

# Chapter 8

## Male–Female Relationships



### 8.1 Introduction

Baboon social diversity offers a number of models and analogies for male–female relationships in early hominins. Several of them may represent the earliest beginnings of human-like family units within the hominin lineage. *Family* is defined here as a long-term social unit consisting of one male affiliated with one or a few females. This describes social units found in the great majority of human societies known to anthropology.

In both humans and baboons, these relationships involve more than sex. However, *sexual strategies* are an important factor. The term refers to patterns of behavior that are likely to produce an adaptive result for the behaving animal. In both humans and baboons, sexual strategies vary from mutual bonding to aggression and resistance. In both humans and baboons, males provide widely varying amounts of parental care to immature individuals.

More than in some other areas of behavior, comparison of reproduction in baboons and hominins requires consideration of differences between them, because these place more stringent limits on analogies. Accordingly, the chapter begins with a brief discussion of baboon sexuality. The basic features are shared with many other primates, so the concepts will be familiar to anyone who has studied or read widely about primate behavior. These features will be briefly summarized for readers without such background.

### 8.2 Some Basic Features of Baboon Sexuality

The topic of sexuality is an example of the need to focus on analogies rather than comprehensive models in comparing baboons with hominins. Differences between baboons and humans show that baboon sexuality cannot be taken as an integrated

“model“for early hominin behavior. Nevertheless, there are specific aspects of baboon sexuality that can provide informative analogies (vide Dixson 2012).

As in other Old World monkeys, a typical adult female baboon who is not pregnant or lactating goes through an ovarian cycle (also called a menstrual cycle). It lasts for roughly a month (there are individual, populational, and species variations). Hormonal and behavioral changes take place around the time of ovulation. This period is often called estrus, a term that is also applied to other mammals. A number of researchers reject this usage because it implies a rigidity that does not characterize monkeys and apes and because it seems to create an artificial distinction between humans and other primates (Dixson 2012). However, the term is still widely used by primatologists and it conveniently denotes a segment of the female cycle during which there are significant hormonal and behavioral changes that are connected with ovulation and thus with the highest probability of conception.

This idea of estrus is useful as long as flexibility in the rest of the cycle is kept in mind. In contrast to most other mammals, copulation may occur at any point in the cycle. It can be said that the female may be sexually receptive at any time, that is, willing or at least able to accept copulation with a male. However, two behavioral changes occur around the time of ovulation (Beach 1976; Dixson 2012) and can be considered features of estrus. One is proceptivity: the female actively seeks copulation. The other is attractivity: the female stimulates greater sexual interest in males.

Female baboons are like females in many other primate species in that a sexual swelling of the perineal area is associated with estrus. The pink swelling is an attractive signal to males. This is one of the most striking differences between baboons and extant humans. Since females of both *Pan* species display comparable swellings, it is not clear what the situation was in early hominins. Whatever the answer to that question might be, not all baboon analogies for male–female relations are affected by the problem.

Whether as a sign of receptivity or proceptivity (depending on the time in the cycle), the female baboon presents her hindquarters to a male. Copulations may take place in the context of consortship (or mate guarding), in which a male tries to stay close to a female and copulate with her multiple times while preventing other males from doing so. The female may be an active participant in the relationship, rejecting other males who try to replace her consort.

Potential baboon-hominin analogies include sexual conflicts, that is, ways in which the reproductive interests of the male and female are somehow contradictory. The most drastic of these is infanticide by males. In baboons, as in other primate species (and other mammals as well), infanticide has been interpreted as a reproductive tactic (Hausfater and Blaffer-Hrdy 1984; van Schaik and Janson 2000). Killing an infant is adaptive for a male who has replaced another male in a relationship with the mother, because it ends the nursing period with the result that the female becomes sexually available. Though the reproductive hypothesis of infanticide is widely accepted, it should be noted that it still has opponents (Rees 2009). Perhaps the most common argument is that there is insufficient evidence for its adaptive significance (Dixson 2012).

An alternative explanation is that the behavior eliminates a rival male's genes. This interpretation is countered by the fact that juveniles are rarely killed (van Schaik and Janson 2000; Muller and Wrangham 2009; Zipple et al. 2017). Sparing juveniles fits the sexual availability hypothesis because, according to the hypothesis, the killing of an infant ends the nursing period and results in a female's return to the estrus cycle. No such advantage comes from killing a juvenile. Rather than being a potential contribution to reproductive success, trying to kill a juvenile may entail costs in terms of energy expenditure, loss of feeding time, neglect of social relationships, and some danger from defense of the juvenile by other adults.

### 8.3 Human Families and Primate Analogies

“One key question in social evolution is the identification of factors that promote the formation and maintenance of stable bonds between females and males beyond the mating context” (Goffe et al. 2016). A useful starting point is the general features of family in extant humans (including recent and historically known), viewed in cross-cultural perspective. Family is loosely defined here as a long-term relationship between one male and one or more females that usually involves reproductive effort (and economic effort in humans, but this does not enter into hominin-baboon comparisons). An operational definition for “long-term” could be persistence from establishment of a bond through the childhood of one offspring (Fisher 1992). However, significantly longer male–female relationships exist in both humans and baboons.

Cross-cultural and historical surveys show that such relationships have been part of human social organization across virtually all cultures and all known time periods. Demography dictated that monogamy was most common, but polygyny was allowed in the majority of societies and desired by many men if not most (Gregersen 1983). The typical human mating relationship has been a relatively long-term association between one male and one to three females (King 2003). Polyandry has occurred in just a few societies under unusual conditions (certain rules of land tenure, for example). A strict rule of monogamy (often violated) became common in the world with the recent spread of Christianity.

Extended families and other larger kinship groups became common with the advent of complex societies, mostly based on farming. The family in the narrow sense became submerged in these groupings, but persisted in virtually every known culture and has become prominent again in modern societies where mobility is greater. The cross-cultural importance of the family suggests an evolutionary origin (Chapais 2008; Swedell and Plummer 2019). This is not to say there is a simple genetic basis for the phenomenon. Rather, the hypothesis is that a complex genetic basis underlies the motivations and behavioral tendencies of human males and females that result in the formation of families.

Baboons provide several perspectives on this process, including the form, social context, and proximal mechanisms that might have been involved in the antecedent

social patterns in early hominins (Chapais 2008; Petersdorf et al. 2019). A crucial factor in analogies between male–female bonds in baboons and early hominins is that this kind of relationship emerged and persisted within communities, whether in troops or multilevel societies.

An alternative evolutionary approach to the human family is comparison with “pair-bonded” species, such as gibbons and titi monkeys. There is an extensive controversy about the definition and nature of pair-bonding itself, which is beyond the scope of this book (see, for example, Fernandez-Duque et al. 2020). The key point here is that, in most of the species originally cited as pair-bonded (e.g., gibbons), each male–female pair is relatively isolated from others. Interactions are largely limited to territorial conflicts and to the transfer of maturing individuals from one group to another.

Humans and baboons differ from such species in several important respects. First, a male may be involved in a long-term affiliation with more than one female. Second, it is rarely (or never) the case that two adult males are in the same relationship with a female. Third, such associations are combined into larger communities (Chapais 2008; Städele et al. 2021).

## 8.4 Male–Female Associations in Troops

Human families in most or all cultures entail several characteristics that can be compared to social patterns in baboon troops: (1) long-term affiliation (generally measured in years) between a particular male and female(s); (2) a sexual relationship between such partners; (3) production of shared offspring; (4) some degree of paternal care or support for the offspring. COKY baboons all display at least some relevant traits. Chacma baboons, yellow baboons, and olive baboons are broadly similar to one another in male–female relationships that are potential analogies for early hominins (Hawley et al. 2023). Kinda baboons seem to differ in several respects, according to initial reports. They may offer an alternative analogy for male–female relationships in early hominins.

### 8.4.1 *Special Friends (Primary Associations)*

Adult males and females in many troops form relationships that have been called “special friendships” (Smuts 1985). These can be defined as “long-term, nonsexual social bonds between unrelated (to the females) males and anestrus females” (McLester 2020). Sexual behavior is not excluded from these relationships; the point of the definition is that the connection involves more than mating (Fig. 8.1). These relationships can lead to any or all of the following social patterns, which are possible analogies for early hominin male–female interactions: copulation, production of offspring, male care for immatures.



**Fig. 8.1** A male olive baboon grooms an anestrus (currently infertile) female, an indicator of Special Friendship. (Photo by Glenn King, Manyara, Tanzania)

Some researchers now use the term “primary associations” instead of special friendships (Hawley et al. 2023; Städele et al. 2021). This seems overly broad to me, since it can literally refer to the mother–offspring relationship as well as others. Long usage has given “special friend” the meaning intended here (McLester 2020). In any event, whatever the terminology, relationships like these could have been the basis for differentiation of families within troops of early hominins (Fogel et al. 2021; Städele et al. 2021; Fig. 8.2).

### 8.4.2 *Benefits of Special Friendships*

The following discussion draws on several recent reviews, where numerous references to earlier literature can be found: Hawley et al. (2023), Städele et al. (2019, 2021). It pertains to chacma baboons, olive baboons, and yellow baboons—abbreviated here as COY (COKY without the Kinda baboons, which differ in some important ways and will be discussed separately). In all of the COY species, some males form close associations with pregnant and lactating females. These associations can be identified by rates of proximity and grooming, and reduced levels of aggression.

Evidence for the significance of these relationships has been gathered from long-term studies of the COY species. Most of it points to the function of the male behavior as being parental rather than mating effort (Fig. 8.3). The males are in many cases the sires of infants born to associated females, to which they devote varying degrees of paternal care. The argument against mating effort comes from genetic analyses that show that a male is not especially likely to father a special friend’s next infant.



**Fig. 8.2** A male olive baboon, with an infant huddled against him, is groomed by a female. This social configuration is typical of Special Friendships in the species. (Photo by Glenn King, Manyara, Tanzania)



**Fig. 8.3** A male olive baboon grooms an infant with a female next to them. (Photo by Glenn King, Manyara, Tanzania)

**Fig. 8.4** A male chacma baboon with an infant, presumably the offspring of a Special Friend. (Photo by Curt Busse. Okavango, Botswana)



In one or more COY species, males provide one or more kinds of care for offspring (Fig. 8.4). These include the following: (1) selectively supporting infants and juveniles in social conflicts; (2) protecting them from predation, infanticide, and/or harassment by other troop members (e.g., female rivals of the mother); (3) providing access to valuable resources, such as high-quality foods, and facilitating efficient feeding. By performing such behaviors, a male may contribute to the perpetuation of his own genes as well as benefiting the fitness of the mother.

The benefits of male–female bonds in humans and baboons extend beyond reproductive success. Noting research findings that humans of both sexes who are more socially integrated have longer lives, Campos et al. (2020) asked whether the same thing applied to yellow baboons for which they had 35 years of life history data. They modeled the factors in age-specific adult mortality in both sexes and compared survival trajectories with social bonds over lifetimes. Both males and females with strong bonds to the opposite sex lived significantly longer. Mortality risk was lowered by about 28% in males and more than 30% in females. Campos and colleagues also found a sex difference in that males with higher dominance rank for their age appeared to have shorter lifespans. This makes clear that longer life in males is actually due to social bonding itself rather than a dominance status that facilitates bonding.

Persistence of the special friend bond varies among *Papio* species. In chacma baboons it ends when the female becomes sexually receptive again (Baniel et al. 2016). In olive baboons it can last for years, entailing intimate behaviors spanning multiple periods when the females are not sexually available (anestrus). Male olive

baboons, for example, spend a great deal of time with anestrus females, groom them, and huddle with them (Smuts 1985; Fig. 8.2).

Olive baboons are distinctive in other ways (Städele et al. 2019). Dominance status is less sharply defined, which suggests that reproductive skew is less than in the other species. Relatively larger testes indicate that sperm competition is a factor. Coalitions diminish the significance of individual dominance (which is also true in yellow baboons). Male olive baboons relate to the infants of special friends in a variety of ways: they greet, inspect, hold, and carry those infants more than any others (Hawley et al. 2023).

Though the emphasis in research findings has shifted to parenting, there is evidence that the special friend relationship may function in pursuit of mating as well as parenting. Hormonal study of yellow baboons determined that increased testosterone in males is positively correlated with both mating effort and paternal behavior (Onyango et al. 2013). Male olive baboons also seem to combine a degree of mating effort with the parenting pattern. A study that combined behavioral and genetic data showed that sires have stronger bonds with their infants' mothers than do other males and that these bonds sometimes persist past weaning age (Städele et al. 2019). In many cases the sire of the previous infant is still a close partner of the female when she nurses her subsequent offspring. Males who have the strongest bonds with females that have resumed cycling, but are not currently sexually receptive, may be likely to sire the female's next offspring. In more than one-third of the cases, a female's successive infants were sired by the same male. The researchers concluded that development of stable breeding bonds and paternal investment seem to be grounded in the formation of close ties between males and anestrus females. All of these features suggest that olive baboons may be the best single-species model for the foundation of the hominin family in a troop context.

Hawley et al. (2023) considered the fact that male care for immatures is rare in mammalian societies with multiple males and females, as opposed to those that live in well-defined pairs. Why are baboon troops an exception to this rule? According to Hawley, this may be the result of unusual characteristics such as higher paternal certainty, high risk of infanticide, and a long juvenile developmental period. The long juvenile period would certainly have applied to early hominins, based on common origin with the *Pan* species. High risk of infanticide is a doubtful explanation since known variation among *Papio* species runs from high (chacma baboons) to relatively low (olive and yellow baboons to virtually zero (Kinda and Guinea baboons). Higher paternal certainty is a questionable attribution for troops, since females may benefit from copulations with multiple males (Nunn 1999). For example, confusion of paternity may counter infanticide. Another possibility is that a female might choose a special friend from among her sexual partners. High paternal certainty may have become a factor in the unimale groups of multilevel societies.

Relationships like that of special friends seem to be rare in chimpanzees, despite occasional signs of male–female affection and a few cases of recurring sexual connections. Städele et al. (2021) noted that comparable associations do take place in



one chimpanzee population and that these differ from baboons in that mating effort seems to be the predominant function. This may be regarded as an alternative analogy for female–male relationships in early hominins. On the other hand, it is plausible that such a pattern existed in the LCA, but later shifted to a system more like that of baboons. Such a shift might have been a response to changing environmental factors, such as increased food competition and predator pressure.

### ***8.4.3 From Special Friends to Families?***

In terms of social structure, the transition from special friendships to human-like families in early hominins need not have been very complicated. A male baboon may have several female special friends. Females may also have more than one, but some evidence (a small amount at this point) suggests that two friends is typical (Städele et al. 2021). Starting with special friends in early hominins, the transition to a family-like structure would have required each female to focus on just one male. Guinea baboons may eventually provide a clue as to why this happened, since females in that species voluntarily associate with one male at a time. As far as hominin males are concerned, concentration on one or two females might have increased the probability of successful reproduction. The male could copulate with the females throughout their cycles, obviating the need for a special signal of ovulation. The male could also provide more concentrated parental effort to his offspring. Groups like these are characteristic of multilevel societies (see below).

### ***8.4.4 Conflicts and Reconciliations***

Conflicts can occur in any relationship (preferred foods are often a source of friction in primates). In many primate species, such conflicts may be followed by reconciliation, that is, positive behaviors (such as certain facial expressions and grooming) that restore the relationship. In chacma baboons, heterosexual opponents exhibit friendly post-conflict reunions, almost exclusively between males and pregnant/lactating females who have formed tight social bonds. This is in accord with the valuable relationship hypothesis, which predicts rates of reconciliation to increase with the fitness consequences of the bond between the erstwhile opponents. In chacma baboons, males are as likely as females to initiate reconciliation, suggesting that males in this species play a role in maintaining heterosexual friendships that is greater than previously appreciated (Webb et al. 2019), bringing them more in line with the other baboon species.

## 8.5 Male–Female Interaction in Kinda Baboons

Kinda baboons seem to have an equivalent of special friendship, although there are distinctive features. Based on measurements of grooming and proximity, Schneider-Crease et al. (2022) determined that each Kinda individual, regardless of sex, had a top male and a top female among their affiliates (Fig. 8.5). Females were likely to have a single top male partner, while being affiliated with more than one female.

Weyher et al. (2014) provided details of grooming patterns that indicated strong male motivation to maintain these relationships. Males initiated 25 of 27 interactions (93%). Females terminated 16 of these interactions, 3 were mutual, and 6 were terminated by males.

Both types of relationship (top male and top female) were correlated with rapid maturation of infant behavior (female rank was also important in this regard). Possible adaptive functions of rapid maturation include lower infant mortality and shorter interbirth intervals for the mother. One possible proximate cause of this phenomenon is that the mother's bonds are used to recruit helpers with infant care. Another is that a more secure mother may invest less in proximity to her mobile infant, facilitating independence.

Petersdorf et al. (2019) argued that Kinda baboons provide a distinctive and perhaps superior model for the hominization of female–male relationships. Compared to other COKY species, Kinda baboons are postulated to be somewhat more like



**Fig. 8.5** A Kinda baboon pair with an infant. Sexual dimorphism in this species is the least pronounced in the genus *Papio*. (Photo by Kenneth Chiou. Kafue National Park, Zambia. Resized for publication. Wikimedia license <https://creativecommons.org/licenses/by-sa/4.0/>)

**Table 8.1** Key features of Kinda baboons compared with other baboon Species

Trait	Kinda baboons	Other COKY baboons
Troop size	200+	Typically <200
Environmental seasonality	Highly seasonal	Varied
Degree of estrous synchrony	High	Low to intermediate
Size of sexual swellings	Small	Medium to large
Relative testis size, mm <sup>3</sup> /kg	2.28	1.61, 1.62, 2.16
Sexual dimorphism in body mass, M:F	1.55	1.71 to 1.83
Sexual dimorphism in canine basal area, M:F	1.96	2.75, 2.89, 3.14
Male immigration	Nonaggressive	Often aggressive
Male–female grooming	Often male-driven	Usually female-driven

The table illustrates several distinctive features of Kinda baboons that are the basis for analogies between Kinda baboon and hominins, as explicated by Petersdorf et al. (2019). It is a simplified version of the table in the Petersdorf paper with additional data from the text

later hominins and modern humans in several respects (Table 8.1). The reasoning is as follows: A large troop in a highly seasonal environment means that many females will be in estrus during a relatively short period of time. Consequently, it would be difficult for one male to monopolize all or even a large percentage of the estrus females. This situation minimizes the value of aggressive competition in males, which leads to a reduction in sexual dimorphism.

The alternative to aggressive competition is sperm competition, that is, a male competes with others by fertilizing females with as much sperm as possible. The genital proportions of Kinda baboons are consistent with this interpretation. Males have large testes that produce competitive quantities of sperm (Petersdorf et al. 2019). Since mating success is nonaggressive, immigrating males are nonaggressive. In addition to sperm production, a viable male strategy is to increase mating opportunities by providing benefits to females—at a minimum, grooming.

According to Petersdorf and colleagues, the key to the evolution of Kinda baboons is their distinctive ecological niche. The Kinda case shows how selective pressures can affect mating systems by shifting them toward traits like those that emerged during hominin evolution. The postulated scenario combines a Kinda model with paleoanthropological information that places early hominins in increasingly seasonal and heterogeneous environments. This factor and/or unusual group size affected male mating opportunities by reducing the potential for monopolization of females. As a consequence, sexual dimorphism declined and female mate choice became more important.

There are problems with this interesting scenario and its use as a model for early hominins. First, Kinda baboons live in a limited geographic area; other baboons have expanded to occupy much the same range of habitats as early hominins. Second, the relative seasonality of the Kinda habitat is in some doubt (Zinner pers. comm.). Third, it is debatable as to whether aggressive competition was diminished in hominins. Reduction in sexual dimorphism, for example, is viewed by some as evidence of reduced aggression; however, it can also be explained by more use of extrasomatic weapons. Fourth, sperm competition is not predominant in humans, as

shown by anatomy and physiology of human male genitalia (Dixon 2012). Evidence from olive baboons suggests that both sperm competition and aggressive competition could have been important in early hominins. Finally, more generally, the small sample size for the species increases the chances of errors in the research results (Fuchs et al. 2018).

## 8.6 Male–Female Associations in Multilevel Societies

In common with special friendships, the unimale groups of multilevel baboon societies entail mating and offspring. However, they differ in having a higher level of paternal certainty. Compared to the special friend relationships in troops, the unimale groups of hamadryas and Guinea baboons are more like human families in two important respects. First, they are associations that combine one male with one or a limited number of females. Second, these associations are embedded in multilevel communities. However, within this common framework, there are crucial differences between the species regarding sociosexual dynamics within unimale groups. These present quite different analogies for the reconstruction of early hominin evolution.

### 8.6.1 *Male-Focal Groups in Guinea Baboons*

In Guinea baboons the male-focal unit (Chap. 7) is based on female choice rather than male coercion. Goffe et al. (2016) found that each female was mainly found in close proximity to one specific male (within 2 m), which they called the “primary male.” The term used here, for comparative purposes is “central male” (Chap. 7). Female–male grooming was mostly confined to the central male. So were ritualized greetings between male and female, which involved hand touches, embraces, hip touches, and mounting. Copulations were almost all confined to the central males, but male–female social interactions were not strongly affected by female reproductive state. Central males handled infants more frequently than other males did.

Each female maintained exclusive social and mating relationships with one male at a time, while males might be affiliated with as many as six females. The stability of these male–female relationships varied considerably because females were free to shift from one male to another (Fischer et al. 2017; Goffe et al. 2016). During a 17-month study period, half of the females transferred between different males one or multiple times. Other than the focus on a single male at a time, female–male relationships in Guinea baboons seem similar to the special friendships in troops with regard to affiliative behavior in both sexes. This suggests one pathway for hominin male–female relations to have transitioned from troop to multilevel society.

### 8.6.2 *One-Male Units in Hamadryas Baboons*

Hamadryas baboons provide a very different model for the transition of male–female relationships into the multilevel context. The basic unit of everyday life in hamadryas baboons is an OMU that typically contains one or two females, although a few units contain many more (Fig. 8.6). Hamadryas females have been accumulated by the male through several different means (Chap.7) and the male restricts their movement.

Females are strongly oriented to the “leader” and their most serious fights with each other concern grooming access to the male. Females do not leave the central male unless appropriated by another male. Benefits received from the leader include protection from predators and from infanticide by outsiders and he shields them during storms. While the group travels, a male will wait for a female who is slowed by age, injury, or carrying a dead infant. The OMU is the reproductive unit. Leaders are not known to copulate with outside females. Females limit overt copulations to the central male. However, they may engage in surreptitious copulations with other males. This could create paternity confusion that would lessen the chance of infanticide by males who could potentially take over the OMU in the future.

Amann et al. (2017) investigated the determinants of takeovers in a population of wild hamadryas with a dataset of 172 events gathered over 20 years. In contrast to other baboon species, hamadryas males show no bias with regard to female reproductive state at the time of the takeover. However, they prefer to assimilate females that have never given birth (as evidenced by their physical features). In other words, the males target females with long-term reproductive potential, a strategy that is consistent with the high degree of stability in OMUs. This preference is paralleled



**Fig. 8.6** A hamadryas male with two females. (Photo by Steven Gotz. Oakland Zoo)



**Fig. 8.7** A hamadryas male with a female and infant. (Photo by Steven Gotz. Oakland Zoo)

by studies of human mating that demonstrate a male preference for a nulliparous female as a potential partner in a long-term relationship.

Hamadryas baboons may be considered an alternative to Guinea baboons as a model for early hominin male–female relationships. An alternative is to view the two species in sequence. Jolly (2020) proposed that hamadryas social organization evolved from a system like that of Guinea baboons. He attributed this development to the distinct environment of hamadryas, but similar pressures may have existed elsewhere. Baboons, like hominins, adapted to arid habitats throughout Africa. If Jolly’s proposed evolutionary sequence for baboons is correct, hominin evolution may have stabilized at a stage comparable to Guinea baboons or it may have gone on to a greater resemblance to hamadryas baboons. This is speculation and the particulars of such a transition in hominins would be the subject of future research and discussion. A related issue of great importance is the role of sexual aggression in hominin evolution (Figs. 8.6 and 8.7).

## 8.7 Sexual Aggression

Sexual threat and violence in humans are of great concern and evolutionary explanations are particularly controversial (Baniel et al. 2017). Different baboon analogies suggest alternative possibilities for early hominins. The interactions in question vary from trivial spats to injurious attacks. There is speculation that sexual violence in hominin evolution is related to the desire for sexual privacy.

### 8.7.1 *Forms of Sexual Aggression*

Several forms of sexual aggression by males against females occur in mammals. Primates are among the orders in which such behavior is most common (Cassini 2021). One of these is infanticide, which is known to occur in four of the six baboon species. The frequency and context vary significantly across the four species..

Forced copulation (“rape”) is rare in primates and is not known to occur in baboons. A questionable explanation is that female resistance is a sufficient deterrent, despite the degree of sexual dimorphism in all baboons. Male baboons seem to have few inhibitions about attacking females. An alternative is that the cries of a female might bring other males to intervene. This might be true in some cases, but not in those where an alpha male is completely dominant. Instead, and contrary to some ideas about rape in humans, male baboons seem not to have any strong motivation to achieve copulations by direct force, much less a specific innate system for such behavior.

The reference to “direct” force is necessary because baboons do provide evidence of more generalized aggression, called *coercion*, that indirectly leads to sexual success. This is characterized as coercion or intimidation. Two other types of sexual aggression will also be considered here. *Harassment* is interference in a copulatory relationship by one or more others. *Punishment* is aggression received by a female from a male in response to actual or perceived copulation with another male.

### 8.7.2 *Sexual Aggression in Troops*

Baniel et al. (2017) began a study of chacma baboons with the problem of human sexual violence in mind. They noted that such behavior is “widespread across human populations” and postulated that their work would have implications for its evolutionary origins. Their specific goal was to test the sexual coercion hypothesis, which interprets male aggression against females as intimidation directed toward dominating a female when she becomes fertile. In other words, the function of repeated male aggression is delayed mating benefits.

Baniel and colleagues observed two troops of chacma baboons in Namibia. Results of the study supported the sexual coercion hypothesis and cast doubt on alternatives. First, male aggression was related to the reproductive state of the targeted females: cycling females were attacked much more often than those in other reproductive stages. Second, the attacks caused injuries, that is, they were costly to the females and could not be ignored. Third, a female who received more aggression from a male during her cycle was more likely to be in a consort relationship with him when ovulating at the end of the cycle. These factors add up to intimidation as a mating strategy for males.

The data ruled out two alternative explanations for the aggression. It was not punishment because aggression rarely followed when females mated with rivals. It was not a signal of prowess to potential mates because there was no correlation between the consort result and the male's general aggression in the troop. Clutton-Brock (2017) commented that, "It would not be surprising if male coercion of females was common in early hominins."

The results of the chacma study were consistent with research on 12 troops of olive baboons in Gombe National Park, Tanzania. A more general study of wounding patterns included the result that cycling females (adult and adolescent) were much more likely to be wounded than females in other reproductive stages (MacCormick et al. 2012). These researchers, like Baniel and colleagues, concluded that sexual coercion was the function of the behavior. Similarly, female yellow baboons in Kenya were at the greatest risk of injury on days when they were most likely to be ovulating (Archie et al. 2014).

Kinda baboons appear to differ from the other COKY species with regard to sexual aggression. This is in accord with the pattern of sperm competition in place of confrontation between males (see above). Sexual dimorphism is less than in other baboons and the thin canines of the males are less suited to attack. Petersdorf et al. (2019) suggested that this is analogous to evolution in the human direction that took place "after *Australopithecus*" (i.e., early *Homo*).

Kinda males make no attempt to monopolize females. Therefore, there is no function for coercion, punishment, or infanticide. As far as forced copulation is concerned, none has been observed. Perhaps female resistance is most likely to be effective in the baboon species with the lowest level of sexual dimorphism.

As was noted previously, the distinctive ecology and demography of the Kinda baboons casts some doubt on their relevance to early hominin behavior. At the least, though, it can be said on the basis of Kinda behavior that troop organization does not entail sexual violence under all circumstances.

### 8.7.3 *Sexual Aggression in Multilevel Societies*

Infanticide and coercion occur in hamadryas baboons, but the pattern differs from COKY species. Infanticide takes place when a male takes over a group of females from another male. The infant mortality rate for these events can be as high as the 67% recorded at Filoha. Under ordinary circumstances, the rate of infant deaths from all causes is 13% (Swedell et al. 2014). If a takeover occurs, pregnant females may respond physiologically with pregnancy termination. This curtails their investment in offspring that are likely to be killed anyway, mitigating the effect of infanticide on their own fitness. As far as humans are concerned, although earlier conclusions may have been exaggerated, recent research confirms that step-fathers are significantly more likely to kill infants than are biological fathers (Nobes et al. 2019). Furthermore, as in baboons and other primates, the behavior is largely limited to infants as opposed to juveniles, with a borderline in humans at about 4 years



of age. This focus on infants is analogous to the pattern in baboons and other primates that functions to return a lactating mother to sexual availability.

In hamadryas baboons there is a high level of aggression directly against the female(s) during any takeover. This is apparently necessary to break the bond with the former leader and coerce the females into following the new leader. Once the new unimale group is consolidated, the rate of aggression declines. In contrast to COKY baboons, there is no need for coercion to promote sexual consorts in a stable unimale group. Another difference between hamadryas and COKY baboons is that punishment, rather than coercion, is an important feature of a stable OMU. A female who goes too far from the group is likely to be chased and attacked with a stereotyped neck bite. Analogous aggressive behavior may have developed in early hominins when the social context shifted to unimale groups in multilevel societies.

While the hamadryas model was the only one available, it seemed that sexual aggression might have been an integral part of the earliest hominin multilevel societies. We now know of a different pattern of behavior in a Guinea baboon population. Little or no aggression between the sexes has been observed. Females are not taken over, herded, or punished (Fischer et al. 2017). Male-driven grooming may facilitate affiliation and sexual interaction.

This possible analogy for early hominins tells us that the origin of the family in a multilevel society does not require rigidly male-dominated OMUs like those in hamadryas baboons. If early hominins were like Guinea baboons, the patterns of sexual violence seen in extant *Homo sapiens* might have come into existence during a later period. Though possibly an evolutionary change under new circumstances, this might also be a case of cultural developments (e.g., patriarchal ideals about lineage) overriding biology.

#### **8.7.4 Concealment of Mating and Sexual Privacy**

Concealment of mating is widespread among humans and in a few other species. Ben Mocha (2020) postulated that this maintains two important relationships for the male: (1) mating control over a partner and (2) continued cooperation with other males that might be jealous or try to intervene if they perceived the sexual behavior.

Baboon evidence suggests the female viewpoint: chacma females initiate fewer copulations in the presence of adult male bystanders. This might be to avoid punishment and/or aggressive interference from rival males (Baniel et al. 2019). A related finding is that female baboons are able to suppress copulation calls that are ordinarily associated with male ejaculation (Vaglio et al. 2020), which could summon other males to the scene and generate competition.

## 8.8 Summary and Discussion

Male–female relationships in baboons offer several perspectives on early hominin behavior and the possible origins of the human family. Salient features of family in this context are (1) a long-term relationship between one male and one or several females (usually no more than two or three); (2) a sexual relationship between the partners with the consequent possibility of offspring; and (3) some degree of male care for the offspring.

Relevant relationships between particular males and females exist in baboon troops. These are called special friendships or primary associations. Either a male or a female can have several special friends. For males these relationships may lead to mating opportunities and the opportunity to care for their own offspring. For females the benefit is protection for themselves as well as their offspring. Protection may be needed against predators, infanticidal males, or harassment by competitive troop members. The minimum duration of a special friendship extends to the time that the offspring is weaned, but is longer in some species. In olive baboons, such relationships may last for years and entail affiliative (affectionate) behaviors such as proximity and huddling. Kinda baboons suggest a modification of this pattern in which there is less competition among males to obtain female associates and more male investment in those associates, manifested in male-driven grooming.

To go from the special friend pattern to something more like the human family would require one or more females to maintain a long-term relationship with just one male. Two possible pathways to this outcome are represented by the one-male units in hamadryas baboons and the male-focal associations in Guinea baboons. Hamadryas one-male units involve coercion of females as they are added to the group. Coercion continues in the form of threats and neck-biting, although females display affiliative behavior toward the male after being integrated into the group. In Guinea baboons, females choose to associate with a particular male and are free to switch from one male to another. Even so, some of these associations last for years. These may be alternatives, but it is also possible that the hamadryas system evolved from ancestors similar to Guinea baboons and that a parallel sequence took place in early hominins.

Sexual aggression is a troublesome issue in human behavior and baboons offer diverse perspectives on possible early hominin origins. Sexual coercion involves persistent attacks on a particular female in order to intimidate her into sexual compliance. This behavior occurs in three of the troop-living species. In hamadryas baboons, intimidation takes place at the time that a female is incorporated into the OMU. Infanticide is another form of sexual aggression that occurs in these baboon species, probably as a way to make newly acquired females sexually available. A tendency toward such behavior in humans may be represented by murder rates that are significantly higher for step-fathers than biological fathers.

Sexual aggression, whether against females or infants, seems not to occur in two *Papio* species: the troop-living Kinda baboons and the multilevel Guinea baboons. Both are less studied than the other species at this point, so sexual aggression may

be seen in future research. However, it seems highly unlikely at this point that sexual aggression occurs at the same level as in other baboons, if at all. If these species represent the origins of human families and sexuality, the sexual violence that occurs in humans might have evolved in a later phase or might be a product of culture in more recent times.

Sexual privacy in humans may be related to sexual aggression in one or more ways. It has been suggested that it allows a male to monopolize a female without direct knowledge of other males. This may preserve male alliances and/or avert danger to both the male and the female. Baboon evidence suggests the female viewpoint: proceptive females initiate fewer copulations in the presence of adult male bystanders. This might be to avoid punishment and/or aggressive interference from rival males. A related finding is that female baboons are able to suppress copulation calls that are ordinarily associated with male ejaculation, which could summon other males to the scene and generate competition.

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