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## Special Friendships Among Baboons



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### Synonyms

[Pair bonding](#); [Social bonds](#); [Special relationships](#)

### Definition

Baboons (*Papio* spp.) form long-term, nonsexual social bonds between unrelated males and asexual females known as “friendships.”

### Introduction

Persistent social bonds between group members known as “friendships” have been described in numerous mammals (e.g., capuchin monkeys, *Cebus* spp.; elephants, *Loxodonta africana*; spotted hyenas, *Crocuta crocuta*; dolphins, *Tursiops aduncus*) (reviewed in Seyfarth and Cheney 2012). Typically, these friendships refer to long-term bonds between nonkin that transcend associations formed in sexual contexts (e.g., during mating periods or consortships). Unlike affiliations with other group members, friendships are

broadly characterized by high rates of association in close spatial proximity; positive, non-harmful social interactions; and mutual tolerance and physical, emotional, and/or social support (Silk 2002; Palombit 2017).

Long-term social bonds between males and females are not commonly observed in many mammals outside of pair-living or small group-living species. Under these social structures, limited reproductive opportunities and high parental certainty should select for increased investment in mating and parenting efforts by males, resulting in the formation of heterosexual pair bonds. In contrast, primates typically live in large, multi-male, multi-female social groups that provide more mating opportunities and lower rates of paternity certainty. Nonetheless, the formation of heterosexual friendships has been observed in a number of primate species (e.g., chimpanzees, *Pan troglodytes*; Assamese macaques, *Macaca assamensis*; Japanese macaques, *M. fuscata*; rhesus macaques, *M. mulatta*; chacma baboons, *Papio ursinus*; olive baboons, *P. anubis*; yellow baboons, *P. cynocephalus*) (Seyfarth and Cheney 2012). Establishing the adaptive benefits of maintaining such male-female bonds in polygynous and polygynandrous species has become a question of interest in both behavioral ecological and anthropological theories. Furthermore, given the likely multi-male multi-female social structures exhibited by early hominins, testing hypotheses of how heterosexual friendships have evolved in similar social structures in extant primates can

inform on how the strong male-female pair bonding found in modern humans may have first evolved.

### Male-Female Friendships in Baboons

Baboons are polygynandrous, mostly female philopatric monkeys that live in multi-male, multi-female groups, and exhibit separate linear dominance hierarchies for each sex. These species provide some of the best-studied examples of friendship in nonhuman primates. The term “friendship” in baboons primarily refers to the social bonds formed between adult males and females that persist beyond the periovulatory period – in contrast to the short-term consortships formed between males and females in estrus. Under the above definition of friendship, positive social interactions between male and female baboon friends include increased rates of mutual grooming, vocalizing, and female tolerance of male alloparenting (Palombit 2017). Friendships are common throughout groups of chacma and olive and yellow baboons in southern and eastern Africa, respectively, although some dynamics vary within groups and between populations (reviewed in Palombit 2017). For example, while it is common for nearly all adult females in a group to have male friends, the opposite is not true – not all males have female friends at any one time. The number of friendships a female engages in can vary both between females and populations – chacma baboon females typically have only one friend, but in olive baboons the number of friendships can extend to three or more simultaneous friendships. In groups where females exhibit multiple concurrent friendships, the number of friendships may also be positively correlated with dominance rank. Similarly, in some yellow and chacma baboon populations, females are more likely to preferentially select male friends with equal or higher dominance ranks to their own. The instigator of a friendship also varies between populations. In olive baboons, males are the primary maintainers of friendships by initiating grooming bouts and reducing spatial proximity – in contrast to chacma baboons, where

females invest a greater effort into maintaining associations (Shur 2008).

### Adaptive Benefits of Friendships for Female Baboons

The pervasiveness of heterosexual friendships among multiple baboon species suggests a substantial adaptive significance to the formation of these bonds. For example, infanticide by males is a well-documented reproductive strategy in non-human primates, particularly in immigrating individuals. By killing an unweaned infant, a male can cause the mother to resume cycling sooner, therefore increasing the number of opportunities for fertilization by the infanticidal male. Evidence from two different methodologies support the hypothesis that for female baboons, a key benefit of friendship with a male is protection against infanticide. First, in a study of chacma baboons during which infanticide was a substantial cause of infant mortality (e.g., 38% of infant deaths), playback experiments found that both male and female friends reacted more strongly to the distress vocalizations of friends under attack compared to non-friends (Palombit 1997). Moreover, male friends responded more strongly to the calls of females with infants compared to females following the death of their infant or when recordings included the calls of a potentially infanticidal male. Second, hormonal analyses of chacma baboon stress responses found that while females experienced higher glucocorticoid levels when their group was taken over by an immigrant male, these levels were significantly lower in lactating females with male friends compared to those without (Beehner et al. 2005). Conversely, males with female friends exhibited increased glucocorticoid levels, but males without friends did not. As such, behavioral and physiological responses in both sexes to behavioral cues in friends and the presence of infanticidal males suggest that female chacma baboons benefit from the active defense of their infants by male friends.

In baboon populations where infanticide by males is less common (e.g., yellow and olive

baboons), friendships are expected to protect against nonlethal harassment. A repeat of the playback experiments conducted in chacma baboons found similar results. Despite a substantially lower risk of infanticide, male olive baboons demonstrated similar protective responses toward female friends in distress. In these cases, female baboons appear to benefit from male friends who can defend them from aggression from other group members targeting themselves or their infants (Nguyen et al. 2009; reviewed in Palombit 2017). More specifically, females benefit from greater protection afforded by higher-ranking male friends, because these males can defend against a higher number of lower-ranking males (Shur 2008). This protection should have a direct fitness benefit, as demonstrated by studies that have shown adult females and infants of mothers who are more closely socially integrated to conspecifics of either sex live longer (e.g., Alberts 2019).

### **Adaptive Benefits of Friendships for Male Baboons**

For male baboons, benefits can be grouped under two hypotheses. Under the parental effort hypothesis, males that have sired the infants of female friends should maintain associations in order to protect their offspring and improve infant survivorship. Paternal care by friends is especially prevalent in populations where paternal certainty is higher, because males are more likely to invest in infant protection, even extending to male friends protecting the unborn offspring of pregnant females, which may be susceptible to abortion induced by immigrant males (Baniel et al. 2016; Städele et al. 2019).

Under the mating effort hypothesis, males should benefit from maintaining heterosexual friendships through increased likelihood that a female will select a male friend to sire subsequent offspring. As such, this hypothesis overlaps with the previous hypothesis of parental effort in that most examples of paternal care likely reflect a form of mating effort if infant care by a male positively influences female mate choice. Nguyen

et al. (2009) and Baniel et al. (2016) found no evidence that friendships generate future mating opportunities for males of any relation to infants after their female friends had weaned and resumed cycling. It is possible however that the effect of prior friendships on mating opportunities may vary between males that have sired their friend's offspring and those that have not (Städele et al. 2019) or if increased mating opportunities occur with the same female friend or a different non-friend (Palombit 2017). Moreover, both the aforementioned studies were conducted in yellow and chacma baboons, respectively. In these species, female mate choice may influence male mating success to a lesser extent compared to male dominance rank (e.g., compared to olive baboons). Städele et al. (2019) found a positive relationship between heterosexual sociality and subsequent male mating success in olive baboons, although there was no effect when considering (1) males who had sired the current infant and (2) lactating females (as opposed to cycling females without sexual swellings). In olive baboons, there is therefore likely a complex interaction between the effects of male friendships and rank on female mate choice, although a female's friendships may have a greater influence than male rank compared to other baboon species.

### **Conclusion**

The conspicuousness of male-female friendships in baboons provides an excellent window into the evolutionary significance of sociality among non-kin in nonhuman primates. While several questions have yet to be explored – for example, the effect of friends in deterring predators and for males the possibility that friends facilitate access to grooming networks or infants for use in agonistic interactions – current data already indicate key selective pressures in baboons through which such stable pair bonds may have evolved. In particular, hypotheses of male mating and parental effort reflect predictions for the origins of pair bonds in early hominins and subsequently modern humans. As such, studies of friendship in baboons, among other nonhuman primates, can

provide useful models for inferring ecological and social determinants of human behavior that are not retained in the fossil record.

## Cross-References

- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Cooperation and Social Cognition](#)
- ▶ [Infanticide in Nonhumans](#)
- ▶ [Nonhuman Primates: Within-Group Conflicts](#)
- ▶ [Nonhuman Primates](#)
- ▶ [Paternal Care](#)
- ▶ [Primate Cooperation](#)
- ▶ [Primate Dominance Hierarchies](#)

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