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Status change during adulthood: life-history by-product or kin selection based on reproductive value?

Stephanie L. Combes[1]† **and Jeanne Altmann**[1,2,3]*

[1]*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA*
[2]*Department of Conservation Biology, Chicago Zoological Society, Brookfield, IL 60513, USA*
[3]*Institute of Primate Research, National Museums of Kenya, PO Box 24481, Nairobi, Kenya*

When dominance status predicts fitness, most adaptive models of dominance relationships among cercopithecine primate females predict lifetime maintenance of status. These models and alternative ones positing rank decline as a non-adaptive by-product have remained largely untested, however, because lifetime status of older adults has been virtually unknown for natural populations. In a 25-year study of adult female savannah baboons (*Papio cynocephalus*), in each of three social groups, rank losses were common among the 66 females that lived past median adult age. These losses were not accounted for by loss in relative rank from group growth or by loss in absolute rank from reversals in rank between members of different maternal families or between sisters. Rather, females that had mature daughters experienced loss of dominance status to these offspring, a characteristic of all but the top-ranking matriline of each group. Among proposed hypotheses for rank reversals between adults, that of kin selection based on relative reproductive value is most clearly supported by these data. In contrast, observed patterns of rank loss are not consistent with alternative models that postulate that changes during adult lifespan are a product of accumulated risk, physical decline during ageing, or coalitionary support among females within or between matrilines.

Keywords: dominance rank; rank loss; reproductive value; kin selection; female primates; ageing

1. INTRODUCTION

Agonistic dominance rank predicts fitness in a number of mammalian species (e.g. elephant seals (Haley *et al.* 1994), red deer (Clutton-Brock *et al.* 1988), wild dogs (Creel *et al.* 1997), spotted hyenas (Holekamp *et al.* 1996), baboons (Altmann *et al.* 1988) and chimpanzees (Pusey *et al.* 1997)). In primates, benefits often associated with high dominance rank include priority of access to higher quality and quantity of resources, lower vulnerability to predation, more beneficial social interactions, and/or differential access to mates (reviewed in Van Schaik 1983; Harcourt 1987; Dunbar 1988). All other things being equal, such benefits enhance biological fitness. The widespread impact of status on individual reproductive success draws attention back to the importance of understanding more fully dominance relationships throughout adulthood, especially among some of the well-studied cercopithecine primates that have provided the classic examples and motivated the models of female dominance hierarchies.

Dominance rank acquisition and lifetime rank maintenance are achieved differently by the two sexes. In many mammals, male dominance status is primarily determined by an individual's current size and strength (red deer (Appleby 1982) and primates (Hrdy & Hrdy 1976)). As a consequence the hierarchies are 'age-graded'; status and age are inversely related among adults. Among many primates, female hierarchies, in contrast, are characterized as 'nepotistic' to varying degrees (Hrdy & Hrdy 1976). Status depends much more on family membership, social skills, tradition and networks than on age and current strength, although potential species differences have been reported in the balance between nepotism and age-graded factors. In macaques and baboons, not only do the next generation of females rank in the same order to each other as their mothers did, but this intermatriline ordering pertains even if one or more mothers are not alive at the time of the daughters' rank acquisition. Within a matriline and with the mother's support, most older juvenile females assume a rank position just below that of the mother and, therefore, just above the juvenile's older sisters (Kawamura 1958; Missakian 1972; Sade 1972; Walters 1980; Horrocks & Hunte 1983*b*). Changes in 'absolute rank' (rank number in an ordering of all females) occur primarily through deaths and maturation events. Changes in 'relative' rank, that is, reversals in rank order between adult females, are uncommon in most cercopithecine populations (for examples of these reversals see Silk *et al.* 1981; Gouzoules *et al.* 1982; Hausfater *et al.* 1982; Goldman & Loy 1997). Life span empirical data have not been available, however, particularly for natural populations to test hypotheses about lifetime maintenance of rank rather than just acquisition of rank.

In the absence of lifetime studies of identified individuals, research on rank maintenance and change over the life span has consisted primarily of simulation models based on relatively short-term empirical studies of rank acquisition by juveniles and rank maintenance over a few years by adults. The models were developed primarily to explain apparent differences between populations or

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*Author for correspondence (altj@princeton.edu).
†Present address: Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27708, USA.

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species in the extent to which they exhibited age-graded and nepotistic systems. Those models, and the one we propose below, all assume that high rank confers a fitness advantage. Beyond this, the models differ considerably in assumptions and conclusions. In particular, the models differ in what aspects of demography and life-history parameters are included as influencing rank relationships and in what strategies females are thought to employ to maximize inclusive fitness (Hrdy & Hrdy 1976; Chapais & Schulman 1980; Schulman & Chapais 1980; Horrocks & Hunte 1983*a*; Hausfater *et al.* 1987; Datta & Beauchamp 1991).

(a) *Predictions of alternative models*

Here, with the opportunity to examine lifetime data for females in a wild baboon population, we revisit the question of female dominance stability and the potential selective pressures that might affect it during the latter half of adulthood. In a study of older adult female baboons, we tested alternative models by using the following distinguishing predictions arising from these models, particularly predictions regarding the pattern of lifetime rank maintenance.

The first prediction is that nepotistic rank attainment between families and mother-assisted rank attainment by younger daughters within families (Kawamura 1958) produce orderings between individuals that remain unaltered throughout adulthood, as predicted by a strictly nepotistic model of rank. Under the strictly nepotistic model, any predictable rank changes during adulthood will derive solely from broad demographic changes. Such changes will alter individuals' absolute rank (see definition above) but will not alter relative rank orderings among individuals, and this will be true within as well as among families. Population growth, decline, or stability will lead to net decrease, increase, or no change, respectively, in the absolute ranks of individuals. Systematic growth of subsets of the population from rank-correlated bias in offspring sex ratios (Altmann & Altmann 1991) would likewise lead to predictable patterns of change in an individual's absolute rank, again without rank reversals (change in rank ordering between individuals). Moreover, these broad demographic processes result in the same predicted direction of change for all females although the magnitude of change may differ among subsets. The strictly nepotistic pattern of rank attainment within and between families of cercopithecine primate females would remain unaltered throughout life.

The second prediction is that status declines with age during adulthood (Hrdy & Hrdy 1976), and relative rank losses during adulthood result from rank reversals between pairs of individuals. This second pattern is predicted by models that are based on two alternative processes. The first postulates that rank loss occurs as a simple non-adaptive by-product of ageing and loss of strength (Hausfater *et al.* 1987); the probability of rank reversal between a pair of individuals will be independent of their relatedness. The second postulates that rank loss during ageing is the adaptive product of past or current selection regimes (Hrdy & Hrdy 1976; Chapais & Shulman 1980; Horrocks & Hunte 1983*a*). For instance, a female may allocate agonistic support differentially to, and among, relatives or may defer to relatives and thereby increase her inclusive fitness. The probability of rank reversal between a pair of individuals will be a positive function of their relatedness. To distinguish between these two models (i.e. by-product and adaptive) we take advantage of the fact that they differ in predictions regarding the effects of relatedness between individuals on the probability of rank reversal between them. Whereas the probability of rank reversal in the simple by-product model is predicted to be independent of relatedness, relatedness is central to an evolutionary model. Data sets adequate to distinguish between these alternative models of rank decline during ageing therefore require known maternal relatedness as well as information on status into later adulthood for long-lived females.

In this paper, we examine the distinguishing predictions of different models and introduce the following simple evolutionary model predicting rank reversals. This model can be viewed as a simplified and more general version of the many-parameter adaptive one of Chapais & Schulman (1980).

(b) *Adaptive model of consensual rank reversal*

We formulate the model predicting 'consensual' rank reversals, i.e. rank reversals without conflict of interest, in terms of fitness enhancement (benefit (b)) to the individual that gains one rank position, and fitness loss (cost (c)) to the one that loses a rank position, along the lines laid out in Trivers (1972, 1974) and subsequent literature. Because rank-associated costs and benefits will continue to accrue over each participant's remaining expected lifetime, we assume that the ratio of the winner's benefit to the loser's cost, b/c, is equal to the ratio of the reproductive value of the winner to the reproductive value of the loser, $b/c = V_w/V_l$.

All other factors being equal, a 'consensual' rank reversal will be favoured through kin selection when $V_w/V_l > 1/r$, where r is the coefficient of relatedness between the interactants.

The values of the ratio, V_w/V_l, will be determined by the ages of the two interacting individuals and by the mortality and fertility schedule of the population. Reproductive value generally increases until the age of first infant production, and generally declines thereafter. In general V_w/V_l increases as a pair of adults ages and will be greater the larger the difference in age between members of the pair. The more closely related a pair of individuals is the lower the reversal threshold predicted by kin selection based on reproductive value. This model can be examined graphically in figure 1, in which we use the example of a mother that will lose rank and a daughter that will gain rank. The reversal threshold, $1/r$, will be 2 for mother–daughter pairs or full siblings, 4 for half-sisters, and 8 or greater for less-related individuals. As can be seen in figure 1, baboon mothers and daughters, especially mothers and later-born daughters, readily reach the threshold for consensual rank reversal; that is, the mother gains inclusive fitness by deferring to her daughter. Less-related pairs are less likely to reach the (higher) threshold for their degree of relatedness, and, therefore, consensual rank reversal is less likely to evolve through kin selection. The predictions that distinguish this model from others, then, are (i) females decline in

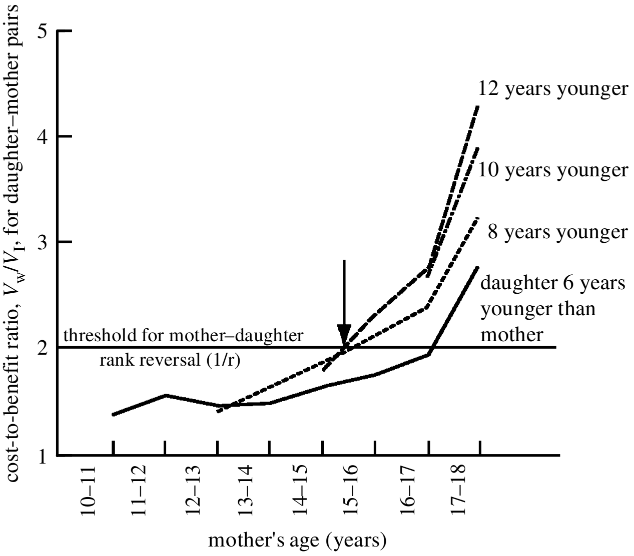

Figure 1. The age at which a female is predicted to first experience a 'consensual' rank reversal with a daughter according to the simple kin-selection model based on reproductive value (see § 1). This prediction is based on the age difference between mother and daughter and on differences in reproductive value of the two, using reproductive values calculated for fully wild-feeding groups in the Amboseli populations (Alberts & Altmann 2001). The threshold for rank reversal between mother and daughter is 2. Mothers are predicted to experience consensual rank reversal with an adjacent daughter on average at age 15 if the daughter is ten years younger (arrow), and not until age 17 if the daughter is six years younger. Pairs of adjacently ranked females that are less closely related than a mother–daughter pair would need to reach a higher threshold value ($1/r$) before consensual reversal is predicted to occur (see § 1b). For example, a female that had a younger sister ranked below her initially would not be predicted to reverse rank with that sister unless they were 12 years apart in age, and the older sister was *ca.* 17 years old. Sisters closer in age are not predicted to reverse rank until even later.

dominance status during adulthood through reversals in rank, and (ii) the closer the relatedness between two adjacently ranked individuals the more likely there will be a rank reversal between them.

2. METHODS

The study was conducted on savannah baboons (*Papio cynocephalus*) living in the semi-arid Amboseli basin and environs at the base of Mount Kiliminjaro. Potential subjects included all adult females belonging to any of three social groups (Alto's, Hook's and Lodge). Alto's and Hook's group members are wild-feeding, whereas the diet of Lodge group is enhanced primarily through foraging at the refuse pit of local tourist lodges (for details see Altmann & Muruthi 1988; Muruthi *et al.* 1991). Animals are individually identified, and matrilineal family relationships are known from reproductive and birth records, for as many as five generations in some cases.

Several aspects of baboon life histories and socioecology are particularly relevant to the present study. The baboon social system consists of multimale, multifemale groups. Typical of many cercopithecine primates (Pusey & Packer 1987), baboon males emigrate as they reach maturity, and females remain in their natal groups. Wild-foraging females reach menarche when a little over four years old, whereas females in food-enhanced groups tend to mature a year earlier; those that reach menarche are referred to herein as 'mature'. Females in wild-feeding Amboseli groups generally assume their adult rank within the female hierarchy approximately one year before reaching menarche (Walters 1980) and two years before they produce their first offspring. Occasionally females live beyond 20 years of age (for life-history parameters of baboon females see Altmann *et al.* 1977, 1988; Altmann 1980; Smuts & Nicolson 1990; Packer *et al.* 2000; Alberts & Altmann 2001). The Amboseli data provide life-history information and behavioural data for 147 adult females. In the wild-feeding groups median age of death was 12 years of age for females that reached menarche (Alberts & Altmann 2001). In order to focus on status relationships during the latter half of adulthood, those 66 Amboseli females (56 wild-feeding, 10 food-enhanced) that reached at least 12 years were included in this study—34 from Alto's group, 22 from Hook's group, and ten from Lodge group. This age was used because in the wild groups 12 years was the median age of a mother when her first daughter matured and was also the median life span for females that reached maturity. Comparable age estimates are not yet available for the food-enhanced groups; for this reason, and to facilitate comparison with the fully wild-foraging groups, we used the same initial age for analysis for Lodge females as for the others.

Dyadic agonistic interactions were recorded *ad libitum* (Altmann 1974) on all observation days for each study group. These were analysed to determine pairwise dominance relationships. Among Amboseli baboons, unlike provisioned and/or captive macaques, agonistic interactions between adults are predominantly dyadic rather than multiparty involving coalitions (Hausfater 1975; J. Altmann and S. C. Alberts, unpublished data). Monthly dominance matrices were constructed, showing a series of wins and losses for each individual. For each agonistic interaction in which only one participant exhibited submissive behaviour and that individual did not exhibit aggressive behaviour, a 'winner' and a 'loser' were designated. A 'win' was scored for the individual that did not perform any submissive behaviour during the interaction, and a 'loss' was scored for the individual that did exhibit one or more submissive behaviours (see Hausfater 1975). Following convention, the individual that consistently wins against all others is assigned rank 1 and so on, to the lowest-ranking individual being assigned the highest rank number. Ranks could thus be traced for all individuals throughout adulthood.

Using our computerized database of long-term behavioural and demographic records, net change in adult rank was determined for each individual by subtracting rank at menarche from rank at time of death or last census. The distribution of net rank changes were tested against a null hypothesis of zero using a Wilcoxon test at a significance level of $p < 0.01$. A more stringent level than 0.05 was used because of the potential lack of independence within families (e.g. Samuels *et al.* 1987; but see § 3). We eliminated a potential confound in interpretation of analyses by initially determining that rank change was not correlated with age at death or last census or the number of years a female was ranked.

'Survival' or 'failure time' analyses (Lee 1980) were then performed for subsets of the data to calculate the proportion of females of each age that continued to maintain their status, i.e. did not experience rank reversal. Survival data are conventionally plotted on a log scale because a constant proportion will be apparent visually and identified statistically as a linear relationship on a log plot. Failure-time analyses used the Lifetest procedure in the SAS system (SAS Institute Statistical Software, v. 6.12 (Allison 1995)).

3. RESULTS

(a) *Rank stability across the adult life span*

Most Amboseli females that survived to 12 years of age experienced a net decline in status during adulthood. The overall median rank change for the 66 females from all three groups pooled was -1.00 ($p < 0.001$, Wilcoxon test) and the mean was -2.79 ($p < 0.0001$, t-test). A similar pattern of left-skewing was seen separately in all three groups. In order to differentiate between rank reversals between close relatives and other sources of change including larger-scale demographic changes, we removed mother–offspring rank reversals from the full data set (i.e. we assumed that these changes did not occur). With those reversals removed, median rank change was zero, and changes were distributed symmetrically about zero ($p = 0.205$, Wilcoxon test), although the mean rank change was still slightly but not significantly negative ($\bar{x} = -0.85 \pm$ s.e. 0.42, $p = 0.05$ for mean different from zero, t-test). This suggested that broad group-level demographic processes, such as increase in the number of females over time or rank-correlated offspring sex-ratio bias, did not account for the observed decline in rank, contrary to the first prediction. Consequently, subsequent analyses focused on relatedness among individuals as a risk factor affecting vulnerability to rank reversals for ageing females because this distinguishes between our model of adaptive rank reversal from ones postulating decline as a non-adaptive by-product.

(b) *Rank reversals as potential sources of rank loss*

(i) *Daughter immediately below in hierarchy*

Thirty-seven (56%) of the adult females that lived at least 12 years produced a daughter that matured (reached menarche) while the mother was still alive, 31 in wild-feeding groups, 6 in the food-enhanced group. The initial rank relationship between these 37 adult females and their mature daughters was always that of the mother ranking above her daughter. For each group considered separately and for the wild groups combined, the proportion of surviving mothers that had not yet fallen in rank to at least one mature daughter declined linearly with age (Alto's $r^2 = 0.94$, $p < 0.0001$; Hook's $r^2 = 0.94$, $p < 0.0001$; Lodge $r^2 = 0.80$, $p < 0.0001$; wild combined $r^2 = 0.98$, $p < 0.0001$; see slopes of the log-plotted curves in figure 2 for the wild groups combined and for Lodge).

Interestingly, one class of females apparently was immune to rank loss from reversals with mature daughters. Members of the highest-ranking matriline in each group did not experience the rank reversals with daughters that females of the other families did despite having many years in which both mother and mature daughter(s) were alive (this set of females included one female from each of two groups and three females from the third group). The only other mothers ($n = 10$) that did not experience loss to their daughters had no apparent characteristics in common except the fact that they died very shortly after a daughter first matured and, therefore, had few years of potential loss to these daughters. Although the samples were inadequate for formal analysis, in each instance the female experienced only three or fewer years in which both she and a mature daughter were alive (in contrast to an average of 4.3 years, range 4.0–8.8 years for other females); if the 'risk period' had been longer, therefore, it seems likely that these females, too, would have reversed rank with a daughter.

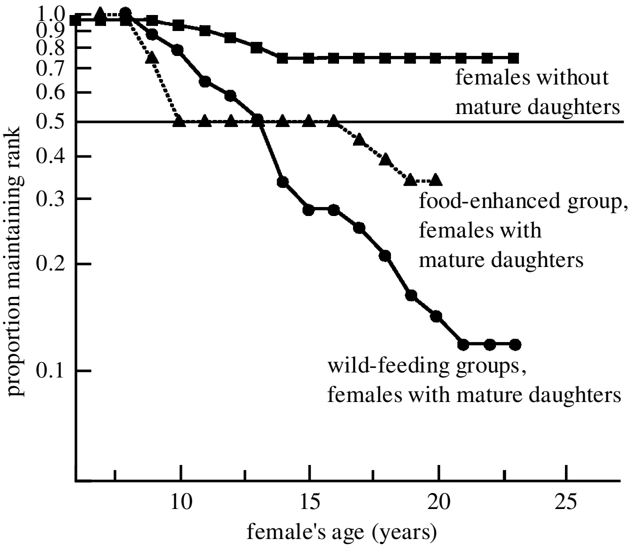

Figure 2. The proportion of females maintaining rank above females of lesser rank. The top curve, (squares), includes any female in the wild-feeding groups (Alto's and Hook's pooled) that did not have a daughter mature during her lifetime. The bottom curve (circles) includes any female that had at least one mature daughter; therefore, it represents the proportion of mothers retaining their dominance rank above their mature daughters. For preliminary comparison, a third curve (triangles), presents data for mothers in a food-enhanced group (Lodge); reproductive values are not yet available for that group. A constant proportion of females fell in rank each year, 0.05 for the wild-feeding females with daughters, 0.04 for the food-enhanced with daughters, 0.02 for wild-feeding females without daughters. See § 3b for further details.

The exceptions to the overall pattern of rank loss to daughters were not due to differential mortality; females that lost rank to a daughter died at the same average age as those that did not lose rank to daughters (17.57 years versus 17.03 years, respectively; $p = 0.54$, Wilcoxon test for difference in survival curves; $n = 22$ and $n = 15$, respectively).

(ii) *Non-daughters immediately below in hierarchy*

Twenty-three wild-feeding females that lived past 12 years did not have a mature daughter during their lifetime and would have risked rank reversal from sisters or less-related females; two others were already at the bottom of the hierarchy in their respective groups. Only 6 out of these 23 females experienced status loss through rank reversal (see figure 2, slope 0.02 per annum versus 0.05 for females with mature daughters). Failure-time analysis confirmed a difference in age-specific ability to maintain rank; at each age, the proportion of females without mature daughters that still maintained rank was significantly greater than the proportion with mature daughters that maintained rank ($p < 0.002$, Wilcoxon test). Only four older females in the food-enhanced group had no mature daughters; none of these females experienced rank reversal. No further analysis could be done of this set.

4. DISCUSSION

Baboon females generally experienced a loss of dominance status if their life span extended beyond average adult life expectancy, and the pattern of loss was as predicted by a simple adaptive model based on reproductive value combined with kin selection. In particular, the presence of mature daughters presented the greatest 'risk' to an adult female maintaining her status rather than rank loss resulting from simple expansion of higher-ranking matrilines, rank reversals between members of different matrilines, even when younger, or rank reversals with younger but lower-ranking sisters. Females of comparable age that did not have mature daughters were unlikely to experience rank reversals, whereas those with a mature daughter were likely to experience reversal with that highest-ranking daughter. Only members of the top-ranking matriline consistently maintained status above adult daughters until death. All other females lost status to daughters if the mother and mature daughter(s) were simultaneously mature for more than a few years.

Hausfater *et al.* (1987) hypothesized that rank reversals during ageing would arise as a simple by-product of the ageing process itself. Declining physical condition in old age could compromise the abilities of aged females to maintain their dominance status, resulting in non-consensual and non-adaptive rank loss. This by-product hypothesis is not supported by the present results. The most compelling evidence against the hypothesis of simple ageing by-product or random chance of reversal over time comes from a comparison of the probability of a rank reversal between adjacent mother–daughter pairs and other pairs. The by-product hypothesis would predict no difference in these probabilities. Nor would simple kin selection, independent of declining reproduction or survival, predict these findings, because the difference in reproductive value between members of a pair is critical in generating the prediction.

In theory, full siblings of appropriate age differences should engage in consensual rank reversal with the same probability as that of mother–daughter pairs. However, full siblings are rare in Amboseli wild-foraging groups (J. Altmann and S. C. Alberts, unpublished data; Altmann 1979; Smith 2000), and they are uncommon even in expanding macaque groups with high rates of natality and survival (Schulman & Chapais 1980). Even when they do occur, full siblings are highly unlikely to be of the age, the age difference, and the order of ranking for which reversals would be predicted based solely on reproductive value as in this model.

Adult females that are more distantly related than mother–offspring or full siblings, or those that are close in age, are extremely unlikely to reach the kin-selection threshold of four or more. Likewise, half siblings and grandmother–granddaughter pairs are unlikely to be positioned during adulthood in the critical adjacent rank positions with older over younger, and the likelihood of reaching the necessary threshold, four, is extremely small, for demographic reasons in both cases (Altmann 1979; Smith 2000). For less-related pairs, the model predicts that consensual reversals would be even less likely.

Consequently, a very simple evolutionary model based on fitness consequences determined solely by reproductive value and relatedness predicts the major and otherwise non-intuitive findings of the present study, whereas neither a by-product model nor one of simple competition, with or without kin selection, does. We propose this simple evolutionary model as a reasonable working hypothesis for predicting rank stability and change during adulthood among females of other populations and species.

Future work and a larger data set for this or other populations will also make possible further exploration and testing of the quantitative details and potential modifications of this model. Two particularly intriguing questions in this regard involve the potential 'invulnerability' of the top-ranking matriline and the characteristics of females that reverse with daughters at younger or older ages than average or than predicted.

With respect to the invulnerability of the top-ranking females to intramatriline status reversals, the models of Chapais & Schulman (1980) and Datta & Beauchamp (1991) are based, to a considerable extent, on the importance of coalitions among matrilines as well as within matrilines. On that basis, Chapais & Schulman (1980), the authors of the most complicated evolutionary model of rank relationships, specifically predicted that the top-ranking families will be most vulnerable to reversals, not least vulnerable, because these families will not have higher-ranking families to enlist as coalition partners. We know of no prior empirical test of this prediction of their model, and the limited data from the current study are clearly contrary to that prediction. Coalitions in the agonistic encounters of wild baboon females (Hausfater 1975; J. Altmann and S. C. Alberts, unpublished data) are rare in contrast to their prevalence in the provisioned or fully captive populations of macaques on which the previous models were based. Greater rank instability for top-ranking females in wild baboon groups relative to that of macaque colonies is therefore not surprising, but one would not *a priori* predict greater stability, either (see also the discussion of conflicts and coalitions in Dunbar 1988). The Hausfater *et al.* (1987) model assumes random pairwise reversals that occur over time. This is also contrary to the present results, including the finding of top-ranking families' invulnerability.

Lack of rank reversals within the top-ranking families of each group might be predicted by our model if the very highest-ranking females did not accrue incremental fitness benefits, i.e. if fitness benefits of higher rank reach a plateau or even reverse at the highest ranks. Packer *et al.* (1995) suggested that among anubis baboons in Gombe, Tanzania, rank benefits do not accrue in the top few ranks; this is based on lower fertility of four high-ranking females in that population. If one assumed very-fine-tuned behaviour on the part of the baboons, these authors' finding might provide an explanation for the stability we observed. However, no such reproductive 'glass ceiling' is observed in Amboseli (Altmann *et al.* 1995; J. Altmann and S. C. Alberts, unpublished data). Therefore, an appeal to that explanation, however tempting, would be unreasonable, at least for the Amboseli population. At this time the invulnerability of females in the top matriline remains puzzling. Comparative data from other groups and females as well as insights gained from a more detailed study of the behavioural dynamics may clarify the generality of the finding and the relevant factors involved.

The timing of mother–daughter rank reversals is intriguing in terms of both the average time of reversal and the variability around that average. Reversals were found to occur on average at slightly younger ages than predicted, and our simple model does ignore one parent–offspring asymmetry that may be important. Cercopithecine mothers that fall in rank are unable to assure that subsequent, younger, daughters attain a rank position above older sisters (reviewed by Walters (1980) for macaques and baboons; also J. Altmann and S. C. Alberts, unpublished data). Therefore, from the perspective of inclusive fitness, both the reversal cost to the mother and the reversal benefit to the daughter with whom rank is reversed, might be greater than assumed in our model. With the addition of that asymmetry, a lower age of reversal would be predicted as well as behavioural conflict resulting from mother–daughter conflict-of-interest. Non-consensual reversals would shift the timing to a younger age. The level of mother–daughter conflict that is thereby introduced might be considered a variant on that envisioned by Horrocks & Hunte (1983*a*). Those authors proposed such conflict as the driving force in the evolution of dominance acquisition in which mothers support juvenile daughters during rank acquisition. If those authors are correct about parent–offspring conflict providing the origin of the widespread pattern of mother-aided rank acquisition among cercopithecine females, then cercopithecine mothers may have gained immunity from daughter coalitions at the cost of risk during later years of rank loss to individual daughters independent of coalitions.

Also of interest is the question of whether variability in age at which females experience reversal is simply stochastic, is simply a predictable outcome of each female's unique demographic situation (e.g. the age of her mature daughters), or is a result of more complex individual traits or family dynamics. Further insights into variability in mean age and variance around the mean will require investigations at various demographic and behavioural levels.

Finally, different demographic and social conditions will result in different distributions of reproductive value across ages, different degrees of relatedness, and different age distributions of daughter production (see, for example, Altmann & Altmann 1979; Dunbar 1979, 1988; Alberts & Altmann 2001). Consequently, the social and demographic conditions will be translated in the model to predictable variability in patterns of rank reversal across the life span and, consequently, predictable patterns of life-history variability. However, little is currently known about the proximate mechanisms by which the metric of relatedness and differences in reproductive value are translated into behavioural interactions. Moreover, if a group's current demographic and social conditions have not existed as long as, for example, in food-provisioned and rapidly growing populations or in recently endangered and declining ones, then the animals' ability to track and respond to those conditions may reflect past environments and selection regimes rather than current ones. Studies of mechanism as well as selective forces and genetic structure will need to be integrated for a full understanding of history, process, and outcome interactions (Chapais & Schulman 1980).

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REFERENCES

Alberts, S. C. & Altmann, J. 2001 Matrix models for primate life history analysis. In *Primate life histories and socioecology* (ed. P. M. Kappeler & M. E. Pereira). (In the press.)

Allison, P. D. 1995 *Survival analysis using the SAS system: a practical guide*. Cary, NC: SAS Institute.

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

Altmann, J. 1979 Age cohorts as paternal sibships. *Behav. Ecol. Sociobiol.* **6**, 161–164.

Altmann, J. 1980 *Baboon mothers and infants*. Cambridge, MA: Harvard University Press.

Altmann, J. & Muruthi, P. 1988 Differences in daily life between semi-provisioned and wild-feeding baboons. *Am. J. Primatol.* **15**, 213–222.

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

Altmann, J., Hausfater, G. & Altmann, S. 1988 Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 403–418. University of Chicago Press.

Altmann, J., Sapolsky, R. & Licht, P. 1995 Baboon fertility and social status. *Nature* **377**, 688–690.

Altmann, M. & Altmann, J. 1991 Models of status-correlated bias in offspring sex-ratio. *Am. Nat.* **137**, 542–555.

Altmann, S. A. & Altmann, J. 1979 Demographic constraints on behaviour and social organisation. In *Primate ecology and human origins* (ed. I. S. Bernstein & E. O. Smith), pp. 47–63. New York: Garland STMP Press.

Appleby, M. C. 1982 The consequences and causes of high social rank in red deer stags. *Behaviour* **80**, 259–273.

Chapais, B. & Schulman, S. 1980 An evolutionary model of female dominance relations in primates. *J. Theor. Biol.* **82**, 47–89.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1988 Reproductive success in male and female red deer. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 325–343. University of Chicago Press.

Creel, S., Creel, N. M., Mills, M. G. L. & Monfort, S. L. 1997 Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behav. Ecol.* **8**, 298–306.

Datta, S. B. & Beauchamp, G. 1991 Effects of group demography on dominance relationships among female primates. I. Mother–daughter and sister–sister relations. *Am. Nat.* **138**, 201–226.

Dunbar, R. I. M. 1979 Population demography, social organisation and mating strategies. In *Primate ecology and human origins* (ed. I. S. Bernstein & E. O. Smith), pp. 65–88. New York: Garland STMP Press.

Dunbar, R. I. M. 1988 *Primate social systems*. New York: Cornell University Press.

Goldman, E. N. & Loy, J. 1997 Longitudinal study of dominance relations among captive patas monkeys. *Am. J. Primatol.* **42**, 41–51.

Gouzoules, H., Gouzoules, S. & Fedigan, L. 1982 Behavioral dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). *Anim. Behav.* **30**, 1138–1150.

Haley, M. P., Deutsch, C. J. & Le Boeuf, B. J. 1994 Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim. Behav.* **48**, 1249–1260.

Harcourt, A. H. 1987 Dominance and fertility in female primates. *J. Zool.* **213**, 471–487.

Hausfater, G. 1975 *Dominance and reproduction in baboons: a quantitative analysis*. Basel, Switzerland: Karger.

Hausfater, G., Altmann, J. & Altmann, S. 1982 Long-term consistency of dominance relations among female baboons (*Papio cynocephalus*). *Science* **217**, 752–755.

Hausfater, G., Cairns, S. & Levin, R. 1987 Variability and stability in the rank relations of nonhuman primate females: analysis of computer simulation. *Am. J. Primatol.* **12**, 55–70.

Holekamp, K. E., Smale, L. & Szykman, M. 1996 Rank and reproduction in the female spotted hyaena. *J. Reprod. Fertil.* **108**, 229–237.

Horrocks, J. A. & Hunte, W. 1983*a* Rank relations in vervet sisters: a critique of the role of reproductive value. *Am. Nat.* **122**, 417–421.

Horrocks, J. & Hunte, W. 1983*b* Maternal rank and offspring rank in vervet monkeys: an appraisal of the mechanisms of rank acquisition. *Anim. Behav.* **31**, 772–782.

Hrdy, S. B. & Hrdy, D. B. 1976 Hierarchical relations among female hanuman langurs. *Science* **193**, 913–915.

Kawamura, S. 1958 Matriarchal social ranks in the Minoo-B troop: a study of the rank system of Japanese monkeys. *Primates* **1**–**2**, 149–156; translated in *Japanese monkeys* 1965 (ed. K. Imanishi & S. A. Altmann), pp. 105–112. Published by the editors.

Lee, E. T. 1980 *Statistical methods for survival data analysis*. Belmont, CA: Lifetime Learning–Wadsworth.

Missakian, E. A. 1972 Genealogical and cross-genealogical dominance relations in a group of free-ranging monkeys on Cayo Santiago. *Primates* **13**, 169–180.

Muruthi, P., Altmann, J. & Altmann, S. 1991 Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia* **87**, 467–472.

Packer, C., Collins, D. A., Sindimwo, A. & Goodall, J. 1995 Reproductive constraints on aggressive competition in female baboons. *Nature* **373**, 60–63.

Packer, C., Collins, D. A. & Eberly, L. E. 2000 Problems with primate sex ratios. *Phil. Trans. R. Soc. Lond.* B **355**, 1627–1635.

Pusey, A. E. & Packer, C. 1987 Dispersal and philopatry. In *Primate societies* (ed. B. B. Smuts, D. L. Cheney, R. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 250–266. University of Chicago Press.

Pusey, A., Williams, J. & Goodall, J. 1997 The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277**, 828–831.

Sade, D. S. 1972 A longitudinal study of social behavior of rhesus monkeys. In *The functional and evolutionary biology of primates* (ed. R. H. Tuttle), pp. 378–398. Chicago, IL: Aldine-Atherton.

Samuels, A., Silk, J. & Altmann, J. 1987 Continuity and change in dominance relationships among female baboons. *Anim. Behav.* **35**, 785–793.

Schulman, S. R. & Chapais, B. 1980 Reproductive value and rank relations among macaque sisters. *Am. Nat.* **115**, 580–593.

Silk, J. B., Samuels, A. & Rodman, P. S. 1981 Hierarchical organization of female *Macaca radiata* in captivity. *Primates* **22**, 84–95.

Smith, K. L. 2000 Do paternal kin matter? The distribution of social behavior among female baboons. PhD thesis, University of Chicago.

Smuts, B. & Nicolson, N. 1990 Reproduction in wild female olive baboons. *Am. J. Primatol.* **19**, 229–246.

Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine.

Trivers, R. L. 1974 Parent–offspring conflict. *Am. Zool.* **14**, 249–264.

Van Schaik, C. P. 1983 Why are diurnal primates living in groups? *Behaviour* **87**, 120–143.

Walters, J. 1980 Interventions and the development of dominance relationships in female baboons. *Folia Primatol.* **34**, 61–89.

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