

## CHAPTER SEVEN

# Reproduction, Mortality, and Female Reproductive Success in Chacma Baboons of the Okavango Delta, Botswana

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## CHAPTER SUMMARY

Predation, food competition, and infanticide all negatively impact female reproductive success. Female dominance rank may mitigate these effects, if

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competitive exclusion allows high-ranking females to gain priority of access to critical food resources. It may also exacerbate them, if low-ranking females are forced to feed or rest in marginal habitats where they are at increased risk. In this chapter, we present data on reproduction, mortality, and female reproductive success from a 10-year study of free-ranging chacma baboons (*Papio hamadryas ursinus*) in the Okavango Delta of Botswana and examine the influence of predation, infanticide, and dominance rank on female reproductive success. Predation appeared to be the cause of most deaths among adult females and juveniles, whereas infanticide was the most likely cause of deaths among infants. Seasonality strongly affected both births and mortality: The majority of conceptions occurred during the period of highest rainfall. Mortality due to predation and infanticide was highest during the 3-month period when flooding was at its peak, most likely because the group was more constrained to move along predictable routes during this time. Those reproductive parameters most likely to be associated with superior competitive ability—interbirth interval and infant growth rates—conferred a slight fitness advantage on high-ranking females. This fitness advantage was counterbalanced, however, by the effects of infanticide and predation. Infanticide affected high- and low-ranking females more than middle-ranking females, while predation affected females of all ranks relatively equally. As a result, there were few rank-related differences in estimated female lifetime reproductive success.

## 1. INTRODUCTION

The relative importance of predation and food competition for the evolution of sociality in baboons (*Papio hamadryas* spp.) and other nonhuman primates is a subject of considerable debate. According to some hypotheses, predation has exerted the primary selective pressure on sociality, because the costs of intragroup feeding competition would otherwise prevent females from living in groups (e.g., van Schaik, 1983, 1989; Janson, 1988, 1998; Sterck et al., 1997; Hill and Dunbar, 1998). Other hypotheses, however, place more weight on the benefits derived from intergroup resource competition (e.g., Wrangham, 1980; Isbell, 1991; Cheney, 1992) or protection against infanticide (Janson and van Schaik, 2000; see also Sterck et al., 1997).

Whatever the benefits of sociality, group life also imposes costs in the form of increased competition for resources and breeding opportunities.

When predation pressure, resource availability, or limited dispersal options make group life essential, breeding may become skewed, with one or a few females monopolizing reproduction (reviewed by, e.g., Vehrencamp, 1983; Keller and Reeve, 1994; Johnstone, 2000). High reproductive skew is especially likely to evolve under severe ecological constraints, when a single female may not be able to produce offspring without the help of nonbreeding adults (e.g., dwarf mongooses, *Helogale parvula*: Creel and Waser, 1997; suricates, *Suricata suricatta*: O’Riain et al., 2000; wild dogs, *Lycaon pictus*: Creel and Creel, 2002; naked mole rats, *Heterocephalus glaber*: Jarvis, 1991). In contrast, low reproductive skew, with relatively egalitarian breeding among all females, is expected to occur when ecological constraints are relaxed and dominant females do not benefit from suppressing the reproduction of subordinates (e.g., lions, *Panthera leo*: Packer et al., 2001; banded mongoose, *Mungos mungo*: Cant, 2000; DeLuca and Ginsberg, 2001; elephants, *Loxodonta africana*: Moss, in press).

The extent of reproductive skew varies widely in the primate order. In the callitrichids, dominant females monopolize reproductive activity and suppress reproduction in subordinates (Goldizen, 1987; Goldizen et al., 1996; French, 1997). In other primates, reproductive skew is considerably reduced, and nearly all adult females produce offspring at more or less regular intervals. Even in species manifesting low reproductive skew reproductive performance may be mediated by dominance rank and access to food resources (e.g., Janson, 1985; Barton, 1993).

Female savannah baboons can be characterized as displaying low, but not insignificant, reproductive skew. Like females in such Old World monkey species as macaques (*Macaca* spp.) and vervet monkeys (*Cercopithecus aethiops*), female baboons form linear, nepotistic dominance hierarchies in which high-ranking females and their close relatives enjoy priority of access to resources (reviewed by Melnick and Pearl, 1987; Silk, 1987, 1993). Although there is no evidence of complete reproductive suppression, low-ranking females may experience reduced fecundity and offspring survival. High-ranking females often give birth at earlier ages (baboons: Altmann et al., 1988; Altmann and Alberts, 2003), have shorter interbirth intervals (baboons: Bulger and Hamilton, 1987; Smuts and Nicholson, 1989; Packer et al., 1995; Barton and Whiten, 1993; Wasser et al., 1998; Altmann and Alberts, 2003; Japanese macaques, *Macaca fuscata*: Sugiyama and Ohsawa, 1982; long-tailed macaques, *M. fascicularis*: van Noordwijk and van Schaik, 1999), or experience

higher offspring survival than low-ranking females (baboons: Bulger and Hamilton, 1987; Rhine et al., 1988; Packer et al., 1995; long-tailed macaques: van Noordwijk and van Schaik, 1999; vervet monkeys: Whitten, 1983; Japanese macaques: Sugiyama and Ohsawa, 1982; see also review by Silk, 1993). Each of these reproductive variables is influenced by nutritional condition and access to food, which is often mediated by dominance rank (Wrangham, 1981; Whitten, 1983; Barton and Whiten, 1993; Barton et al., 1996).

Not all studies, however, have documented significant differences in lifetime reproductive success between high- and low-ranking females (baboons: Altmann et al., 1988; Packer et al. 1995; vervets: Cheney et al., 1988a,b; reviewed by Silk, 1993). The lack of a consistently strong relationship between female rank and reproductive success is probably a consequence of at least two factors. First, the effects of food competition on reproduction are likely to be most evident under extreme ecological conditions, such as during severe drought (Alberts et al., 2005). At other times these effects may be smaller and more difficult to measure, especially over the short term (van Noordwijk and van Schaik, 1999). Second, causes of mortality unrelated to food competition, such as infanticide and predation, may affect high- and low-ranking females relatively equally, thereby masking the impact of food competition.

The interaction of feeding competition and predation pressure may especially be costly to low-ranking animals. Because low-ranking animals may be excluded from safe feeding sites toward the center of the group and forced to feed in more peripheral areas, they may suffer increased predation. Again, however, data in support of this hypothesis are inconsistent. Although some studies have documented a relationship between low rank and increased vulnerability (baboons: Ron et al., 1996; long-tailed macaques: van Noordwijk and van Schaik, 1987), others have not (baboons: Bulger and Hamilton, 1987; vervet monkeys: Cheney et al., 1988a,b).

We provide here a descriptive account of female reproduction and mortality over a 10.5-year period (July 1992–December 2002) in one group of chacma baboons inhabiting the Moremi Reserve in the Okavango Delta of Botswana. Because baboon females can live for over 20 years in the wild (Packer et al., 1995; Altmann and Alberts, 2003), our data do not provide a complete analysis of the factors that influence lifetime reproductive success. They do, however, permit evaluations of the relative influences of predation,

infanticide, interbirth intervals, and infant survival on the reproductive success of females of different ages and dominance ranks.

## 2. STUDY GROUP AND HABITAT

The focus of this study was a group of free-ranging chacma baboons (*Papio hamadryas ursinus*) inhabiting the Moremi Game Reserve in the Okavango Delta of Botswana. Grasslands in the delta flood annually (usually between June and October), leaving elevated “islands” edged with woodland. Baboons feed extensively on a number of tree species in these edged woodlands, including wild or strangler figs (*Ficus thonningii*), sycamore figs (*F. sycamorus*), sausage trees (*Kigelia africana*), African mangosteens (*Garcinia livingstonei*), jackalberries or African ebonies (*Diospyros mespiliformis*), marula trees (*Sclerocarya birrea*), camelthorn acacias (*Acacia erioloba*), candle-pod acacias (*Acacia hebeclada*), knobthorn acacias (*Acacia nigrescens*), and real fan palms (*Hyphaene ventricosa*) (Hamilton et al., 1976; Bulger and Hamilton, 1987; Ross, 1987; Ellery et al., 1993; Roodt, 1998). Islands can be less than one to hundreds of hectares in size. During floods, baboons ford the submerged plains and move between islands throughout an approximately 5 km<sup>2</sup> range. The population density of baboons in this area is considerably higher than in other areas of Africa (approximately 24/km<sup>2</sup>; Hamilton et al., 1976, unpublished data).

Predation is the most important cause of mortality for juveniles and adults in Moremi (described in detail in Cheney et al., 2004; see also Busse, 1982; Cowlishaw, 1994). Most predation is due to leopards (*Panthera pardus*) and lions (*Panthera leo*). Although we have also observed several attacks by crocodiles (*Crocodilus niloticus*), we have not been able to confirm any deaths due to crocodile predation. Other potential, but unconfirmed, predators include hyenas (*Crocuta crocuta*), wild dogs (*Lycan pictus*), and pythons (*Python sebae*).

The study group, C, has been observed since 1978, with almost daily observations since mid-1992. The ages and matrilineal relatedness of all natal animals are known, as are the origins and destinations of many immigrant males. During the course of this study, the group averaged around 75 individuals. The number of adult females in the group ranged from 19 to 26, while the number of adult males ranged from 3 to 12. As in most other baboon populations, females remain in their natal groups throughout their

lives, but males typically emigrate to neighboring groups after attaining sexual maturity.

Dominance ranks among adult females were determined by the direction of approach–retreat interactions (Silk et al., 1999). Female dominance ranks remained stable over the 10-year period of this study, with daughters assuming ranks similar to those of their mothers (Silk et al., 1999, unpublished data). Younger sisters have typically risen in rank over older sisters, while ranks between mothers and daughters have not been as predictable. Some mothers have continued to rank higher than their adult daughters, while others have dropped below their daughters (see Combes and Altmann, 2001). One female, which was orphaned at 9 months, achieved a rank different from (in this case, higher than) that of her closest female relatives.

Females were assigned ranks according to the proportion of females dominated, which largely controls for variation in the number of females present in the group across time. When assessing the effects of female rank on particular demographic events (e.g., infant death), we used each female's rank at the time of the event. When considering lifetime reproductive success, we calculated the female's mean rank across years. For the purposes of the analyses described here, we divided females into high-, middle-, and low-rank categories. No females changed from one rank category to another across time.

Infants were defined as animals under the age of 1 year. Juveniles were animals aged 1–5 years in the case of females and 1–6 years in the case of males. Females were considered to be adult at 6 years of age, and males at 7 years of age. No male was known to emigrate from his natal group before 8.5 years of age.

Most of the data presented in this chapter were gathered between 1992 and 2002. For one analysis that estimates lifetime reproductive success, however, we also used demographic data on births and deaths gathered prior to 1992. These data were collected by W. J. Hamilton, J. B. Bulger, and colleagues during the 1980s and early 1990s. Because these records did not always include the exact dates of all demographic events or precise information on causes of mortality, we have not used them for the bulk of our analysis. Disappearances were classified into several categories (Table 1), with additional categories for cases of infanticide (Table 2).

**Table 1.** Classification of disappearances and causes of mortality

Ill	An animal disappeared after appearing to be ill or listless within the previous 24 hr. Individuals that disappeared after appearing ill were not included as victims of predation or infanticide
Confirmed predation	The predation event was witnessed by observers, or a predator was observed with the carcass of a known individual who had been observed, apparently healthy, within the previous 24 hr, or the carcass of an individual known to be healthy was found in conjunction with predator tracks and feces containing baboon remains
Suspected predation	A baboon who had been seen, apparently healthy, within the previous 24 hr disappeared in contexts in which predation was strongly suspected. These contexts included alarm calls and the sighting of predators or predator tracks in close proximity to the baboons at the time of the individual's disappearance
Disappear apparently healthy	The disappearance of an apparently healthy animal within 24 hr of being seen. Animals were classified as "apparently healthy" if they were not obviously diseased or listless at the time of their disappearance. Clearly, however, it remains possible that such individuals might have suffered from illnesses that were not detectable to observers. Infants, juveniles, and adult females that disappeared were presumed to have died. We have observed no cases of female emigration in this study group. Baboons are able to swim even at a very young age, so it is unlikely that any disappearances during times of flooding were due to drowning

Annual mortality rates were calculated for 10 years (1 August 1992–31 July 2002), based on the number of individuals in each age/sex class on 1 August of each year. All individuals aged less than 1 year as of 1 August plus all individuals born between 1 August and 31 July were included in the "infant" class for that year. Thus the same individual might be counted as an infant in two successive years.

**Table 2.** Classification of cases of infanticide

Confirmed infanticide	The infanticidal attack was witnessed by observers
Strongly suspected infanticide	An infant disappeared after a fight involving a male and female, and after sustaining wounds suggestive of a baboon bite, or at the same time that its mother sustained wounds suggestive of a baboon bite. In one suspected case, a male, which had been observed killing other infants, was seen eating a carcass that appeared to be that of an infant baboon
Suspected infanticide	An apparently healthy infant disappeared at around the same time that a male was confirmed to have killed other infants

### 3. FEMALE REPRODUCTION

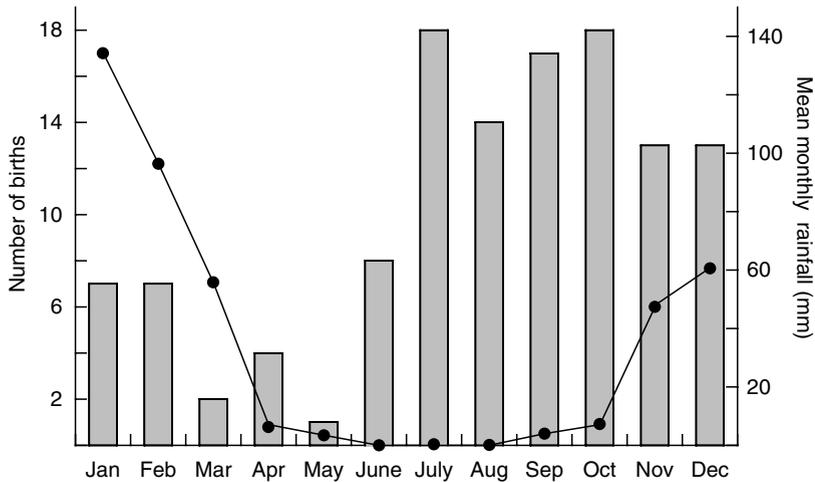
#### 3.1. Seasonality

Although baboons produce offspring throughout the year, a number of studies have documented birth peaks that are correlated with seasonal fluctuation in rainfall. Most conceptions occur during the rainy season, and births tend to peak during the dry season or winter months (Mikumi, Tanzania: Rhine et al., 1988, 1989; Amboseli, Kenya: Alberts et al., 2005; de Hoop and Drakensberg Mountains, South Africa: Barrett et al., this volume). In Moremi, births showed seasonal variation, with 76 percent of 122 births occurring in the 6 months from July through December (Figure 1; two-tailed chi square one-sample test,  $df = 1$ ,  $\chi^2 = 33.58$ ,  $P < 0.001$ ). This seasonal effect held for females of all ranks, although high-ranking females' births appeared to be slightly less seasonal than those of middle- and low-ranking females. While 83 percent of middle- and low-ranking females' births occurred from July through December, only 65 percent high-ranking females' infants were born during this period.

As in other baboon populations, birth seasonality in Moremi appeared to be influenced by seasonal fluctuations in rainfall (Figure 1). Rainfall in the Okavango Delta is highly variable, but most rain falls during the months of November–March, usually peaking in January and February. Baboon gestation periods are approximately 6 months in length. Thus, if females were most likely to become pregnant after periods of high rainfall when food was more plentiful, births would be expected to peak in the months immediately following July and August.

#### 3.2. First Birth

Females first gave birth at an average age of 6 years, 9 months (range 5 years, 9 months to 7 years, 11 months; median age: 6 years, 6 months;  $N=28$  females). In contrast to some other baboon populations (see "Introduction"), age at first birth appeared to be unrelated to female rank. Females in the top third of the female dominance hierarchy first gave birth at a mean age of 6 years, 7 months (median: 6 years, 7 months;  $N=11$ ). Those in the mid-third gave birth at a mean age of 7 years, 0 months (median: 6 years, 11 months;  $N=9$ ), and those in the bottom third at a mean age of 6 years, 8 months (median: 6 years, 6 months;  $N=8$ ).

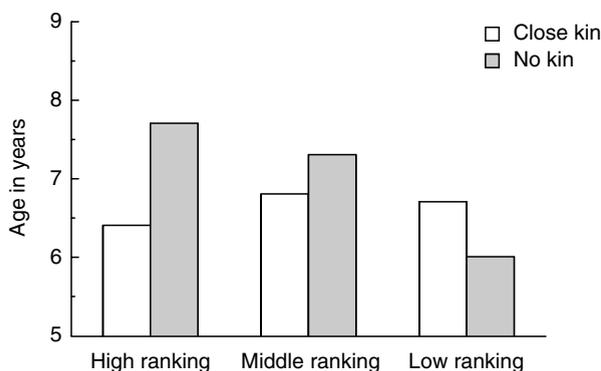


**Figure 1.** Relationship between the number of births per month from August 1992 through July 2002 (bars) and the mean monthly rainfall for each month (in mm; solid line) (two-tailed chi square one-sample test,  $df=1$ ,  $\chi^2=33.58$ ,  $P < 0.001$ ). Data on rainfall are based on records from 1992 to 1999 ([http://tao.atmos.washington.edu/data\\_sets/wilmott](http://tao.atmos.washington.edu/data_sets/wilmott)). Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.

The presence of adult maternal kin (i.e., mothers and/or maternal sisters) appeared to influence age at first birth, but this effect varied according to female rank. Whereas high- or middle-ranking females with a living mother or adult sister gave birth for the first time at significantly younger ages than females without close kin, the reverse was true for low-ranking females: Low-ranking females with living kin gave birth at older ages than those without kin (Figure 2; general linear model (GLM) with rank and presence of female kin; significant interaction between presence of female kin and rank,  $F = 10.1$ ,  $df = 2, 22$ ;  $P < 0.01$ ).

### 3.3. InterBirth Intervals

We used a GLMM (general linear mixed effect model; maximum likelihood estimation) to assess whether sex of the previous infant, infant survival to 1 year, presence of female kin, rank, and female age had an effect on inter-birth interval. With this analysis, repeated measures from the same individual can be analyzed. We used data from 20 females (using female identity as a



**Figure 2.** Mean age at first birth for females with and without living adult kin. High-ranking females:  $N=11$ ; middle-ranking female:  $N=9$ ; low-ranking females:  $N=8$ . A general linear model (GLM) with rank and presence of female kin yielded a significant interaction between presence of female kin and rank ( $F=10.1$ ,  $df=2, 22$ ;  $P < 0.01$ ). Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.

random factor in the analysis) and randomly selected one data point per female in the “infant survived” and one in the “infant died before 1 year of age” category. We first calculated the initial model with all factors and then examined different models using Akaike’s information criterion (Pinheiro and Bates, 2000) to identify the best one.

Although there was no significant effect of infant sex on interbirth interval, there was a significant interaction between infant survival and infant sex: If the infant survived and was male, the interbirth interval was longer ( $759 \pm 84$  days as opposed to  $718 \pm 85$  days for female infants). However, if the infant died and was male, the interbirth interval was significantly shorter ( $429 \pm 91$  as opposed to  $506 \pm 78$  days for female infants;  $F=4.6$ ,  $df=1, 34.4$ ,  $P < 0.05$ ). Interbirth intervals for females aged 15 years or older were somewhat longer ( $812 \pm 106$  days,  $N=3$  females) than for younger females ( $721 \pm 76$  days,  $N=17$ ), but only if the infant survived to 1 year of age (if the infant died the average interbirth interval was  $428 \pm 85$  versus  $470 \pm 94$  days).

As in several previous studies of baboons and macaques (see “Introduction”), interbirth intervals for females whose previous infant survived tended to be shorter for high-ranking females (mean =  $682 \pm 78$  days,  $N=6$ ) than for middle-ranking (mean =  $759 \pm 66$  days,  $N=8$ ) and low-ranking females (mean

=  $754 \pm 101$  days,  $N=6$ ). If a female's previous infant had died, rank-related differences in interbirth intervals were less obvious. The mean interbirth interval for high-ranking females whose previous infant had died was 475 days, compared with 447 and 464 for middle- and low-ranking females, respectively. Interbirth intervals for females that had living adult female kin were shorter ( $724 \pm 80$ ,  $N=14$ ) than for females without such kin ( $760 \pm 96$ ,  $N=6$ ). However, none of these effects reached statistical significance.

### 3.4. Infant Sex Ratios

A long-term study of a population of baboons in Amboseli, Kenya, has documented a female-biased sex ratio among high-ranking females, possibly reflecting local competition for resources (Altmann et al., 1988). A similar bias has been reported for captive bonnet macaques (*M. radiata*; Silk, 1983). Rank-related biases have not consistently been documented, however, in other baboon populations (Rhine et al., 1992) or in other populations of monkeys (e.g., vervet monkeys: Cheney et al., 1988a,b). In fact, rank-related sex ratio biases may result largely from the errors inherent in small samples, as the effects of maternal rank on birth sex ratios disappear as sample size increases (Brown and Silk, 2002).

In Moremi, overall birth sex ratios were almost even ( $N=70$  female births, 62 male births, and 1 birth of unknown sex from June 1992 through December 2002). There was no evidence for a rank-related difference in birth sex ratios. The mean female/male infant sex ratio for high-ranking females ( $N=14$ ) was 0.52, compared with 0.51 for middle-ranking females ( $N=15$ ) and 0.55 for low-ranking females ( $N=13$ ).

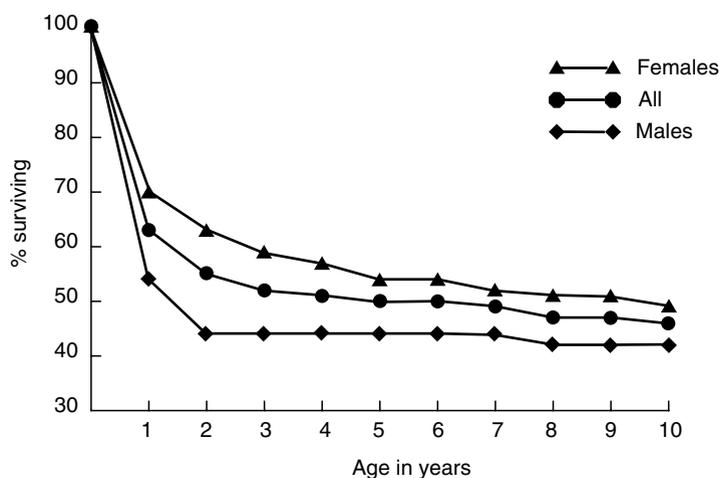
## 4. MORTALITY

### 4.1. Age-Specific Mortality

Figure 3 presents data on age-specific mortality rates for males and females from birth to 10 years of age. The highest mortality rates occurred among infants, with juveniles and young adults experiencing relatively low mortality.

### 4.2. Adult Female Mortality

Confirming the observations made by Bulger and Hamilton (1987) in an earlier study of the same group, almost all adult female deaths appeared to be



**Figure 3.** Age-specific mortality estimates for males and females from birth through 10 years of age. Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.

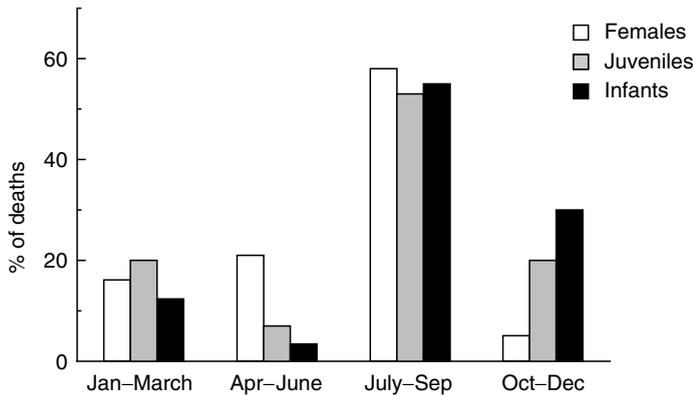
due to predation (Table 3). Only one female was ill or listless at the time of her disappearance. Leopard predation on four females was confirmed, and in six other cases predation by leopards ( $N=2$ ) and lions ( $N=4$ ) was strongly suspected. An additional thirteen females disappeared after having been observed, apparently healthy, on the previous day.

Female mortality peaked between the months of July and September, during maximal flooding. Overall, 58 percent of the 19 known or suspected cases of predation on females occurred in these months, significantly more than

**Table 3.** Causes of mortality among adult females, juveniles, and infants

	<i>N</i>	Ill	Confirmed predation	Suspected predation	Disappear healthy	Confirmed infanticide	Suspected infanticide	M's death
Adult females	24	1	4	6	13			
Juv. females	12	0	1	2	9			
Juv. males	7	0	0	1	6			
Infants	46	7	0	1	6	11	14	7

See Tables 1 and 2 for definitions. “M’s Death” stands for infant died following mother’s death. “Suspected Infanticide” includes both strongly suspected and suspected cases of infanticide. An additional three infants disappeared when observers were absent for more than 24 hr. Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.



**Figure 4.** Proportion of all deaths among adult females, juveniles, and infants between August 1992 and July 2002 that occurred in each 3-month period. Of the 19 known or suspected cases of predation on adult females, 58 percent occurred in July–September, significantly more than would be expected by chance (chi square one-sample test,  $\chi^2=8.99$ ,  $df=1$ ,  $P < 0.01$ ); of 15 juvenile deaths between August 1992 and July 2002, 53 percent occurred in July–September ( $\chi^2=6.43$ ,  $df=1$ ,  $P < 0.05$ ); and of the 33 infants that disappeared healthy, 55 percent disappeared in July–September ( $\chi^2=15.37$ ,  $df=1$ ,  $P < 0.01$ ). Analysis excludes individuals that disappeared ill and, in the case of infants, after the deaths of their mothers. Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.

would have been expected by chance (Figure 4; chi square one-sample test,  $\chi^2=8.99$ ,  $df=1$ ,  $P < 0.01$ ).

Adult females experienced an annual mortality rate of 0.09 (s.d.=0.04). Mortality rates fluctuated between 0.04 and 0.16, indicating that females encountered substantially higher predation rates in some years than in others. For example, during 2002 seven of 29 females in the group disappeared (24 percent), all apparently victims of predation. A drought and widespread fires during this year caused the group to scatter over large distances while foraging, possibly increasing females’ vulnerability to predation. Bulger and Hamilton (1987) noted a similar surge in female mortality in 1980–1981, when 40 percent of the group’s females died, all apparently due to predation.

Little rank-related variation in mortality rates was apparent. Of 24 female deaths, 29 percent occurred among high-ranking females, 38 percent among middle-ranking females, and 33 percent among low-ranking females. Females ranked in the top third of the dominance hierarchy experienced a mean annual mortality rate of 0.08 (sd=0.11). Females ranked in the mid-third

experienced a mortality rate of 0.11 ( $sd=0.13$ ), and those in the bottom third a rate of 0.11 ( $s.d.=0.13$ ) (Figure 5; Kruskal–Wallis one-way analysis of variance,  $H=1.46$ ,  $df=2$ ,  $P > 0.10$ ).

The average age of death for all females was 13 years, 11 months (median age: 13 years, 7 months). Five females are known to have been over 20 years of age at the time of death. High-ranking females tended to die at slightly younger ages than middle- and low-ranking females, although these differences were not significant. The average age of death for high-ranking females was 13 years, 5 months (median: 10 years, 4 months;  $N=7$ ), compared with 13 years, 7 months (median: 13 years, 7 months;  $N=9$ ) for middle-ranking females and 14 years, 8 months (median: 14 years, 8 months;  $N=8$ ) for low-ranking females.

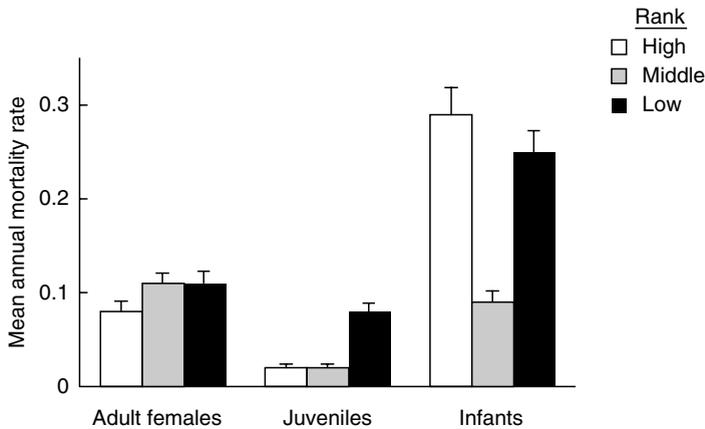
Pregnant females may have been particularly vulnerable to predation. At least 13 of the 23 females (56 percent) that died of apparent predation were pregnant when they died. By comparison, only 4 (19 percent) females with infants under the age of 6 months, the approximate length of gestation in baboons, died.

### 4.3. Juvenile Mortality

All juvenile deaths appeared to be due to predation (Table 3). Of the 19 juveniles that disappeared, 1 was killed by a lion, 2 were suspected to have been killed by lions, and 1 disappeared after sustaining injuries that appeared to be crocodile-inflicted. An additional 15 juveniles disappeared when healthy. As in the case of adult females, juvenile mortality increased during the period of greatest flooding; 53 percent of 15 juvenile deaths between August 1992 and July 2002 occurred during the months of July–September (Figure 4;  $\chi^2 = 6.43$ ,  $df = 1$ ,  $P < 0.05$ ).

Mortality rates among juveniles were generally lower than those for adult females and infants (Figure 5). Juveniles of both sexes experienced an average annual mortality rate of 0.04 (females = 0.04,  $sd=0.04$ ; males = 0.04,  $sd = 0.04$ ).

Previous research on this study group has suggested that the juvenile offspring of low-ranking mothers may be more vulnerable to predation than other juveniles, because they are more likely to feed in peripheral areas (Johnson, 2003). Indeed, the juvenile offspring of low-ranking females suffered higher levels of mortality. Ten (53 percent) of the juveniles that died of apparent predation had mothers who ranked in the bottom third of the female dominance hierarchy, compared with five (26 percent) and four (21 percent) for offspring of high- and middle-ranking females, respectively.



**Figure 5.** Mean annual mortality rates for high-, middle-, and low-ranking females and their offspring (Kruskal–Wallis one-way analysis of variance; adult females:  $H=1.46$ ,  $df=2$ ,  $P > 0.10$ ; juveniles:  $H=6.78$ ,  $df=2$ ,  $P < 0.05$ ; infants:  $H=7.25$ ,  $df=2$ ,  $P < 0.05$ ). Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.

The average annual mortality rate among the juvenile offspring of low-ranking females was 0.08, compared with a rate of 0.02 for the offspring of both high- and middle-ranking females (Figure 5;  $H=6.78$ ,  $df=2$ ,  $P < 0.05$ ).

Though sample sizes are small, there was some indication that juvenile male mortality decreased with increasing age, whereas juvenile female mortality did not. Only one (14 percent) of the seven deaths among juvenile males occurred after 2 years of age. In contrast, eight (67 percent) of the twelve juvenile females who died were over 2 years of age (two-tailed Fisher exact probability test,  $P < 0.05$ ). After about the age of 2 years, juvenile males begin to dominate juvenile females in competitive interactions, regardless of their mothers’ relative ranks (Pereira, 1988; Lee and Johnson, 1992; unpublished Moremi data). The juvenile daughters of low-ranking females may have been forced to forage in more peripheral areas than juvenile males, thereby increasing their vulnerability to predation.

#### 4.4. Infant Mortality

##### 4.4.1. Causes and Patterns of Infant Mortality

Of 120 infants born in the group, 46 (38 percent) died before reaching the age of 1 year (Figure 3). Seven infants either died on the day of birth or appeared

to be ill at the time of death (Table 3). Seven others died when their mothers were killed by predators. Three infants disappeared while observers were absent for more than 24 hr and three infants disappeared within 24 hr of having been observed apparently healthy. Infanticide accounted for the majority of infant deaths, ranging from at least 23 percent to as much as 70 percent annually (see also Palombit et al., 2000). Observers witnessed 11 cases of infanticide by resident adult males and another nine cases of infanticide were strongly suspected (Table 3). Five other apparently healthy infants disappeared when other infants were known to have been killed by adult males. The majority (64 percent) of the 25 infants known or suspected to have been killed by males were under 3 months of age and still being carried by their mothers.

As with predation, infanticide was most frequent during the period of peak flooding (July–September). Six (55%) of the eleven cases of observed infanticide occurred from July through September, while 44 percent of the nine infants strongly suspected to have been killed by infanticide also disappeared during this time. Overall, a significant proportion (55 percent) of the 33 infants that disappeared healthy between August 1992 and July 2002 died during these 3 months ( $\chi^2 = 15.37$ ,  $df = 1$ ,  $P < 0.01$ ).

Seasonal peaks in the frequency of infanticide were not obviously related to seasonal fluctuations in male immigration patterns. Of the 40 males that immigrated into the group from July 1992 through December 2002, 30 percent immigrated in January–March, 32 percent in April–June, 25 percent in July–September, and 13 percent in October–December.

Mortality rates among infants fluctuated more widely than mortality in other age classes, ranging from 0.03 to 0.57 annually. The average annual mortality rate for infants was 0.21 ( $sd = 0.15$ ).

The infants of high-ranking females were not more likely to survive than the infants of lower-ranking females. Of the 42 infants born to high-ranking females, 45 percent died before the age of 1, compared with 31 percent of infants born to middle-ranking females ( $N = 43$ ), and 37 percent of infants born to low-ranking females ( $N = 35$ ). The average annual mortality rate for infants of high-ranking females was 0.29, higher than the mean mortality rate for low-ranking (0.25) and especially middle-ranking females (0.09) (Figure 5;  $H = 7.25$ ,  $df = 2$ ,  $P < 0.05$ ).

The infants of middle-ranking females appeared to be less vulnerable to infanticide than the infants of high- and low-ranking females. Only 12 percent of the 25 infants suspected of being killed by infanticide were the offspring of

middle-ranking mothers. In contrast, 53 percent were the offspring of high-ranking females and 36 percent the offspring of low-ranking females.

Primiparous females experienced higher infant mortality (44 percent;  $N = 25$  births) than multiparous females (35 percent;  $N = 97$ ). This was particularly true for low-ranking primiparous females. A majority (71 percent) of the infants born to primiparous low-ranking females died before reaching 1 year of age ( $N = 7$ ), compared with 30 percent ( $N = 10$ ) and 38 percent ( $N = 8$ ) of the infants born to high-ranking and middle-ranking primiparous females, respectively. This difference, however, did not reach statistical significance.

#### 4.4.2. *Factors affecting infant survival*

We used logistic regression to identify factors that predict infant survival to 1 year of age, using the  $-2$  log likelihood (Tabachnik and Fidell, 2001) to identify the best model. We examined the following factors: infant sex, age category of the mother (5–7.9, 8–14.9, 15, and older), season when infant was born (quarter of the year), parity of the mother (primiparous or multiparous), rank of the mother (high, middle, low), and the presence of close adult female kin. The analysis included the 119 infants for whom there were no missing values.

Mother's age had a significant effect on infant survival (likelihood ratio test,  $\chi^2 = 8.65$ ,  $df = 2$ ,  $P = 0.013$ ), with middle-aged females experiencing lower infant mortality rates (27 percent;  $N = 64$ ) than young (41 percent;  $N = 29$ ) or old (62 percent;  $N = 26$ ) females. The mortality rate was significantly different between young and middle-aged females ( $\chi^2 = 3.83$ ,  $df = 1$ ,  $P = 0.05$ ,  $\exp(B) = 0.303$ ), and between middle-aged and old females ( $\chi^2 = 8.143$ ,  $df = 1$ ,  $P < 0.01$ ,  $\exp(B) = 0.299$ ).

Season of birth tended to have some effect on infant survival (likelihood ratio,  $\chi^2 = 6.67$ ,  $df = 3$ ,  $P = 0.083$ ). Mortality was highest among infants born in the second quarter of the year, which was also the time of the fewest births (see above). There were significant differences in the mortality rates between the second and the fourth quarter ( $\chi^2 = 6.11$ ,  $df = 1$ ,  $P < 0.05$ ,  $\exp(B) = 0.174$ ).

As in other populations of baboons (Altmann and Alberts, 2003), males tended to experience higher mortality than females (likelihood ratio,  $\chi^2 = 3.03$ ,  $df = 1$ ,  $P = 0.082$ ): 46 percent of males ( $N = 56$ ) and 30 percent of females ( $N = 63$ ; one infant could not be sexed before death) died before the age of one year ( $\chi^2 = 2.97$ ,  $df = 1$ ,  $P < 0.10$ ,  $\exp(B) = 2.08$ ).

Neither maternal rank, parity, nor the presence of living kin contributed significantly to infant survival in this analysis (Cheney et al., 2004).

## 5. FEMALE LIFETIME REPRODUCTIVE SUCCESS

Because we have not yet followed a large sample of females from birth to death, we cannot specify precisely the extent to which lifespan, fecundity, and offspring survival influence female lifetime reproductive success. As a first pass at such an analysis, we calculated the number of breeding years, fecundity, and offspring survival for all females present in the group between 1992 and 2002, including all offspring produced by these females prior to 1992. Ideally, this analysis would have been restricted to females whose entire reproductive history was known. However, given small sample sizes and the relatively short duration of the study, our first analysis included all females present in the group between 1992 and 2002 for whom complete birth records were available ( $N=42$  females, average age of all females = 13 years, 7 months). In a separate analysis, we removed females that were still alive and restricted our sample to females whose reproductive lives were completed ( $N=24$  females, average age = 13 years, 11 months).

Similarly, our calculations of offspring survival would ideally have included only those offspring that survived to adulthood. Again due to small sample size, however, we calculated offspring survival in terms of infant survival to one year. Table 4 presents mean values of  $L$  (number of breeding years),  $F$  (fecundity, or number of offspring/ $L$ ), and two measures of  $S$  (the proportion of offspring surviving to 1 year,  $S_1$ , and to reproductive age,  $S_a$ ) for all 42 breeding females, divided into high-, middle-, and low-rank categories. Table 5 presents the same data for the 24 deceased females. Both tables also show values for mean lifetime reproductive success, calculated as the product of  $LFS$ .

We detected few consistent rank-related differences in reproductive success, particularly when the analysis was restricted to deceased females whose reproductive lives were complete (Tables 4 and 5). Fecundity was higher among high-ranking females, while middle-ranking females on average experienced higher offspring survival. Lifetime reproductive success, however, was similar for high- and middle-ranking females. Indeed, what seems most notable about the calculations is the high degree of variance within every rank category for each measure of reproductive success. This variance was particularly striking for high- and low-ranking females.

**Table 4.** Mean (+variance) values for life history traits for all breeding females present in group between 1992 and 2002

	All ( <i>N</i> = 42)	High ranking ( <i>N</i> = 14)	Middle ranking ( <i>N</i> = 15)	Low ranking ( <i>N</i> = 13)	Kruskal–Wallis <i>H</i> (df =2)
<i>L</i>	7.35 (23.38)	7.66 (29.24)	6.61 (16.18)	7.87 (28.24)	7.07
<i>F</i>	0.63 (0.04)	0.66 (0.05)	0.64 (0.02)	0.58 (0.05)	9.91*
<i>S</i> <sub>1</sub>	0.62 (0.09)	0.53 (0.08)	0.75 (0.05)	0.55 (0.11)	3.41
<i>S</i> <sub>a</sub>	0.39 (0.07)	0.34 (0.11)	0.50 (0.06)	0.34 (0.04)	1.80
<i>LFS</i> <sub>1</sub>	2.79 (3.58)	3.01 (4.65)	2.73 (2.15)	2.62 (4.61)	7.43
<i>LFS</i> <sub>a</sub>	2.17 (2.99)	2.32 (5.25)	2.22 (1.34)	1.95 (2.68)	0.63

*L* is the number of breeding years; *F* is the fecundity; *S*<sub>1</sub> is the percentage of offspring surviving to 1; *S*<sub>a</sub> is the percentage of offspring surviving to adult. Data exclude five females over the age of 6 that had either not produced offspring or whose offspring had not yet reached 1 year of age by 31 December 2002. Kruskal–Wallis one-way analysis of variance test compares high-, middle-, and low-ranking females. \* = *P* < 0.05, after Bonferroni adjustment. See text for description of each life history trait. Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.

**Table 5.** Mean (+variance) values for four life history traits for all now-deceased adult females present in group between 1992 and 2002

	All ( <i>N</i> = 24)	High ranking ( <i>N</i> = 7)	Middle ranking ( <i>N</i> = 9)	Low ranking ( <i>N</i> = 8)	Kruskal–Wallis <i>H</i> (df =2)
<i>L</i>	7.85 (30.52)	6.96 (48.13)	7.40 (18.39)	9.14 (35.06)	0.51
<i>F</i>	0.58 (0.05)	0.63 (0.10)	0.60 (0.01)	0.51 (0.05)	2.28
<i>S</i> <sub>1</sub>	0.53 (0.09)	0.37 (0.09)	0.69 (0.05)	0.46 (0.08)	11.57*
<i>S</i> <sub>a</sub>	0.43 (0.07)	0.30 (0.09)	0.55 (0.07)	0.39 (0.04)	2.46
<i>LFS</i> <sub>1</sub>	2.58 (4.13)	2.43 (7.63)	2.69 (1.99)	2.76 (5.96)	0.33
<i>LFS</i> <sub>a</sub>	2.33 (3.30)	2.38 (6.86)	2.34 (1.84)	2.27 (3.14)	0.87

Legend as in Table 4. Reprinted from Cheney et al., “Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana,” *International Journal of Primatology* 25:401–428, with the kind permission of Springer.

We next subjected these calculations to the model developed by Brown (1988) for partitioning variance in lifetime reproductive success into additive contributions due to variation in single components, and to variation and covariation among groups of components (for discussions of this method, see Brown, 1988; Grafen, 1988). Table 6 presents the estimated overall variance in lifetime reproductive success among all females who survived to breeding age (approximately 56 percent). Table 7 presents the same calculations for all deceased females. In both tables, values show the percentage of *V(LFS)* accounted for by variation in *L*, *F*, *S*, and their products, with the diagonal containing single component contributions. Due to small sample sizes, *S* was calculated as the proportion of offspring reaching 1 year of age (*S*<sub>1</sub>), a value that overestimates actual *S*.

**Table 6.** Percentage contribution of the components of lifetime reproductive success to variation in *LRS* for all females of breeding age between 1992 and 2002

	<i>L</i>	<i>F</i>	<i>S</i>
<i>L</i>	49.59		
<i>F</i>	-7.82	5.52	
$S_1$	-21.64	-5.73	29.84
<i>LFS</i>	-2.673		

N = 42 females. See text for explanation of analysis. Reprinted from Cheney et al., "Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana," *International Journal of Primatology* 25:401-428, with the kind permission of Springer.

**Table 7.** Percentage contribution of the components of lifetime reproductive success to variation in *LRS* for all deceased females of breeding age between 1992 and 2002

	<i>L</i>	<i>F</i>	<i>S</i>
<i>L</i>	38.58		
<i>F</i>	-0.45	4.90	
$S_1$	-8.57	-11.78	30.54
<i>LFS</i>	-0.34		

N = 24 females. See text for explanation of analysis. Reprinted from Cheney et al., "Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana," *International Journal of Primatology* 25:401-428, with the kind permission of Springer.

Even when only those females that survived to breeding age were considered in the analysis and offspring survival was overestimated, *L*, or the number of breeding years, accounted for the highest proportion of variance in lifetime reproductive success. Offspring (infant) survival accounted for the second highest proportion. Both fecundity and offspring survival negatively covaried with lifespan, with the result that their effect on the product reduced its variance rather than increasing it. The same was true of the covariance between fecundity and survival.

These trends remained the same when calculations were performed separately for high-, middle-, and low-ranking females. Because most adult and juvenile mortality was due to predation, and most infant mortality was due to infanticide, these two factors appeared to be the most important variables influencing female lifetime reproductive success.

## 6. DISCUSSION

Female baboons, like many other species of Old World monkeys, form nepotistic dominance hierarchies. Regardless of their rank, however, all females are

able to breed. As a result, differences in the reproductive success of high- and low-ranking females are not as obvious as they are in species with high reproductive skew, in which some females do not breed at all (see “Introduction”).

Because one of the primary advantages of high rank is increased access to food, the reproductive benefits associated with high rank are likely to be most obvious in times of food scarcity or drought (Alberts et al., 2005). In the Moremi population, linear dominance relations among adult females were unambiguous, and there was competition among adult females and juveniles for food (Johnson, 2003). There was little evidence, however, of rank-related illness or malnutrition, and any functional effects of food competition on female reproductive success were subtle. As in many other populations of Old World monkeys (see “Introduction”), high-ranking females experienced somewhat shorter interbirth intervals than mid- or low-ranking females. Like baboons in Amboseli, Kenya (Altmann and Alberts, 2003), their infant and juvenile daughters also grew at faster rates and achieved higher weights for their age (Johnson, 2003, this volume). In contrast to Amboseli, however, these faster growth rates did not result in a younger age at first birth.

In Amboseli, female baboons with extensive social networks have significantly higher offspring survival than females without such networks (Silk *et al.*, 2003). Although this effect was not evident in the Moremi population, we did find that females with close female kin gave birth at younger ages and had shorter interbirth intervals. This pattern, however, was apparent only in high- and middle-ranking females. In captive vervet monkeys, primiparous females with living mothers experience significantly reduced infant mortality (Fairbanks and McGuire, 1986). This effect is particularly striking among high-ranking females, whose mothers take a more active role in care-giving than lower-ranking grandmothers (Fairbanks, 1988). Similarly, in baboons (Cheney, 1992; Silk et al., 1999, 2003, 2004) and rhesus macaques (*M. mulatta*; Berman, 1980), female members of high-ranking matriline tend to maintain greater proximity, groom each other at higher rates, and support each other at higher rates than the members of low-ranking matriline. The presence of female kin may accelerate reproduction in high- and middle-ranking individuals, for example, by enhancing access to resources or reducing stress levels. These effects may be less evident in less cohesive low-ranking matriline, where the presence of kin may even decrease females’ competitive access to food.

Unlike females in some other populations of baboons and Old World monkeys (see “Introduction”), high-ranking females in this study did not experience

higher infant survival, probably because infant survival was not entirely condition dependent. Infanticide was the primary cause of infant mortality, and it affected females regardless of their competitive abilities. Adult male baboons have nearly twice the body mass of adult females, and even high-ranking females are unable to defend themselves or their infants against infanticidal males. Female alliances appear to be equally ineffective in resisting such attacks (Palombit et al., 2000). Perhaps as a result, high-ranking females and females with adult kin did not experience higher infant survival than other females.

Although females of all ranks were vulnerable to infanticide, middle-ranking females appeared to be less susceptible than high- and low-ranking females. Several factors may have contributed to high- and low-ranking females' increased risk of infanticide. First, males and high-ranking females enjoy priority of access to high-quality food resources, with the result that high-ranking females may be more likely than other females to feed in close proximity to a potentially infanticidal male. Second, high-ranking females are more successful than lower-ranking females at competing for "friendships" with high-ranking males (Palombit et al., 2001). These males, however, are also more likely than lower-ranking males to compete with other males for access to estrous females, which may again expose high-ranking females to potentially infanticidal males. Low-ranking females, in contrast, are more likely to feed or take refuge in more peripheral areas (van Noordwijk and van Schaik, 1987; Ron et al., 1996; Johnson, 2001) and to form friendships with low-ranking males who may be unable to resist attacks by higher-ranking males. Both factors may increase the vulnerability of low-ranking females to infanticide.

As in previous studies of this same population, predation was the primary cause of mortality among juveniles and adults (Busse, 1982; Bulger and Hamilton, 1987) and appeared to be a major determinant of female lifetime reproductive success. The intensity of predation fluctuated strongly, even over short periods of time. In some years, females experienced relatively low mortality rates. In one year, however, 24 percent of the group's adult females died of apparent predation (see also Bulger and Hamilton, 1987).

For female baboons at Moremi, two factors in particular accounted for the highest proportions of variance in lifetime reproductive success: a female's number of breeding years and the survival of her infants. This finding is unsurprising: Baboons are long-lived mammals that give birth to single offspring requiring extensive maternal investment. Indeed, similar analyses on other populations of baboons (Rhine et al., 2000; Altmann and Alberts, 2003), other

monkeys (e.g., Cheney et al., 1988a,b), and other mammals (e.g., lions: Packer et al., 1988; elephant seals, *Mirounga angustirostris*: Le Boeuf and Reiter, 1988) have also shown that lifespan (number of breeding years) and offspring survival contribute substantially more to lifetime reproductive success than fecundity. The negative covariations between the products of  $L$ ,  $F$ , and  $S$  shown in Tables 6 and 7 are also expected. It is well known that offspring survival decreases female fecundity, and that investment in offspring may reduce the number of breeding years. More interesting, perhaps, is the lack of any effect of female dominance rank on the components contributing to lifetime reproductive success. High-ranking females did not live significantly longer than low-ranking females, and their infants suffered relatively high mortality rates. Both factors appeared to offset any advantages in increased fecundity that high-ranking females might have gained through priority of access to food.

There were strong seasonal effects on mortality. Most deaths among females, juveniles, and infants occurred during the 3 months of peak seasonal flooding. Throughout this period, the baboons took highly predictable routes with limited numbers of escape options when moving between islands, which may have increased their vulnerability to both predation and infanticide. Infanticide was not obviously correlated with the timing of male immigration, however, probably because not all immigrant males assumed high rank and those that did achieved this status at varying intervals after immigrating. Moreover, male immigration was not itself seasonal.

In a previous study of baboons in Amboseli, lactating females were found to experience higher mortality than females in other reproductive states (Altmann et al., 1988). In this study, by contrast, mortality appeared to be highest among pregnant females. One possible cause for this difference is that the friendships formed between adult males and lactating female baboons in Moremi are particularly strong and enduring (Palombit et al., 1997). In addition to reducing the probability of infanticide, friendships may have also reduced lactating females' own vulnerability to predation (Busse, 1984; Cowlishaw, 1999). In contrast, pregnant females spend more time feeding and less time engaged in social activities than other females (Silk, 1987), which may in turn increase their vulnerability to predation.

The findings reported here may be compared with those of an earlier 8-year study of the same group living at a similar population density (Bulger and Hamilton, 1987). In that study, high-ranking females also had shorter

interbirth intervals. In this study, however, high-ranking females also experienced lower infant mortality and higher adult mortality. These differences in rank-related correlates of reproductive success serve to emphasize that the factors influencing reproduction and survival are both facultative and variable, even over short periods of time.

In sum, those reproductive parameters most likely to be associated with superior competitive ability—interbirth interval and infant growth rates—conferred a slight fitness advantage on high-ranking females. This fitness advantage was counteracted, however, by the effects of infanticide and predation. Infanticide affected high- and low-ranking females more than middle-ranking females, while predation affected females of all ranks relatively equally. As a result, there were few rank-related differences in estimated lifetime reproductive success.

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BEHAVIORAL, ECOLOGICAL,  
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PERSPECTIVES

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