

PART I

Reproductive Behavior and Mating Strategies

CHAPTER TWO

Infant Mortality, Paternity Certainty, and Female Reproductive Strategies in Hamadryas Baboons

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CHAPTER SUMMARY

Hamadryas differ from other *Papio* baboons in that their social organization centers around reproductively exclusive one-male units. Infanticide and aggression toward infants are risks for hamadryas and other baboons and, as has been suggested for other primates, these risks may have played a role in shaping female baboon reproductive strategies. One way that females may reduce aggression toward (and promote protection of) infants is by increasing paternity uncertainty through promiscuity and the incitement of male contest and sperm competition. Presentations to multiple males, postcopulation darts, and copulation calling in particular have been suggested as mechanisms whereby females may incite male competition at both the pre- and postcopulatory levels. Accordingly, a coupling of infanticide risk and multiple mating by females (and the associated male competition)

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characterizes many baboon societies. Another, alternate route to ensure protection against infanticide and other forms of infant mortality is association and exclusive copulation with a single protective male. Paternity certainty is probably quite high among hamadryas leader males, and protective behavior toward infants has likely been selected for. Correspondingly, compared to other baboons, female hamadryas are less promiscuous, do not frequently initiate copulation, and rarely behave in ways that might incite male–male competition. We suggest that, while all baboon females use a combination of paternity concentration and confusion to varying degrees, hamadryas baboon females in particular focus on paternity concentration rather than confusion and that this can be explained by changes in male and female reproductive strategies during the evolution of hamadryas social organization.

1. INTRODUCTION

While olive (*Papio hamadryas anubis*), yellow (*P. h. cynocephalus*), and most populations of chacma (*P. h. ursinus*) baboons are characterized by a multi-male, multifemale social system in which there is little consistent substructuring, hamadryas baboon (*P. h. hamadryas*) social groups split regularly and consistently into progressively smaller subsets (Kummer, 1968; Swedell, 2006). The smallest stable social unit in hamadryas society is the one-male unit (OMU), consisting of a single “leader male” and several females. OMUs are often accompanied by *follower males*, which socialize with, but do not usually have sexual access to, the unit’s females. Several OMUs comprise a *clan*, whose male members are thought to be related (Abegglen, 1984; Swedell, 2006), and two or more clans comprise large aggregations called *bands*, analogous to the “groups” or “troops” of other baboons. Finally, two or more bands may assemble at sleeping cliffs for the night, forming *troops*.

Hamadryas female behavior is different from that of other female baboons in that it is, on the surface at least, largely controlled by males. Male herding—through visual threats, chasing, and neckbiting—is the cohesive force holding OMUs together, and each female is conditioned by her leader male to remain near him, copulate only with him, and avoid interaction with individuals outside the unit. Within such a society, it is hard to imagine that females have social or reproductive strategies of their own, or that they are able to exert such strategies.

As with other females, however, we expect female hamadryas to act in ways that maximize individual reproductive success. From a female's point of view, enhancing the "quality" of each of her offspring (e.g., through better nutrition, socialization, or protection) is one of the most important ways in which she can do so. Ultimately, the fitness of a female baboon is determined by the survival and eventual reproductive success of her infants.

As shown by Cheney and colleagues for the Moremi chacma baboon population (Cheney et al., this volume), infant survival may be impacted by ecological factors such as seasonality and predation as well as social factors such as infanticide by males. In many primates and other mammals, immigrant or newly dominant males sometimes kill dependent infants that are present at the time of the immigration or takeover (Hrdy, 1974, 1977; Brooks, 1984; Packer and Pusey, 1984; Vogel and Loch, 1984; Sommer, 1994; Blumstein, 2000; van Schaik, 2000a,c). In most of these taxa, such behavior appears to be a male competitive strategy that has evolved via sexual selection (Hrdy, 1979; Hausfater and Hrdy, 1984; van Schaik, 2000a). Infanticide and attempted infanticide by males—either directly observed or strongly inferred—has been reported for most populations of baboons that have been studied to date (summarized in Palombit, 2003). While there is wide variation among baboon populations in its occurrence, the prevalence of infanticide in the genus *Papio* as a whole would suggest that it is a behavioral predisposition shared by all baboon males (Palombit, 2003). Palombit (2003) argues that variation in infanticide rate across baboon populations can be best explained by looking at specific demographic and reproductive characteristics of each population. He explains the high rate of infanticide among chacma baboons of the Drakensberg of South Africa as resulting from a combination of long interbirth intervals, low infant mortality (from sources other than infanticide), and high reproductive skew (see Barrett et al., this volume for further discussion of this population). At least the latter two of these factors—high reproductive skew and low infant mortality—are shared by hamadryas as well, suggesting that hamadryas females should, in theory, confront at least as high a risk of infanticide as females in other baboon populations.

But what evidence is there for infanticide in hamadryas baboons? Reports of infanticide in hamadryas derive mainly from captive populations, in some of which an exceptionally high rate of infanticide occurs (Angst and Thommen, 1977; Rijksen, 1981; Gomendio and Colmenares, 1989; Kaumanns et al., 1989; Chalyan and Meishvili, 1990; Zinner et al., 1993).

Infanticide also takes place in the wild (Kummer et al., 1974; Swedell, 2000, 2006; Swedell and Tesfaye, 2003), but at a far lower frequency. The first incidence of infanticide among wild hamadryas occurred during the field experiments reported by Kummer et al. (1974): Two mothers with infants were moved into new OMUs, after which one infant disappeared and the other was found dead with large canine-inflicted wounds on its skull and thighs. Although the evidence was only circumstantial, these infants may well have been killed by their mothers' new leader males. More recent evidence of infanticide in wild hamadryas derives from the Filoha population: After four takeovers of known females, the only black infant (aged less than 6 months) associated with each takeover either (a) disappeared (in two cases), (b) was the victim of prolonged kidnapping with no protective behavior on the part of its mother's new leader male (in one case), or (c) was attacked and killed by its mother's new leader male (in one case; Swedell, 2000; Swedell and Tesfaye, 2003). The first two cases were initially conservatively interpreted as accidental infant death by prolonged kidnapping resulting from a lack of protection by the females' new leader males (Swedell, 2000, 2006). Hamadryas leader males normally defend infants from harassment and kidnapping by extra-unit individuals, and the absence of such protection is unusual within the context of hamadryas society (Swedell, 2006). The more recent observation of direct infanticide in the same wild population, however, suggests the possibility that the first two infants may have been killed, rather than just neglected, by their mothers' new leader males (Swedell and Tesfaye, 2003; Swedell, 2006).

The relatively few observations of infanticide in hamadryas baboons compared to other taxa, including those on other baboons and other mammals living in one-male groups, might suggest that infanticide in hamadryas is a relatively rare occurrence and not much of a risk for females. This apparent rarity is misleading, however, for two reasons. The first is that the number of observation hours spent on individually identified wild hamadryas baboons is a tiny fraction of that spent on groups of other monkeys in which infanticide has been reported. For example, the Hanuman langurs of Ramnagar, Nepal (e.g., Borries et al., 1999) and the baboons of the Moremi Game Reserve in Botswana (e.g., Palombit et al., 1997, 2000; Cheney et al., this volume; Johnson, this volume) have each been observed for tens of thousands of hours over several decades, compared to less than 1,500 hr of observation for the hamadryas baboons at the Filoha site in Ethiopia. The second reason

behind the apparent rarity of infanticide in hamadryas is that its occurrence appears to be closely tied to OMU takeovers, which are in themselves rare occurrences, having been observed only a handful of times (see Swedell 2000; Swedell and Tesfaye 2003). When takeovers do occur, typically only 1–4 females are involved, most of which may not have a black infant at the time. Thus, the circumstances under which infanticide would be expected to occur—male takeovers of females with young infants—do not arise very often. Overall, therefore, the actual rate of infanticide in hamadryas populations is probably quite low, but it is still undoubtedly a risk for females after takeovers. This can be described in terms of chronic versus acute risk: In savanna baboon populations such as that at Moremi (e.g., Palombit et al., 2000; Cheney et al., this volume; Johnson, this volume), where adult males are commonly in contact with infants they likely did not sire, there is a *chronic* risk of infanticide. In hamadryas populations, however, the chronic risk of infanticide is quite low but the *acute* risk after takeovers is high. In fact, the normally high rate of infant survival in hamadryas baboons (Sigg et al., 1982; Swedell, 2006) coupled with the observed and inferred infant mortality after takeovers (Swedell 2000; Swedell and Tesfaye 2003) suggests that infanticide may be the primary cause of death for hamadryas baboon infants.

Regardless of the actual number of successful infanticides that occur, infanticide is clearly a selective factor affecting hamadryas and other baboon females. Even if infanticide occurs, on average, only once in a female's lifetime, it reduces her lifetime reproductive success by negating a period of maternal investment and should therefore have an impact on the evolution of female behavior (van Schaik et al., 1999; van Schaik, 2000b). In female baboons, adaptive responses to male infanticide may include minimizing one's losses through abortion, premature birth or weaning, or an otherwise earlier return to reproductive condition following immigration or takeovers (Pereira, 1983; Colmenares and Gomendio, 1988; Alberts et al., 1992; Swedell, 2000, 2006); the manipulation of paternity assessment through "pseudoestrus" (Zinner and Deschner, 2000) or mating with multiple males (Hausfater, 1975; Smuts, 1985; Bercovitch, 1987b; Swedell, 2006); and social bonding with a protective male to obtain protection for one's infants (Smuts, 1985; Palombit et al., 1997; Weingrill, 2000; Swedell 2006). van Schaik et al. (1999) emphasize the duality of female counter-strategies to infanticide, hypothesizing that "female sexuality in species vulnerable to male infanticide has been molded by the dual need for paternity

concentration and confusion: concentration in order to elicit infant protection from the likely father, confusion in order to prevent infanticide from non-likely fathers” (p. 207).

In this chapter, we compare four components of female sexual behavior across baboons as a preliminary examination of the qualitative and quantitative differences between the reproductive strategies of hamadryas females and females of other baboon subspecies. We regard our interpretations as hypotheses for further testing rather than empirically supported conclusions. We begin with the assumption that baboon infants are at a risk of mortality from infanticide or other sources and that female baboons may employ one of the two general strategies—paternity concentration and paternity confusion—to counteract this risk. We focus on four components of behavior in particular: female exclusivity of mating, female initiation of mating, postcopulatory darts, and copulation calls. We have chosen these behavioral elements because they are largely female initiated and thus indicative of sexual motivation and underlying strategies of females rather than behavioral compromises between females and males (which would be reflected by measures such as copulation frequency and grooming rates). Each of these variables is used for heuristic purposes only and is simply meant to give us an indication of whether females are using a general strategy of paternity confusion or paternity concentration (cf. van Schaik et al., 1999). We use female *exclusivity of mating* as a direct measure of the number of males that each female mates with during an estrus period. We acknowledge that the number of males with whom a female ultimately copulates is, in part, a result of male as well as female strategies. Nevertheless, we expect this number to increase with a general strategy of paternity confusion and decrease with a strategy of paternity concentration. We use the variable *female initiation of mating* as a second measure of female promiscuity. We assume that females that are using a paternity confusion strategy would be more likely to initiate copulations with multiple males than females using a paternity concentration strategy. On the other hand, females using a paternity concentration strategy have little need to expend energy in either initiating copulations or even maintaining this behavioral element in their repertoire. We acknowledge, however, that a behavioral pattern whereby a female repeatedly initiates copulations with only one male would not be indicative of a general strategy of paternity confusion. Finally, we use female *postcopulatory darts* (the postcopulation withdrawal response, in which females run away from a male at the end of a copulation) and

copulation calls (loud vocalizations given by females during or just after copulation) as measures of a female's motivation to mate with multiple males. Both behavioral elements have been interpreted as means by which females attract attention of other males during copulation and thereby incite competition among males (O'Connell and Cowlshaw, 1994, 1995). While we recognize that copulation calls have conversely been argued to be mechanisms to assure paternity certainty and promote mate guarding (Henzi, 1996; Maestripieri et al., 2005), we view the male-male competition hypothesis to be better supported by the available evidence and use it as our working assumption for the purposes of this chapter (Hamilton and Arrowood, 1978; Oda and Masataka, 1995; Cowlshaw and O'Connell, 1996; but see Maestripieri et al., 2005).

We compare data from hamadryas baboons at the Filoha site in Ethiopia to reports of sexual behavior drawn from the literature in olive, yellow, and chacma baboons, all of which are generally characterized by a multimale, multifemale social structure (except mountain chacmas) and a female-bonded social organization. Where possible, we also include Guinea baboons, *P. h. papio*, in our comparisons.

2. METHODS

Behavioral data on hamadryas baboons, *P. h. hamadryas*, were collected from a population inhabiting the lowlands of the northern Rift Valley of East Africa. The study site is the Filoha outpost of the Awash National Park in Ethiopia (see Swedell, 2002a, b, 2006 for details). At least five different groups ("bands" cf. Kummer, 1968) of hamadryas baboons range throughout the Filoha area, each showing the characteristic hamadryas social structure (OMUs nested within clans and bands, as described above) and frequent male herding and neckbiting described by Kummer (1968). The main study group at Filoha consists of about 200 baboons, including about 25 one-male units and about 55 reproductively active females. This group has been under observation on and off over a 6-year period: 986 hr from October 1996 through September 1998 and over 250 hr from 2000 to 2004 (outlined in more detail in Swedell and Tesfaye, 2003; Swedell, 2006).

Comparative data from other baboon subspecies were drawn from the literature. Due to both the limitations of our hamadryas data set and differences in methods and presentation of results among studies, we restrict our

comparison to the four behavioral elements listed below. Because we have ranges of values for each behavioral element from only one subspecies and cannot assume that the single values obtained from the literature are robust indicators of the distribution of those data in other subspecies, we cannot perform statistical comparisons with sufficient power. Instead, we have contrasted the values graphically for heuristic purposes.

We compared the following four behavioral elements:

1. *Exclusivity of mating*: average number of different males that a female typically copulates with during the sexually swollen phase of one monthly cycle.
2. *Female initiation of copulation*: percentage of copulations or consortships initiated by females. For most populations, we refer here to percentage of *copulations* initiated by either a female presentation of the hindquarters with the tail raised, commonly referred to as a “sexual present,” or an approach. (This measure is somewhat inconsistent across studies because some authors consider an approach by a female to be an initiation of copulation while others limit their definition to a sexual present.) For one data point, we use Bercovitch’s (1991) measure of initiation of *consortships* rather than copulations, because females at Gilgil apparently initiated consortships by sexually presenting to males but then did not initiate the actual copulations once in consort (Bercovitch, 1991). For hamadryas, we consider only sexual presents to be initiation of copulation because females are frequently herded and often approach males in response to a threat or a brief look, and thus an approach alone is not indicative of a female’s motivation to copulate. In fact, female hamadryas also often present to males in response to threats, so our measure of female-initiated copulations for hamadryas is likely an overestimate. Unfortunately, for most of the copulations reported here we do not know if the female presentations were preceded by a male threat, so we cannot control for this factor in this preliminary analysis.
3. *Postcopulatory darts*: percentage of copulations followed by the postcopulation withdrawal response, or postcopulatory dart, described by Hall (1962) as a “short running-away by the female” during or after the male’s dismount. It has been suggested that postcopulatory darts function to incite male–male competition in baboons by drawing attention to the copulating pair (O’Connell and Cowlishaw, 1995).

4. *Copulation calls*: percentage of copulations accompanied or followed by copulation calls, vocalizations by females that are largely, though not exclusively, given during copulation. These calls have been described as “intermittent roars” (Bolwig, 1959), “staccato grunts” (Saayman, 1970), “gurgling growls” (Hall, 1962), or “a series of grunts...accompanied by loud barks in longer calls” (O’Connell and Cowlshaw, 1994). Females have been reported to give these vocalizations while defecating as well (Hall, 1962; Boese, 1973; Bercovitch, 1985), and the calls may thus be an involuntary reaction to compression of the vaginal wall. Many authors suggest, however, that copulation calls are costly signals and therefore must serve a communicative function, one of which may be the incitation of competition among males (Hamilton and Arrowood, 1978; Dunbar, 1988; Dixon, 1998; O’Connell and Cowlshaw, 1994).

3. RESULTS

3.1. Exclusivity of Mating

Female exclusivity in mating, compared across the four subspecies, is shown in Figure 1. In olive baboons at Gilgil, Kenya (Smuts, 1985; Bercovitch, 1987b), and yellow baboons at Amboseli (Hausfater, 1975), females copulate

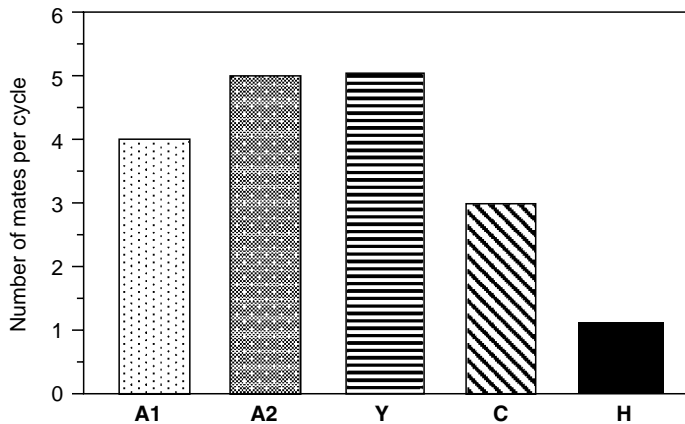


Figure 1. Female exclusivity of mating, defined as the average number of different males that a female typically copulates with during the sexually swollen phase of her monthly cycle. **A1** = olive baboons at Gilgil (Bercovitch, 1987); **A2** = olive baboons at Gilgil (Smuts, 1985); **Y** = yellow baboons at Amboseli (Hausfater, 1975); **C** = chacma baboons at Cape Point (Hall, 1962); and **H** = hamadryas baboons at Filoha (this study).

with an average of four to five different males during a single cycle. In chacma baboons, the alpha male usually has priority of access during peak estrus (Bulger, 1993), but Hall (1962) reported that females often copulated with all three adult males in the group on a given day (though the frequency of mating by each male was highly variable). In olive and yellow baboons, turnovers in sexual consortship are quite frequent (Hall and DeVore, 1965; Smuts, 1985; Bercovitch, 1988; Noë and Sluijter, 1990), and, unless a female is in a multiday consortship (as is common in chacmas), she will often copulate with more than one male each day (Hausfater, 1975; Noë and Sluijter, 1990). While olive and yellow baboon males occasionally monopolize a female for her entire period of probable conception, this is the exception rather than the rule (Hausfater, 1975; Bercovitch, 1987b). For example, of the 19 conceptive cycles reported by Bercovitch (1987b), only one of them included the monopolization of a female by a single male throughout her entire period of probable conception.

In hamadryas baboons, by contrast, most females copulate with only their leader male. Of the 76 copulations observed at Filoha for which the identity of the male could be determined, 15 were with nonleader males. Of these, 6 were with juvenile males (3–5 years of age using the age classes of Sigg et al., 1982; Swedell, 2006), 5 with adolescent males (5–6 years), and 4 with subadult males (6–9 years). No multiple mounts with nonleader males were observed, and only one of these copulations, with a young male (aged 5 or 6), included an ejaculatory pause. In captive Guinea baboons, copulation also occurs mainly between females and the one adult male in their subgroup (analogous to one-male units of hamadryas), though females do apparently copulate with other males as well on occasion (Boese, 1973; Maestripieri et al., 2005). Because these observations of Guinea baboons are from captivity, they are not included in our graphical comparisons.

3.2. Female Initiation of Copulation

Figure 2 shows the proportion of observed copulations (or consortships; see below) initiated by females in the four subspecies. In most baboons, females initiate at least 20 percent and often up to three-quarters of all copulations observed. Hausfater (1975) found that female yellow baboons initiate 44 percent of copulations, and Hall (1962) and Seyfarth (1978) found that

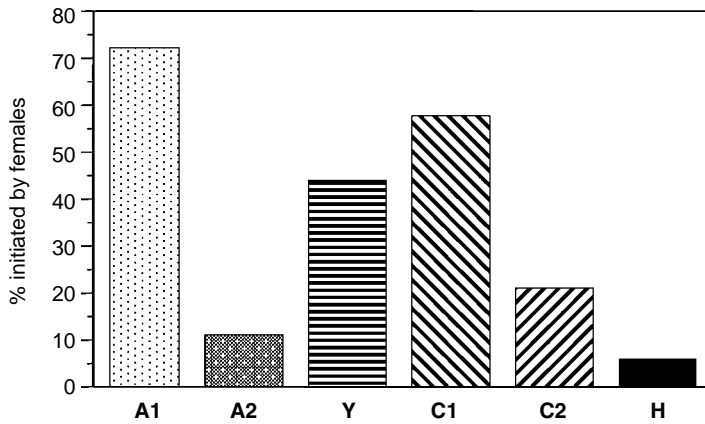


Figure 2. Percentage of copulations or consortships initiated by females. **A1** = percentage of consortships initiated by females in olive baboons at Gilgil (Bercovitch, 1991). **A2** = percentage of copulations initiated by females in olive baboons at Gombe (Ransom, 1981); **Y** = percentage of copulations initiated by females in yellow baboons at Amboseli (Hausfater, 1975); **C1** = percentage of copulations initiated by females in chacma baboons at Cape Point (Hall, 1962); **C2** = percentage of copulations initiated by females in chacma baboons at Mountain Zebra National Park, South Africa (Seyfarth, 1978); and **H** = percentage of copulations initiated by females in hamadryas baboons at Filoha (this study).

female chacmas initiate 58 percent and 21 percent of copulations, respectively. For olive baboons, Ransom (1981) found that females initiate only 11 percent of copulations, but Bercovitch (1991) pointed out that, while females do not often initiate copulation itself, they initiate 72 percent of *consortships* by presenting to males. Olive baboon females also regularly present to one male while in consort with another, often leading to consort turnovers (Smuts, 1985). In hamadryas, by contrast, only 4 of the 48 copulations (8 percent) for which the initiator of the copulation could be determined were initiated by females. In Guinea baboons, both Boese (1973) and Galat-Luong (pers. commun.) observed females presenting to males, and Galat-Luong et al. (this volume) report that females initiate slightly fewer copulations than do males. As these are only preliminary observations and the sample size is quite small, we did not include these data in our graphical representation.

3.3. Postcopulatory Darts

The postcopulation withdrawal response, or postcopulatory dart, is commonly seen in olive, yellow, and chacma baboons (Hall and DeVore, 1965; Ransom, 1981; Smuts, 1985; Bercovitch, 1995; O'Connell and Cowlishaw, 1995; K. Rasmussen, pers. commun.; Semple, pers. commun.). It varies in its occurrence from 25 percent (Ransom, 1981) to 92 percent (Bercovitch, 1985) in olive baboons, but occurs after at least 75 percent of copulations in chacmas (78 percent: Hall, 1962; 75 percent: Hall and DeVore, 1965; 86–89 percent: Saayman, 1970) (Figure 3). In olive baboons, females have been observed to run away from one male (with whom copulation had just occurred) and directly to another (Hall and DeVore, 1965), and such behavior often leads to consort turnovers (Smuts, 1985). We have not included yellow baboons in our graphical comparison because we could not find any published reports of quantitative data on darting, though we have been told that yellow baboon females dart after 80 percent (K. Rasmussen, pers. commun.) to virtually 100 percent (Semple, pers. commun.) of observed copulations. In hamadryas baboons, we have seen postcopulatory darts only by (a) adolescent females and (b) females that were mounted by males other

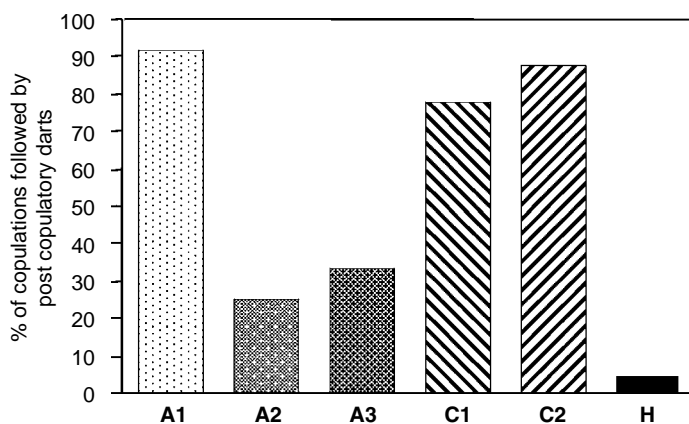


Figure 3. Percentage of copulations followed by postcopulatory darts. **A1** = olive baboons at Gilgil (Bercovitch, 1985); **A2** = olive baboons at Gombe (Ransom, 1981); **A3** = olive baboons at Nairobi Park (Hall and DeVore, 1965); **C1** = chacma baboons at Cape Point (Hall, 1962); **C2** = chacma baboons at Honnet (Saayman, 1970); and **H** = hamadryas (this study).

than their leader male, and postcopulatory darts occurred after only 6 percent of observed copulations for which the postcopulatory behavior was also observed ($N=69$). While Galat-Luong et al. (this volume) report that Guinea baboon females sometimes dart after copulations, their sample size was too small to include here.

3.4. Copulation Calls

In chacma, yellow, and some populations of olive baboons, females often give loud vocalizations, or copulation calls, during and/or just after copulation, and in most populations these calls are given in the majority of copulations that occur (Hamilton and Arrowood, 1978; O'Connell and Cowlishaw, 1994). Figure 4 shows the frequency of copulation calling in each subspecies. In Guinea baboons, copulation calls occur in 39 percent (Boese, 1973) of observed copulations; in olive baboons they occur in 19 percent (Ransom, 1981) to 68 percent (Bercovitch, 1985) of copulations (68 percent with subadult males and 62 percent with adult males, the latter of which is shown in Figure 4); in yellow baboons they occur in 80 percent (Collins, 1981) to 97 percent (Semple, 2001; Semple et al., 2002) of copulations; and in chacma

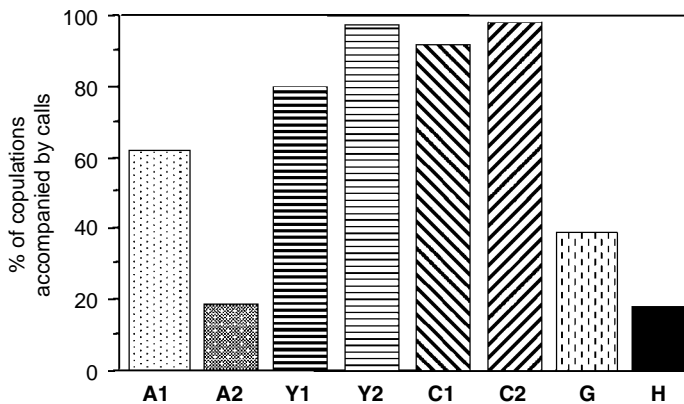


Figure 4. Percentage of copulations accompanied or followed by copulation calls. **A1** = olive baboons at Gilgil (Bercovitch, 1985); **A2** = olive baboons at Gombe (Ransom, 1981); **Y1** = yellow baboons in Tanzania (Collins, 1981); **Y2** = yellow baboons at Amboseli (Semple, 2001; Semple et al., 2002); **C1** = chacma baboons at Cape Point (Hall, 1962); **C2** = chacma baboons at Honnet (Saayman, 1970); **G** = Guinea baboons at Niokolo Koba (Boese, 1973); and **H** = hamadryas (this study).

baboons they occur in 92 percent (Hall, 1962) to 98 percent (Saayman, 1970) of copulations.

In hamadryas, only about 18 percent of observed copulations ($N=86$) included female calls, and copulation calls were given by only 30 percent (4 out of 13) of the females in the study group who were observed both sexually swollen and copulating. When calls were examined individually, we found that those of hamadryas were quieter and substantially reduced in both length and complexity compared to those of chacma and yellow baboons. For purposes of comparison, Figure 5 shows a representative call of (a) a female chacma baboon from the De Hoop Nature Reserve in South Africa and (b) a

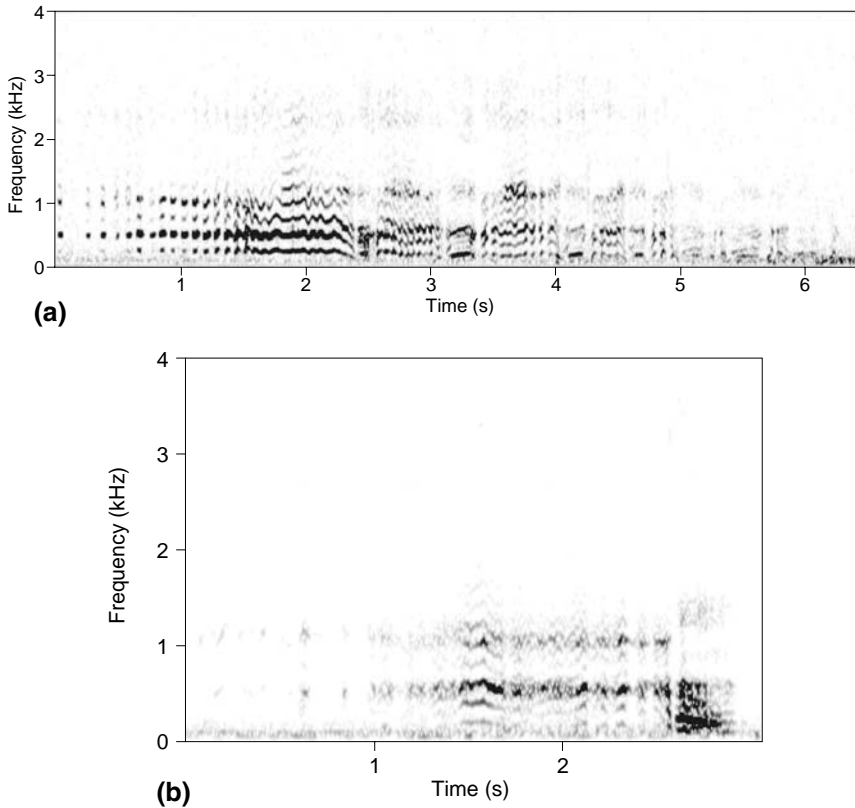


Figure 5. Spectrographic representations of (a) a copulation call of a female chacma baboon from the De Hoop Nature Reserve in South Africa and (b) a copulation call of a female hamadryas baboon from the Filoha field site in Ethiopia.

female hamadryas baboon from the Filoha field site in Ethiopia. A quantitative comparison of the copulation calls of chacma and hamadryas baboons will be reported elsewhere (Saunders, in preparation).

4. DISCUSSION

4.1. Comparisons Among Baboon Taxa

The most obvious difference between hamadryas and most other baboons is the number of males with whom each female copulates during the sexually swollen phase of her monthly cycle. In olive, yellow, and chacma baboons, this number typically approaches the number of males in the group as a whole (Hall and DeVore, 1965; Hausfater, 1975; Bercovitch, 1995). While the highest-ranking male in the group often manages to exclude other males during the peak of a female's sexual swelling, females do copulate with other males before and after maximal swelling and are generally characterized as "promiscuous" in their mating behavior (Hall and DeVore, 1965; Saayman, 1970; Hausfater, 1975; Seyfarth, 1978; Smuts, 1985; Bercovitch, 1987b). Even in chacmas, in which the alpha male usually consorts exclusively with females during peak estrus (Bulger, 1993; Weingrill et al., 2000), promiscuity may be the rule for females at other times: "The roving, appetitive behaviour of inflating females from one male to another was conspicuous. It was not uncommon for an inflating female to present to, and be mounted by, as many as three males within the space of two or three minutes" (Saayman, 1970, p. 86).

By contrast, in hamadryas baboons, most females have never been observed to sexually solicit or copulate with more than a single male in a given cycle, and that male is invariably the leader male of her OMU. The few copulations with nonleader males that have been observed in the Filoha population were with subadult males, and most did not appear to include ejaculation (see below). This relative exclusivity of hamadryas mating patterns confirms reports from previous observational field studies of wild hamadryas (Kummer, 1968; Abegglen, 1984) as well as a management "experiment" conducted by Biquand et al. (1994) in Saudi Arabia in which leader males were vasectomized and their females did not subsequently reproduce (though this study is not conclusive, as the only nonleader male in the group died shortly after the vasectomies of the leader males, so the females had few, if any, options other than their infertile leader male).

The proportion of copulations initiated by females also differs dramatically between hamadryas and other baboons. While most baboon females initiate either most copulations or the consortships themselves, hamadryas females initiate copulation only infrequently. Interestingly, female yellow and chacma baboons are less likely to initiate copulation when they are in consort with a male than when they are out of consort (Hall and DeVore, 1965; Seyfarth, 1978), and in olive baboons, females initiate consortships but do not usually initiate the actual copulations once they are in consort (Ransom, 1981; Bercovitch, 1995). If female baboons in general initiate copulations outside of consort but not while in consort, then female hamadryas are no different from other baboon females insofar as they can be viewed as being in a permanent consortship with their leader male.

The frequency of postcopulatory darts and copulation calls also differs between hamadryas and other baboon populations, though the patterns shown by these two behavioral elements are somewhat inconsistent. While olive baboon populations in general are quite variable in the percentage of copulations followed by darts, females in chacma and yellow populations as well as the olive baboon population at Gilgil dart away from males after the majority of copulations. Similarly, while olive baboon females vary in their tendency to give copulation calls, yellow and chacma baboons give calls during (or after) the majority of their copulations. Compared to olive, yellow, and chacma baboons as a whole, hamadryas females engage in both of these behavioral elements far less frequently.

Differences among baboons in their tendency to give copulation calls may be related to differences in their physiology. Because female baboons have been reported to give copulation calls while defecating as well (Hall, 1962; Boese, 1973; Bercovitch, 1985), it has been suggested that the calls are simply an involuntary reaction to compression of the vaginal wall. Whether during copulation or defecation, calls are almost invariably given when a female is sexually swollen, and Bercovitch (1985) suggested that they be called “sexual swelling vocalizations” rather than copulation calls for that reason. If variation in calling is tied to the size of a female’s sexual swelling, then we would expect sexual swellings to be smaller in hamadryas than in other baboons. This does not appear to be the case, however. There may be other physiological differences among baboon subspecies that underlie differences in copulation calling, though it is not obvious what those differences might be other than the slightly smaller body size of hamadryas females compared to other female baboons.

4.2. Reproductive Strategies in Female Baboons: Overall Patterns

If we apply van Schaik et al.'s (1999) framework to baboons and assume that the risk of infanticide is present (either today or in ancestral populations), it appears that most populations of "savanna" baboons use a predominant strategy of paternity *confusion* to counteract male infanticide and other sources of infant mortality (Hall and DeVore, 1965; Hausfater, 1975; Bercovitch, 1991, 1995). Sexual presentations to multiple males, copulation with multiple males, postcopulatory darts, and copulation calls may all serve to elicit male–male contest and/or sperm competition and confuse paternity among males, which may in turn elicit protection of infants by multiple males and inhibit infanticide (O'Connell and Cowlishaw, 1994, 1995; Dixson, 1998; Soltis, 2002). Even in chacma baboons, in which the alpha or resident male has exclusive access to females during their periovulatory period, females expend what appears to be a substantial amount of energy soliciting and mating with *other* males earlier and later in their cycles. Such behavior would have the effect of confusing paternity from the perspective of these other males, even if paternity is *not* confused from the female's (or the alpha male's) perspective.

This pattern of behavior can be viewed as a high-energy strategy with fitness costs. Not only are such behavioral elements likely to be energetically demanding, but if they result in an increase in male–male competition then they are also likely to increase a female's risk of injury from male aggression (Manson, 1994). Moreover, these behavioral elements are likely to both render a female more conspicuous to predators and decrease her time spent engaged in predator and social vigilance, the combination of which may further reduce her fitness. Overall, the energetic demands on females that use a strategy of paternity confusion—as manifested in the above ways— are likely to be relatively high.

The general pattern shown by female hamadryas, on the other hand, appears to be one of lower energy expenditure, a high degree of concentration on a single male, and fewer behavioral elements that would promote male–male competition and increase a female's risk of injury. Further evidence of monandry in hamadryas females and the consequent reduced (or absent) sperm competition in hamadryas males can be drawn from the smaller testis size of hamadryas compared to olive baboons reported by Jolly and Phillips-Conroy (2003, this volume).

One might argue that the hamadryas social system in itself is an outcome of a high degree of male–male competition, leading to a constant high risk of injury for females. However, overt competition among males for sexual access to females is not a regular occurrence in hamadryas society and generally only occurs during takeovers and attempted takeovers. Similarly, one might argue that hamadryas females incur daily aggression from their leader males through neckbiting and are thus more prone to injury in general than nonhamadryas females. While this may be true, we do not view herding and neckbiting to be elements of the hamadryas *female* reproductive strategy, but rather of the hamadryas *male*'s. Moreover, the behavioral elements comprising a paternity confusion strategy, if used in a hamadryas social system, would undoubtedly increase a hamadryas female's risk of injury. Thus, in the context of the hamadryas social system, if hamadryas females are to attempt to confuse paternity, they must do so surreptitiously.

4.3. Energetic Limitations on Hamadryas Baboon Females

Compared to other baboons, hamadryas inhabit drier, more resource-limited habitats in which female time budgets are likely constrained by foraging needs. Although found today in a wide range of ecosystems (Nagel, 1973; Zinner et al., 2001), the majority of hamadryas distribution coincides with the semidesert regions of the Horn of Africa and the southwestern Arabian peninsula. Hamadryas baboons likely spent most of their evolutionary history since divergence from other baboons in a dry, semidesert region (possibly the Arabian peninsula: Kummer et al., 1981; Kamal et al., 1994; Wildman, 2000), and it is this environment that may have provided the selective pressures leading to their rigid, male-dominated social organization (Kummer, 1968, 1971, 1990).

Food availability is closely tied to reproduction in baboons: Females with access to fewer food resources have been shown to either spend more time foraging during lactation, when their energetic needs are highest (Dunbar et al., 2002), or suffer from lowered fertility (Strum and Western, 1982; Bercovitch, 1987a; Bercovitch and Strum, 1993; Barton, 1990). Evidence from mountain chacmas (Lycett et al., 1998) as well as cross-subspecies comparative analyses (Hill et al., 2000; Barrett et al., this volume) suggest that severe environmental conditions lengthen interbirth intervals in female

baboons, thereby reducing female reproductive output. Moreover, low-ranking females—i.e., those at a competitive disadvantage with regard to access to food—not only have longer interbirth intervals (see Cheney et al., this volume) but also give birth to infants with lower growth rates than high-ranking females (Johnson, this volume). Current evidence does not point to shorter interbirth intervals in hamadryas than in other baboons (Sigg and Stolba, 1981; Hill et al., 2000; Swedell, 2006), but available reproductive data on wild hamadryas females derive from relatively mild habitats compared to those in most of the hamadryas range. If interbirth intervals are longer in hamadryas baboons as a whole compared to other baboons, then hamadryas females would incur an increased cost of infanticide, as an already high cost of reproduction would be exacerbated by a short-term loss in maternal investment.

In addition to yielding lower-quality food resources, hamadryas habitats are also hotter year round than those of other baboons, which may impose an additional cost on hamadryas females. The mean annual afternoon temperature at the Filoha site is about 34°C with no more than four degrees of variation (32.7–36.0°C) throughout the year (Swedell, 2006). This is higher than, for example, both the average (23°C) and the maximum (33°C) temperatures reported for Amboseli, Kenya (Bronikowski and Altmann, 1996), and is generally expected to be higher than most other habitats in which baboons are found (with the exception of desert chacmas, e.g., in Namibia: Brain and Mitchell, 1999). Hill et al. (2003) demonstrated that the mean annual temperature affects the amount of time that baboons spend in different activities: Higher temperatures are associated with less time spent feeding and moving as well as more time spent resting, presumably to compensate for the high heat load. Likewise, Brain (1991) found that desert chacmas were far less active during intergroup encounters after several days of water deprivation, compared to high rates of activity during such encounters when they had drunk water more recently. Hamadryas are arguably heat stressed year round and appear to thermoregulate by seeking shade throughout the day regardless of the season. Most other baboons, by contrast, live in more seasonally variable habitats in which females are probably environmentally stressed during only parts of the year. The costs of an energetically demanding paternity confusion strategy may therefore be especially high for hamadryas females compared to other female baboons.

4.4. Paternity Concentration in Hamadryas Baboons

A strategy of paternity concentration by hamadryas females is intrinsically tied to, and likely evolved in association with, the very specific behavioral strategy of hamadryas males. Instead of competing for access to any estrous female like other baboons, male hamadryas mate exclusively with a small subgroup of females, their “possession” of which is “respected” by other leader males (Kummer et al., 1974). Assuming that leader males sire most, if not all, of the infants born into their units, paternity certainty is probably quite high and protective behavior by leader males of infants born into their units (and their mothers) is likely to be selected for. That protection of infants by leader males is important in hamadryas society is suggested by two lines of evidence from this population: (1) leader males often threaten and ultimately retrieve infants from individuals outside the unit who handle those infants and (2) females tend to remain closer to their leader male during the first month after the birth of an infant, when the infant is most vulnerable, compared to subsequent months or when pregnant (Swedell, 2006; unpublished data). Rohrhuber (1987 (in German), cited in Kaumanns et al., 1989) found that, in a group of captive hamadryas with an unusually high rate of infanticide, a high rate of grooming as well as close proximity between a female and her leader male lowered the probability that her offspring would be killed. This suggests that hamadryas leader males play an important role in infant survival and that females benefit reproductively from associating with and copulating exclusively with a protective leader male. Sigg et al. (1982) pointed out that infant survival is higher in hamadryas than in other baboons and suggested that the OMU social structure might provide a safer environment for infants and juveniles than the multimale, multifemale social structure of yellow or olive baboons. Such a conclusion is supported by both the findings of Beehner and Bergman (this volume), who found a higher survival rate of infants born to hybrid females in OMUs compared to those born to non-OMU females, and the lower infant mortality found in chacma baboons living in one-male groups compared to those living in multimale groups (Lycett et al., 1998; Barrett et al., this volume). A hamadryas female’s leader male is her main protector from aggression, whether it be toward herself or her offspring, and, consequently, she probably benefits from ensuring his paternity.

Such an extreme version of a paternity concentration strategy can be explained by the coevolution of male and female strategies in hamadryas

baboons. It is probable that the evolution of hamadryas social organization began with a larger group splintering into foraging parties (consisting of female kin groups and a few associated males) due to the low food availability in their arid, semidesert habitat (Kummer, 1990). Males would presumably have found it advantageous to remain with small groups of females on a semipermanent basis so as to be nearby when females came into estrus, and those that managed to keep these small groups of females with them at all times via herding and neckbiting would have been favored by natural selection. Once this began, a powerful evolutionary feedback loop would have led rather quickly to the system we see today because of the dual advantages of such a system to both males and females (Henzi and Barrett, 2003). For males, it would have become even more advantageous to maintain exclusive access to a small group of females due to the high degree of paternity certainty that would result and the corresponding reduction in fitness incurred by males that did not adopt this strategy. For females, it would have become advantageous to participate in such a system because of the protection they would receive for themselves and their infants. Such protection may be even more important for hamadryas than other baboon females due to the high energetic costs of reproduction in a semidesert habitat. Ironically, a system would have evolved that, while protecting females against infanticide, would have also inherently increased the potential risk of infanticide by extra-unit males (due to their far lower chance of paternity), thereby increasing the power of the feedback loop.

4.5. Promiscuity in Hamadryas Baboons

Despite their near exclusivity in mating, hamadryas females also occasionally copulate with nonleader males. In the Filoha population, females copulated with nonleader males in 15 of the 76 copulations for which individual identities were known, and one of these copulations included an ejaculatory pause. Kummer (1968) also reported copulations between females and nonleader males. Noting that these males were almost always subadult, Kummer suggested that they were probably not sexually mature and that such copulations were probably unlikely to ever result in pregnancy. Jolly and Phillips-Conroy (2003, this volume), however, found that hamadryas males undergo testicular enlargement at an earlier age than other baboon subspecies and suggested that copulations between hamadryas females and subadult nonleader males

may, in fact, result in fertilization. Whether or not they ever do is not yet known.

Most copulations with nonleader males, both at Filoha and Erer Gota, appear to be surreptitious (Kummer, 1968; Swedell, 2006). At Filoha, most took place while the OMU was traveling and the leader male was ahead of the copulating pair and unable to see them. Likewise, Kummer (1968) reported such copulations to take place mainly “behind the backs of” the females’ leader males (pp. 41–42). In these cases, such copulations may still be interpreted as part of a general strategy of paternity concentration. Provided that (a) the leader male provides the protective benefits consistent with such a strategy, as outlined above, and (b) the majority of a female’s offspring are sired by her leader male, a strategy of paternity concentration with occasional inseminations by nonleader males could still be selected for. This assumes, of course, that leader males cannot distinguish their own offspring from those of other males, an assumption that does not appear to be met in yellow baboons (Alberts, 1999; Buchan et al., 2003).

If, as has been suggested by Kummer (1968) and Abegglen (1984), leader males and their followers are usually closely related, then copulations between females and follower males may actually provide inclusive fitness benefits to the leader male. On three occasions, copulations with nonleader males took place in full view of the females’ leader males. In two of these cases, the nonleader male was a follower of that unit and may have been a close relative of the leader male.

It is possible that some hamadryas females, in effect, combine the two strategies of paternity concentration and confusion. Females may “concentrate” paternity by engaging in multiple-mount copulations with their leader males around the time of ovulation, but they might also “confuse” paternity via occasional, surreptitious single-mount copulations with nonleader males. Although such copulations probably rarely result in conception, they would nevertheless have the outcome of confusing paternity from the perspective of the nonleader male. A nonleader male should be selected to protect, tolerate, or at least avoid killing infants of any female with whom he has copulated recently as long as the chances of inseminating her are greater than zero. Whether or not the female gains—or the leader male loses—fitness benefits from these extra-unit copulations, the fact that they occur at all suggests that, at the very least, hamadryas females retain the behavioral motivation to mate promiscuously that presumably characterized the ancestral female baboon.

Our observations suggest that for most females, this motivation is unexpressed, but for a few females, it is strong enough to act upon despite the associated risk of aggression from their leader males.

4.6. Paternity Concentration and Confusion in Baboons

Such a system whereby males and females engage in mutualistic strategies of close association, protection, and (relatively) exclusive mating has evolved to an extreme only in hamadryas baboons, but it appears to exist to varying degrees in other baboon subspecies as well (Boese, 1973; Smuts, 1985; Anderson, 1989, 1990; Palombit et al., 1997). For example, many researchers have described strong social bonds between baboon females and specific adult males, sometimes called “friendships,” and have suggested that these relationships benefit females via protection from infanticide or aggression by males (Smuts, 1985; Palombit et al., 1997; Weingrill, 2000; also see Beehner and Bergman, this volume). In chacma baboons in particular, females may be in effect pursuing a strategy of paternity concentration by focusing their periovulatory mating on the alpha male (or the resident male in one-male groups), while, at the same time, confusing paternity by mating with other males at other times. As with hamadryas, such a strategy would have the outcome of confusing paternity from the perspective of these other males and could thus provide a female the protective benefits gained via both strategies. As long as the alpha (or resident) male fathered most of a female’s offspring while the chances of other males’ paternity was greater than zero, such a pattern could be selected for in both males and females.

Obviously, we must bear in mind that female reproductive strategies do not exist outside of the context of those of males. Neither chacma nor hamadryas females may be “choosing” to mate exclusively with one male. Rather, one male is able to exclude other males from a female for a longer period than is typical in other baboons. The ability of chacma and hamadryas males to do this may be related to the absence in these taxa of the coalitionary behavior seen in olive and yellow baboons. The concentration of paternity in a single male for hamadryas and chacma baboon females, therefore, may be as much of a consequence of male mating strategies as those of females. Females in these two subspecies can thus be viewed as “making the best out of a bad situation” in that they likely garner benefits from close association with a single male even though such relationships may in effect be imposed on them by males.

In chacma baboons living at high altitudes, the similarities to hamadryas are more striking: Compared to lowland chacmas, mountain chacmas are more commonly found in one-male groups, cross-sex bonds are stronger, female–female bonds are weaker, and herding behavior by males occurs more frequently (Anderson, 1981, Anderson, 1990; Byrne et al., 1987, 1989; Whiten et al., 1987; Henzi et al., 1990; Hamilton and Bulger, 1992; Henzi et al., 1999). These features, however, are not seen to the extent that they are in hamadryas, and chacma one-male groups do not coalesce to form the larger bands seen in hamadryas. That chacma one-male groups with exclusive mating are more prevalent at high altitudes than at low altitudes suggests that, as in hamadryas, one-male groups and strong cross-sex relationships are adaptive responses to food scarcity and reduced predator pressure (Whiten et al., 1987; Byrne et al., 1987, 1989; Henzi et al., 1990, 1999; Anderson, 1990).

Some authors have suggested that the evolution and maintenance of strong cross-sex relationships in *all* baboons is related primarily to protection from infanticide or aggression by males rather than to ecological factors (Busse and Hamilton, 1981; Smuts, 1985; Palombit et al., 1997; Weingrill, 2000). Palombit (1999), for example, discusses infanticide avoidance as a primary reason for close bonds between female chacma baboons and adult males, and attributes a significant portion of infant mortality in this species to sexually selected infanticide. He points out that in both chacma baboons and gorillas, infanticide accounts for a large portion of infant mortality *and* females develop and maintain bonds with males. In both taxa it is the females, not the males, which are most responsible for proximity maintenance and do most of the grooming. Weingrill (2000) points out the prevalence of close relationships between chacma baboon females and the likely sires of their offspring specifically during the periods of pregnancy and lactation. As infanticide by males has been observed in the same population, Weingrill suggests that the driving force behind such associations may be infanticide avoidance. Many authors have suggested that infanticide and aggression toward infants has been a primary selective force leading to strong intersexual bonds in primates as a whole (Wrangham, 1979, 1982; Fossey, 1984; Watts, 1989; van Schaik and Dunbar, 1990; Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995; Sterck et al., 1997; Palombit, 1999; van Schaik et al., 1999). Treves (1998) proposes the conspecific-threat hypothesis for the evolution of primate social systems, an extension of Brereton's (1995) coercion–defense

hypothesis, in which females are always at risk of aggression (to themselves or their infants) from unrelated males, and so must adopt one or more defensive strategies, one of which is the association with a male for protection.

4.7. CONCLUSIONS

As a means of ensuring protection for their infants—whether it be from infanticide or other sources—most primate females, and baboons in particular, seem to show some combination of paternity concentration and paternity confusion (Bercovitch, 1991, 1995; Palombit et al., 1997; Henzi and Barrett, 2003). Olive and yellow baboon females can be described as focusing largely on paternity confusion, as suggested by the prevalence of multiple mating and behavioral elements that incite male–male competition. Hamadryas females, by contrast, focus mainly, though not exclusively, on the concentration of paternity in a single male. Chacma baboon females appear to combine these two general strategies by focusing on a single male around ovulation and mating promiscuously at other times. The predominance of one strategy over the other may depend on both demographic factors such as sex ratio and ecological factors such as seasonality, food availability, and predator pressure (Wrangham, 1980; van Schaik, 1989; Dunbar, 1992; Barrett et al., submitted). The collection of additional data from other populations of wild baboons—and in particular from Guinea baboons, for which we know very little—promises to shed further light on both the variation among and flexibility of baboon females in their responses to infanticide and other threats to the survival of their offspring.

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