Chapter 9
Female–Female Relationships

9.1 Introduction

Baboon analogies suggest various ways in which early hominin females may have related to each other. Enduring relationships between females occur in troops and in multilevel societies. Females maintain dyadic relationships with each other as well as network connections. Female–female interactions include competition as well as affiliation. Food, unless abundant, is a primary source of conflict. In some species, females may compete for preferred males.

Competitive behaviors among females resemble those of males: displacement, threat, and physical aggression. Physical attacks between females seem to be generally of low intensity (though escalated under certain circumstances). Females never engage in aggressive displays such as the wahoo contests of male chacma baboons. Baboon evidence is consistent with many recent findings about female–female relationships in humans regarding both affiliation and competition, which suggests that they originated in (or were perpetuated in) early hominins,

9.2 Female–Female Affiliation

Some contributors to a recent symposium on relationships between women demonstrated interest in possible evolutionary origins for these relationships. Fox et al. (2022) allowed that the capacity of women to form bonds with each other might come from "a long evolutionary history." Chimpanzees, and especially human hunter-gatherers, were prominent in some of these discussions, but many of the points made are amenable to comparison with baboon behavior. Differentiated affiliative relationships between pairs of female baboons are common in troops. These are often, but not always, based on kinship. Kramer (2022) endorsed the

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evolutionary perspective, noting that "an ancient feature of human sociality is living in multilevel societies." This applies to early hominins as well as humans, and leads to analogies in hamadryas and Guinea baboons.

9.2.1 Female Affiliation in Humans

Patrilocality is a human social pattern in which the marriage of a woman entails taking up residence with her husband and his family, often in another community. It is the human equivalent of male philopatry. Patrilocality has been depicted as a fundamental feature of human evolution (Reynolds 2022), but this view has been strongly challenged. Based on considerable cross-cultural evidence, including hunter-gatherers, Rucas and Alami (2022) argue that patrilocality was far from universal in the human evolutionary past. Perhaps more important, they note that patrilocality rarely resulted in complete isolation of female blood relatives. In recent forager cultures (most of them with flexible residence patterns), a woman was often related to at least a few others in her husband's community. In societies with polygyny, a woman had about a 10% chance of being in a household with a sister or other close relative. In addition, women were in many cases free to visit relatives in other groups.

Reynolds (2022) maintained that female friends were important to women because "many female ancestors were surrounded by unrelated individuals upon marriage." Although this may be somewhat exaggerated (Rucas and Alami 2022), it must have been true that many women were in such situations during some significant part of their lives. Research shows that women and girls are more strongly attached to friends than are males. They place great value on these relationships and report higher levels of trust and communication than do males.

Female kin and friends provided cooperation in a variety of endeavors, such as food processing and child care. Beyond immediate cooperation for various purposes, "a large body of evidence" shows that such social support is strongly linked to better health and increased longevity. Social ties are more critical predictors of disease risk than body weight or physical exercise (Reynolds 2022). Friends as well as kin can be allies in conflicts and both can help a woman with child care and other needs. Studies of various human societies have amassed evidence that access to kin and other close affiliates has a positive effect on fertility. In Gambian women, for example, the presence of mother and sisters is associated with enhanced fertility (Kramer 2022).

9.2.2 Female–Female Dyads in Troops

The trend toward downgrading patrilocality in human evolution fits comfortably with the hypothesis that very early hominin societies were like the female-philopatric troops of baboons. More specifically, baboon troops display female–female relationships that are comparable to those described above for humans. The evidence is especially strong for kinship, but also suggests a role for friendship (Fig. 9.1). Primate societies like baboon troops have been characterized as "female-bonded" (Wrangham 1980).

Two studies of Amboseli yellow baboons (Silk et al. 2006a, b) and a study of Okavango chacma baboons (Silk et al. 2010) investigated the strength and durability of female–female bonds in troops. The results for both species showed that adult females formed close, equitable, supportive, and enduring social relationships. Based on measures of proximity and grooming, the strongest bonds connected a female with her mother and sisters; beyond that, bond strength decreased as relatedness decreased. The details of relationships in the two studies were somewhat different, but the theme of strong female–female bonds emerged from both. The durability of social bonds in yellow baboons followed the same patterns as bond strength. Fourteen dyads maintained close relationships for at least 5 years: mother/daughter (five pairs), maternal sisters (five), paternal kin (three).

These studies also indicated that if close maternal kin are not available, females seek alternatives. Bonds formed with paternal sisters are ordinarily intermediate in strength between ties to maternal sisters and to nonkin. A strong attraction to similar-aged females may be explained by the fact that such peers are often paternal

Fig. 9.1 A young female olive baboon grooms an older female. They may be mother and daughter. (Photo by Glenn King. Manyara, Tanzania)

half-sisters or cousins. However, some of these peers might actually be unrelated, and, even if related, the baboons might not be aware of the relationship. In short, the motivation to create these bonds might be a need for friendship such as was described above for human females.

The baboons also paralleled humans with regard to the physiological effects of social ties. Other research concluded that females' bonds with other females enhanced reproductive success, as in humans. This effect was independent of infant attractiveness or long-term bonds with specific males, that is, special friends (Silk et al. 2009). Females who formed the strongest social bonds with other adult females had the highest survivorship among their daughters and sons (at least after the age of high infanticidal risk). These benefits were unrelated to female dominance rank and increased quantitatively with the strength of a female's social bonds. Although females formed the strongest bonds with their closest kin, the mere presence of kin seemed to be less important to offspring survival than the quality of those relationships.

Several proximate factors might contribute to the connection between a female's social bonds and her offspring's survival. The first is related to predation, which is the primary cause of juvenile and adult mortality in the Okavango baboons (Cheney et al. 2004). Females with stronger and more secure social relationships may be less spatially peripheral to the troop while they are feeding during the day and while perching in sleeping trees at night. These positions could make them and their offspring less vulnerable to predators. Second, females with strong social bonds may be better shielded from social conflict within the troop and therefore able to feed more efficiently (Silk et al. 2003).

9.2.3 Female Groups and Networks in Humans and Baboons

More extensive connections than dyads have linked human females together in the historical and evolutionary past (Kramer 2022). These ranged from small groups to extensive networks. Some groups of women are informal and temporary (though often recurrent), forming for specific purposes such as collecting or processing food. Less frequently, female coalitions countered male aggression. Women's social networks coordinated a variety of activities such as visiting, helping, or exchange. For example, a gift-giving network among Kalahari foragers covered extensive areas and linked female partners who could provide each other with refuge during local environmental crises (Kramer 2022).

More formal networks called sodalities organize women (and men) to carry out a variety of functions (Kramer 2022). Some support individuals, such as the sick, old, and widowed. Others have societal functions, such as coordination of ceremonies. Despite the varied cultural definitions of networks and sodalities, the cross-cultural ubiquity of these social structures suggests an underlying evolutionary basis. All of these relationships have been culturally elaborated, but the tendency to form similar social structures can be seen in baboons, which suggests that there are

roots in human evolution. Baboon analogies show how the foundations for these entities might have evolved and developed in early hominins.

Cooperative food collection does not occur in baboons, but females do group together in the course of foraging. King et al. (2011) investigated the factors involved in co-feeding in desert-living chacma baboons. They found that feeding groups were significantly correlated with social bonds measured by grooming rather than kinship. Females followed male grooming partners to favorable food patches and were joined by other females with whom they had social bonds. Similar grouping tendencies in early hominins might have provided the basis for more cooperative food collection and sharing as savanna expansion made good food patches harder to find. If the primary basis was social bonding rather than kinship, as in these baboons, this would have added flexibility to the formation of the hominin groups.

In addition to organizing ordinary activities, grooming connections can alleviate stress during difficult times. Wittig et al. (2008) tracked stress in female chacmas, measured by glucocorticoid levels, during a period of social instability caused by dominance competition between males. Stress increased in the week after the upheaval and females narrowed their grooming activities to a few preferred partners, mostly close kin. Changes in GC levels were not related to giving or receiving grooming. Rather, stress was relieved by participating in small grooming networks with reliable preferred partners. Wittig and colleagues noted research with humans that showed women to be more likely than men to seek social contact in times of stress and to turn to smaller support groups (see also Crockford et al. 2008).

Female baboons do not group together to counter aggression from the much larger males, but they do occasionally display the capacity to form coalitions in competition with each other. In a study of females in several yellow baboon troops, a little more than 2% of all dyadic disputes led to intervention by a third female (Silk et al. 2004). In most cases, high-ranking females supported others of high rank who were maternal relatives. That is, they supported the existing hierarchy. However, coalitions played an important role in reorganization of the female hierarchy in the troop that was ancestral to the three troops in the study.

Silk et al. (2004) cited other reports of female coalitions, some of which might represent greater frequency of the behavior. Yellow baboon females at another site intervened "regularly" and attacked other females "jointly." Female olive baboons intervened in disputes once every 14 h. Female chacma baboons intervened in 32 disputes during 15 months of observation. A similar capability in early hominin females might have been increasingly devoted to mutual defense against male aggression during the evolutionary reduction of sexual dimorphism in size.

A social network analysis of chacma baboons evaluated the comparative benefits of dyadic bonds against several network measures (Cheney et al. 2016). Results suggested that females with strong dyadic bonds also showed high *eigenvector centrality*, a measure of the extent to which an individual's partners are connected to others in the network. Eigenvector centrality was a better predictor of offspring survival than dyadic bond strength. Having preferred partners who are themselves the preferred partners of several others may facilitate social interactions by making encounters more predictable and less stressful. Similarly, such connections may

facilitate the formation of new bonds if a female's primary partner dies. The offspring of individuals with high eigenvector centrality may also be less peripheral and at lower risk of predation—the primary cause of mortality for juveniles and adults in this population.

Parallels with modern humans suggest that the baboon patterns are analogous with adaptations of early hominins. Baboon researchers compared their findings to epidemiological and clinical studies of humans that indicate that social support has beneficial effects on health and well-being across the life span, including direct effects on reproduction such as the birth of heavier infants (Archie et al. 2014; Silk et al. 2003). Experimental studies in humans suggest that social integration is the cause not the consequence of improved health outcomes. Social support is thought to moderate the deleterious effects of chronic stress and thereby enhance well-being. Human studies have varied considerably in their measures of social support, ranging from detailed measures of the strength and quality of individual social bonds to composite measures of individual social integration and experience. All point to reduced mortality risk**.**

In some baboon field studies female relationships with other adults of both sexes are correlated with offspring survivorship, an effect that was unrelated to dominance rank or ecological conditions (Silk et al. 2003). Complementary work focused on longevity (Archie et al. 2014). Females with social connections to either males or females lived longer than isolated individuals. Females with strong connectedness to individuals of both sexes lived longest.

9.3 Female–Female Relationships in Multilevel Societies

In one view of hominin evolution presented earlier, troops were replaced by multilevel societies. Baboon multilevel societies, in comparison to troops, are characterized by shifts from female to male philopatry and from multi-male organization to unimale groups within larger communities. Nevertheless, some of the same female–female relationships and interactions can be seen in both kinds of society. Assuming a transition from troops to multilevel societies in early hominins, analogy indicates that such connections would have been preserved, though presumably in modified form. Two *Papio* species suggest the possibilities.

9.3.1 Female–Female Relationships in Guinea Baboons

Relatively little is as yet known about female–female relationships in Guinea baboons. Given the freedom of choice that females in that species have, a similar hominin multilevel system would presumably have made it easy for particular females to stay together or at least in contact. However, a captive study (Maestripieri et al. 2007) suggests complications. A large zoo enclosure contained 11 "harems"

with 1–4 females per group. Focal female subjects were randomly selected from five of these unimale groups. These subjects displayed a tendency to initiate contact and grooming *less* often when they had *more* relatives in the group. On the other hand, subjects who had more relatives *outside* their own groups initiated interactions with non-group females more often than those with fewer outside relatives. The researchers noted that the latter pattern resembled behavior in hamadryas baboons reported by Swedell (2002).

Interactions within the groups were both affiliative and agonistic (Maestripieri et al. 2007). Each female received more contact and grooming from other females than from the central male and these interactions were largely symmetrical. On the other hand, group-mates exchanged more threats and avoidance than with non-group females. Overall, group cohesion was maintained by approaches among all members, rather than by male coercion.

9.3.2 Female–Female Relationships in Hamadryas Baboons

Female hamadryas baboons are usually separated from kin through coercive formation and maintenance of one-male units. Nevertheless, females find ways to assert affiliation with some of their relatives. Genetic data suggest that, despite the social system, female hamadryas are more likely to be found in an OMU with maternal relatives than would be expected by chance. At least a third of these maternally related dyads are mother–daughter pairs (Städele et al. 2016). This situation is facilitated by the fact that hamadryas females are generally more philopatric within clans and bands than previously thought, presumably because more takeovers occur within clans and bands than between them (Swedell and Plummer 2019).

It may be that the baboons can recognize maternal kin and can find a way to express choice in at least some takeover situations and/or transfer between specific pairs of units due to a relationship between the two leader males. The situation implies that an ancestral maternal kin bias has been retained in hamadryas society (Städele et al. 2016). This suggests that female relationships like those found in troops could have persisted in a hominin transition to multilevel societies (Fig. 9.2). Observation of a captive colony confirmed the maintenance of kinship bonds by hamadryas females and found that mother–daughter dyads did the most grooming. Among wild hamadryas baboons, females risk punishment from their central males in order to visit females in other OMUs, possibly relatives.

Fig. 9.2 An old female hamadryas baboon after the death of a sister who was her "inseparable companion." She is embraced by an adolescent male. (Photo and information from Steven Gotz. Oakland Zoo)

9.4 Further Evolution of Hominin Female Relationships: Two Scenarios

Baboon analogies indicate that female–female cooperation was limited, if not minimal, in early hominins. It may have been limited to temporary coalitions. However, the underlying affiliations suggest that the roots of human female cooperation may be found in that evolutionary era. A scenario based on hamadryas baboons suggests an intermediate step in the transition to human patterns. This effort can be compared with another recent scenario that ignores baboons entirely.

9.4.1 The Swedell/Plummer Scenario

This scenario for later hominin evolution was based on information described above regarding persistence of female kinship bonds in hamadryas OMUs despite coerced transfers. It envisioned modifications resulting from changes in ecological conditions, subsistence patterns, and costs of reproduction for females (Swedell and Plummer 2012, 2019). The scenario postulates female subgrouping into small social units in which females assisted one another with food procurement as well as care and provisioning of offspring. Kinship bonds would have strengthened such groups, which might have led to multiple generations of related females. These cooperative breeding units may have aggregated around "favored places" as they tracked seasonally changing food sources.

This view of female bonds in relation to subsistence can be connected with a discussion above about co-feeding groups in chacma baboons. King et al. (2011)

found that co-feeding groups were significantly correlated with social bonds (measured by grooming) and not necessarily with kinship. Females joined other females with whom they had bonded, presumably as friends, perhaps because they were age-mates. Similar grouping tendencies in early hominins might have provided the basis for more cooperative food collection and sharing as savanna expansion made good food patches harder to find.

9.4.2 The Newson/Richerson Scenario

Newson and Richerson (2021) presented what they considered to be a new model for the evolution of *Australopithecus*, although there are numerous similarities to the Swedell-Plummer scenario. Both scenarios alluded to the rigors of open country, including widely spaced resources, increased predator danger, and debilitating heat. Both proposed that hominin mothers adapted to these new problems by grouping together to help each other. They imagined the mothers and their young at a "central place" (cf. "favored place") with cover and water that could be defended. Infants would stay there with some mothers while others took turns going out to forage, a concept that some primatologists have labeled the *creche*. Females would have to trust that others would protect and perhaps feed their infants and that food would be shared in order to overcome different levels of success.

Newson and Richerson find this scenario to be "reasonable" because it evolved in sperm whale mothers. There is some irony in using an oceanic analogy to address the problem of how mothers raised their young "in drier habitats." Another anomaly is the use of sperm whales to model a situation in which predator risk has substantially increased. The size of a female sperm whale is far greater than that of any potential predator, with the possible exception of the giant squid. The only other probable dangers are pods of orcas or perhaps multiple sharks. Of course, predators would probably attack infants. But early hominins would have had the same problem in the face of enemies much more like those that confront baboons. Primatologists have made use of cetacean comparisons in the past (as noted in Chap. 2), but these should be juxtaposed with competing (or supplementary) hypotheses derived from primates.

9.4.3 Female Bands with Males

The adaptations of many baboon populations provide analogies for hominins in hot, dry, open habitats. Among these populations there are various analogies that suggest how and why the postulated female foraging bands might have retained one or a few male associates. To begin with, the baboon troop's subtrooping potential models a society in which groups of mothers might have become differentiated while remaining members of the larger community. There are strong affiliative bonds among

groups of females within a baboon troop. Many of these relationships are based on kinship, but not all of them.

Hominin females, smaller than males, would have faced a wide array of larger predators. Foraging by a lone individual or a small party of females would probably have been very dangerous, especially in areas where trees were far apart. The baboon analogy suggests that one or a few males in the party would have considerably reduced the risk. Foraging subtroops of chacma and olive baboons often contain several adult females with one adult male. Hamadryas OMUs have one male protector and sometimes an additional male. As sexual dimorphism in hominins declined, the postulated female bands (in either the Newson-Richerson or Swedell-Plummer scenario) might have been more inclined to retain one or a few males to enhance predator defense, perhaps in positions of equality or even subordination.

The Newson-Richerson scenario suggested that the creche pattern created risks of omission: that females at the "home base" might not protect or feed the young of others. Baboon analogy indicates a more dynamic risk: that females at the home base might actually harm the offspring of others, whether through direct attack or "rough handling" (Fig. 9.3). Baboon analogy also suggests a solution: the young might be protected by adult males who were invested in them (Chap. 8).

Newson and Richerson argued that their speculation about a band of mothers is superior to theories of savanna survival based on "pair bonding." Their concept of pair bonding was clearly based on primate species such as gibbons, tamarins, and titi monkeys. None of these or any other pair-bonded primates are savanna dwellers in the same sense as early hominins and baboons. As described in previous sections, baboons provide a different view of long-term relations between males and females

Fig. 9.3 A hamadryas baboon female displays interest in another female's infant. The outcome of such interactions may be affectionate allocare, but it is sometimes "rough handling" (discussed in text). (Photo by Steven Gotz. Oakland Zoo)

in savanna troops, as well as multilevel societies. Special friendships in baboon troops and unimale groups in multilevel baboon societies suggest that close associations of male and female early hominins persisted from woodlands into savannas and from troops into multilevel societies. This view is more in accord with the human pattern that we see in cross-cultural evidence (cf. Chapais 2008).

9.5 Female–Female Competition

Cross-culturally, women behave more competitively than men in same-sex situations. In 91% of societies sampled, female aggression targeted other women (Reynolds 2022). Rucas and Alami (2022) added that rates of aggression between women were only slightly higher for in-laws than for kin. Sisters were the main target in 8% of the societies and mothers/daughters in 10%.

In a stable baboon society, competition is most often manifested in dominance relationships. Overt aggression, the most obvious representation of competition, is in the behavioral repertoire of female as well as male baboons. Physical aggression also occurs among human females, but is often controlled by cultural factors. On the other hand, humans can manifest competitiveness and hostility in verbal aggression.

Women display less physical aggression than men because they risk their children as well as themselves. Evidence from diverse populations shows that the loss of a mother is much more detrimental to the survival of children than the loss of a father (Campbell 2013). Women prefer less dangerous responses to conflict, such as social isolation of targeted individuals (Reynolds 2022). Throughout the world and in all historical periods, physical aggression between women has been less frequent, less lethal, and less injurious than among men.

9.5.1 Competition for Food

Affiliation among women often revolves around gathering and processing of food, whether there is a practical need for cooperation or simply an opportunity for socializing. There is also ample opportunity for conflict over food. In a study of the Tsimane of Bolivia, for example, 19% of women's arguments were about food (the rest were about men and social relationships) (Campbell 2013).

There is no cooperative food-getting in baboons and so the relationship among adults is neutral or competitive. Analogies suggest that competitive tendencies in early hominins were affected by food preferences, whether for differences in the quality of foods or for patches with readily available quantities. Among olive baboons at Gombe (Packer 1995), high-ranking females had shorter interbirth intervals, better infant survival, and accelerated maturation of daughters. Researchers attributed these advantages to nutrition. One criterion for dominance ranking was the ability to supplant others from food.

A study of olive baboons on the Laikipia Plateau of Kenya examined the relative importance of food and mates in shaping patterns of aggression between females (Patterson et al. 2021). The most aggressive females were those that were pregnant or lactating, that is, in the stages of reproduction that require the most energy replenishment. There was no evidence that "sexually receptive" females (presumably those in estrus) were more involved in aggression than any others. Neither was there evidence for competition for male caretakers or for reproductive suppression through attacks on other females. The researchers concluded that competition over food played a more important role than competition over mates in this population.

In a stable dominance hierarchy in a baboon troop, grooming may be a tactic to obtain access to resources. Grooming is hygienic, but the fact that it is pleasurable to the recipient makes it socially useful. Females may spend hours of each day in grooming, perhaps because alliances are so important. Subordinates woo dominant females by grooming them. Females without effective allies may transfer from one troop to another, which raises the question of whether alliances are the *cause* of female philopatry rather than an effect (Barton 2000). Baboon evidence suggests that hominin females used such affiliative tactics as well as occasional aggression to pursue dominance and resources.

Barrett et al. (2002) used data from a natural experiment on adult female chacma baboons to test the hypothesis that variation in aggression through time influences patterns of grooming reciprocity within a social group. Due to a change in the competitive regime, they were able to compare data from periods when aggression was high (period 1) and low (period 2). During period 2, the slope of the relationship between aggression and rank was significantly shallower than during period 1 and less aggression was directed at the lowest-ranking females. The researchers attributed this change to reduced effectiveness of dominance as a means of excluding other females from feeding resources.

The reduction in aggression during period 2 was accompanied by an increase in grooming reciprocity between dyads suggesting that high-ranking females no longer attracted grooming by subordinates in exchange for tolerance, and that grooming in period 2 was exchanged for its intrinsic benefits. The loss of rank-related effects on grooming reciprocity in period 2 compared with period 1 further confirmed this. These findings show that female baboons are able to respond flexibly and swiftly to changes in their social circumstances (Barrett et al. 2002). Presumably early hominins were no less adaptable.

9.5.2 Competition for Males

Despite negative findings in some studies (e.g., Patterson et al. 2021, above), there is considerable evidence that female baboons compete for male services and that these behavior patterns parallel findings for human females. In a recent collection of papers, writers examined competitive behavior in human females. The primary article by Reynolds (2022) made several points relevant here, based on broad

cross-cultural comparisons and similar findings in industrial societies. She saw "traces" of "ancestral" behavior in modern women. Reynolds placed these patterns in a historical setting: However, several of these female patterns are subject to comparison with other primates. In the discussion below, points made by Reynolds are italicized. Each of them is followed by comments on the paper (which was a "target article") and by relevant statements from other researchers on the subject. Then comparisons are made with baboon behavior. The underlying postulate is, of course, that the similarities might be analogous to behavior patterns in early hominins.

Throughout most of history women had to compete for the "romantic" partners most likely to acquire resources and to make a long-term commitment to provisioning those resources.

A cross-cultural survey found that aggression between women "often" revolved around competition to acquire and retain mates (Campbell 2013). For example, in the Tsimane study cited above, 25% of women's arguments were about men (vs. 19% about food). For girls under the age of 20, men were the leading cause of conflict (early marriage was characteristic of the culture). Women in "every communal condition" compete over material and social resources, including mates (Rucas and Alami 2022).

Male baboons as mates provide services rather than material resources. These are (potentially) protection and parental investment (Chap. 8). Female chacma baboons at Moremi competed for males as mates and as possible protectors of offspring. This competition among chacma females may be especially intense because the threat of infanticide is higher than in other baboon species (Cheney et al. 2012). Within the OMUs of hamadryas baboons, females compete for access to the central male (Kummer 1968).

In large cross-cultural samples, men often prioritize physical attractiveness in romantic partners. Similar studies show that women experienced more distress and jealousy when confronted with attractive rivals. In Western societies, women considered to be attractive were more likely to marry, to marry highly educated and/or higher earning men, and more likely to have children.

Girls who emphasize attractiveness with clothing, makeup, or behavior are likely to be targeted by other girls (Campbell 2013). In baboons, attractiveness is a function of the sexual swelling. Among chacma baboons studied at Tsaobis, "sexually receptive" females received high levels of aggression from others who were in the same condition. Researchers interpreted this to be consistent with competition for mating opportunities (Baniel et al. 2018a). They reported no evidence for food competition.

At Mikumi, Tanzania, female yellow baboons received the highest rates of coalition attacks from other females when in reproductive states most vulnerable to reproductive suppression (Wasser and Starling 1988). Pregnant females were the most frequent attackers in coalitions. Other, less frequent, attackers were cycling females and then lactating females. These attacks were followed by decreased reproductive performance due to longer periods of cycling before conception, possibly due to lingering stress caused by the attacks.

Women are more intolerant of sexual promiscuity than men. One possible explanation is that they perceive a threat to established relationships. Cross-cultural evidence shows that women who are attractive and who engage in casual sex are most successful in poaching mates. Other women are likely to be inclined to punish such women.

Regardless of social class, race, or ethnicity, accusations of promiscuity are a powerful form of verbal attack because such behavior jeopardizes the possibility of having a reliable long-term mate (Campbell 2013).

At Tsaobis, pregnant and lactating chacma baboons were more aggressive to estrus females when (a) the attackers had recently conceived, and (b) when an estrus female was mate-guarded and sexually active with one of their male friends (Baniel et al. 2018b). Reduced probability of conception in targeted females seemed to suggest reproductive suppression against a rival (however, Baniel et al. 2018a stated that there was no evidence for reproductive suppression).

Similar attacks took place among yellow baboons at Amboseli (Samuels et al. 1987). Physical aggression, including biting, resulted in injuries to 14 of 19 females and "some wounds clearly endangered females' lives" (p.788). Aggression included "mob" attacks and 15 of 18 occurred during the "turgescent" phase of the loser (about half of the cycle).

Silk et al. (2004) investigated such female coalitions and found that third-party interventions occurred in no more than 4% of all disputes. Females did not reciprocate agonistic support nor exchange it for grooming. They supported close maternal kin more often than others (Silk et al. 2006b). Sexual competition probably occurred among early hominin females, as it does in humans and baboons. However, the baboon evidence indicates that group action, though occasionally intense, was sporadic and usually included few individuals.

The competitive behavior of women is affected by the operational sex ratio, that is, the preponderance of one sex (men in this case) over the other at a given time. Cross-culturally this is associated with heightened levels of casual sex and mate poaching. In experiments, women who believe they are in such a situation behave more aggressively toward other women who are attractive.

According to Campbell (2013) the local sex ratio "determines" the intensity of mate competition and that ratio has been often badly skewed against girls in urban neighborhoods. Adding to the problem is variance in male resources. Physical aggression is more likely to occur in these settings and mothers sometimes participate in support of daughters. Three reasons for young women to use "physical interference competition" are that mates and resources are in short supply; a husband is shared; and kin are absent (Benenson 2013).

Among chacma baboons at Moremi, rates of aggression increased with greater skew in sex ratio, especially from low-ranking females. The behavior included coalitionary ("mob") attacks by low-ranking females, mostly against estrus females in consort (i.e., attractive females with mates), resulting in some changes in dominance hierarchy. Rates were higher when there was a larger proportion of nulliparous females. These were more likely to challenge older and more dominant females and also attack other cycling females.

Social instability can have a similar effect. During such a period, rates of aggression increased among chacma females. Under these circumstances, the probability of infanticide increases, protection from a single alpha male becomes vital, and opportunities to mate with the alpha male become the focus of competition among females (Baniel et al. 2018a, b; Huchard and Cowlishaw 2011).

When females live in groups with less reproductive skew and little danger of infanticide, as do the olive baboons at Laikipia, access to the alpha male may not provide major fitness benefits. In addition, there may be less competition over access to special friends because females share these friends with relatively few other females. Instead, female fitness may be more strongly affected by access to nutritional resources, as discussed above (Patterson et al. 2021). Differences in the pattern of aggression between these two baboon populations in different habitats seem to suggest that evolution has "finely tuned" female baboons'responses to the challenges that they face in their local environments**.**

9.6 Summary and Discussion

Female baboons display a variety of relationships with each other that may represent early hominin behavior in ways that suggest parallels with recent humans. These patterns may have provided evolutionary foundations for human female social relationships. First, there are dyadic associations that are often composed of close kin but not limited to this basis. Second, there are groups and networks of females that perform a variety of functions. Whatever their other purposes or functions, these bonds were subject to evolution by natural selection because they increased the fitness of participants through better health, longer life, and more successful reproduction. Stress reduction probably made a major contribution. Research with modern humans shows that all of these positive results of social bonds also apply to women.

Patrilocality has been thought to be a barrier to female affiliation in human evolution. However, this rule of postmarital residence has rarely had a rigid application, especially among the hunter-gatherers who probably represent our Paleolithic ancestors. In any case, women who were compelled to live in their husbands' communities could make friends there and could visit their relatives in other communities.

The ability of females to maintain their bonds has been demonstrated even in the coercive societies of hamadryas baboons. Females find ways to end up in the same OMUs as their female relatives more often than would be expected by chance, despite separations caused by competition among males. If female early hominins lived in a multilevel society like that of Guinea baboons (rather than hamadryas), their freedom would have been greater. If earlier hominins lived in troops like those of the COKY baboons, the foundation for female affiliation would have been initiated in a system of female philopatry (comparable to matrilocality in humans).

Two recently published scenarios have imagined the changing relationships of females in *Australopithecus* and early *Homo*. Both posit increasing cooperation among females, independent of males. The main difference between them is that the Swedell and Plummer scenario, based on hamadryas baboons, was first presented in 2012. The Boyd and Richardson scenario, which ignores baboons, was published in 2021. An important shortcoming of both scenarios, from the viewpoint here, is the assumption that cooperative female defense would have been sufficient in very dangerous circumstances. These bands of mothers would have benefitted from some male presence (this has been called the "hired gun hypothesis"). The male presence need not have been coercive and dominant, as demonstrated by analogies with Kinda baboons and Guinea baboons.

Early hominin females must have competed with one another, on behalf of themselves and their offspring. The baboon perspective indicates that food and males would have been the goals. Food competition was contingent on the abundance of the general food supply and the availability of preferred foods. Males would have been a source of contention everywhere, though also somewhat contingent on the supply. Certain individuals would always have been preferred as mates and (with greater variation) as protectors and caretakers of offspring. Stable dominance hierarchies would have guided competitive regimes in many societies, but occasional physical aggression would have occasionally altered dominance relationships, expressed rivalries, and perhaps resulted in reproductive suppression. In a few instances aggressive females would have joined in small coalitions.

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