, in turn, will determine the distribution of resources and, consequently, the variance in reproductive output across individuals. Dominance hierarchies thus reveal two related continuums in animal societies: the continuum between equal and unequal sharing of resources and the continuum between egalitarian reproduction and despotic/highly skewed reproduction (Hemelrijk, 1999; Kokko & Johnstone, 1999; Packer, Pusey, & Eberly, 2001; Vehrencamp, 1983).

Our results point to a third continuum that has been little examined: the continuum between size/strength-based rank systems and rank systems determined by familial relationships and kin support, as in nepotistic societies (see Clutton-Brock & Huchard, 2013 for a related discussion). Specifically, our analyses suggests that female baboon societies, and by implication many other societies, may in fact fall along the continuum between strictly size/strength-based dominance hierarchies and strictly nepotistic dominance hierarchies. That is, while our results reveal complex and nuanced influences of kin on dominance rank in female baboons, two pieces of evidence suggest that female rank may partly depend on individual strength, even in this classically nepotistic species. First, an orphaned female was more likely to rise above her matriline than a nonorphan, raising the possibility that a female’s own strength and fighting ability determine her rank position if her mother is absent. Second, females that ranked lower than expected at menarche often ‘corrected’ their position by first live birth: a greater proportion of females ranked with their matriline and showed youngest ascendancy at first live birth (compared to menarche). Because female baboons continue to grow for several years after menarche (and specifically gain in body mass index, a measure of mass-for-stature; Altmann et al., 2010),

this temporal pattern suggests that individual size and/or strength may influence dominance rank in female baboons.

Some species certainly lie at the extremes of the continuum between strictly size/strength-based and strictly nepotistic dominance hierarchies: African elephant females, for instance, show a strictly size-based hierarchy (Archie et al., 2006), while spotted hyaenas show a strongly nepotistic hierarchy, albeit one that may be heavily mediated by the strong influence of maternal dominance rank on offspring size and growth rates (Holekamp & Dloniak, 2009; Höner et al., 2010). However, evidence from several other species places them along the continuum between these two extremes. For instance, in many ungulates, age and/or body condition are strong predictors of female dominance rank (Clutton-Brock et al., 1982; Côté, 2000; Favre, Martin, & Festa-Bianchet, 2008; Festa-Bianchet, 1991); however, in some species, maternal rank is also a predictor of offspring rank (Clutton-Brock, Albon, & Guinness, 1986; Clutton-Brock, Albon, & Guinness, 1984; Guilhem, Gerard, & Bideau, 2002). In other words, while generally showing a size/strength-based hierarchy, ungulates also have a nepotistic component to their rank system. This ‘nepotistic’ similarity between maternal dominance rank and offspring rank is likely mediated by the well-documented influence of maternal rank on offspring growth and body condition (i.e. the offspring of high-ranking female ungulates tend to be larger: Clutton-Brock et al., 1987; Green & Rothstein, 1991; Guilhem et al., 2002). However, red deer mothers do occasionally intervene on behalf of their offspring in agonistic encounters (Dusek, Bartos, & Svecova, 2007), raising the possibility that similarities between maternal rank and offspring rank may be partially explained by direct maternal behaviours (as observed in classically nepotistic cercopithecine species; reviewed in: Clutton-Brock & Huchard, 2013; Walters, 1987). Taken together, our results, and the work of others, suggest that variation in dominance rank may often be explained by both competitive ability and familial relationships. In addition, our results suggest that an examination of the role of size and body condition in classically nepotistic species, such as cercopithecine primates, is long overdue.

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Supplementary Material

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