

Bonnet Macaques: Evolutionary Perspectives on Females' Lives

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I have spent a good part of the last 20 years studying the social behavior of an obscure monkey, the bonnet macaque (*Macaca radiata*). Bonnet macaques (Figure 1) are indigenous to southern India where they live in groups of about 30. Many bonnets were imported to the United States from India for biomedical research in the 1960's. Some of these animals found their way into behavioral research projects, including the founding members of a group of monkeys that I observed at the California Regional Primate Research Center at the University of California, Davis. In the Davis group, bonnets reared offspring, developed relationships, conducted courtships, and grew old under the watchful eyes of observers.

I spent hundreds and hundreds of hours standing outside the bonnet's enclosure, sweating under the hot Central Valley sun and shivering in the damp Valley fog. Over the years, I got to know dozens of monkeys. I learned to recognize their faces, admire their punk hair-do's, and appreciate their distinctive personalities.

My research on this group of bonnet macaques did not begin the way scientific projects are supposed to start. When students start thinking about conducting research they are usually advised to identify an important and tractable theoretical question and then choose a biological model which is appropriate for studying the question they have chosen. This is wise advice, and I am sure that the other distinguished contributors to this volume followed it. But my own research followed a different trajectory---I started studying a species I knew very little about, devised a completely intractable research project, and then let the monkeys lead me from one research question to another. I don't advise students to follow my example. But it might be useful to remember that nearly

every researcher makes false starts, commits errors, encounters obstacles, and confronts dead ends. But most of us are also blessed by surprises, serendipity, and dumb luck.

I began graduate school at an exciting time. It was 1976. E.O. Wilson's massive tome on evolutionary biology, *Sociobiology: The New Synthesis*, had been published just one year earlier. Wilson popularized the theoretical work of W.D. Hamilton, Robert Trivers, John Maynard Smith, and many others and compiled a vast amount of empirical information about the form and function of behavior. This body of work generated considerable intellectual excitement within biology and the behavioral sciences, provoking intense debates within the biological research community about the units of selection, the nature of adaptation, and the effects of selective forces on the evolution of social behavior. A flood of empirical and theoretical work followed. These ideas became the foundation of my graduate training.

Like many students, I was anxious to apply my academic knowledge to my own research project. My choice of taxa was limited to primates for several reasons. As an undergraduate, I had spent nearly a year studying chimpanzees at the Gombe Stream Reserve under the supervision of Jane Goodall. That experience led me to the graduate program in Anthropology at the University of California at Davis. One branch of anthropology, biological anthropology, is concerned with human evolution and adaptation. Biological anthropologists study primates because we share a common evolutionary history and we are similar to other primates in our physiology, morphology, life history, and behavior. Academic custom dictates that anthropologists study primates, but not other kinds of animals.

So, I was limited to primates. Although the first primates originated in North America, they have been gone from this continent for nearly 70 million years. However, I was lucky that U.C. Davis is the site of the California Regional Primate Research Center (CRPRC) which houses a large population of Old World monkeys. My graduate advisor suggested that I join him and another student, Amy Samuels, in studying a group of bonnet macaques there. Although I knew virtually nothing about these animals, I accepted his offer. I passed the obligatory TB test, was issued a white lab coat, and started bicycling out to the primate center several days a week.

I decided to study female mate choice in the bonnet group. I wanted to know how females' preferences affected male reproductive success and why females preferred some males over the others (or vice versa). This project was grounded in evolutionary theory, but it was completely intractable empirically. Three fundamental problems emerged. First, female bonnet macaques provide no visible external signs of their ovulatory status. This meant I couldn't determine when females were sexually receptive or likely to conceive. Second, I couldn't assess whether females' preferences were effective in determining who fathered their offspring because newly developed immunological techniques could not be used to assess paternity in this species. Third, it became clear that females' choices were sometimes constrained by male-male competition, making it difficult to discern their true preferences. By the end of the first mating season, I knew the project would not work¹.

¹ Today, the situation is very different because newly developed genetic techniques allow questions about paternity to be resolved. One of my graduate students has successfully examined female mate choice in Japanese macaques (*Macaca fuscata*; Soltis et al. 1997a, 1997b) and resolved nearly all of the questions that plagued my research on bonnets.

But in those months, I'd learned a lot about the bonnets. Life in a macaque group is like a soap opera in which all the leading roles are played by females: relationships are formed, conflicts erupt, compromises are negotiated, and support is provided. Like despots everywhere, the dominant females in the group enjoyed the advantages of their rank. They regularly supplanted lower ranking females from drinking fountains, disrupted peaceful grooming parties, appropriated the shadiest resting spots in the summer, and installed themselves in the warmest and driest refuges in the winter.

We also noticed that high-ranking females had larger families than low-ranking females. The relationship between females' rank and the size of their families interested us because variation in reproductive success provides the raw material upon which natural selection acts. Thus, any factors that create systematic differences in reproductive success among individuals should be subject to strong selective pressure. However, there had been very few attempts to measure the source and significance of variation in reproductive success among mammalian females. This was partly due to the fact that the reproductive success of mammalian males potentially varies more than that of females who are constrained by the demands of gestation and lactation (Bateman 1948). Since variance in female reproductive success was relatively low, it was assumed to be of little adaptive importance.

But the conventional wisdom didn't seem to fit what we saw among the bonnets—reproductive success among females varied considerably. The females in the highest ranking family had healthy infants year after year, while the lowest ranking female produced one nonsurviving infant after another. Thus, we set out to identify the

sources of variation in female reproductive success and to examine the processes that contributed to this variation.

Life History of Female Bonnet Macaques

All other things being equal, a reproductively successful female will be one who has a long reproductive career, produces infants at regular intervals, and rears her infants successfully. Variation in any of these parameters can create variation in females' reproductive success.

It is important to realize that not all the factors that affect female reproductive success are likely to produce systematic variation in reproductive success among females. This is because some factors, such as age, have roughly the same effect upon all females. Among primates, young females routinely reproduce less successfully than mature females do (Fairbanks and McGuire 1995; Small and Rodman 1981; Wilson et al. 1983), while females' fertility becomes progressively more variable as they reach old age (Caro et al. 1995). All other things being equal, age-related changes in fertility do not produce variation in reproductive success among females because all females grow old. Some factors generate variation in reproductive success, but are not subject to natural selection because they are not based upon heritable traits. Thus, environmental events (like floods, droughts, predation, disease) may generate variation in individual reproductive success. But if vulnerability to environmental catastrophes is not linked to heritable traits, then this variation will not be subject to selection. However, there are some factors that have consistent effects upon different individuals, and may contribute to systematic variance in reproductive success among females. Thus, the ability to acquire valuable resources, the

choice of a good mate, or the ability to protect offspring from environmental hazards may cause female reproductive success to vary systematically. If the traits that enhance females' reproductive success are transmitted genetically to offspring, they will be subject to natural selection.

For macaque females, there is good reason to think that dominance rank might contribute to differential reproductive success. The reproductive success of female mammals is limited by their access to food, while male reproductive success is mainly limited by access to receptive females (Wrangham 1980). There is good evidence that fertility of primate females and the growth of primate populations is influenced by the availability of food (e.g. Altmann et al. 1993; Dittus 1979, 1980; Fujii 1975; Koford 1965; Koyama et al. 1975; Kurland 1977; Masui et al. 1975; Sugiyama and Ohsawa 1975; Takahata 1980). Moreover, many primates, including macaques, rely on foods that occur in clumps that can be monopolized, making competition over access to food sites profitable (Isbell 1991; van Schaik 1989; van Hooff and van Schaik 1992). In many primate species access to resources is regulated by dominance relationships, as dominants maintain priority of access (e.g. Cheney et al. 1981; Dittus 1979, 1986; Whitten 1983; Wrangham 1981). Thus, dominance rank may influence females' nutritional condition and ability to reproduce successfully.

Although this logic seems compelling now, there was little evidence that it was correct when we began our work. In one provisioned population established on an island in the Caribbean, Drickamer (1974) found high and middle-ranking females' daughters produced their first infants at slightly earlier ages than low-ranking females' daughters did. Moreover, he found that high-ranking females were more likely to produce

infants each year than lower ranking females, and the infants of high-ranking females' were more likely to survive to 6 months than the infants of low-ranking females were. However, these trends emerged only among females who had been born in the wild, not females who had been born in the colony. Drickamer (1974) suggested that this discrepancy was due to the fact that the wild-born females were all older than the captive-born females, but he was unable to assess the effects of birthplace, age, and rank independently. Shortly afterwards, Sade et al. (1976) reported that high ranking lineages grew at faster rates than low ranking ones, providing further evidence that dominance rank influenced females' reproductive performance. We were encouraged by these results because they showed that there was substantial variation in female reproductive success and suggested that female dominance rank contributed to that variation.

Sources of Variation in Female reproductive success

The first step was to establish the basic parameters that define females' reproductive careers. Female macaques usually reproduce seasonally (Lindburg 1987), restricting conceptions and births to discrete periods with the year. Among the bonnets in Davis, most conceptions took place between October and December, while births followed approximately 5½ months later in March, April and May (Figure 1, Silk 1989). Females' reproductive careers began when they conceived their first infant at about 3½ years of age (Silk 1988; Silk et al. 1981a) and they continued to reproduce until their deaths, although fertility declined as females aged (Caro et al. 1995). The oldest females in the group lived about 20 years, but not many females survived to this age (Caro et al. 1995).

Most females in the group produced their first infant when they were between 47 and 50 months of age (Silk 1988; Silk et al. 1981a), but a few females gave birth before they reached this age and a few females did not give birth until they were older. In this group the variance in age at first birth is mainly a function of when females themselves were born themselves. Eleven of the 13 females who produced their first infants when they were younger than 47 months or older than 50 months of age were born outside the normal mating season. Thus, they were either younger or older than other members of their cohorts. Females' dominance rank had no consistent effect on the age of first birth (Silk et al. 1981a).

The length of interbirth intervals varied over the course of females' reproductive careers. Intervals following surviving births lasted, on average, 15 months, while intervals following nonsurviving infants lasted 13 months on average (Silk 1988; Silk et al. 1981a). This difference in the length of IBI following surviving and nonsurviving infants reflects the energetic costs of rearing infants. These costs appear to be most pronounced for young females (Wilson et al. 1983). Females' whose first-born infant survived had IBI's that lasted on average 21 months, while females whose first-born infant did not survive had IBI's that lasted 14 months on average. Fertility was generally highest among middle-aged females, but as females aged their fertility declined (Caro et al. 1995). Female dominance rank had virtually no effect on the length of intervals following surviving or nonsurviving births (Silk 1988).

Approximately one-half of all infants born in the group survived to the age of six months (Silk 1988; Silk et al. 1981a). First-born infants were somewhat less likely to

survive than other infants (Silk 1988). However, for multiparous females, there was no consistent relationship between parity and infant survival (Silk 1988).

Maternal rank was directly related to infant survivorship, as 62% of the offspring of high-ranking females survived their first 6 months of life, while only 38% of the offspring of low-ranking females survived to this age (Silk 1988). Differences in infant survivorship also contributed to differences in survival to reproductive age. 46% of the offspring of high-ranking females survived to the age of four years, while only 27% of the offspring of low-ranking females survived to this age. Moreover, rank-related variation in reproductive success was perpetuated in the next generation. High-ranking females were more likely to produce daughters who survived to reproductive age, and their daughters were more likely to reproduce successfully than the surviving daughters of low-ranking females (Silk 1988).

Adaptive significance of the relationship between female dominance rank and reproductive success

We have subsequently discovered that dominance rank is related to reproductive success in many primate species (reviewed by Harcourt 1987; Silk 1987, 1993). This does not mean that rank is positively correlated with all components of reproductive success in every group (e.g. Altmann et al. 1988; Gouzoules et al. 1982), or that statistically significant correlations between dominance rank and reproductive success are established in every study (e.g. Cheney et al. 1988; Packer et al. 1995). Moreover, a growing body of theoretical and empirical work indicates that the strength of the relationship between female rank and reproductive success depends partly on local ecological conditions, particularly the abundance and distribution of food (Isbell 1991;

van Hooff and van Schaik 1992; van Schaik 1989; Wrangham 1980). However, there is no evidence that *low* rank ever confers unambiguous advantages upon females.

For macaques, the adaptive significance of the relationship between dominance rank and reproductive success is compounded by the relationship between female dominance rank and matrilineal kinship. Juvenile macaques typically acquire ranks just below their mothers, and females maintain these ranks when they mature (reviewed by Chapais 1992). The inheritance of maternal rank creates female dominance hierarchies in which members of the same matriline occupy contiguous ranks and all members of a given matriline rank above or below all the members of other matrilines. Matrilineal dominance hierarchies have now been documented in at least seven species of macaques (Chapais 1992), including the bonnet macaques in Davis (Silk et al. 1981b). Matrilineal dominance hierarchies are also observed among savannah baboons and vervet monkeys (Chapais 1992).

The acquisition of maternal dominance rank has important reproductive consequences for females because matrilineal dominance hierarchies tend to be very stable over time (Hausfater et al. 1982; Isbell and Pruett 1998; Lee 1983; Kawai 1958; Sade 1967). For example, researchers observed no challenges to higher ranking females during a four-year study of vervet monkeys (Isbell and Pruett 1998). In the bonnet group, the dominance hierarchy remained relatively stable for over a decade. This means that a female who is born into low-ranking lineage is likely to become low-ranking and reproduce unsuccessfully for most of her life, while a female born into a high-ranking lineage is apt to become high-ranking and raise many healthy offspring.

The formation of matrilineal dominance relationships is generally thought to be the product of kin selection (Hamilton 1964) which favors altruistic behavior toward kin. Altruistic acts, which are defined as acts which increase the genetic fitness of the recipient at some cost to the actor, are not favored by natural selection because they reduce the fitness of the actor. However, altruism can evolve via kin selection. The general logic of kin selection is based upon the fact that individuals who behave altruistically to their relatives have some chance of conferring benefits upon individuals who carry copies of their own genes which they have acquired through descent from a common ancestor. Hamilton showed that altruism can evolve when the benefits to the recipient (b) devalued by the degree of relatedness between the actor and the recipient (c) exceed the costs to the actor (c), or $rb > c$. This has come to be known as Hamilton's rule.

Macaques behave as if they had studied Hamilton's rule. For example, they spend much of their time in close proximity to their relatives, devote more time to grooming kin than nonkin, and are more tolerant of kin than nonkin when they are feeding (reviewed by Dugatkin 1997; Gouzoules and Gouzoules 1987). Females also support their offspring and other close kin when they are involved in agonistic encounters. Both naturalistic and experimental studies have demonstrated that support from kin is largely responsible for the acquisition of maternal rank and the formation of matrilineal dominance hierarchies (reviewed by Chapais 1992).

These observations suggest that kin selection has shaped the evolution of behavior in macaque groups. In fact, the strength of kin selection is likely to be enhanced by the relationship between maternal rank, kinship, and reproductive success. To see how

Local resource competition and harassment of females

In nature, the growth of primate populations is generally limited by the availability of resources, or local resource competition (references above). In matrilineal species, including macaques, baboons, and vervets, males are the dispersing sex, while females are philopatric (Pusey and Packer 1987). If local resource competition limits females' fertility, then females' reproductive opportunities will be affected by the amount of competition that they encounter in their natal groups. Local resource competition will influence the reproductive success of their daughters, who will remain in their natal groups throughout their lives. In contrast, the extent of competition for local resources may have little impact on the reproductive success of males, who will immigrate when they reach puberty. Thus, natural selection may favor behaviors which enable females to minimize the amount of competition that they and their daughters will encounter in the future.

One way for females to limit the extent of local resource competition is to reduce the the number of unrelated infants born and raised in their groups. There is good evidence that some bonnet females do just that. Infants and juveniles were sometimes threatened, chased, and attacked by adult females. Not all infants were equally vulnerable to harassment. The offspring of low-ranking females were harassed at higher rates than the offspring of high-ranking females, and rates of aggression toward immature females were generally higher than rates of aggression toward immature males (Silk et al. 1981b). Females persistently targeted certain immature monkeys, who sometimes sustained injuries during these attacks. Over the years, several infants had to be removed from the

group for veterinary treatment, and several eventually died from their injuries. The pattern of injuries reflected the pattern of harassment: offspring of low-ranking females were more likely to be injured than the offspring of high-ranking females, and immature females were more likely to be injured than immature males (Silk 1991; Silk et al. 1981b).

Infant survivorship was also influenced by maternal rank and infant sex. The sons of high- and low-ranking females were equally likely to survive to four years of age, but the daughters of high-ranking females were three times as likely to survive to reproductive age as the daughters of low-ranking females (Figure 3; Silk 1983; 1988). Adult females were at least partly responsible for the high rates of mortality among the daughters of low-ranking females.

The selective harassment of immature females that we observed in the bonnet group may be a form of reproductive competition which results from local resource competition. This idea is supported by the fact that data from other studies also indicates that juvenile females are harassed at higher rates than males (Dittus 1977, 1979, 1980; Maestriperi 1994; Pereira 1988; Simpson and Simpson 1985). Comparative analyses indicate that in female-bonded species, like macaques, baboons, and vervets, juvenile females suffer higher mortality than males do when food is limited (van Schaik and de Visser 1990). This suggests that local resource competition favors behaviors which reduce the viability of young females, and limits the recruitment of potential competitors.

What's a mother to do?

In the bonnet group, daughters of low-ranking females faced daunting odds: they were most likely to be harassed, most likely to be injured, and least likely to survive to

adulthood. If they did survive to reproductive age, they were apt to inherit their mothers' low rank and reproduce unsuccessfully themselves.

The dismal prospects for the daughters of low-ranking females may be linked to skews in the secondary sex ratio. Over the years, more males than females have been born in the bonnet group (1.29 males per female, $n = 245$; Silk 1988). Low ranking females were largely responsible for this imbalance. While high-ranking females produced approximately equal numbers of male and female offspring (0.98 males per female), low-ranking females produced significantly more males than females (1.67 males per female).

It seemed plausible that the relationship between offspring sex and maternal rank was linked to the fact that the benefits derived from producing male and female offspring differ for high- and low-ranking females. High ranking females' daughters are likely to become high-ranking and reproductively successful, while their sons disperse and meet uncertain fates in nonnatal groups. Low-ranking females' daughters are unlikely to survive to adulthood, and if they do, they are likely to become low-ranking and reproduce unsuccessfully. Their sons will disperse and may have a greater chance of reproducing successfully than their daughters. Thus, low-ranking females who invest more heavily in sons than daughters might achieve higher fitness than low-ranking females who produce equal numbers of sons and daughters (Altmann et al. 1988; Gomendio et al. 1990; Silk 1983, 1984; van Schaik and Hrdy 1991).

Although this hypothesis made sense from what we know about matrilineal primate species, it did not fit the conventional understanding of how natural selection shapes sex ratios. R.A. Fisher (1930) showed that sex ratios will be balanced at

equilibrium because every infant has two parents. When males are less common than females, the average fitness of males in the population will be higher than the average fitness of females, and vice versa. Natural selection will always favor parents who bias investment in offspring of the less common sex (because they will on average have higher fitness than members of the more common sex), leading to balanced sex ratios at equilibrium. Thus, there was a general consensus that sex ratios would hover around unity.

However, as we published our first analyses of the relationship between maternal rank and infant sex, the consensus was being eroded by new theoretical developments. Trivers and Willard (1973) imagined a situation in which offspring of one sex benefited more from maternal investment than another, and females varied in their ability to invest in their offspring. In this situation, they argued, females in good condition would invest more heavily in the sex that benefited most from that investment, while females in poor condition would invest more heavily in the other sex. Thus, natural selection would favor the ability to adjust offspring sex ratios in relation to maternal condition. Trivers and Willard originally imagined that males would be the sex that benefited most from additional investment, but in matrilineal primate societies the opposite pattern might hold because high-ranking females can have a greater impact upon the fitness of their daughters than of their sons. Trivers and Willard's model is faithful to Fisher's basic logic because sex ratios remain balanced within the population.

Skewed sex ratios may evolve if the population is subdivided into discrete groups (Hamilton 1967; Silk 1984; Wilson & Colwell 1981), a factor that Fisher did not consider. In these models, there is a balance between natural selection operating within

groups and natural selection operating between groups. Forces operating within groups may favor biased sex ratios. Thus, in some haplo-diploid insects, females lay all of their eggs in one spot, and offspring compete for mates with their siblings. When there is local mate competition, females benefit by producing just enough male offspring to fertilize each of their female offspring (Hamilton 1967). In this situation, selection within local groups favors balanced sex ratios because males have higher fitness than females. However, selection between groups favors biased sex ratios because females who produce few sons have many daughters who carry the sex-ratio-biasing allele and will contribute to the global population.

Using the same logic, Clark (1978) argued that when there is local resource competition, females might benefit from producing a surfeit of sons who will disperse to form new groups and limiting production of daughters who will remain in the natal area and compete for local resources. We can take this argument one step further to consider what happens when the competitive abilities of females vary, and some females are able to protect their daughters better than others (Silk 1983, 1984). For females whose daughters are most vulnerable to harassment, it will be very costly to rear female offspring successfully. These females are likely to bias investment most heavily in favor of males. Under these conditions, natural selection will favor adaptations which enable females to adjust the sex ratio of their progeny in relation to their own dominance rank (Silk 1984).

I suggested that the interaction between maternal rank and infant sex that we observed in the bonnet group reflected the effects of local resource competition (Silk 1983, 1983). Similar patterns among free-ranging baboons in Amboseli, Kenya (Altmann

1980, Altmann et al. 1988) and captive rhesus macaques (Simpson and Simpson 1982; Gomendio et al. 1990) seemed consistent with this explanation. However, as more and more information about the relationship between maternal rank and infant sex became available, the picture became more complicated (reviewed by Clutton-Brock and Iason 1986; van Schaik and Hrdy 1991). Some of the new data fit the local resource competition hypothesis. Thus, in chimpanzees and spider monkeys, where males are the philopatric sex rather than females, high-ranking females invested more heavily in sons than daughters (Boesch 1997; Symington 1987). However, other data did not fit the local resource competition hypothesis. In some populations, high-ranking females produced more sons than daughters, the opposite of the pattern that we had seen among the bonnetts (e.g. Meikle et al. 1984; Paul and Kuester 1987, 1988; van Schaik et al. 1989). In other populations, there was no consistent relationship between maternal rank and infant sex (e.g. Berman 1988; Small and Hrdy 1986).

This contradictory body of data produced considerable controversy among primatologists. This dispute generated more heat than light, until Hrdy and van Schaik (1991) found one way to make sense of the observed variation. They discovered that the extent of local resource competition, measured in terms of the population growth rate, was associated with sex ratio biases. When local resource competition is intense, and reproductive opportunities for females are limited, high-ranking females invest more heavily in daughters than low-ranking females do. When local resource competition is relaxed, high-ranking females shift investment more toward their sons. Thus, much of the variation in the relationship between maternal rank and offspring sex can be explained as a function of the nature of the selective pressures perating on females and their offspring.

Evolved strategies in captive environments

I have argued that harassment of immature offspring of unrelated, lower ranking females is a form of competition over reproductive opportunities. One way that females respond to these pressures is to adjust investment in male and female offspring. However, it may seem odd that captive monkeys, who have abundant food, are motivated to compete for reproductive opportunities. Indeed, the intensity of competition and the variation in reproductive success among females is more pronounced than we see in many free-ranging groups (Harcourt 1987). There are several possible explanations of this paradox. The behavior that produces rank-related variance in reproductive success in captive populations might simply be maladaptive. However, if that were the case, it is surprising that the patterns that we observe in captivity are so consistent and generally similar to the patterns observed in the wild. It seems more likely that the bonnets' behavior reflects an evolved predisposition to respond to certain conditions in certain ways. These predispositions may produce adaptive behavior in the environments in which they evolved, but they may produce "inappropriate" outcomes when environmental conditions are radically altered. The bonnets' evolved psychology might have prepared them to prosper in the forests of Southern India, but might not have provided them with behavioral responses that are appropriate for life in a cage in California.

For macaques, whose populations are normally limited by the availability of resources, the size of their groups or the density of the local population may be a good index of the intensity of local resource competition. If this is the case, then females may

react to changes in group size or population density. Among the bonnet macaques, there is some evidence that this is the case. The size and demographic composition of the bonnet group varied from year to year, as animals were born, matured, or died. In addition, natal males were sometimes removed from the group when they matured to prevent inbreeding and simulate dispersal, while nonnatal males were occasionally added to the group.

Variation in the demographic composition of the group was associated with variation in female fertility. Female fecundity (likelihood of conceiving) was lowest in years in which there were many adult females in the group (Figure 4; Silk 1988). Female fecundity was not consistently related to the total size of the group or the number of members of any other age-sex classes. Thus, females were most likely to conceive in years when the number of other females in the group was relatively low. The density of the group was also related to the survivorship of infants. As the number of females increased, the number of infants born increase, but the proportion of infants who survived declined. Thus, high density seemed to depress females' fecundity and reduce the viability of their infants.

Similar effects can also be seen when we examine the timing of conceptions. As noted earlier, the bonnets reproduced seasonally. Although the mating lasted for six months, most conceptions were concentrated during a few months of the year. This means that some infants were conceived at the same time as many others while others were conceived when few other infants were conceived. An infant's chance of surviving was closely related to the number of other infants who were conceived at the same time. For this analysis, "synchronous conceptions" were defined as those which occurred

within 14 days. The number of synchronous conceptions was negatively correlated with the likelihood of survival. Low ranking females were particularly sensitive to the number of synchronous conceptions. Their infants were less likely to survive if they were conceived at the same time as many other infants, while the number of synchronous conceptions had little impact on survivorship of offspring of high-ranking females.

The high mortality among infants conceived during the peak of the mating season may have been behaviorally-induced. Behavioral data indicated that monthly rates of aggression corresponded roughly to the number of conceptions (Silk 1989). That is, months in which conceptions were common were months in which rates of harassment were high. These data suggest that harassment of cycling females near the time of conception may have reduced the viability of their fetuses, although there is no direct evidence to tie harassment of conceiving females to infant mortality.

Sensitivity to changes in demographic parameters, such as group size or population density, may have been favored by natural selection if these variables provided an accurate measure of the intensity of present and/or future reproductive competition. In captive situations, this evolved mechanism may “misfire”, generating behavioral responses which are not adaptive in current environments. Thus, the bonnets may have been sensitive to changes in the size or composition of the group because in the environments in which they evolved, these variables provided reliable cues of environmental conditions.

Beyond Conflict and Competition

The bonnet group in Davis has been disbanded, a casualty of changing funding priorities and new management policies. I continue to encounter the bonnets in my computer and my memories of them animate the entries in my data files, but my research is no longer focused on bonnet macaques. I have shifted continents and genera. In the last few years, I have been studying the social behavior of free-ranging savanna baboons (*Papio cyncocephalus*). The questions that I am investigating are closely related to the questions that guided my work on bonnets.

We have seen that in matrilineal primate species like macaques, baboons, and vervets females sometimes respond to competitive pressures by forming cooperative relationships. These alliances play an important role in the acquisition and maintenance of dominance rank, which is in turn correlated with reproductive success. To facilitate and sustain cooperation, monkeys must forge social bonds and develop networks of support. Researchers have begun to appreciate how important these relationships are to females, and to document how social relationships are established and preserved (Cords 1997). For example, De Waal and his colleagues have hypothesized that primates employ special tactics for reconciling former adversaries and repairing social relationships that have been damaged by conflict (e.g. Cords and Thurnheer 1993; Cords and Killen 1998; de Waal and Aureli 1996; de Waal and van Roosmalen 1979). Others have focused on the the role of grooming in reinforcing social bonds and cementing alliances (Dunbar 1991; Seyfarth 1977).

Social relationships, which represent the accumulated history of interactions among individuals (Hinde 1983), are shaped by the same kinds of evolutionary forces that shape competitive interactions. We know that kin selection and reciprocal altruism

influence the distribution of social interactions and support among female primates (reviewed by Gouzoules and Gouzoules 1987; Silk 1987; Dugatkin 1997). But it is not entirely clear how natural selection shapes the form and structure of social bonds or how females benefit from them, although there is some evidence that primate females exchange grooming for support (di Bitetti 1997; Hemelrijk and Ek 1991; Seyfarth 1980) and may cultivate relationships selectively with those who support them most (Cords 1997). To understand these issues more fully, we need more information about the structure of female relationships and a better understanding of how natural selection shapes social bonds. These issues lie at the heart of my present research agenda.

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Figure Legends

Figure 1. A female bonnet macaque holds her newborn infant.

Figure 2. In Davis, most births occurred in the months of March, April, and May.

Macaques typically breed seasonally in the wild as well.

Figure 3. Survivorship to reproductive age (4 years) is a function of maternal rank and sex. The daughters of low ranking females were less likely to survive than the sons of low ranking females or the offspring of high ranking females.

Figure 4. During years in which there were many adult females in the group, the proportion of females who produced infants declined. In general, female fertility was correlated with the number of adult females in the group, but not with the overall size of the group.