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Determinants of Reproductive Success in Savannah Baboons, *Papio cynocephalus*

Jeanne Altmann, Glenn Hausfater, and Stuart A. Altmann

BABOONS (FIG. 25.1) ARE AMONG the largest, most sexually dimorphic, and most terrestrial of monkeys. The presence in baboons of externally visible correlates of reproductive physiology (Gillman 1935; Gillman and Gilbert 1946; Kriewaldt and Hendrickx 1968; S. Altmann 1970) aids studies of their reproductive success, and their ground-dwelling habit in the African grasslands facilitates observation. Conversely, other characteristics of baboons—their slow maturation, litter size of one, long period of parental care, behavioral flexibility, and long adulthood that spans changing ecological and social conditions—all complicate attempts to measure and account for reproduc-



Figure 25.1: Savannah baboons, *Papio cynocephalus*, in Amboseli National Park.

tive success. However, based on over thirteen years of data from known individual savannah baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya, we can now provide fairly good estimates for some reproductive and survival parameters and tentative estimates for others.

Despite the emphasis on male behavior and mating success in the first studies of this and other primate species, knowledge of males' life histories remains much less complete than knowledge of females'. Male baboons take several years longer to reach full maturity. They are the sex that disperses: they leave their natal group near maturity and sometimes change groups once or more during adulthood. One often cannot determine what has happened to a male that disappears from a group or determine his reproductive success in a new group even if one knows that he successfully transferred. For the same reason, one does not usually have much prior information on males that immigrate into study groups. In addition, information about paternity, particularly in noninterventive studies but also in studies that have included attempts at genetic analysis, remains much poorer than for maternity. Consequently, our analyses of female reproductive success are more complete than those of male success.

25.1 Background

The data on which this chapter is based come from almost daily records on all individuals of "Alto's Group," a group that varied in size from about thirty-five to sixty-five during the study period, averaging approximately forty-five animals including an average of fourteen adult females and nine adult males. Records on each day of observation include presence or absence of each individual, checks for wounds and other pathologies, the condition of each female's sexual and paracallosal skin and the presence or absence of menstruation, partners involved in the exclusive sexual consortships that are characteristic of this species (Rasmussen 1985), copulations, and ad libitum records of agonistic interactions to determine dominance relationships. (Details of the methodology can be found in Hausfater 1975; J. Altmann 1980; Altmann, Altmann, and Hausfater 1981; Hausfater, Altmann, and Altmann 1982.)

In baboons, because the time of ovulation can be well determined from changes in sexual skin swellings and because menstruation is externally visible, delayed menstruation, indicating a possible pregnancy, can readily be detected. In addition, pregnancy can be confirmed within a few weeks of a missed menstruation through reddening of the paracallosal skin (S. Altmann 1970); moreover, the skin loses its pinkness if the fetus is later miscarried. Consequently, we can identify fetal wastage as well as later offspring loss. Because pregnancy can be detected shortly after implantation and because few miscarriages have occurred thereafter, we can determine infant sex ratios not only at birth but near the time of conception.

Once an infant is born, its fate can be followed through age six, because group transfer is extremely rare before that age. Because dead infants are carried for several days by their mothers, the cause of death can sometimes be estimated and its occurrence confirmed for infants, though not often for juveniles.

Approximately one hundred conceptions occurred in Alto's Group during 1971-83 and have been used here for analysis. We do not have information on all variables of interest for all conceptions, so sample sizes vary from analysis to analysis. For example, age of mother is known or well estimated only for those mothers that reached maturity since 1971, whereas dominance rank of mother is known for all conceptions. Season of conception and birth is known for all, rainfall at that time for most. For conceptions starting with those in 1979, we have determined probable paternity based on mating and consortship records during the days of most likely conception; in addition to mating records, dominance rank and length of residency in the group was known for each male during this five-year period.

Reproductive success involves more than conception, of course. We know offspring survival through infancy for all conceptions, through age six (age of first reproduction for females and age of attaining the subadult stage for males) for a fraction of these.

The present report includes data on twenty-eight adult females and thirty-eight adult males. However, for most of the subjects the study period overlaps only a portion of their life span or even of their reproductive span. Similarly, only a fraction of the infants they produced during this period have had time to reach maturity. Thus our reconstruction of reproductive success necessarily involves both cross-sectional as well as longitudinal analyses. Wherever possible, we have done both types of analysis to verify that the results are consistent. We have also been able to replicate some of the findings during a shorter, more recent study of a second group (Hook's Group) in a slightly different habitat within the same park.

Unfortunately, because many of the life spans are incomplete, because the factors determining reproductive success in our animals are not independent (see below), and because we cannot yet evaluate most factors that determine life span, the results of our studies cannot yet be translated directly into quantitative estimates of contribution to variance in lifetime reproductive success. Moreover, because primate populations are age structured, with overlapping generations and overlap of reproduction, we have not been able to take advantage of analytical techniques developed by Arnold and Wade (1984a,b) for evaluating selection.

We begin with an investigation of factors affecting conception success first in females, then in males. Next we examine sources of variability in offspring survival. Finally, we consider determinants of the length of an individual's reproductive span.

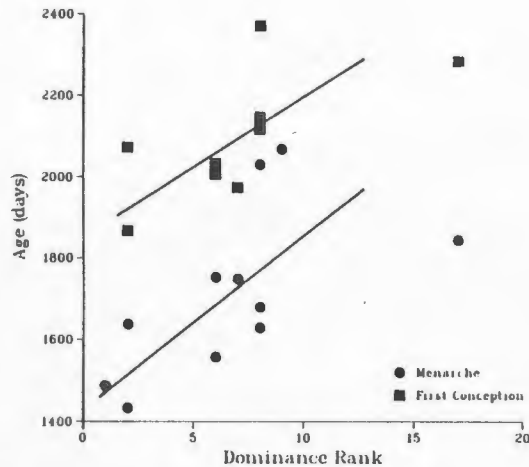


Figure 25.2: The effect of a mother's dominance rank when her daughter was conceived on the age at which the daughter reaches menarche ($y = 23.5x + 1525$; $r^2 = .37$, $p < .05$). The highest-ranking female is, by convention, indicated as having the lowest rank number, one.

25.2 Results

Conception Success of Females

Attainment of full reproductive capacity is a gradual process in female baboons, and its first externally visible stage is menarche. In captivity, a female reaches menarche at three to three and a half years of age and conceives her first infant within the next year (Snow 1967; Gilbert and Gillman 1960). In Amboseli, however, menarche occurs when females are approximately four and a half to five years old, and conception first occurs at age six (Altmann et al. 1977; Altmann, Altmann, and Hausfater 1981; also Nicolson 1982 for olive baboons). Daughters of high-ranking females attain reproductive maturity younger than do daughters of low-ranking females: they reach menarche about three hundred days earlier, and they conceive their first infant two hundred days earlier on the average (fig. 25.2). This provides a high-ranking female with an additional half-infant advantage—roughly a 7% adult life span advantage—relative to an average of seven offspring conceived (two surviving to adulthood) per female.

Once a female reaches age six, her fertility remains relatively constant over at least the next ten or twelve years. If a female lives to an old age, nonreproductive pathologies, such as extreme tooth wear and stomach tumors, as well as reproductive pathologies, particularly tumors, will increasingly interfere with reproduction (Lapin et al. 1979, based on captive animals). In the absence of pathologies, most nonhuman primate females, including baboons, continue to produce offspring until death (see summary in Graham, Kling, and Steiner 1979 for data on the existence of menopause in a few individual captive macaques and its absence in other

nonhuman primates, and see Strum and Western 1982 for reproductive decline from unknown causes in several free-ranging olive baboons estimated to be very old). In Amboseli, the variance but not the mean in reproductive parameters, including interbirth interval, seems to increase after age fifteen, but the sample of known-age elderly females is limited, and no data are available on factors that might be affecting age changes in reproduction.

The probability of conception is strongly affected by the survival of the immediately preceding offspring. If an infant dies, its mother's postpartum amenorrhea terminates within a few weeks, and she conceives in only one or two cycles, whereas if the infant survives, postpartum amenorrhea lasts approximately twelve months, and three or four menstrual cycles usually occur before conception (Altmann, Altmann, and Hausfater 1978). Thus the absence of strong birth seasonality means that baboons have a greater ability than seasonally breeding primates (e.g., vervets, Cheney et al., this volume, chap. 24) to recoup losses from infant mortality. In addition, fewer females will simultaneously be in estrus or giving birth. As a result, female/female reproductive competition may be less than in primates that are highly seasonal and thus more synchronous in their reproduction.

Finally, ecological factors affect conception rates (J. Altmann 1980; Strum and Western 1982). In our population this occurs through effects on the probability of cycling. In Alto's Group, the proportion of females that are cycling in the group is higher during wet seasons than during dry ones, because then it is easier both for females to attain menarche and for postpartum females to resume menstrual cycling (unpublished data). Once females are cycling, however, we can detect no effect of season on the probability of conception.

Although overall conception rates are not related to dominance rank, infant sex ratios shortly after conception are correlated with maternal rank. The highest-ranking third of females produce three to four females to each male offspring, and the lowest-ranking third produce two males to each female (fig. 25.3). We suggest that differences in offspring sex ratios are an immediate effect of social stress on behavior or physiology, as through timing of conception with respect to ovulation or changes in vaginal pH, and that this stress is a function of the number of females that dominate the conceiving female. Offspring sex ratio is not a function of maternal age or parity. As we describe below, the initial offspring sex-ratio bias is further exaggerated by an interaction between maternal rank and sex-specific offspring survivorship.

Conception Success of Males

When females first conceive at age six, the males of their cohort are just reaching subadulthood. Although physiologically capable of inseminating a female, six-year-old males are about half the weight of fully adult males and rank below them in the dominance hierarchy. It takes several

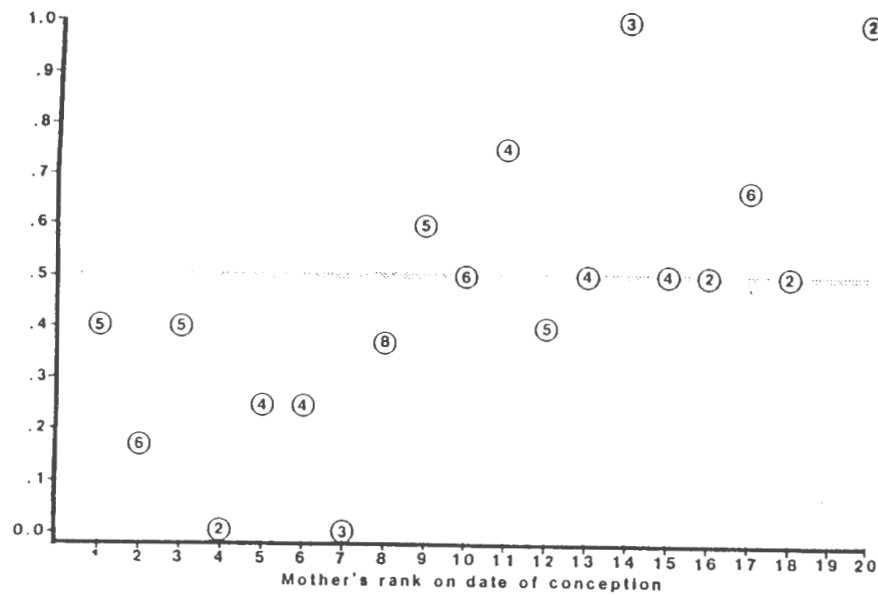


Figure 25.3: The effect of a female's dominance rank at the time she conceives on the probability that the offspring will be a male (July 1971–June 1981). The sample size of conceptions at each dominance rank is indicated within the circle marking the sex ratio for that rank. We determined a female's absolute dominance rank at the time of each conception; deaths, maturations, and rarely, rank changes among adults sometimes result in a female's having different rank numbers at the conception of successive offspring.

more years before these young males attain the size and social relationships that facilitate their fathering infants in the group.

Only rarely do matings during the days of likely conception occur outside the exclusive consortships maintained by adult females and males. Sometimes a single male is a female's only consort throughout these days, at other times consortships are maintained by two or more males successively within and between days (Hausfater 1975; Rasmussen 1985).

Juvenile males occasionally appear in the mating (but not consortship) records for females during the days of likely conception, but subadult males are virtually absent from both records: in this situation, juveniles but not subadults are tolerated by adult males (Hausfater 1975). Males reach subadulthood at approximately six years (Altmann, Altmann, and Hausfater 1981) and by seven and a half years of age they are large and strong enough to rise in the adult male dominance hierarchy, often precipitously, commonly becoming second or third ranking. During this age, usually after the rise in rank, the males often leave their group for a few days at a time, but of nineteen males who reached age six in Alto's Group, only one is known to have transferred groups successfully before age eight. One other subadult male died, two almost surely died, two others either emigrated or died, and the remaining thirteen stayed in the group through their eighth birthday. After rising in rank, these males

sometimes mate with fertile females in their natal group. However, these matings are rarer than for fully mature males of the same rank. In sum, most males (68%) survive subadulthood in their natal group but are unlikely to produce offspring there during this period.

The situation changes dramatically after age eight. Males of this age are usually high in rank and well within the size range of fully adult males even though their growth is not yet complete. Of the thirteen males who reached both subadulthood and adulthood in Alto's Group, eight are known or thought to have emigrated from the group between ages eight and nine. Two others died or emigrated in their tenth year. At that same age, two males that emigrated a year earlier returned to their natal group. Finally, one male in his tenth year is still in Alto's Group.

At least four males who reached subadulthood in Alto's Group—known or presumed to be their natal group—have stayed or returned there during adulthood. If males do stay or return as adults, they become fully participating mating adults within the group. The small sample available thus far does not suggest any pattern of maternal rank, male rank, or presence of adult female relatives that distinguish the "leavers" from the "stayers" and "returners." Approximately 20% of males reaching subadulthood or almost 30% of those reaching adulthood in Alto's Group may have spent their entire reproductive career there, but this is apparently a less common pattern in other baboon populations (Packer 1979a).

The remainder of this section focuses on the reproductive success of adult males who leave their natal group and reproduce elsewhere and is based on an analysis of patterns of residency, rank occupancy, and consortship for males that immigrated into Alto's Group or were there at the start of the study.

We first consider the data on residency duration, using actuarial estimates for incomplete durations (Cutler and Ederer 1958). Of residency durations for males that did not mature in Alto's Group, 32% were ten months or less, and 3% lasted for eleven to twenty months, 8% each for twenty-one to thirty months and thirty-one to forty months, none for forty-one to fifty months, 14% for fifty-one to sixty months, and the remaining 35% for more than sixty months. Males who were recorded as having more than one period of residency in the group had two periods, usually consisting of a short period (less than ten months) and then a second residency period of several years. Overall, the median time from when a male was first associated with the group to the last date of association (ignoring gaps due to absences) was thirty-four months for males who immigrated into the group during the study, and males who were with the group at the start of the study stayed for a median of fifty-one months subsequently.

Within thirty days of entering the group, most (12/18) immigrant males had obtained the highest position in the dominance order of adult males that they would ever achieve, and virtually all males (17/18) had done so by the middle of their first year of residency in the group. Furthermore, the initial rank position of immigrant males proved to be a

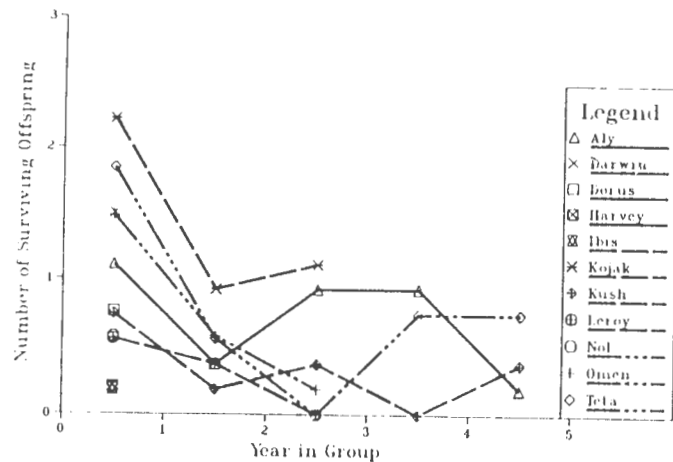


Figure 25.4: The yearly reproductive success of males as a function of the length of time they have been resident in a group. Each symbol represents a different adult male. For methods used to calculate number of surviving offspring for males see text.

good predictor of their subsequent duration of residency in the group: rank occupancy patterns and residency duration were not independent attributes of an adult male's life history. Specifically, immigrant males who obtained only an initial rank position in the lower half of the hierarchy among adult males remained with the group for a median of eighteen months (range 2–90+). In contrast, those males that initially obtained a rank position in the upper half of the adult male dominance order subsequently remained with the group for a median of sixty-seven months (range 44–89).

For each infant conceived during the five-year period 1979–83, we examined our daily monitoring records for its mother's matings and consortships on the days of likely conception. A male who appeared in those records for several matings or was recorded as a consort was considered a "likely father" of that infant. Almost all infants had one to three likely fathers, and overall the average was two likely fathers. Consequently, for the purpose of the present chapter, the number of infants a male was considered to have fathered was taken as half of those for which he was one of the likely fathers. Beyond that, the number of surviving offspring for males was taken as the number of infants fathered multiplied by the average rate of survival to age six.

A linear regression of cumulative reproductive success on duration of residency accounted for 56% of the variance in male reproductive success (fig. 25.4). Note that in this analysis the duration of residency for some males represents their complete stay in the group, while for others it is how long they had been in the group as of the end of 1983, the cutoff time for these data. Thus, at any duration shown in figure 25.4 the values include the cumulative reproductive success both of males who departed after staying that long and of those who had been there that long as of the

end of 1983 but were still in the group. In particular, the first-year results include both low-success males who left after a brief residency and high-success males who entered in 1983 and stayed for several years thereafter. Long-association males were the likely fathers of more infants in their *first* year of residency in the group than was the case for short-association males.

Recently completed analyses of lifetime rank occupancy sequences for the adult males of Alto's Group have demonstrated that the average rank occupied by males declined steadily with each additional year they associated with the group. This slow decline in male rank over time may be the main factor responsible for the finding that the per annum reproductive success of males was substantially reduced in their second and later years with the group compared with their first year with the group (fig. 25.5). Nevertheless, males that stayed with the group even for very long periods were likely fathers of infants in almost all years of their residency. The total number of offspring attributable to each male varied considerably both across year of residency and when summed over all years with the group (figs. 25.4, 25.5). Year-to-year fluctuations in the number of conceptions in the group, duration of occupancy in the top few dominance ranks during the first years of residency, and development of mating-partner preferences by the females all probably contribute to this variance.

Females exercise mate choice by the extent to which they contribute to or thwart consort formation or maintenance. At one extreme, they frequently approach (follow) the male, present sexually, and stand for male mountings. At the other extreme, they move away at most approaches by the male, present rarely and only at male instigation, and walk out from under the male as he starts to mount. Consequently, the time and

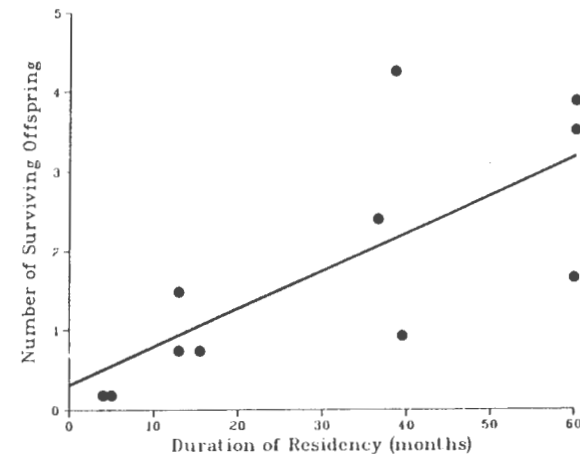


Figure 25.5: Cumulative male reproductive success as a function of the length of time the male has been resident in the group. See text for method used to calculate number of surviving offspring for males ($y = 0.05x + 0.26$; $r^2 = .56$, $p < .01$).

energy a male must expend per copulation and ultimately the number of copulations he achieves and his likelihood of fathering an infant will vary considerably as result of female behavior. Although quantitative data are not yet available, it appears that a low-ranking male will fight higher-ranking males for access to consort females primarily if these are females with whom the low-ranking male has mutually cooperative relationships. The nondominance basis for female choice remains to be determined (see also Rassmussen 1980; Smuts 1985; Bercovitch 1985).

Survival of a Female's Offspring

To attain high reproductive success, not only must individuals conceive offspring, but those conceptions must result in offspring that survive and reproduce. In most primates, few offspring are produced in a lifetime, usually one at a time. Consequently the fate of each greatly affects a parent's ultimate reproductive success.

In Alto's Group, 10% ($n = 95$) of pregnancies result in miscarriage or stillbirth. Mortality is approximately 25% in each of the first two years of life and declines in the next two years to virtually zero for the later juvenile period (J. Altmann 1980 and below). In this section and the subsequent one, we consider, first for female and then for male parents, what factors are related to variability in offspring mortality. We examine survivorship through the first two years, because infancy lasts between one and two years, and through age six, because that is the age of first conceptions in females and attainment of subadulthood in males.

The probability that an infant will survive is affected by maternal parity, but only in separating first pregnancies from later ones. The rate of miscarriage and stillbirth is the same for both parity groups, but live-born infants of primiparous females are half as likely (.29, $n = 17$) as later ones (.63, $n = 70$) to survive to two years of age. Survival success for second conceptions is indistinguishable from that for higher parities (.62, $n = 16$ vs. .63, $n = 54$). Variability in survival of first offspring is not accounted for by variability in age of the mothers at first conception.

Social dominance rank of mothers bears no simple relationship to offspring survival in Amboseli. Survivorship is .43 through two years of age and .35 through age six for the conceptions of the top-ranking females, .45 and .31 for those of the low-ranking ones. Because further analysis requires partitioning of our limited data sets, we will need more data and data on other groups to pursue complex interactions with confidence. However, several suggestive patterns, discussed below, emerge in the data now available.

Offspring survival is an interactive function of infant sex and maternal dominance rank: for both high- and low-ranking females, the offspring of the sex toward which birth ratios are biased have higher probabilities of survival. Considering the upper third (ranks 1-7) and lower third (ranks 14-20) of the dominance hierarchy, those in which sex ratio is biased, daughters of high-ranking females have a better chance of surviving to age

six (.47, $n = 15$) than do sons of high-ranking females (.00, $n = 5$) or daughters of low-ranking females (.25, $n = 4$). Likewise, sons of low-ranking females are more likely to survive (.33, $n = 9$) than are daughters of low-ranking females (.25, $n = 4$) or sons of high-ranking females (.00, $n = 5$). The ranks that have the most divergent sex ratios, the highest third of the ranks, have the greatest survival advantage conferred on the preferred sex.

Sex bias in offspring mortality affects the offspring of low-ranking females at a different age than it does offspring of high-ranking females. The daughters of low-ranking females are not at greater mortality risk during infancy, perhaps as a result of their mothers' greater protectiveness (J. Altmann 1980), but they are more vulnerable as juveniles, as also suggested for macaques (Dittus 1979 for wild toque macaques; Silk et al. 1981 for captive bonnet macaques). In contrast, so far only one son of a high-ranking female has survived the first two years ($n = 7$).

Because the sample of "wrong sex" offspring is small, we have not yet been able to identify likely sources of the mortality differences, particularly in the case of sons of high-ranking females. However, available data reveal that "right-sex" offspring have gestations that are a few days longer, their mothers experience a postpartum amenorrhea that is one month longer, and the mothers' cycling time to next pregnancy is also one month longer, suggesting prolonged maternal care. Gestation length is positively correlated with probability of survival in Amboseli baboons (unpublished data) as it is in humans (Van Valen and Mellin 1967). The differences in postpartum amenorrhea and in the subsequent time spent cycling are of the order of 10% to 25%. These several differences do not yet reach statistical significance. However, each is consistent with the initial sex-ratio biases and with the survival differences. The complete set of results is consistent with the hypothesis that the observed offspring sex biases are adaptive.

Survival of a Male's Offspring

A male's reproductive success, like that of a female, will depend not only on achieving conceptions but also on any factors that lead to the survival of those offspring he does father. Males provide both direct and indirect care for infants (DeVore 1963; Ransom and Rowell 1972) and for young juveniles, primarily for those that are likely to be their own (see, e.g., J. Altmann 1980; Nicolson 1982; Stein 1984). Such care is sometimes dramatic in life-threatening situations, but it also occurs more subtly on a daily basis. Data are not yet available on the effectiveness of this care.

Males differ in the extent of care they provide. These differences have not yet been quantified, however, nor is it clear to what extent they represent life-stage differences or whether they result in lifetime differences in reproductive success. It appears that differences are partially related to life stage and, though not independently, to dominance rank: a

male who is top ranking does not seem to provide as much care as those who are middle and low ranking.

The survival of a male's offspring will also depend on those maternal factors that affect successful gestations and infant and juvenile survival, so that mate selection by males may be a key component of their reproductive success. Several studies document selectivity among baboons (e.g., Hausfater 1975; Rasmussen 1985; Smuts 1985), but it is still unclear to what extent the selectivity results from female choice versus male choice. Moreover, much of the basis of choice remains to be elucidated, as noted above. These studies failed to find any indication that males are selective among females by dominance rank. Two studies report that adult males select multiparous females as consorts in preference to nulliparous ones (Rasmussen 1985; Takacs 1982). Unfortunately, these studies pooled data from females at all stages of adolescence; our (unpublished) data and those of Scott (1984) suggest that there is a major shift in adult male interest late in adolescence, when the females are likely to conceive. Judging by the poor survival chances for a female's first offspring, males should mate with nulliparous females only if it does not reduce their chances of fathering an infant by a female who has already had at least one infant or if doing so appreciably increases the likelihood that the young female will choose him as a mate in subsequent years.

Adult Reproductive Span and Survival

Age emerges as a major factor affecting cumulative female reproductive success, accounting for 79% of the variance in the linear regression (fig. 25.6). However, in a number of cases the data points are based on adult spans that are not yet complete. Consequently we cannot yet estimate the variance in life span or specify the proportion of lifetime reproductive success accounted for by life span. Because the expected survival of a newly adult female is approximately ten to twelve years, and because no known factors seem to have a very strong influence on adult span, we cannot yet predict individual differences in female reproductive success based on predictors of longevity.

Our data do indicate, however, that mortality rates are higher for females who are caring for young infants. Females spend approximately half their adult years in postpartum amenorrhea, caring for an infant (Altmann et al. 1977), and we would therefore expect that half the females who die would be in this reproductive state if probability of death is independent of reproductive condition. Three females who died were suspected of having pathologies that interfered with reproduction and were excluded from the analyses, although their inclusion would not have changed the results: one cycled continuously for the eight years before her death, the other two had extended periods of postpartum amenorrhea until death. Of the remaining thirteen females that died, eleven were in postpartum amenorrhea (chance $p = .01$) at the time of their deaths. The remaining two were pregnant. We conclude that there is a mortality cost of

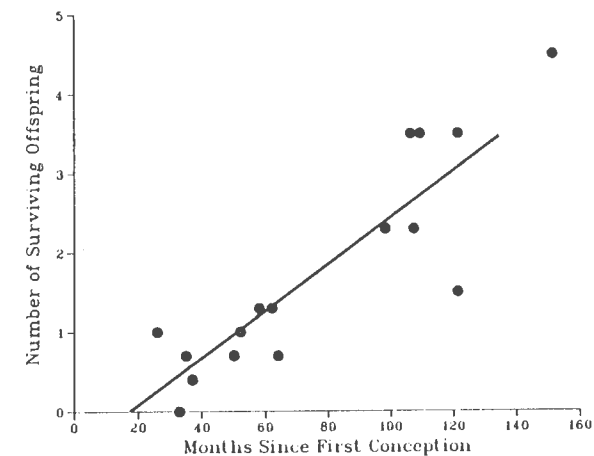


Figure 25.6: Cumulative female reproductive success as a function of months since first conception. The actual survival of each offspring was used for this graph. For any offspring that was alive and less than six years of age at the time the calculations were done, we used survival probabilities from that age through age six based on the longitudinal data for Alto's Group ($y = 0.03x - 0.59$; $r^2 = .79$; $p < .005$).

reproduction (J. Altmann 1980, 1983). Females that repeatedly lose young infants and therefore produce more infants in compensation for this loss may have a higher mortality rate, which could emerge as a source of individual differences in life span and consequently in reproductive success.

For males, we rarely know if we have observed their whole reproductive span, even if data are complete for their time in a single group. Some reproduction may occur in the natal group before a male leaves, and a male may live and reproduce in more than one nonnatal group before he dies (unpublished Amboseli data; also Packer 1979a; Strum 1982). We do not know whether males that are unsuccessful in one nonnatal group and stay only briefly subsequently make a successful transfer into another group. Moreover, there is considerable variability in total reproductive success, at least in the short term, among groups within the same population (Altmann, Hausfater, and Altmann 1985), so that attaining high relative reproductive success in different groups may have different absolute values. Thus, though the present data suggest that age, or at least length of residency in a group, is a major determinant of reproductive success for males as well as females, factors that we cannot yet evaluate may confound the relationship.

25.3 Summary and Discussion

Agonistic dominance among males has long been recognized as a feature of baboon society and as a factor affecting differential access to fertile females (see Packer 1979b and references therein). A quantitative study by Hausfater (1975) demonstrated that dominance accounted for approxi-

mately half of the short-term variance among males in the frequency of matings with females around the time of ovulation. It took longer to appreciate the importance of female dominance relationships, even though these are much more stable than those of males (Hausfater 1975), not only within generations but between them (Hausfater, Altmann, and Altmann 1982). However, a relationship between female dominance status and reproductive success remained uninvestigated (but see, e.g., Dunbar and Dunbar 1977 and Dunbar 1984 for geladas; and Drickamer 1974 and Gouzoules, Gouzoules, and Fedigan 1982 for macaques), partially as a result of the expectation from evolutionary theory that females in sexually dimorphic mammals with a somewhat polygynous mating system would have low reproductive variance and might choose among mates but not compete reproductively.

We have presented longitudinal data that demonstrate the effect of dominance on the reproductive success of female baboons, and also the limitations of that effect for both males and females. With respect to female reproductive success, daughters of high-ranking females attained reproductive maturity earlier than did daughters of low-ranking females. However, no dominance effect on conception rates could be demonstrated beyond first conception, nor could we discern any simple relationship between dominance and adult survival or offspring survival, the other main factors affecting lifetime reproductive success.

Dominance did affect sex-specific conception rates and survival of offspring. High-ranking females produced more daughters than sons. These daughters appeared to garner somewhat greater maternal investment, and they were more likely to survive infancy than were sons of these high-ranking mothers. In contrast, low-ranking females produced offspring sex ratios that were biased toward males. These males appeared to garner more maternal investment, and although the males did not have higher chances of surviving infancy, they were more likely than daughters of low-ranking mothers to survive the juvenile years and reach sexual maturity.

Questions regarding parental biasing of offspring sex ratios and subsequent investment have been of considerable interest in the evolutionary literature. Conditions that might favor the production of one sex over the other include environmental/nutritional stress, social stress, and the ability of the parent of each sex to affect its own reproductive success and that of each sex of offspring. Authors rarely treat these factors separately or consider that for any given species or population these factors may work in opposing directions rather than the same direction. Adequate information on these effects would result, for different species, in predictions of sex-ratio biases that differ in direction—or no bias—when the several factors are taken together. The absence of the necessary empirical evidence often results in a posteriori explanations of observed sex-ratio bias or of their absence.

Several recent studies of cercopithecine primates, including the two

in this volume, differ in the relationships found between maternal dominance rank and offspring sex ratio (see J. Altmann 1980; Silk et al. 1981; Simpson and Simpson 1982; Paul and Thommen 1984; van Schaik and van Noordwijk 1983; Meilke, Tilford, and Vessey 1984; for other cercopithecine data). Whether these differences represent methodological differences, small-sample differences, or real differences remains to be seen. Likewise, in the absence of relevant measurements of those variables that are predicted to favor selection for parental influence on sex ratio, we cannot evaluate whether any or all of these sex ratios are those that would be predicted on the basis of adaptive arguments even if the results are "real." Finally, despite suggestive results on the relationship between timing of conception and offspring sex ratios in several mammalian species, neither the relevant normative physiological nor behavioral evidence is available for nonhuman primates.

Adult male immigrants who stayed at least a year in their new group tended to be high ranking and to produce the most infants during that first year. However, high rank is at least partially a temporary life-history stage for males rather than a stable trait, thus diluting over a lifetime the short-term reproductive advantages (Hausfater 1975; Saunders and Hausfater 1978). Elapsed residency in a group, inversely correlated with dominance rank, affected the estimated per annum number of offspring for males. Nonetheless, males continued to mate with fertile females, subsequent to rank loss, for the remaining years they were in the group, resulting in a strong correlation between length of residency and estimated reproductive success.

Instability of dominance for males, biased offspring sex ratios at conception and in offspring survival for females, yet-to-be-determined roles of mate choice in males and females, and undetermined contributions of fathers to offspring survival left adult survival as the apparent predominant factor affecting within-sex variance in reproductive success in our investigations thus far. It remains for future studies to determine the magnitude of these unmeasured effects as well as the extent of variance in adult survival and the identification of those factors that affect adult survival.

Studies of artificially fed macaques (e.g., Mori 1979; Sugiyama and Ohsawa 1982) demonstrate greater differential effects of female dominance on reproductive success under conditions of artificial feeding than otherwise. Because the artificial feeding resulted in a more concentrated food resource as well as a higher average nutritional plane, it is hard to disentangle these two factors (see J. Altmann 1986). However, it is clear that the proportion of variance in reproductive success attributable to various factors may vary with ecological and demographic conditions. This is further illustrated by the fact that infant survival is the major factor affecting conception rates in Amboseli (Altmann, Altmann, and Hausfater 1978 and unpublished data), where infant mortality is appreciable, whereas food availability has been identified as the major factor in olive baboons at

Gilgil, Kenya, where infant mortality is negligible (Strum and Western 1982). Any rank-related variability in infant survival or in food availability might have different effects on conception at these sites.

Male and female baboons appear to have alternative strategies for increasing their rates of conception and the survival of their offspring, thereby reducing the variance in reproductive success. Biasing sex ratios, adapting different styles of maternal care, choosing mates, and taking advantage of potential social resources all seem to be utilized by baboon females. Males differ in choice of group in which to mate, decision to emigrate, timing of one or more migrations, choice of and extent of competition for mates, and care of potential offspring. We have much yet to learn about the causes and consequences of these various behavioral and life-history patterns.

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