Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*

SUSAN C. ALBERTS*†, HEATHER E. WATTS*, JEANNE ALTMANN†‡§

*Department of Biology, Duke University
†Institute for Primate Research, National Museums of Kenya
‡Department of Ecology and Evolutionary Biology, Princeton University
§Department of Conservation Biology, Chicago Zoological Society

In many animals, variance in male mating success is strongly correlated with male dominance rank or some other measure of fighting ability. Studies in primates, however, have varied greatly in whether they detect a relationship between male dominance rank and mating success. This variability has led to debate about the nature of the relation between rank and mating success in male primates. We contribute to the resolution of this debate by presenting an analysis of the relationship between dominance rank and male mating success over 32 group-years in a population of wild savannah baboons. When data were pooled over the entire period, higher-ranking males had greater access to fertile females. However, when we examined successive 6-month blocks, we found variance in the extent to which rank predicted mating success. In some periods, the dominance hierarchy functioned as a queue in which males waited for mating opportunities, so that rank predicted mating success. In other periods, the queuing system broke down, and rank failed to predict mating success when many adult males were in the group, when males in the group differed greatly in age, and when the highest-ranking male maintained his rank for only short periods. The variance within this single population is similar to the variance observed between populations of baboons and between species of primates. Our long-term results provide strong support for the proposition that this variance is not an artefact of methodological differences between short-term studies, but is due to true variance in the extent to which high-ranking males are able to monopolize access to females.

In mammalian species that live in multifemale assemblages, male fighting ability or dominance rank often predicts male mating success (e.g. red deer, *Cervus elaphus*: Clutton–Brock et al. 1982; fallow deer, *Dama dama*: Moore et al. 1995; chimpanzees, *Pan troglodytes*: Constable et al. 2001; domestic cats, *Felis catus* L.: Say et al. 2001). This is especially true when mate guarding is the predominant means by which males gain matings (e.g. elephant seals, *Mirounga angustirostris*: LeBouef 1974; African elephants, *Loxodonta africana*: Poole 1989; Soay sheep, *Ovis aries*: Preston et al. 2001). The result of such a system is considerable short-term variance in male mating success. This variance is of interest in light of two distinct but related research areas in evolutionary

Correspondence and present address: S. Alberts, Department of Biology, Duke University, Box 90338, Durham, NC 27708, U.S.A. (email: alberts@duke.edu). H. E. Watts is now at the Department of Zoology, Michigan State University, East Lansing, MI 48824, U.S.A. J. Altman is at the Department of Ecology and Evolutionary Biology, Princeton University, Guyot 401, Princeton, NJ 08544, U.S.A.

biology. On one hand, variance in male mating success due to fighting ability is one source of sexual selection pressure on males (e.g. Andersson 1994). On the other hand, variance in male mating success due to fighting ability can be seen as but one process leading to 'reproductive skew' (i.e. the unequal distribution of reproductive opportunities) that characterizes most if not all animal societies (Vehrencamp 1983; Keller & Reeve 1994; Bourke 1997; Emlen 1995, 1997; Reeve 2000; Reeve & Keller 2001). Although most of the research on reproductive skew has focused on societies where skew is extreme and is associated with nearly complete reproductive control by one group member, the goal of recent research in reproductive skew has been to develop a single, unified framework to describe the evolution of reproductive skew in all types of animal societies (e.g. Reeve & Keller 2001).

For sexual selection research and for reproductive skew models, adequate descriptions of the nature of the variance in reproductive success between group members are crucial. However, for mammals in particular, data on

variance in reproductive success tend to come from studies that are short term relative to the life span of the study subjects. Hence, these studies often fail to capture lifetime variance in reproductive success and, equally importantly, variance over time in the extent of reproductive skew.

One taxonomic group with an unusually rich array of data on male reproductive skew is the primates. In particular, many studies exist on the relation between male rank and mating success in a wide range of primate species. This relationship is quite variable (see reviews in Dewsbury 1982; Cowlishaw & Dunbar 1991; Ellis 1995). Although many early primate studies reported that high-ranking males had higher mating success (e.g. Maslow 1936; Carpenter 1942; DeVore 1965; Suarez & Ackerman 1971; Hausfater 1975; Packer 1979a), many others reported that rank did not predict mating success (Strum 1982; Smuts 1985; Bercovitch 1986; Noë & Sluijter 1990; reviewed in Cowlishaw & Dunbar 1991). Published discussions failed to resolve whether these differences were methodological, so that one set of findings was 'right' and one was 'wrong', or were due to real differences between populations or species in the extent to which rank predicted mating success (Bernstein 1981; Dewsbury 1982; Berenstain & Wade 1983; Fedigan 1983; Bercovitch 1986, 1992a, b; McMillan 1989; Barton & Simpson 1992; Cowlishaw & Dunbar 1992; Dunbar & Cowlishaw 1992).

Two studies influenced our perception of the problem. Cowlishaw & Dunbar (1991, 1992) found that, over a wide range of primate species, variance in the correlation between male rank and mating success was partly explained by group size. In particular, as group size increases, high-ranking males lose their ability to monopolize access to females. Cowlishaw & Dunbar (1991) reasoned that this was because, as the number of males increases, either power differentials between males decrease, or the number and frequency of challenges to high-ranking males increases, or both. The second important paper was Bulger's (1993) summary of 18 studies in 10 populations of savannah baboons, which showed that rank and mating success were positively correlated in most populations, but that the correlation showed considerable variance in both magnitude and direction. Bulger suggested a number of possible explanations for this range of relationships, including different degrees of female synchrony across studies, variance in the prevalence of male–male coalitions across populations and demographic factors, such as number of adult males, that affected the stability of the male dominance hierarchy.

These papers signalled an emerging consensus in the primate literature that the relation between male dominance rank and mating success, across and within species, shows true variance, not just error variance. However, three important questions remain unanswered about the relation between dominance rank and mating success. First, what is the mechanism by which rank functions to determine mating success? Second, when and how does the mechanism that connects rank to mating success break down? This is equivalent to asking, what are the sources of variance in the relationship between rank and mating success? Third, to what extent do other species display the patterns we observe in primates?

Queueing and Queue-jumping

We suggest that the answer to the first question, concerning mechanism, is that, for baboons and similar primates, male dominance rank functions as a queue for mating opportunities, as first proposed by Altmann (1962; Suarez & Ackerman 1971; Hausfater 1975; Chapais 1983; Bulger 1993; for similar analyses in nonprimate species, see Say et al. 2001; Engh et al. 2002). The queuing model, more widely known as the priority-of-access model (Altmann 1962) posits that males wait for mating opportunities, so that when only one female is fertile, only the highest-ranking male will mate with her; when two females are simultaneously fertile, the highest- and second-ranking males will mate, and so on.

We propose that the answer to the second question, concerning sources of variance, is that the queuing system breaks down whenever males successfully use strategies that allow them to jump the queue (i.e. to mate when they would not otherwise be able to do so). Five possible mechanisms of queue-jumping exist for baboons and similar primates. Each mechanism has been explored independently in short-term studies, but this is the first study to examine long-term patterns in the relationship between rank and mating success, and to examine the effect of two queue-jumping mechanisms.

The first possible mechanism is solo competition. Savannah baboons mate in the context of mate-guarding episodes, in which one male persistently follows, maintains proximity to and mates with a fertile female (e.g. Hausfater 1975; Packer 1979a). Queue-jumping would occur if a lower-ranking male successfully challenged a higher-ranking male for a mate-guarding opportunity without permanently changing his rank position. In general, we expect that successful challenges will lead to rank reversals; however, in some circumstances, a lower-ranking male may gain temporary access to a particular resource (a fertile female) without permanently changing his rank position. He would thereby obtain more mating opportunities than expected for his rank position.

The second is male coalitionary behaviour, in which males team up to challenge higher-ranking males (e.g. Packer 1977; Noë & Sluijter 1990). Coalitions can be an effective means of distracting and displacing a mate-guarding male; one of the coalitionary members, but not both, then initiates mate guarding with the fertile female (Packer 1977; Bercovitch 1986; Noë & Sluijter 1990). As a result, that male obtains more mating opportunities than expected from his rank position. As with queue-jumping through solo competition, coalitions allow males to gain mating opportunities without changing their rank position.

Energetic constraints associated with mate guarding (Packer 1979a; Alberts et al. 1996) may lead to queue-jumping if high-ranking males abandon their place in the queue when their energy reserves are depleted. Mate guarding imposes energetic constraints in many species (e.g. LeBoeuf 1974; Poole 1989; Cuthill & MacDonald

1990), but males face special challenges in year-round breeders such as baboons. In particular, males may not have the energy reserves to mate-guard without rests if fertile females are continuously available for many consecutive weeks. In such cases, we expect that high-ranking males would forgo some mating opportunities, and lower-ranking males would obtain more mating opportunities than expected for their rank positions.

The fourth possible mechanism is female choice. Female baboons express clear mating preferences for particular males (Seyfarth 1978a, b; Rasmussen 1983; Smuts 1985; Bercovitch 1995). These preferences increase the probability that the preferred male will form a consortship with the preferring female (Smuts 1985). Consortships involving preferred males also tend to last longer than those involving unpreferred males (Bercovitch 1995). However, such consortships do not result in a higher ejaculation rate or more total ejaculations than consortships with unpreferred males (Bercovitch 1995), although they do result in a higher total mount rate (Rasmussen 1983). Bercovitch (1995) concluded that, overall, these female effects are small relative to the effects of male reproductive strategies (i.e. solo and coalitionary aggressive behaviour) on male mating and reproductive success in this species.

The final possible mechanism is sneak copulation, which occurs when males seek opportunities to mate surreptitiously. This is a widely distributed male mating tactic, seen in both vertebrates (e.g. LeBoeuf 1974; Gross 1985; Gibbs et al. 1990; Manson 1992) and invertebrates (e.g. Parker 1970; Alcock et al. 1977). Sneak copulations are limited but not absent (e.g. Manson 1992) in species such as baboons, which tend to live in open habitats with high visibility, and in which males maintain close and continuous proximity to the females they are mate guarding. In our study population, sneak copulations appear to have relatively little effect on overall mating patterns; genetic analysis (Altmann et al. 1996; J. Altmann & S. C. Alberts, unpublished data) indicates that observed matings correlate well with actual paternity in the study population.

Goals of the Current Study

We had three goals. Our first goal was to examine the correlation between rank and mating success for male baboons in our study population. In particular, we sought to describe variance in the correlation between rank and mating success in our population, and to compare this intrapopulation variance with Bulger's (1993) intraspecific variance and with Cowlishaw & Dunbar's (1991) interspecific variance.

However, the correlation coefficient provides limited biological information. It is descriptive rather than predictive, and allows no inferences to be drawn about biological mechanisms underlying the relationship. Hence, our second goal was to test the priority-of-access model (Altmann 1962) using long-term data on baboons. The priority-of-access model posits an explicit mechanism by which rank affects mating success, namely that

Table 1. Periods for which data were available on each study group

Study group	Study period	N
Alto's	1980–1988	18
Dotty's (Alto's fission product)	1997–1998	4
Nyayo's (Alto's fission product)	1997–1998	4
Hook's	1982–1994	26
Linda's (Hook's fission product)	1996–1998	6
Weaver's (Hook's fission product)	1996–1998	6
All group-periods		64

N=the number of 6-month blocks available for analysis from each group.

the dominance hierarchy functions as a queue in which males wait for mating opportunities.

Our third goal was to determine the relative importance for queue-jumping of particular demographic variables that are likely to contribute to two of the mechanisms of queue-jumping outlined above, solo competition and coalitionary behaviour. We tested the extent to which these demographic variables predicted the fit between observed and expected (priority-of-access) mating patterns.

METHODS

Study Population and Data Set

The study population resides in the Amboseli basin at the base of Mt Kilimanjaro and has been the subject of ongoing research since 1971 (e.g. Hausfater 1975; Altmann et al. 1988; Alberts & Altmann 1995a, b; Altmann et al. 1996). The data used in this analysis were collected routinely as part of daily monitoring of study groups. The current analysis involves data spanning 19 chronological years, 32 group-years, and six study groups (Alto's group and its fission products, and Hook's group and its fission products; Table 1, Fig. 1). We restricted our analysis to (1) the period after our data collection methods were completely standardized for both dominance rank and mate guarding (which occurred in approximately 1980), (2) periods in which groups were undergoing neither fusions nor fissions (processes that sometimes occurred over many months or even years) and (3) periods when we contacted each group at least several times per week. We also excluded the one study group (Lodge group) and its fission products that foraged part-time at a refuse site associated with a tourist lodge. We found that the priority-of-access model predicted reproductive success very well in Lodge group for the study period prior to 1989 (Altmann et al. 1996). However, this group experienced no immigration by nonnatal males and reduced emigration by natal males during 12 years of intensive monitoring. The consequence was that, after 1989, increased levels of relatedness between potential mating partners and resulting patterns of inbreeding avoidance were likely to add substantial and atypical variance to the relationship between male rank and mating success (Altmann et al. 1996; Alberts 1999).
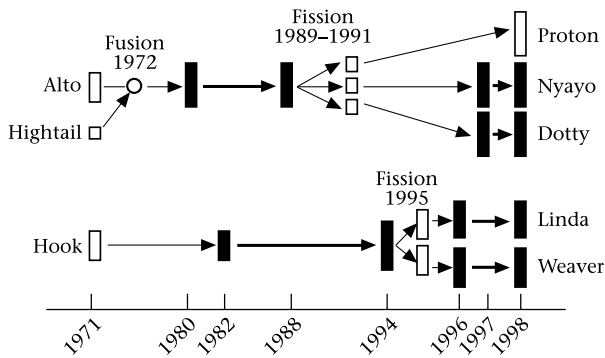
Figure 1. Amboseli study groups through time. Dark boxes and heavy lines represent groups and time periods for which data were analysed in this study. We restricted our analysis to periods when data collection methods were completely standardized, groups were not undergoing fission, and our observations of the group occurred at least several times per week. See Table 1.

Figure 2. Mean (±SE) absolute male dominance rank as a function of age. Numbers above points represent the number of males that contributed to the value. Arrow indicates average age at which adulthood is reached (Alberts & Altmann 1995a).

Baboon reproductive biology

Savannah baboons mate in the context of mate-guarding episodes, generally known as sexual consortships, which are conspicuous episodes of close, persistent following of females by males accompanied by sexual activity. Mate-guarding episodes may last from several hours to several days. Data on the identity of male and female partners in all mate-guarding episodes were collected routinely as part of regular daily monitoring of study groups.

Mate-guarding episodes occur while females are in the second half of the follicular phase of the sexual cycle. During this phase, females have sexual swellings that increase (turgesce) until around the time of ovulation. In the luteal phase of the cycle, the swelling decreases in size (deturgesces) until the sex skin is flat. The follicular phase lasts several weeks, but we restricted our analysis of mate guarding to the window of time 5 days before the onset of deturgescence, because this encompasses the period in which ovulation and conception are most likely to occur (Hendrickx & Kraemer 1969; Wildt et al. 1977; Shaikh et al. 1982). We calculated the duration of all consort time that occurred within 5 days before the onset of deturgescence, and considered this to represent the total available consort time of fertile females. We defined the mating success of each male as the proportion of this available consort time of fertile females that he obtained. Because this measure of mating success is a good predictor of genetic paternity in this population (Altmann et al. 1996), we view it as a good proxy for actual reproductive success in our population. Similar results have been reported for other wild mammal populations (e.g. red deer: Pemberton et al. 1992; longtailed macaques, *Macaca fascicularis*: de Ruiter et al. 1994; Soay sheep: Coltman et al. 1999: chimpanzees: Constable et al. 2001).

Dominance rank and fighting ability

Male dominance ranks were determined by assigning wins and losses in dyadic agonistic encounters between males. Males were considered to win agonistic encounters in which their opponent gave only submissive gestures,
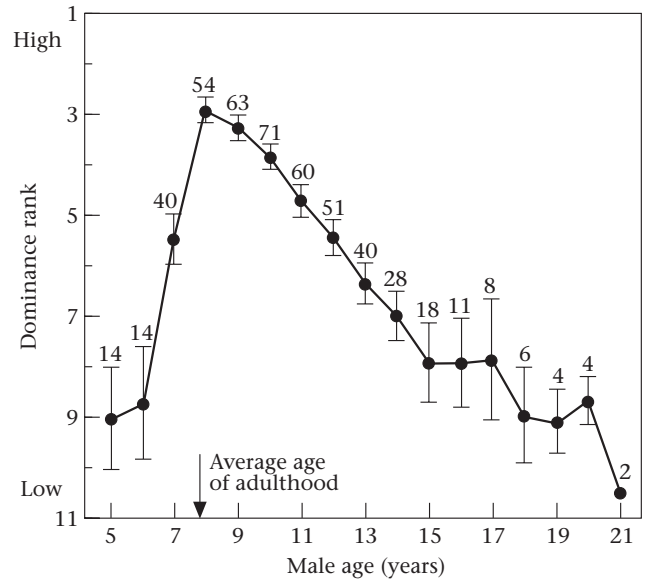
while they gave only aggressive or neutral (nonsubmissive) gestures (Hausfater 1975). This procedure of assigning wins and losses allowed the construction of a square matrix of interactions in which entries below the diagonal (which would represent wins by the lower-ranking animal) were few or zero.

Dominance rank is a good assay of fighting ability for male baboons (see discussions in Packer 1979a, b; Hamilton & Bulger 1990; Noë & Sluijter 1995). Two pieces of evidence support this view. First, dominance rank follows a striking pattern of age dependence in baboons; males attain high rank when they are young and in their prime, and fall in rank throughout their lives (Fig. 2; see also Packer et al. 2000). Second, dominance rank in male baboons does not change as a consequence of multiparty interactions or male coalitions (Packer 1977; J. Altmann & S. C. Alberts, unupublished data). Thus, dominance rank (as measured in this and most studies) reflects the outcome of repeated one-on-one conflicts between pairs of males, independent of social context or the influence of others.

Adult versus subadult males

Subadults were excluded from the current analysis; only adult males were included. Subadulthood was defined as the prolonged period of growth, low dominance rank and reproductive inactivity that males in many sexually dimorphic species experience after reaching puberty. Adulthood began when males attained a dominance rank among the adult males in their current social group (Alberts & Altmann 1995a). This was a discrete event, defined by the first nonreversed win in a dyadic interaction with another adult male, and occurred at a median age of 7.4 years. Newly adult males typically

rose quickly in the dominance hierarchy, winning over many other adult males in the group within a few months of their first nonreversed win (Hamilton & Bulger 1990; Alberts & Altmann 1995a).

We explicitly excluded subadults because Bercovitch (1986) and McMillan (1989) have raised the question of whether the correlation between rank and mating success was artificially inflated in some studies due to the inclusion of subadult males, who rank below adult males and do not engage in mate guarding. In the Amboseli population, it was extremely rare for subadult males to engage in mate guarding. Of 7623 consortships recorded over 32 group-years, only nine were attributable to subadult males. Of the subset of 3937 consortships that occurred within 5 days before the onset of deturgescence, only six were attributable to subadult males. These consortships by subadult males were always relatively brief, lasting between 20 min and 2 h. Thus, our exclusion of subadult males both avoided the concern raised by Bercovitch (1986) and McMillan (1989) and included all but a small fraction of mate-guarding episodes.

Immigrants versus natal males

During the majority of group periods, all adult males were immigrants. During some group periods (20/64), one adult male in the group was a natal male; during four group periods, two or more adult males were natal. After first attaining adulthood, natal males typically rose quickly in rank and emigrated within a few months. They usually engaged in mate guarding before emigrating (Alberts & Altmann 1995a). In two cases, natal males remained as high-ranking, and then as middle-ranking males in their natal groups for several years. Their mating behaviour was indistinguishable from that of immigrant males except that they each avoided their few female maternal relatives as mates (Alberts & Altmann 1995a, b).

Data partitioning

To identify variance in the relation between rank and mating success, we needed to partition the 32 group-years into shorter periods and to quantify the relation between rank and mating success for each short period. We partitioned the 32 group-years of data into 64 6-month group-periods for this analysis. As with any analysis of temporal variation, the duration of the periods used as the units of analysis is important because of the potential for lack of independence among successive periods, which would result in pseudoreplication of effects. Partitioning a large set of data on a temporal basis will inevitably result in some lack of independence between successive time periods. From another view point, not doing so (for instance, by treating the social group, rather than 6-month group-periods, as the unit of analysis) will obscure true temporal variance in the measures of interest. Our goal in choosing 6-month blocks was to maximize our ability to identify true variance in the relationship between rank and mating success while minimizing error variance and lack of independence. For the most part, our predictor variables showed variation on a time scale less than 6 months. The number of adult

males in each group changed, on average, every 2.9 months (range 1–14 months, median 2 months) through immigration, emigration, maturation and death. Rank tenure (rank stability) of the highest-ranking male averaged 8 months, and the range for mean rank tenure for each 6-month block was 1.3–26.5 months. However, rank stability of the second- and third-ranking males averaged only 2.8 months, and rank changes occurred somewhere in the male hierarchy every 1–2 months, on average. Hence, successive 6-month periods represented successive mixed sets of demographic conditions that varied substantially from one period to the next.

Data Analysis

Data analysis occurred in three steps. In the first step, we examined the correlation between rank and mating success, for comparison to other studies. In the second step, we tested the priority-of-access model for the entire 32 group-years pooled. In the third step, we used the partitioned data to examine variance in the fit to the priority-of-access model, and to identify predictors of the fit.

Step 1: correlation analysis

Using the partitioned data, we calculated Spearman's correlation coefficient between rank and mating success for each of the 64 6-month group-periods. We then examined the distribution of the 64 correlation coefficients and calculated their mean and standard error.

Step 2: testing the priority-of-access model using the pooled data

We obtained the proportion of all days during our 32 group-years on which only a single female was fertile (i.e. was within 5 days of the onset of deturgescence), the proportion of days when two females were fertile simultaneously, the proportion of days when three females were fertile simultaneously, and so on. The priority-of-access model predicts that when only one female is fertile, only the highest-ranking male will mate-guard, when two females are fertile, the highest- and second-ranking males will mate, and so on. Consequently, we used these data to predict the proportion of all available female consort time that should have been obtained by each male rank position. We compared these expected proportions with the observed proportion of all consort time of fertile females that was obtained by males of each rank, pooling over the entire 32 group-year period.

Step 3: examining variance in the fit to the priority-of-access model using the partitioned data

We examined variance in the relationship between male rank and mating success by calculating, for each 6-month group-period, the priority-of-access model expectation for the proportion of mate-guarding episodes obtained by males of each rank, and comparing that expectation to the observed proportions for that 6-month period. We then used a multiple regression analysis to examine the effect of five predictor variables on the

Table 2. The five predictor variables we evaluated for their effects on the relation between male dominance rank and mating success

Predictor variable	Predicted response of Departure-from-Model	Calculation
N adult males	Increases with increasing number of adult males	$\dfrac{\Sigma\ N\ \text{adult males each month}}{6}$
N adult females	Increases with increasing number of adult females	$\dfrac{\Sigma\ N\ \text{adult females each month}}{6}$
Age difference of the three highest-ranking males.	Increases as age difference decreases	$\dfrac{(\Sigma\ \text{AgeDiff}\ 1-2)+(\Sigma\ \text{AgeDiff}\ 2-3)}{12}$
Rank stability of highest-ranking male	Increases with shorter tenures	$\dfrac{\Sigma\ N\ \text{successive months in rank 1}}{6}$
Rank stability of 2nd- and 3rd-ranking males	Increases with shorter tenures	$\dfrac{\Sigma\ N\ \text{successive months in ranks 2 and 3}}{6}$

For each 6-month group-period, we used the mean value of each variable over those 6 months (second column).
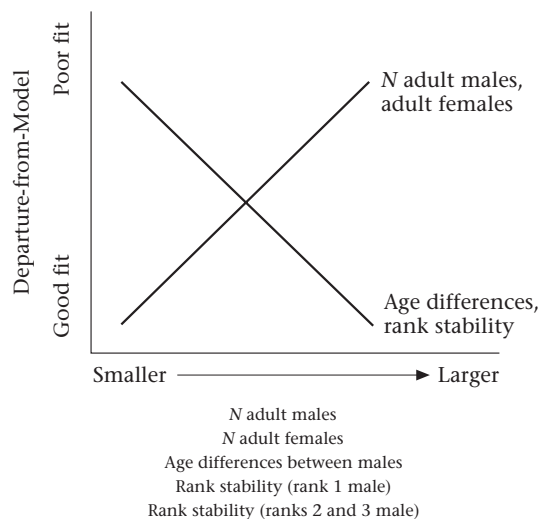

Figure 3. Schematic representation of predicted relation between predictor variables and the response variable, Departure-from-Model.

extent to which observed levels of mating success differed from expected.

Predictor variables. We identified five variables as predictors of the extent to which male rank affects mating success (Table 2, Fig. 3). We calculated, for each variable, its mean value within each group over each 6-month period (Appendix).

(1) Number of adult males in the group. Cowlishaw & Dunbar (1991, 1992) showed in their interspecific analysis that at small group sizes (low densities of males), rank is a good predictor of mating success, and at large group sizes (higher densities of males), rank is a relatively poor predictor of mating success. They proposed that this is because when more males are in the group, the highest-ranking male will receive more challenges, and hence more successful challenges, both from individuals and from coalitions; that is, both solo competition and coali-

tionary behaviour will be more successful as queue-jumping mechanisms. Hence, we expected a poorer fit to the priority-of-access model as male number increased (Fig. 3). Mean number of adult males for each 6-month block ranged from 2 to 14.2 in our data set (Appendix).

(2) Number of adult females in the group. Like number of adult males in the group, this is correlated with overall group size. It was also strongly correlated with number of adult males in our study (Spearman rank correlation: $r_S=0.70$, $N=64$, $P<0.0001$), a phenomenon found in both interspecific and intraspecific analyses (Andelman 1986; Mitani et al. 1996; Nunn 1999; Altmann 2000). We included it as a separate predictor variable from number of adult males because Cowlishaw & Dunbar (1991) proposed a different, independent mechanism by which it affects the relationship between male rank and mating success. They proposed that when more females are in the group, more of these females will be cycling at any one time, and because males cannot control access to more than one female at a time, this will weaken the relationship between rank and mating success (e.g. domestic cats: Say et al. 2001). However, the consequences of oestrous synchrony are already built into the priority-of-access model that we tested here. That is, the model's expectations for high-ranking males incorporate the fact that when females are synchronously fertile, high-ranking males are unable to monopolize them. Hence, including number of adult females as a predictor variable in our multiple regression was equivalent to asking, does the number of adult females, independent of the number of simultaneously fertile females, affect the extent to which the highest-ranking male monopolizes mating opportunities? This is a different question than that posed by Cowlishaw & Dunbar (1991) when they included number of adult females in their analysis. However, including the variable seemed important for comparative purposes with their study, and to clarify possible mechanisms by which number of adult females might affect male mating behaviour. Although it is difficult to conceive of a direct effect of number of adult females, independent of number of simultaneously fertile ones, on the relative

mating success of the highest-ranking male, indirect effects might occur. For instance, the number of adult females is a good predictor of male dispersal (Alberts & Altmann 1995b; Altmann 2000); thus, number of adult females might indirectly affect male–male competition through its effects on male dispersal. We predicted that, if number of adult females affects the fit to the priority-of-access model at all, it will affect it in the same manner as number of adult males; the fit to the priority-of-access model will be poorer as female number increases (Fig. 3). Mean number of adult females for each 6-month block ranged from 8.3 to 23.8 in our data set (Appendix).

(3) The mean age difference of the three highest-ranking adult males. As noted, male dominance rank is age dependent in baboons. Dominance rank peaks soon after attainment of adulthood, declines relatively mono-tonically during the rest of life and does not change as a consequence of coalitionary activity (Fig. 2; see also Packer et al. 2000). Thus, male dominance rank is a good measure of male fighting ability. Hence, when males are close in age, they are also likely to be close in fighting ability, and when they differ greatly in age, they usually will also differ greatly in fighting ability. We predicted that the solo competition strategy for queue-jumping, in which a lower-ranking male challenges a higher-ranking male for a mate-guarding opportunity without perma-nently changing rank positions, would be more effective when males were close in fighting ability. In such a situation, we might expect that cardinal ranks (quantita-tive measures of absolute rank differences), if they were available, should be more accurate predictors of the fit to the priority-of-access model than would the ordinal ranks that we obtained (Boyd & Silk 1983). That is, males may be of adjacent ordinal ranks and be close in fighting ability, particularly if they are close in age, or far apart in fighting ability, particularly if they are far apart in age. Therefore, we predicted that our data would not fit the priority-of-access model well when high-ranking males were closer in age (Fig. 3), because in this situation, we predicted that solo competition would be a more effective means of queue-jumping. In our data set, mean age difference of the three highest-ranking males ranged from 1 month ($N=10$ males/group) to 6.4 years ($N=4$ males/group; see Appendix).

(4) The rank stability of the highest-ranking male (how long he had been the highest-ranking male; see Table 2) and (5) the rank stability of the second- and third-ranking males both represent measures of social and demographic stability. We predicted that departure from the priority-of-access model would be greater with shorter rank tenure (greater rank instability). Cowlishaw & Dunbar (1991) hypothesized that rank instability reflects a situation in which several males are close to each other in fighting ability or resource holding potential. In such situations, ordinal ranks of two males may reverse frequently while their relative mating successes remain the same, weaken-ing the relation between rank and mating success. Alter-natively, males experiencing frequent rank changes may have to forgo mating opportunities while they attempt to maintain rank. This, too, will weaken the relationship between rank and mating success. We predicted that the

fit to the priority-of-access model would be good when ranks were stable for long periods, and would become poorer as high-ranking males changed ranks more often (Fig. 3). In our data set, mean rank stability ranged from 1.3 to 26.5 months for rank 1, and from 1.2 to 10.5 months for ranks 2 and 3 combined (Appendix).

The response variable, 'Departure-from-Model'. For the dependent variable in the multiple regression analysis, we needed a single measure of the extent to which observed mating success for each rank differed from that expected under the priority-of-access model. We identified three candidate response variables, each of which measured particular aspects of the observed–expected relationship as follows.

(1) The sum of the positive differences between observed and expected values across all rank positions ('SumDev'). Like the chi-square statistic, it uses the sum of the deviations between observed and expected. We were unable to use the chi-square statistic itself because it involves division of the squared deviation by the expected value; in our data set, a large number of expected values were equal to zero, which made the chi-square statistic (and others like it) impossible to cal-culate. However, SumDev captures the pattern of depar-ture from expected in a manner similar to the chi-square statistic, because it uses the same parameter as the numerator of the chi-square statistic.

(2) The rank position that acquired the largest pro-portion of female consort time in each 6-month block ('RankMax'). The priority-of-access model predicts that this will always be rank one (i.e. that the highest-ranking male will always acquire the largest proportion of female consort time).

(3) The mean proportion of female consort time obtained minus the median proportion of female consort time obtained ('Mean − Median'). This is a measure of skew in the distribution; when mate-guarding episodes are evenly distributed across males, the mean is equal to the median. The priority-of-access model predicts that the mean will always be larger than the median (i.e. that the distribution will always be skewed towards the highest-ranking male).

All three of these response variables captured important aspects of the extent to which observed mating success departed from expected mating success. The magnitude of the departure was particularly well captured by the first variable, and the second and third variables measured the pattern of departure and the extent of skew in the distribution. It was necessary to unite them into a single measure of the difference between observed and expected. We did so by combining them in a linear equation, which we termed Departure-from-Model:

Departure-from-Model=
$$0.84(\text{SumDev})+0.12(\text{RankMax}) - 0.21(\text{Mean} - \text{Median})$$

This linear equation is empirically derived from our data via a canonical correlation between our set of five predic-tor variables and our three response variables. Canonical correlation is used to analyse the correlation between two sets of variables (simple correlation is a special case of

canonical correlation, in which each set contains only one variable). For each set of variables, the canonical correlation returns linear equations ('canonical variables'; Dillon & Goldstein 1984; Allen et al. 1990) that describe the relationship within each set of variables that maximizes the correlation between the two sets.

Canonical correlation is often used to explore the manner in which the two sets of variables covary, so it would have been an appropriate method of analysing the relationship between our predictor and response variables. However, canonical correlation requires multivariate normality among the variables, which our data set did not have. Hence, we simply used the linear equation, Departure-from-Model, which was itself normally distributed, as the dependent variable in a multiple regression.

Multiple regressions. We next examined the multiple regression of our response variable (Departure-from-Model) on our five predictor variables. For each 6-month period for each group, we had a single value for each of the five predictor variables and a single value for Departure-from-Model, the response variable. We first performed the multiple regression for the entire data set, which encompassed 64 group-periods in six groups (Table 1, Fig. 1, Appendix). Our subsequent goal was to examine the six subsets of the data that corresponded to individual social groups alone, but the only two groups for which we had a reasonable sample size were Hook's group alone ($N=26$ group-periods) and Alto's group alone ($N=18$ group-periods). The response variable, Departure-from-Model, did not differ significantly from a normal distribution for these subsets of data.

In all three analyses, the same predictor variables emerged as either significant at $P<0.05$, or as tendencies with P values between 0.05 and 0.10. Because of our limited sample size, particularly for the two analyses examining individual social groups, we treated as potentially important all predictor variables with P values less than 0.10, and highlighted these predictor variables in our results (Tables 3–5).

RESULTS

Is the Dominance Hierarchy a Mating Queue?

Step 1: correlation results

The mean ($\pm$ SE) Spearman's coefficient for the correlation between male dominance rank and mating success over 64 group-periods was 0.56 ± 0.04 (range -0.7–1.00), and almost all (60 of 64 coefficients) were positive (Fig. 4). The distribution of correlation coefficients within our study population is similar to the intraspecific distribution reported by Bulger (1993, range -0.58–1.00, with 15 of 18 positive) and to the interspecific distribution reported by Cowlishaw & Dunbar (1991, range -0.63–1.00, with 28 of 37 positive).

Step 2: testing the priority-of-access model using the pooled data

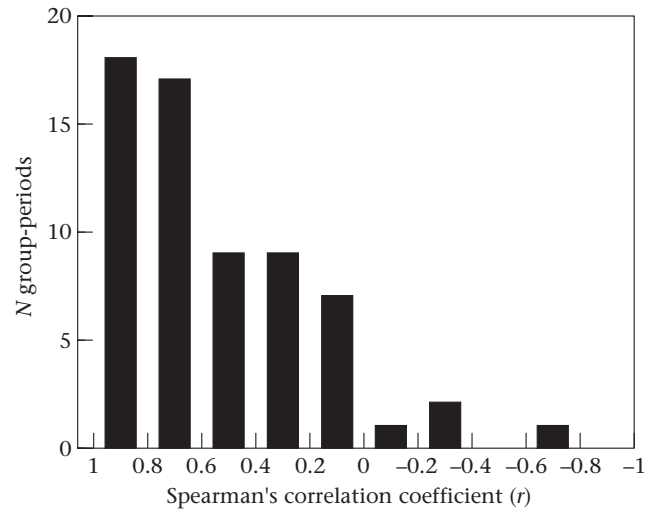The priority-of-access model tested for the entire 32 group-years pooled revealed that, although the highest

Figure 4. Frequency distribution of the correlation coefficients between male dominance rank and mating success for 64 group-periods in Amboseli.
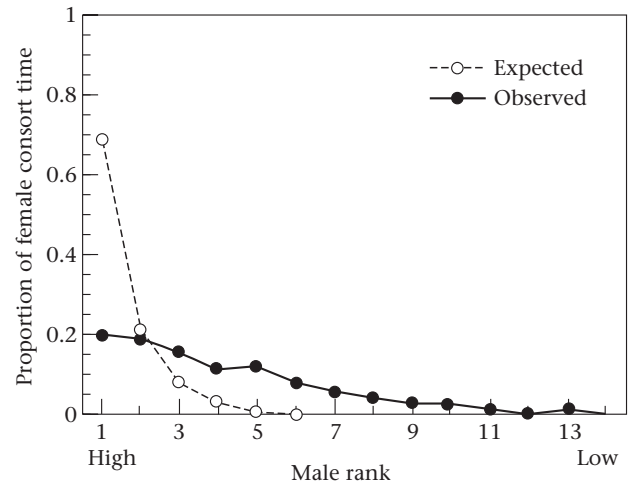

Figure 5. Expected proportion of female consort hours obtained by males of each rank, based on the priority-of-access model, and the observed proportion. Data are pooled over 32 group-years (i.e. many different males contribute to each observed value).

rank position obtained the largest proportion of female consort time, as predicted by the model, the quantitative fit of the data to the model was poor (Fig. 5). The largest departure was seen for rank 1; the priority-of-access model predicts that the highest-ranking male will obtain nearly 70% of the female consort time over the 32 group-years pooled, but the observed value was 20% (Fig. 5). Furthermore, the priority-of-access model predicts that males below rank 5 will obtain no consort time at all, but males as low as rank 13 obtained some (admittedly small) proportion of the available consort time of fertile females. In other words, although higher-ranking males obtained more mating access than did lower-ranking males, the dominance hierarchy does not function strictly as a queue over the long term.

Is the poor fit between observed and expected mating success because the dominance hierarchy never
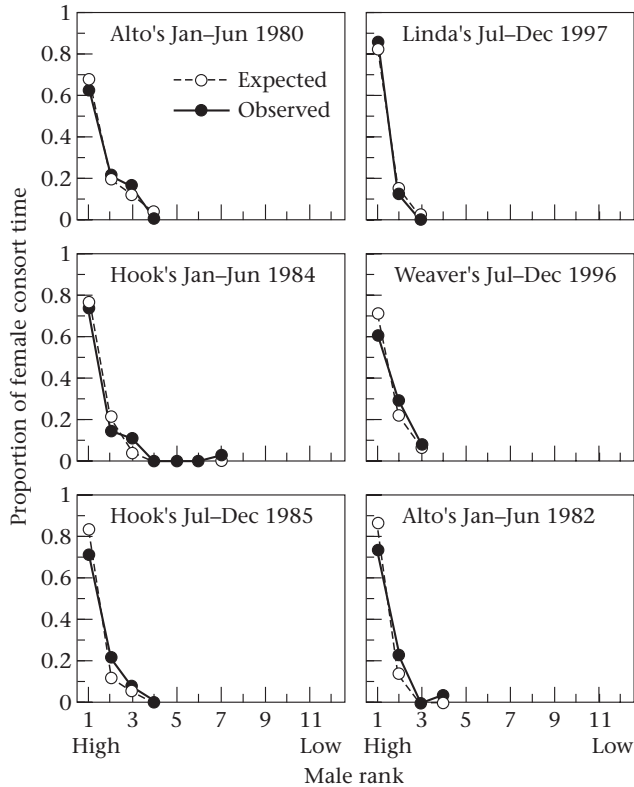
Figure 6. The six group-periods with the best fit to the priority-of-access model, as measured by our response variable, Departure-from-Model. These correspond to the six smallest values of Departure-from-Model (black bars, Fig. 8).

Figure 7. The six group-periods with the largest deviation from the priority-of-access model, as measured by our response variable, Departure-from-Model. These correspond to the six largest values of Departure-from-Model (black bars, Fig. 8).

effectively functions as a queue, so that the biological mechanism posited by the model is wrong? Or is it because the hierarchy sometimes functions as a queue, but at other times queue-jumping predominates? To address this question, we returned to the partitioned data.

Step 3: testing the priority-of-access model using the partitioned data

For some 6-month blocks, the priority-of-access model predicted nearly perfectly the proportion of mate guarding that each male obtained (Fig. 6). For other periods it did not do so at all (Fig. 7). No consistent pattern of departure from the priority-of-access model was apparent in those periods where the fit was poor; the examples shown in Fig. 7 are the most extreme cases of departure, and in each case the pattern of departure was slightly different. In all cases, however, the highest-ranking male obtained much less consort time than expected, and lower-ranking males obtained much more. This situation is different from that shown in Fig. 6, which reveals a very close fit between observed and expected in each of the periods.

Similarly, our response variable, Departure-from-Model, showed a wide range of values, with high values representing a poor fit to the priority-of-access model and low values representing a good fit (Fig. 8). These analyses make it evident that the extent to which the priority-of-
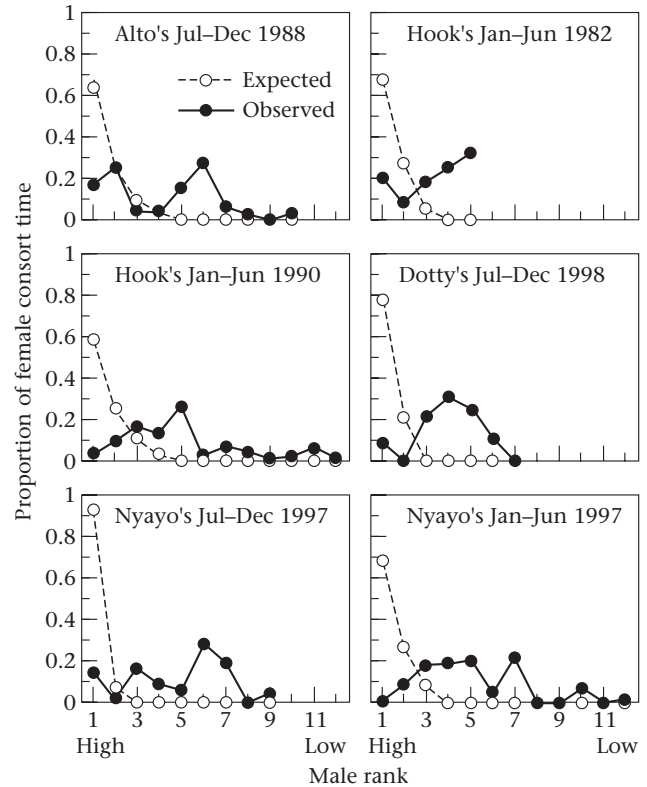
access model predicted male mating success was highly variable over time within a single population.

When Does the Queue Break Down?

Variables that predicted Departure-from-Model

Is this variability in the rank–mating success relationship stochastic, or is it structured in predictable ways? That is, how well do our predictor variables explain variance in Departure-from-Model?

Departure-from-Model was strongly predicted by the number of adult males, by the rank stability of the highest-ranking male, and to a lesser extent by the age differences of the three highest-ranking males (R^2_{adj}=0.40, $P<0.001$ for the whole model; $P=0.0064$, $P=0.0002$ and $P=0.0847$ for the partial regression coefficients; Table 3, Fig. 9). As number of adult males increased from 2 to 14.2, Departure-from-Model increased as predicted (Fig. 9). Similarly, as the highest-ranking male's tenure at rank increased from 1.3 to 26.5 months, Departure-from-Model decreased as predicted (Fig. 9). However, the observed effect of age differences was opposite to the predicted effect: when the three highest-ranking males were closer in age, Departure-from-Model was smaller (the fit to the priority-of-access model was better), and Departure-from-Model increased as age differences between males increased (Fig. 9). The number of adult females, and the rank stability of the second- and
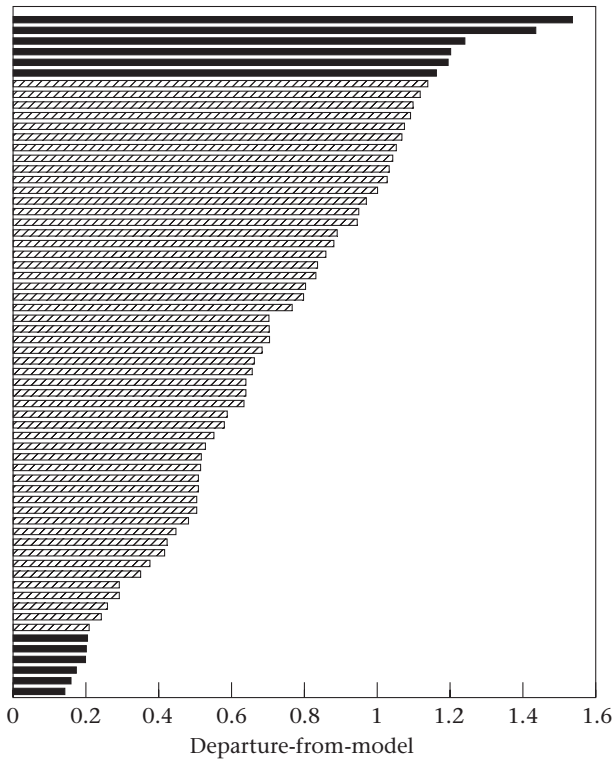
Figure 8. Values of Departure-from-Model, our measure of the extent to which observed male mating success matched the expectation of the priority-of-access model. Values for all 64 group-periods are shown, ordered by magnitude. The values for the six group-periods with the best fit (six smallest values) and the values for the six group-periods with the worst fit (six largest values) are in black (see Figs 6, 7).

third-ranking males did not contribute significantly to Departure-from-Model.

A similar pattern occurred in Alto's group alone, in spite of the much reduced sample size (N=18 group-periods). Number of adult males, rank stability of the highest-ranking male, and age differences contributed most to the model (R^2_{adj}=0.67, P=0.0016 for the whole model; P=0.1007, P=0.0626 and P=0.0306 for the partial regression coefficients; Table 4). For Hook's group alone (N=26 group-periods), the number of males in the group failed to contribute significantly to the overall model; only rank stability of the highest-ranking male and age differences among males had significant partial correlation coefficients (R^2_{adj}=0.39, P=0.0096 for the whole model; P=0.019 and P=0.0216 for the partial regression coefficients; Table 5). The fact that number of adult males had no effect in this data set may reflect that number of adult males was significantly less variable here than in the larger data set. Hook's group ranged from 6 to 11.8 males, compared to all group-periods excluding Hook's, which ranged from 2 to 14.2 males (Brown-Forsythe test of homogeneity of variance: $F_{1,62}$=24.55, P<0.0001), or compared to Alto's, which ranged from 3 to 14.2 males ($F_{1,42}$=6.996, P=0.0114). In other words, when variance in number of adult males is low (when male density does not change much in the data set), the rank stability of the highest-ranking male and the age differences of the
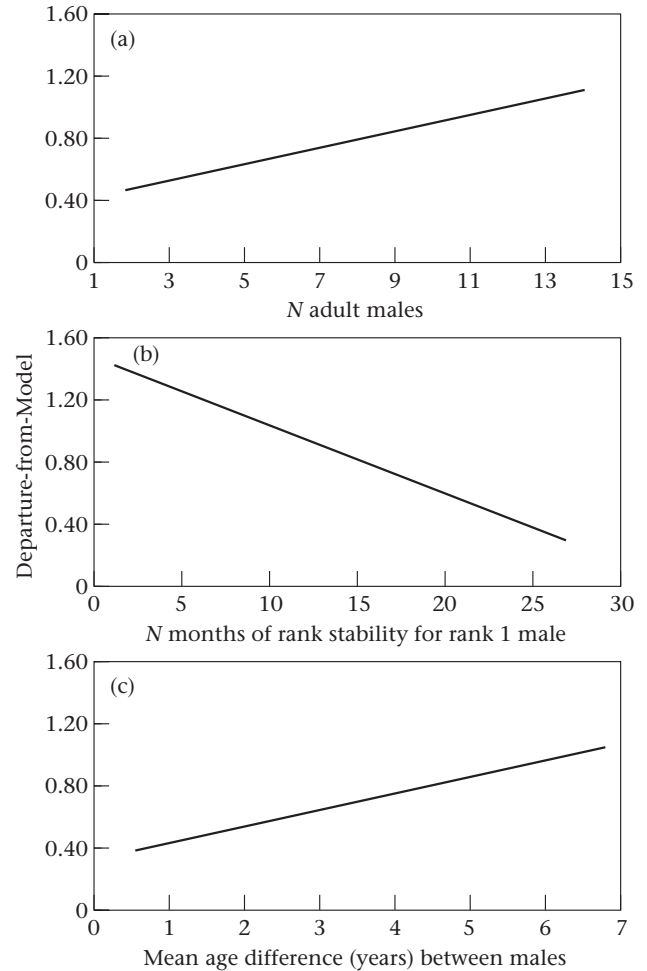

Figure 9. Observed effects on Departure-from-Model of (a) number of adult males, (b) rank stability of highest-ranking male, and (c) age differences between the three highest-ranking males. Slopes are based on the magnitude and sign of the partial regression coefficents (Table 3). X axes show actual ranges for the variables.

highest-ranking males contribute proportionately more to Departure-from-Model.

A posteriori tests

Did changes in male membership contribute to Departure-from-Model? Because the rank stability of the highest-ranking male and the number of adult males were important in predicting Departure-from-Model, we asked whether a different measure of demographic stability, variability in the number of adult males in each 6-month period, also predicted Departure-from-Model. That is, we wanted to know whether 6-month periods with more changes in the number of adult males were also 6-month periods in which Departure-from-Model was greater. Hence, in an a posteriori analysis, we added the coefficient of variation (CV) of the number of adult males in each 6-month period to the original multiple regression. The CV ranged from 0 to 0.38, but when added to the model, did not increase the proportion of variance explained. R^2_{adj} for the modified model was 0.41 (compared to 0.40 for the original model), and the partial

Table 3. Multiple regression of Departure-from-Model on five predictor variables (all group-periods pooled)

Source	R^2_{adj}	df	Mean square	F	P
Overall model					
Model	0.40	5	0.672	9.300	**<0.0001**
Error		58	0.072		
Total		63			
			Parameter		
Predictor variables		df	estimate	t ratio	P
Number of adult males		1	0.05	8.016	**0.0064**
Rank stability, (rank 1)		1	−0.03	1.336	**0.0002**
Age differences		1	0.07	3.077	**0.0847**
Number of adult females		1	0	0.0001	0.9934
Rank stability (ranks 2 and 3)		1	−0.002	0.008	0.9271

Among the predictor variables, P values ≤0.10 are in bold.

Table 4. Multiple regression of Departure-from-Model on five predictor variables (Alto's group alone)

Source	R^2_{adj}	df	Mean square	F	P
Overall model					
Model	0.67	5	0.214	7.949	**0.0016**
Error		11	0.027		
Total		16			
			Parameter		
Predictor variables		df	estimate	t ratio	P
Number of adult males		1	0.03	1.78	**0.1007**
Rank stability (rank 1)		1	−0.03	−2.05	**0.0626**
Age differences		1	0.21	2.45	**0.0306**
Number of adult females		1	0.05	1.38	0.1931
Rank stability (ranks 2 and 3)		1	−0.03	−1.07	0.3073

Among the predictor variables, P values ≤0.10 are in bold.

Table 5. Multiple regression of Departure-from-Model on five predictor variables (Hook's group alone)

Source	R^2_{adj}	df	Mean square	F	P
Overall model					
Model	0.39	5	0.270	4.142	**0.0096**
Error		20	0.065		
Total		25			
			Parameter		
Predictor variables		df	estimate	t ratio	P
Number of adult males		1	−0.01	−0.42	0.6759
Rank stability (rank 1)		1	−0.03	−3.56	**0.0019**
Age differences		1	0.23	2.49	**0.0216**
Number of adult females		1	0.01	0.58	0.5664
Rank stability (ranks 2 and 3)		1	0	0	0.9962

Among the predictor variables P values ≤0.10 are in bold.

regression coefficient for CV of number of adult males was not significant ($P=0.17$).

What predicted the rank stability of the highest-ranking male? We postulated that the tenure of the highest-ranking male at rank one, an important variable in predicting Departure-from-Model, would vary as a direct consequence of male demography. Consequently, we treated rank tenure of the highest-ranking male as the response variable in a multiple regression on three measures of male demography: number of adult males in the group, the coefficient of variation of the number of adult males and the age differences among the three highest-ranking males. The tenure of the highest-ranking

male was predicted most strongly by the number of adult males in the group, and not by variance in number of adult males or age differences between males ($R^2_{adj}=0.14$, $P=0.007$ for the whole model, $P=0.014$ for the partial regression coefficient of number of males; Table 6). However, most of the variance in rank stability remained unexplained by male demography.

Does Departure-from-Model show bias dependent on sample size? Finally, we examined Departure-from-Model to rule out the possibility of sample-size-dependent bias in this measure. Barton & Simpson (1992) pointed out that the correlation coefficient is not a true measure of the strength of the relationship between rank and mating

Table 6. Multiple regression of tenure (rank stability) of the highest-ranking male on demographic variables

Source	R^2_{adj}	df	Mean square	F	P
Overall model					
Model	0.14	3	143.0	4.408	**0.0072**
Error		60	32.4		
Total		63			
			Parameter		
Predictor variables		df	estimate	t ratio	P
Number of adult males		1	−0.75	−2.54	**0.0138**
CV of number of adult males		1	3.52	0.40	0.6885
Age differences		1	0.35	0.48	0.6365

Among the predictor variables, significant P values are in bold.

Table 7. Departure-from-Model does not show sample size-dependent bias

Number of males in sample	R^2_{adj}	Overall model (P)	N males (P of partial regression coefficient)*
≥3 (excluding periods with 2 males)	0.35	0.0001	**0.011**
≥4 (excluding periods with 2 or 3 males)	0.31	0.0003	**0.038**
≥5 (etc.)	0.30	0.0004	**0.091**
≥6	0.30	0.0007	**0.077**
≥7	0.38	0.0004	0.784
≤13 (excluding periods with >13 males)	0.41	0.0001	**0.003**
≤12 (excluding periods with >12 males)	0.41	0.0001	**0.003**
≤11 (etc.)	0.42	0.0001	**0.038**
≤10	0.41	0.0001	**0.034**
≤9	0.46	0.0001	0.144

Following Barton & Simpson (1992), we systematically excluded periods with small samples of males, and our model did not lose explanatory power, nor did number of males lose its effect until we reached ≥7 males. We also systematically excluded periods with a large rather than a small number of males; results indicate that this loss of effect was probably a result of the restricted range of the variable.
*P values ≤0.10 are in bold.

success, because it is biased by sample size. When only two males are in a group, the correlation coefficient can take on only two values, +1.0 and −1.0; when three males are in a group, it can take on only four values, and so on. Barton & Simpson performed a computer simulation that demonstrated a sample-size-dependent bias in the correlation coefficient. The nature of Departure-from-Model, which compares a single observed to a single expected value for each rank position, precludes a simple computer simulation of the type they performed (a resampling procedure from a cloud of points with an overall correlation of 0.7). However, following Barton & Simpson (1992), we did examine the effect of excluding from our analysis periods with small sample sizes. Barton & Simpson showed that when the smallest sample sizes (samples with two or three males) were excluded from Cowlishaw & Dunbar's (1991) analysis, the correlation between rank and mating success became nonsignificant. In contrast, our overall regression and the effect of number of males remained significant or as a trend when we successively excluded periods with fewer than 3, 4, 5 or 6 males (Table 7). The effect of number of males (but not the overall model) became nonsignificant when we excluded periods with fewer than seven males. However, this result was probably because our variable, number of

males, now had a limited range of values. In support of this interpretation, the same thing happened when we systematically excluded the periods with the largest rather than the smallest sample sizes. Both our overall regression and the number of males remained significant when we excluded periods with more than 13, 12, 11 and 10 males, but number of males lost significance when we excluded periods with more than nine males (Table 7).

DISCUSSION

Our results make three contributions towards resolving the ongoing debate over male rank and mating success in primates, and have general implications for understanding variance in mating success. First, they confirm the findings of a number of authors over the past several decades, that dominance rank is an important predictor of mating success for male baboons. A majority of correlations between rank and mating success in our study were positive; males who maintain high rank for extended periods will, on average, experience an overall advantage over males who fail to do so (Figs 4, 5).

Second, our results help to resolve the apparent contradictions between studies in whether dominance rank predicts mating success. The extent to which

high-ranking males monopolize access to fertile females varies, not only between populations and species (Cowlishaw & Dunbar 1991; Bulger 1993) but within a single population of a single species (Figs 6, 7, 8).

Third, we have identified key processes that contribute to this variance: density dependence of the ability to enforce queuing; age dependence of fighting ability and coalitionary activity; and individual differences in the ability to maintain high dominance rank. These processes are probably general to many social systems. We therefore predict that the patterns that we report here may apply to a wide range of mammalian species living in multifemale assemblages. Therefore, estimates of variance in mating success based on one-time measures of reproductive skew should not be taken as species typical (i.e. as robust measures of the constant force of selection on male fighting ability in a given species).

When is the Queue Not a Queue?

For some proportion of time, the dominance hierarchy functions as a queue in which male baboons wait for mating opportunities. This occurs when groups are small, when males in the group are relatively close in age, or when the highest-ranking male's position has been stable for long periods (Fig. 9). However, under some circumstances the highest-ranking male is unable to enforce queuing, and queue-jumping predominates. Queue-jumping is more common when many males are in the group (Fig. 9), which occurs more often when groups have many females and many fertile females (Altmann 2000). Queue-jumping is also prevalent when age differences between males in the group are large, or when the highest-ranking male has maintained his position for only a short time (Fig. 9).

Queue-jumping is density dependent

In our study, a high-ranking male's ability to monopolize access to fertile females was density dependent, a result comparable to that found in Cowlishaw & Dunbar's (1991) interspecific analysis. This will translate into density-dependent sexual selection on the ability to attain high dominance rank; when rank predicts mating success, selection on the ability to attain high rank will be relatively strong. When rank does not predict mating success, selection on the ability to attain high rank will be relaxed. Density-dependent sexual selection has been documented in a number of invertebrate and vertebrate species (McLain 1982; Conner 1989; Clutton–Brock et al. 1997; Pilastro et al. 1997; Coltman et al. 1999; Nielsen & Watt 2000). Density-dependent selection is a mechanism by which genetic variation may be maintained for traits that affect fitness, and is important to document in trying to understand how sexual selection has shaped mating strategies.

Queue-jumping depends on characteristics of the highest-ranking male

Cowlishaw & Dunbar (1991) predicted that high-ranking males will monopolize fertile females more successfully when the dominance hierarchy is more stable. Although our results are consistent with this prediction, the effect appears to depend only on the rank tenure of the highest-ranking male. The rank tenure of the second- and third-ranking males had no effect on Departure-from-Model, nor did variability in the number of males in a group. The rank tenure of the highest-ranking male depends, in turn, on how long he has been in the group and on his relative fighting ability. Thus, high-ranking males with low rank tenure may simply be males that have only been in the group for a short time. Alternatively, they may be males that have been resident in the group for some time but have changed ranks frequently, because when they reach rank one they do not have the fighting ability to maintain it (Table 2). Whichever of these is the more important in any given case, Departure-from-Model will depend heavily on the highest-ranking male's fighting ability and the time he has been in the group, and relatively little on characteristics of other males or on general demographic stability.

This result in turn supports the observation made by several authors (Smuts 1985; Noë & Sluijter 1990) that high-ranking males that have recently immigrated perform particularly poorly relative to priority-of-access expectations. Apparently, newly immigrant males must both achieve and then maintain high rank for an extended period before their status forces other males into a queue. Why should this be? Strum (1982) and Smuts (1985) assigned a relatively important role to female choice for long-resident males and to the social skills of these males in cultivating associations with females. However, Bercovitch (1995) has shown that, although female preferences have a measurable effect on male mate guarding, this effect is small relative to the effects of male strategies. An alternative explanation for the effect of rank stability on Departure-from-Model is that establishing high dominance rank may require substantial time and energy in the first months a male is in a group and may therefore preclude extensive mating activity.

The effect of age differences on queue-jumping

The effects of age differences were opposite in direction to what we predicted (cf. Fig. 3 and Fig. 9). We proposed that when the three highest-ranking males were close in age they would be less likely to queue, because the second- and third-ranking males would more successfully queue-jump through solo competition. In contrast, males were more likely to queue when age differences between high-ranking males were small, and the queue was more likely to break down when males in the group differed greatly in age. This finding rules out the possibility that small power differentials between high-ranking males inherently lead to rank instability and a breakdown of the priority-of-access queue. Apparently, high-ranking males with relatively small power differentials may coexist in a stable priority-of-access queuing system.

Why would Departure-from-Model be greater when males are further apart in age and presumably have larger power differentials? This pattern may reflect the fact that

coalition formation is both the major alternative mating strategy for male baboons and is expressed in a highly age-dependent fashion. When the second- and third-ranking males are far in age from the highest-ranking male, they are more likely to belong to the age group that engages in extensive coalitionary activity. This interpretation is supported by several lines of evidence. Noë & Sluijter (1990) found that high-ranking males gained the majority of their mating opportunities through individual contests, but middle-ranking males gained the majority of their consortships by forming coalitions with other males (see also Strum 1982; Smuts 1985). Bercovitch (1988) also noted that the most frequent coalition participants were middle- and low-ranking males. Noë & Sluijter (1990) and Bercovitch (1988) lacked age data, but we know that rank is age dependent in baboons (Packer et al. 2000; Fig. 2). Our results, in combination with those of others (Strum 1982; Smuts 1985; Bercovitch 1988; Noë & Sluijter 1990), strongly suggest that age-dependent expression of coalitionary activity may account for much of Departure-from-Model.

Male coalitionary behaviour, rank and queuing

Additional strong support for the hypothesis that male coalitionary activity is a major determinant of whether the dominance hierarchy functions as a queue in baboons comes from comparative data across subspecies. Studies of chacma baboons, *Papio c. ursinus*, consistently report both a total absence of male–male coalitionary behaviour and a near-perfect fit of observed data to the priority-of-access model, regardless of the number of males in the group (reviewed in Bulger 1993). In contrast, virtually all studies of yellow, *P. c. cynocephalus*, and anubis baboons, *P. c. anubis*, document both coalitionary activity and imperfect correlations between rank and mating success (Bulger 1993). The reasons for this subspecific difference in coalition behaviour remain obscure. Henzi et al. (1999) argue that chacma baboons, living in arid environments below the 23rd parallel, tend to live in smaller groups than do the other subspecies, which afford fewer opportunities for coalition formation and hence weaker selection on the behavioural tendency to form social alliances that might lead to coalitions. This inference is debatable, because chacma baboons in fact live in groups that range almost as greatly in size as do yellow and anubis baboons, even though the mean size is smaller (Henzi et al. 1999). However, the intriguing hypothesis remains that coalitionary behaviour simply has not evolved in chacma baboons, in contrast to the yellow and anubis subspecies (Henzi et al. 1999). Comparisons between baboon subspecies may yield great insight into both sexual selection in this species and the evolution of the complex behaviour of coalition formation.

Other Potentially Important Processes

The energetic demands of mate guarding

Mate guarding constrains foraging activity in male baboons (Packer 1979a; Alberts et al. 1996), and a substantial proportion of consortships end through aban-donment by the male (Bercovitch 1988). The costs of mate guarding reduce the potential of a single male to take advantage of the apparently greater mating opportunities that he would have when females cycle asynchronously rather than synchronously. This is because, when females cycle asynchronously year round, males may experience extended periods when fertile females are continuously or nearly continuously available. This will be especially likely in large groups with many females, and the energetic demands of mate guarding may constrain males from continuous guarding in these situations. Hence, although lack of synchrony generally will facilitate a state in which 'one male takes all', in general, this effect will be greater in small groups than in large groups because of the energetic demands of mate guarding. In the current study, increasing group size (measured here as increasing numbers of adult males) may have resulted in larger values of Departure-from-Model in part because, as group size increases, one or more oestrous females become more continuously available, and high-ranking males are unable to meet the energetic demands of continuous mate guarding.

The energetic demands of consorting may also have indirect effects on Departure-from-Model if it affects male mate choice. Female baboons in Amboseli vary in both their fertility and in the growth rates and survival of their offspring, providing a basis for male mate choice (Altmann 1997; J. Altmann & S. C. Alberts, unpublished data). Although male mate choice should be most evident when females are simultaneously in oestrus, males may also express mate choice when only one female is available. That is, even if a male has sufficient energy reserves for a particular mate-guarding episode, he may forgo the opportunity entirely if energetic demands are high and the available female is unpreferred.

Female choice

Evidence suggests that female choice may have an important effect on the fitness of individual male baboons at particular times (Seyfarth 1978a, b; Rasmussen 1983; Smuts 1985; Bercovitch 1995). Might female choice also be an important mechanism of queue-jumping over the long term, or are its effects small enough when measured at the population level that they will be swamped in the type of analysis presented here?

This remains an unanswered question. On one hand, detailed analyses of female preferences and their effects on behaviour during consortships suggest that these preferences exert only small effects on male mating success (Rasmussen 1983; Bercovitch 1995). Furthermore, chacma baboons, in which females do express preferences (Seyfarth 1978a, b) but males do not form coalitions (Bulger 1983; Henzi et al. 1999), consistently show very strong correlations between rank and mating success (reviewed in Bulger 1993). This result suggests that female choice does not affect the highest-ranking male's ability to enforce queuing most of the time, at least in chacma baboons.

On the other hand, female preferences require detailed data to measure, and female strategies for expressing

those preferences may be subtle and various. This means that it will be difficult to rule out female choice as a potential source of the unexplained variance in Departure-from-Model. Thus, female choice may not only have occasional consequences for the fitness of individual males; its effects may also be strong enough overall that it introduces significant variance in the relation between male rank and mating success. This issue will be difficult to resolve without extensive long-term data on female preferences, and more importantly good methods of quantifying potential effects of these preferences on mate guarding. Even if female choice is not an important source of variance in Departure-from-Model, developing bonds with females may still be important for individual males, depending on their demographic context and their consequent success with other strategies.

Implications for Male Life Histories and Sexual Selection

Why do young males queue and older males attempt to jump the queue?

The dominance hierarchy functions less effectively as a queue when males are very different in age. Why should this be? Males of different ages but of equal rank should be equally likely to jump the queue. If a male's dominance rank is three, for instance, he generally has a low probability of gaining consortships by queuing, regardless of his age (see expected values for males of rank three, Figs 5, 6, 7), and he should attempt queue-jumping more often than not. However, our data indicate that if he is relatively young (relatively close in age to the highest-ranking male), he is less likely to queue-jump than if he is much older than the highest-ranking male.

This puzzling result might have one of three different explanations. First, our conclusion, based on our results and the studies described above, is that the main mechanism of queue-jumping is coalition formation. This may be wrong. Female preference for longer resident, older males (Strum 1982; Smuts 1985) may be playing a larger role than we suppose. If this is true, it begs the question of why female choice acts differently in yellow and olive baboons than in chacma baboons, in which queue-jumping is rare or absent. Second, we may be correct that the main mechanism of queue-jumping is coalition formation, and young males may be attempting to form coalitions as frequently as older males, but may be less successful at doing so. This view is supported by data on coalition formation in other studies (Bercovitch 1988; Noë & Sluijter 1995), which suggest that middle- and low-ranking males (usually older males) view high-ranking (relatively young) males as poor coalition partners, perhaps because their fighting advantage means that they will disproportionately reap the benefits of the coalition. We therefore expect coalition formation by a particular male to be a function not only of his age, but of the age distribution of other males in the group. Third, young males may simply not attempt to form coalitions as frequently as older males (i.e. coalition formation may be truly age dependent and young males may lack

the flexibility to express this behaviour). This third explanation, if true, would be surprising. Baboons, like most primates, show remarkable behavioural flexibility. However, it remains a possibility that young males require considerable time to observe and develop the skill of coalition formation, and hence do not express this behaviour until middle age.

Regardless of when males begin to express alternative mating strategies, our evidence of queue-jumping, combined with results of many other studies (Packer 1977, 1979a; Strum 1982; Smuts 1985; Bercovitch 1988, 1995; Noë & Sluijter 1990, 1995; Bulger 1993) make it clear that male baboons do use alternatives to rank attainment and queuing for mating opportunities. Queue-jumping, the result of alternative strategies, may occur for a variety of reasons; to the extent that it relies on either coalitions or female choice, queue-jumping requires social skills and established relationships. Furthermore, males who do not successfully queue-jump as they age will suffer the equivalent of reproductive death as soon as they drop below rank three or four. The life-history consequences of this should result in strong selective pressure on males to engage in alternative strategies that allow queue-jumping. Although sexual selection has contributed to several obvious sexually dimorphic traits in baboons (large size, large canine teeth and a moderately developed mane on the head and shoulders, all expressed in males), it has clearly also acted on the ability of males, at least in the olive and yellow subspecies, to form complex social alliances with conspecifics of both sexes. A pressing question, again, is why this has not occurred in chacma baboon populations.

The effect of demographic context on male dispersal strategies

If demographic variables predict the relationship between rank and mating success, males should be selected to modify their dispersal strategies in response to particular demographic contexts, in a manner that is both age specific and also potentially highly individualistic. Between and sometimes within primate species, dispersal patterns can be understood as a means by which males simply distribute themselves across available females (Packer 1979b; Andelman 1986; Sussman 1992; Alberts & Altmann 1995b; Altmann 2000; Olupot & Waser 2001).

However, based on some intrapopulational studies, males do not preferentially disperse in ways that increase the number of fertile females they encounter (e.g. Borries 2000; van Noordwijk & van Schaik 2001). This may reflect the fact that, as our results emphasize, the best dispersal strategy will differ between males, depending on their relative age, their relative fighting ability, whether they have immature offspring in which they can invest, and the demographic structures of the social groups available to them (Altmann 2000). For instance, past-prime male baboons, if they cannot locate groups in which they can attain and maintain the highest rank position, may do better by seeking out larger groups in which they can form coalitions with other males. Some such males, however, may maximize their mating success

by remaining as long residents in groups where they have developed social bonds with females (Strum 1982; Smuts 1985; Bercovitch 1995), or where they have immature offspring in which to invest. Young males, in contrast, should tend to seek small groups in which they can maintain high rank for long periods, even if overall female availability is low in such groups. Dispersal patterns should thus reflect both characteristics of the individual (age, relative fighting ability, residence and relationship patterns) and demographic characteristics of social groups (age structure of adult males, and group size).

Summary

The disproportionate acquisition of mating opportunities by a small subset of individuals in the population (reproductive skew) has important evolutionary consequences. It may represent differences in relative fitnesses among phenotypes, with greater variance resulting in larger fitness differences among individuals and stronger selection on the traits that contribute to the variance. One of the central goals of behavioural ecology can be described as understanding behavioural sources of reproductive variance within species, and of differences in reproductive variance between species.

Our results indicate considerable short-term variance in the extent to which attaining high rank results in improved mating success for male baboons. This variance probably translates into variance in the strength of selection on fighting ability. However, on average, males that attain high rank will experience fitness advantages over those that do not. Furthermore, successful coalitionary activity itself probably depends on fighting ability (Bercovitch 1988; Noë & Sluijter 1995). Thus, our results and those of others suggest that fighting ability remains important to males throughout their lives and plays a continuous, critical role in determining mating success.

A number of key questions remain. The roles of female choice and energetic constraints remain unclear in producing the patterns described here and in a number of species with mating systems similar to that of baboons. The behavioural difference between chacma and other savannah baboons seems a critical and understudied phenomenon that may have general relevance for population-level differences in male mating behaviour in other species. Finally, to what extent do males modify their dispersal strategies in response not just to female availability, but to their own prospects for mating and contributing to offspring survival in different demographic contexts? These remain open questions to study in baboons and other mammalian species living in multifemale assemblages.

Acknowledgments

References

Alberts, S. C. 1999. Paternal kin discrimination in wild baboons. *Proceedings of the Royal Society of London, Series B,* **266,** 1501–1506.

Alberts, S. C. & Altmann, J. 1995a. Preparation and activation: determinants of age at reproductive maturity in male baboons. *Behavioral Ecology and Sociobiology,* **36,** 397–406.

Alberts, S. C. & Altmann, J. 1995b. Balancing costs and opportunities: dispersal in male baboons. *American Naturalist,* **145,** 279–306.

Alberts, S. C., Altmann, J. & Wilson, M. L. 1996. Mate guarding constrains foraging activity of male baboons. *Animal Behaviour,* **51,** 1269–1277.

Alcock, J., Jones, C. E. & Buchmann, S. L. 1977. Male mating strategies in the bee *Centris pallida* Fox (Hymenoptera: Anthrophoridae). *American Naturalist,* **111,** 145–155.

Allen, J. F., Ashton, J. J., Cohen, B. L., Cornell, R. J., Early, R., Luginbuhl, R. C., Gear, J. C., Meek, G., Schlotzhauer, S. D. & Yeo, C. 1990. Chapter 15: The CANCORR procedure. In: *SAS/STAT User's Guide.* Cary, North Carolina: SAS Institute.

Altmann, S. A. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta. Annals of the New York Academy of Sciences,* **102,** 338–435.

Altmann, J. 1997. Mate choice and intrasexual reproductive competition: contributions to reproduction that go beyond acquiring more mates. In: *Feminism and Evolutionary Theory* (Ed. by P. A. Gowaty), pp. 320–333. New York: Chapman & Hall.

Altmann, J. 2000. Models of outcome and process: predicting the number of males in primate groups. In: *Primate Males: Causes and Consequences of Variation in Group Composition* (Ed. by P. M. Kappeler), pp. 236–247. Cambridge: Cambridge University Press.

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

Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D., Mututua, R. S., Sayialel, S. N., Wayne, R. K., Lacy, R. C. & Bruford, M. W. 1996. Behavior predicts genetic structure in a wild primate group. *Proceedings of the Naional Academy of Sciences, U.S.A.,* **93,** 5797–5801.

Andelman, S. J. 1986. Ecological and social determinants of cerco-pithecine mating patterns. In: *Ecology and Social Evolution: Birds and Mammals* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 201–216. Princeton, New Jersey: Princeton University Press.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Barton, R. A. & Simpson, A. J. 1992. Does the number of males influence the relationship between dominance and mating success in primates? *Animal Behaviour*, **44**, 1159–1161.

Bercovitch, F. B. 1986. Male rank and reproductive activity in savanna baboons. *International Journal of Primatology*, **7**, 533–550.

Bercovitch, F. B. 1988. Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour*, **36**, 1198–1209.

Bercovitch, F. B. 1992a. Re-examining the relationship between rank and reproduction in male primates. *Animal Behaviour*, **44**, 1168–1170.

Bercovitch, F. B. 1992b. Dominance rank, reproductive success and reproductive tactics in male primates: a reply to Dunbar and Cowlishaw. *Animal Behaviour*, **44**, 1174–1182.

Bercovitch, F. B. 1995. Female cooperation, consortship mainten-ance, and male mating success in savanna baboons. *Animal Behaviour*, **50**, 137–149.

Berenstain, L. & Wade, T. D. 1983. Intrasexual selection and male mating strategies in baboons and macaques. *International Journal of Primatology*, **4**, 201–235.

Bernstein, I. S. 1981. Dominance: the baby and the bathwater. *Behavioral and Brain Sciences*, **4**, 419–457.

Borries, C. 2000. Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. In: *Primate Males: Causes and Consequences of Variation in Group Composition* (Ed. by P. M. Kappeler), pp. 146–158. Cambridge: Cambridge University Press.

Bourke, A. F. G. 1997. Sociality and kin selection in insects. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 203–227. Oxford: Blackwell Scientific.

Boyd, R. & Silk, J. 1983. A method for assigning cardinal dominance ranks. *Animal Behaviour*, **31**, 45–58.

Bulger, J. B. 1993. Dominance rank and access to estrous females in male savanna baboons. *Behaviour*, **127**, 67–103.

Carpenter, C. R. 1942. Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). I. Specimens, procedures and behav-ioral characteristics of estrus. *Journal of Comparative Psychology*, **33**, 113–142.

Chapais, B. 1983. Reproductive activity in relation to male domi-nance and the likelihood of ovulation in rhesus monkeys. *Behavioral Ecology and Sociobiology*, **12**, 215–228.

Clutton–Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press.

Clutton–Brock, T. H., Rose, K. E. & Guinness, F. E. 1997. Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society of London, Series B*, **264**, 1509–1516.

Coltman, D. W., Bancroft, D. R., Robertson, A., Smith, J. A., Clutton–Brock, T. H. & Pemberton, J. M. 1999. Male reproduc-tive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology*, **8**, 1199–1209.

Conner, J. 1989. Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. *Evolution*, **43**, 1378–1386.

Constable, J., Ashley, M., Goodall, J. & Pusey, A. 2001. Non-invasive paternity assignment in Gombe chimpanzees. *Molecular Ecology*, **10**, 1279–1300.

Cowlishaw, G. & Dunbar, R. I. M. 1991. Dominance rank and mating success in male primates. *Animal Behaviour*, **41**, 1045–1056.

Cowlishaw, G. & Dunbar, R. I. M. 1992. Dominance and mating success: a reply to Barton and Simpson. *Animal Behaviour*, **44**, 1162–1163.

Cuthill, I. C. & Macdonald, W. A. 1990. Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. *Behavioral Ecology and Sociobiology*, **26**, 209–216.

DeVore, I. 1965. Male dominance and mating behavior in baboons. In: *Sex and Behavior* (Ed. by F. A. Beach), pp. 266–289. New York: J. Wiley.

Dewsbury, D. A. 1982. Dominance rank, copulatory behavior and differential reproduction. *Quarterly Review of Biology*, **57**, 135–159.

Dillon, W. R. & Goldstein, M. 1984. *Multivariate Analysis: Methods and Applications*. New York: J. Wiley.

Dunbar, R. I. M. & Cowlishaw, G. 1992. Mating success in male primates: dominance rank, sperm competition and alternative strategies. *Animal Behaviour*, **44**, 1171–1173.

Ellis, L. 1995. Dominance and reproductive success among non-human animals: a cross-species comparison. *Ethology and Socio-biology*, **16**, 257–333.

Emlen, S. T. 1995. An evolutionary theory of the family. *Proceedings of the National Academy of Sciences, U.S.A.*, **92**, 8092–8099.

Emlen, S. T. 1997. Predicting family dynamics in social vertebrates. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 228–253. Oxford: Blackwell Scientific.

Engh, A. L., Funk, S. M., Van Horn, R. C., Cribner, K. T., Bruford, M. W., Libants, S., Szykjam, M., Smale, L. & Holekamp, K. E. 2002. Reproductive skew among males in a female-dominated mammalian society. *Behavioral Ecology*, **13**, 193–200.

Fedigan, L. M. 1983. Dominance and reproductive success in primates. *Yearbook of Physical Anthropology*, **26**, 91–129.

Gibbs, H. L., Weatherhead, P. J., Boag, P. T., White, B. N., Tabak, L. M. & Hoysak, D. J. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science*, **250**, 1394–1397.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature*, **313**, 47–48.

Hamilton, W. J., III & Bulger, J. B. 1990. Natal male baboon rank rises and successful challenges to resident alpha males. *Behavioral Ecology and Sociobiology*, **26**, 357–362.

Hausfater, G. 1975. *Dominance and Reproduction in Baboons* (Papio cynocephalus). Basel: Karger.

Hendrickx, A. G. & Kraemer, D. C. 1969. Observations on the menstrual cycle, optimal mating time and pre-implantation embryos of the baboon, *Papio anubis* and *Papio cynocephalus*. *Journal of Reproduction and Fertility, Supplement*, **6**, 119–128.

Henzi, S. P., Weingrill, T. & Barrett, L. 1999. Male behaviour and the evolutionary ecology of chacma baboons. *South African Journal of Science*, **95**, 240–242.

Keller, L. & Reeve, H. K. 1994. Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution*, **9**, 98–102.

LeBoeuf, B. J. 1974. Male–male competition and reproductive success in elephant seals. *American Zoologist*, **14**, 163–176.

McLain, D. K. 1982. Density-dependent sexual selection and posi-tive phenotypic assortative mating in natural populations of the soldier beetle, *Chauliognathus pennsylvanicus*. *Evolution*, **36**, 1227–1235.

McMillan, C. 1989. Male age, dominance, and mating success among rhesus monkeys. *American Journal of Physical Anthropology*, **80**, 83–89.

Manson, J. 1992. Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, **44**, 405–416.

Maslow, A. 1936. The role of dominance in the social and sexual behavior of infra-human primates: observations at Vilas Park Zoo. *Journal of Genetic Psychology*, **48**, 261–277.

Mitani, J. C., Gros-Louis, J. & Manson, J. H. 1996. Number of males in primate groups: comparative tests of competing hypotheses. *American Journal of Primatology*, **38**, 315–332.

Moore, N. P., Kelly, P. F., Cahill, J. P. & Hayden, T. J. 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behavioral Ecology and Sociobiology*, **36**, 91–100.

Nielsen, M. G. & Watt, W. B. 2000. Interference competition and sexual selection promote polymorphism in *Colias* (Lepidoptera, Pieridae). *Functional Ecology*, **14**, 718–730.

Noë, R. & Sluijter, A. A. 1990. Reproductive tactics of male savanna baboons. *Behaviour*, **113**, 117–170.

Noë, R. & Sluijter, A. A. 1995. Which adult male savanna baboons form coalitions? *International Journal of Primatology*, **16**, 77–105.

van Noordwijk, M. A. & van Schaik, C. P. 2001. Career moves: transfer and rank challenge decisions by male long-tailed macaques. *Behaviour*, **138**, 359–395.

Nunn, C. L. 1999. The number of males in primate social groups: a comparative test of the socioecological model. *Behavioral Ecology and Sociobiology*, **46**, 1–13.

Olupot, W. & Waser, P. M. 2001. Correlates of intergroup transfer in male grey-cheeked mangabeys. *International Journal of Primatology*, **22**, 169–187.

Packer, C. 1977. Reciprocal altruism in *Papio anubis*. *Nature*, **265**, 441–443.

Packer, C. 1979a. Male dominance and reproductive activity in *Papio anubis*. *Animal Behaviour*, **27**, 37–45.

Packer, C. 1979b. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Animal Behaviour*, **27**, 1–36.

Packer, C., Collins, D. A. & Eberly, L. E. 2000. Problems with primate sex ratios. *Philosophical Transactions of the Royal Society of London*, **355**, 1627–1635.

Parker, G. A. 1970. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. IV. Epigamic recognition and competition between males for the possession of females. *Behaviour*, **37**, 113–139.

Pemberton, J. M., Albon, S. D., Guinness, F. E., Clutton–Brock, T. H. & Dover, G. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behavioral Ecology*, **3**, 66–75.

Pilastro, A., Giacomello, E. & Bisazza, A. 1997. Sexual selection for small size in male mosquitofish (*Gambusia holbrooki*). *Proceedings of the Royal Society of London, Series B*, **264**, 1125–1129.

Poole, J. H. 1989. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour*, **37**, 842–849.

Preston, B. T., Stevenson, I. R., Pemberton, J. M. & Wilson, K. 2001. Dominant rams lose out by sperm production. *Nature*, **409**, 681–682.

Rasmussen, K. L. R. 1983. Influence of affiliative preferences upon the behaviour of male and female baboons during sexual consortships. In: *Primate Social Relationships: an Integrated Approach* (Ed. by R. A. Hinde), pp. 116–120. Oxford: Blackwell Scientific.

Reeve, H. K. 2000. A transactional theory of within-group conflict. *American Naturalist*, **155**, 365–382.

Reeve, H. K. & Keller, L. 2001. Tests of reproductive-skew models in social insects. *Annual Review of Entomology*, **46**, 347–385.

de Ruiter, J. R., van Hooff, J. A. R. A. M. & Scheffrahn, W. 1994. Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour*, **129**, 203–224.

Say, L., Pontier, D. & Natoli, E. 2001. Influence of oestrus synchronization on male reproductive success in the domestic cat (*Felis catus* L.). *Proceedings of the Royal Society of London, Series B*, **268**, 1049–1053.

Seyfarth, R. M. 1978a. Social relationships among adult male and female baboons. I. Behaviour during sexual consortship. *Behaviour*, **64**, 204–226.

Seyfarth, R. M. 1978b. Social relationships among adult male and female baboons. II. Behaviour throughout the female reproductive cycle. *Behaviour*, **64**, 227–247.

Shaikh, A. A., Celaya, C. L., Gomez, I. & Shaikh, S. A. 1982. Temporal relationship of hormonal peaks to ovulation and sex skin deturgescence in the baboon. *Primates*, **23**, 444–452.

Smuts, B. B. 1985. *Sex and Friendship in Baboons*. New York: Aldine.

Strum, S. C. 1982. Agonistic dominance in male baboons: an alternative view. *International Journal of Primatology*, **3**, 175–202.

Suarez, B. & Ackerman, D. 1971. Social dominance and reproductive behavior in male rhesus monkeys. *American Journal of Physical Anthropology*, **35**, 219–222.

Sussman, R. W. 1992. Male life history and intergroup mobility among ringtailed lenurs (*Lemur catta*). *International Journal of Primatology*, **13**, 395–414.

Vehrencamp, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, **31**, 667–682.

Wildt, D. E., Doyle, L. L., Stone, S. C. & Harrison, R. M. 1977. Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology, and ovarian follicular development during the baboon reproductive cycle. *Primates*, **18**, 261–270.

Appendix

Table A1. Demographic variables and values of Departure-from-Model for each of the 64 group-periods used in the analysis

Group	Period	Mean number of adults		Mean rank tenure		Mean age difference (years)	Departure-from-Model
		Males	Females	Rank 1 (months)	Ranks 2 and 3 (months)		
Alto's	1980–1	3.00	15.50	13.50	9.50	2.07	0.1367
	1980–2	4.33	17.00	7.00	5.17	1.75	0.5088
	1981–1	6.00	17.00	6.50	2.83	1.37	0.7972
	1981–2	6.00	17.00	12.50	5.50	1.60	0.4754
	1982–1	6.50	17.17	18.50	2.83	1.68	0.1979
	1982–2	8.67	17.83	12.50	1.33	1.27	0.5758
	1983–1	11.00	18.00	6.50	1.33	1.15	0.6971
	1983–2	12.00	18.33	12.50	2.00	2.74	1.0715
	1984–1	13.33	17.67	7.17	2.00	0.57	0.6998
	1984–2	11.00	17.00	2.33	1.83	0.65	0.6579
	1985–1	11.33	19.00	3.50	2.67	0.66	0.4381
	1985–2	14.17	18.00	2.33	1.67	0.46	0.9649
	1986–1	13.33	18.33	4.83	2.17	0.99	0.7613
	1986–2	11.00	20.17	2.33	1.17	2.04	1.0463
	1987–1	13.50	18.83	5.50	4.50	1.68	0.9409
	1987–2	12.17	17.50	6.00	2.00	0.83	0.8345
	1988–1	12.00	19.17	6.50	5.17	1.09	0.8546
	1988–2	10.33	21.50	6.17	1.67	1.31	1.1575
Nyayo's	1997–1	11.33	14.33	7.50	3.50	2.11	1.5283
	1997–2	10.00	15.00	3.50	3.50	1.59	1.4282
	1998–1	8.17	15.67	9.50	9.50	1.59	0.5779
	1998–2	9.00	16.00	1.67	1.50	2.05	0.8786
Dotty's	1997–1	5.50	14.00	2.17	1.17	1.36	1.0022
	1997–2	6.83	13.17	5.50	2.33	3.49	0.8877
	1998–1	8.00	13.17	2.17	1.67	1.25	1.1387
	1998–2	7.50	14.00	7.50	2.83	2.21	1.2345
Hook's	1982–1	6.83	15.33	3.17	1.17	2.24	1.1881
	1982–2	7.00	16.00	2.17	1.67	0.30	1.1150
	1983–1	8.17	13.50	7.50	1.67	0.84	0.6494
	1983–2	8.33	13.00	8.83	1.83	0.30	0.6797
	1984–1	8.00	13.83	5.50	5.50	0.23	0.1639
	1984–2	7.33	13.00	11.50	1.17	0.31	0.2849
	1985–1	6.00	12.17	17.50	2.17	1.00	0.4154
	1985–2	6.67	13.67	23.50	3.00	1.17	0.1941
	1986–1	7.33	15.00	24.33	4.00	2.33	0.5022
	1986–2	9.00	17.67	2.50	1.83	1.17	0.4950
	1987–1	9.83	18.00	6.50	2.33	0.47	0.4966
	1987–2	8.83	19.33	12.50	1.67	0.61	0.3469
	1988–1	7.67	19.67	18.50	4.50	0.51	0.2873
	1988–2	9.83	22.17	20.17	2.67	1.71	0.6322
	1989–1	9.67	23.00	4.50	2.00	1.16	0.5470
	1989–2	10.33	22.83	4.00	2.33	0.76	0.5221
	1990–1	10.50	20.83	1.33	1.17	1.23	1.1985
	1990–2	8.83	20.67	5.50	4.50	0.15	1.0633
	1991–1	9.50	21.83	3.00	1.50	0.63	0.6285
	1991–2	11.00	19.67	3.00	2.50	0.53	1.0923
	1992–1	11.83	21.50	4.17	1.67	0.76	0.7948
	1992–2	10.00	23.00	5.50	2.17	0.05	0.5088
	1993–1	7.17	23.83	2.83	2.17	0.36	0.8289
	1993–2	8.50	22.67	3.50	2.67	1.25	1.0913
	1994–1	9.83	20.17	6.50	2.50	1.25	1.0255
	1994–2	8.17	16.67	4.17	2.83	1.13	1.0326
Linda's	1996–1	5.33	8.33	2.67	1.33	4.71	1.0405
	1996–2	3.00	9.00	8.50	2.50	2.96	0.5046
	1997–1	3.17	9.00	14.50	3.67	3.16	0.2369
	1997–2	2.83	9.67	20.50	4.50	4.14	0.1539
	1998–1	2.00	11.17	26.50	10.50	3.62	0.2551
	1998–2	3.83	12.00	11.83	1.50	2.87	0.4110

Table A1. *Continued*

Group	Period	Mean number of adults		Mean rank tenure		Mean age difference (years)	Departure-from-Model
		Males	Females	Rank 1 (months)	Ranks 2 and 3 (months)		
Weaver's	1996–1	2.67	8.33	8.50	2.83	2.09	0.2014
	1996–2	3.67	9.50	14.50	2.00	6.41	0.1883
	1997–1	4.33	11.50	5.50	2.33	2.69	0.6347
	1997–2	6.83	13.00	8.50	2.83	2.25	0.9503
	1998–1	6.00	13.00	2.00	1.33	2.56	0.6980
	1998–2	6.00	13.00	3.50	2.67	3.74	0.3681

'Period' indicates the year followed by 1 (for 6-month blocks from January to June) or 2 (for 6-month blocks from July to December). Table 3 describes how each predictor variable was calculated; see text for calculation of Departure-from-Model.