Chapter 7
Social Organization and Male–Male Relationships

7.1 Introduction

Baboons provide diverse options for hypotheses about early hominin social organization. They pertain to both synchronic variation and long-term changes. This chapter begins with the ideas of some archeologists about prehistoric human social ecology, and goes on to explore ways in which baboon social patterns articulate with the archeological model. As in traditional ideas about baboon and human societies, males play important roles. These are considered here and used to evaluate a longstanding idea about male–male relationships in human evolution that has been called "men in groups." The role of females in early hominin evolution will become increasingly prominent in Chaps. 8 and 9.

7.2 Archeological Perspectives on Prehistoric Hominin Society

Archeologists and paleoanthropologists have often turned to extant and recent human hunter-gatherers for models of prehistoric hominin behavior. As biologically modern humans, these peoples can only represent the later stages of human evolution. Primates like baboons and chimpanzees are more appropriate for the earlier stages. However, human and primate sources can be articulated with one another to develop a more dynamic view of hominin social evolution.

Archeologists at a recent conference largely agreed on several inferences about prehistoric human society (Goren-Inbar and Belfer-Cohen 2020), using concepts that are readily applied to early hominin societies as modeled by baboons. First, groupings of 20–50 individuals were common. Second, these groups were not rigidly separated from one another. Third, group size was dynamic, varying from small

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bands to large aggregations. Fourth, the various groupings served a variety of functions and purposes, including subsistence and predator defense. This "elasticity" probably derived from both social behavior and ecological constraints.

There was general agreement among the archeologists that larger groups facilitated increased vigilance and stronger cooperation. These features would be adaptive in defense against predators and rival hominin groups, as well as in competition with predators and other hominins for hunted or scavenged prey. Presumably, these social features would have been especially important in earlier hominin evolution when safety in numbers compensated for limited technology. Further developments, perhaps including cooperative hunting, would have stimulated major changes in brain, behavior, technology, and life history (Stout et al. 2018). The period around 2-1.7 mya may have been pivotal for the developments that transformed the genus *Homo* (Chaps. 4 and 5).

Some archeological research provides direct evidence for a relatively late shift in social organization, well after the first appearance of *Homo*. Comparison of two Early Pleistocene archeological sites revealed the same spatial pattern in the accumulation of bones and stone tools. Statistical tests showed intense interdependence between both types of materials in both spatial distribution and intensity (Dominguez-Rodrigo and Cobo-Sanchez 2017). The researchers inferred that the high-density single clusters characterizing these sites represent communal use of the same spot for processing and consuming animal carcasses. They argued that this does not support the presence of individual nuclear families, which would indicate human-like social organization. Multiple clusters of remains characterize the assemblages left by the camps of recent hunter-gatherers. Baboon behavior articulates with hunter-gatherer models and archeological evidence in a multidimensional reconstruction of early hominin social organization and its transformations.

7.3 The Troop: A Baboon Model for Early Hominin Society

Baboons fall into two broad categories as far as basic social structure is concerned (Fischer et al. 2019). The simpler form occurs in the "COKY" species—chacma, olive, Kinda, and yellow baboons (Jolly 2020). This is the troop, typically composed of multiple males and females of all age categories (Fig. 2.2). The troop usually travels as a unit and, if it spreads out for feeding, contact is maintained with vocalizations. Troop size varies from roughly 10–200, but many troops fall into the 20–50 range postulated by the archeologists.

Dunbar et al. (2018) studied recurring troop sizes in three baboon species and hypothesized an underlying pattern that makes certain values particularly common. The values were approximations to 20, 40, 80, and 160. The researchers posited that these tendencies are responses to varying demographic factors. The lower end of the scale is determined by predation risk, because larger groups are needed for increased vigilance and defense. The upper end is determined by the maximum size that can be attained before limits on resource availability require that the troop split

permanently, usually into two daughter groups. Baboons observed in a habitat with high predator density fissioned at a mean size of about 65 while the mean size in a low-predator habitat was about 30. Analysis of the data suggested an optimal size of about 40, which is close to the mean group size for the whole genus. In the terms discussed in Chap. 3, application of these data to early hominins entails a genus-level referential model, strengthened by a conceptual context based on ecological and demographic principles.

The term *troop* has been used in some cases to designate groupings of primates (including baboons) that are larger than the COKY troops and organized differently (e.g., Kummer 1968). To avoid confusion, I will use the term *maximum social group* (MSG) to denote the largest group to which individuals belong in any primate social system. More specifically, this is the largest group that involves its members in any kind of affiliative or tolerant social interactions with any regularity. The troop is the maximum social group of COKY baboons in every habitat that they have occupied. Given such adaptability, a similar society could have persisted in early hominins as they expanded from woodlands into a wide variety of mosaic habitats and eventually survived in relatively open savannas.

7.3.1 Relations Between Troops

The baboon perspective suggests that intergroup relationships of early hominins were complex and variable. Intertroop relationships of baboons vary from hostility to avoidance to tolerance to occasional brief associations that give rise to supratroop groupings. Research on wild baboons has never discovered anything like the highly publicized "wars" between chimpanzee communities. Some early accounts described aggression between troops, especially among chacma baboons (reputed to be the most aggressive species). However, there were virtually no fatalities in these reports. For example, Saayman (1971) observed 58 encounters among four chacma troops in South Africa. Seventy-six percent of these meetings were nonantagonistic and occasionally two troops intermingled and traveled together for a while. There was "overt fighting" in just 14 of the 58 encounters, and two "spectacular and tumultuous fights" took place. Yet Saayman did not mention any serious injuries, much less deaths. Chacma baboons, with a reputation for aggression, provide evidence suggesting that hominin competition for resources entailed only limited fighting and encounters that more often involved noncontact behaviors.

Baboon troops commonly avoid each other rather than be drawn into conflict. This was often true of chacma baboons as well as other species (DeVore and Hall 1965). Continuing research with more sophisticated methods has confirmed the pattern. Markham et al. (2013) used GPS to investigate temporal landscape partitioning in yellow baboons. They monitored collared subjects to synchronously record the hourly locations of five troops for about 900 days. They used behavioral, demographic, and life history data to measure factors affecting the use of overlap areas. On an annual scale, home ranges of neighboring groups overlapped substantially.

However, home ranges overlapped less when space use was assessed over shorter time scales, indicating that the troops were seldom in the same area at the same time. Neighboring groups were in close spatial proximity to one another on fewer days than expected from random movement. Nevertheless, yellow baboons engaged in some significant intergroup competition (Markham et al. 2013). When direct conflict occurred, losing groups used the area surrounding the interaction less than previously. Visual contact usually resulted in displacement of one group by the other.

In circumstances of scarcity, baboon groups might fight each other over sleeping places (cliffs or trees) or water sources (Altmann and Altmann 1970; Stolz and Saayman 1970). Similar conflicts probably took place among early hominins. They needed water from scarce sources in dry savannas and they needed arboreal refuges from predators until they found ways to sleep safely on the ground. Competition could arise if tall trees or cliffs were scarce. Competition for females may be another factor in hostility between troops. In some baboon species, troop females are herded away from other groups during conflicts (Kitchen et al. 2004; Saayman 1971).

Baboons may defend space and boundaries, but these patterns are ultimately related to resources (Hamilton et al. 1976). Two chacma troops in the Namib Desert defended a boundary near a waterhole. In the Okavango Swamp in Botswana, large troops defended well-defined boundaries of small home ranges that were relatively dense in plant species and energy sources. The size and configuration of troop space and the arrangement of resources within each space influence the likelihood of intertroop encounters and the expression of spatial defense.

The diverse interrelationships of baboon troops and resources suggest that early hominins engaged in a variety of intergroup encounters, ranging from hostility to avoidance to temporary affiliation. These diverse options contradict some popular ideas about intergroup violence and warfare being fundamental features of human evolution. If anything, the expansion into more open habitats almost certainly resulted in larger home ranges with reduced contact between troops, except possibly in the case of limited crucial resources such as water.

7.3.2 Fission–Fusion

Troop organization is often somewhat flexible and allows for groupings of various sizes (as envisioned by the archeologists for prehistoric hominins). A troop usually moves as a unit but in some circumstances, especially food scarcity, subgroups forage independently and then reunite. In this respect baboons sometimes resemble the chimpanzee system of fission-fusion. Baboons differ from chimpanzees in that the parties come together again as a single troop. This temporary fission should not be confused with the kind of fission in which a baboon troop permanently divides into two or more "daughter" troops.

Anderson (1981) described "subtrooping" in two troops of chacma baboons in South Africa. It varied with the season, being more frequent when temperatures and food availability decreased. Some subtroops frequented only certain parts of the

larger troop range and remained separate from other groups for up to several days. Anderson speculated that lack of predation, coupled with genetic isolation for several generations, might have facilitated the pattern that she observed. From a functional viewpoint, it probably increased the efficiency of resource use during less favorable seasons, especially for less dominant individuals.

Comparing her observations with those of others, Anderson found that her population was "relatively unique" with regard to seasonality of the phenomenon, consistency of membership in subgroups, and the frequent occurrence of one-male subtroops. Nevertheless, she suggested that subtrooping is a facultative potential of all baboon species that requires little genetic change to develop. Her hypothesis is supported by later research on olive baboons living in a different kind of environment in a different part of Africa—the Gashaka forest in Nigeria. The larger troop of the two that were studied displayed "regular subgrouping" into parties averaging 15 individuals (Kunz and Linsenmair 2008). Aldrich-Blake et al. (1971) reported subtrooping in arid conditions in Ethiopia.

There may be an ecological convergence with chimpanzees here. The olive baboons used the forests more often than expected by chance, had large home ranges, and were highly frugivorous. They spent about 50% of their feeding time on the fruits and seeds of at least 79 woody plant species. In contrast to Anderson's chacma baboons, fission–fusion at Gashaka was a response to abundance (of fruit) rather than scarcity.

Since early hominins probably shared a strong preference for fruit with *Pan* (and other apes), fission–fusion may have been more prominent in the woodland hominin populations. Later on, during the expansion into arid habitats, the same capability would have been available to deal with scarcity as in the South African baboons. The fission–fusion capability is consistent with the social flexibility of human hunter-gatherers envisioned by the archeological conference (Goren-Inbar and Belfer-Cohen 2020).

In the context of fission–fusion, one-male subgroups are prominent in the reports of chacma baboons in South Africa (Anderson 1981) and olive baboons at Gashaka, Nigeria (Kunz and Linsenmair 2008). In the latter case, for example, the proportion of one-male groups varied from 50% to 63%. Differentiation of these one-male groups within troops may be a model for the origin of multilevel societies in baboons and early hominins.

7.4 Multilevel Societies

Hamadryas and Guinea baboons display the multilevel society, in which smaller social groups are nested within larger ones, creating three or four levels of social organization. In both species the foundation of the system is a tier composed of one-male groups, each containing one adult male with one or more adult females. Affiliation at the different levels serves varied (but overlapping) biological, ecological, and social functions, including foraging, predator defense, and shared sleeping

locations (Fischer et al. 2019; Kummer 1968; cf. Goren-Inbar and Belfer-Cohen 2020). In contrast to these complex societies, the COKY troop is essentially an independent one-level system. Departures from that status, such as subtrooping or affiliation between two troops are occasional and temporary.

The two main categories of baboon social organization—the troop and the multilevel society—can be linked to each other and to early hominins in two alternative ways. One model places them in a sequence, with multilevel societies emerging from troops (e.g., Swedell and Plummer 2019). The alternative is to place one or the other at the base of hominin evolution and derive species-typical forms of human social organization directly from it.

Multilevel organization, whether viewed as the original form of hominin society or an intermediate stage, fits well with the archeological model described at the beginning of this chapter (Goren-Inbar and Belfer-Cohen 2020). Large groups regularly separate into smaller groups and then come together again. Some groups within the structure typically fall into the 20–50 range. These intermediate social units contain semi-independent subgroups and belong to a larger community that may number several hundred. The groupings at different levels provide somewhat different contributions to basic functions.

The basic social unit in both multilevel baboon species is a group that revolves around one male who is affiliated with one or more females as social and reproductive partners. The hamadryas male in this position has been termed the "leader." The comparable figure in Guinea baboons is called the "primary male." The term *central male* will be used here to encompass both. It distinguishes the adult male with a pivotal role from other members of the group. The others may include one or more additional adult or nearly adult males that are subordinate in social and reproductive terms. This basic unit has been given different names by students of hamadryas baboons and Guinea baboons. Here, the term *unimale group* (cf. Hex et al. 2021) will be applied to both.

7.4.1 Multilevel Society in Hamadryas Baboons

The following description of hamadryas society is based on two recent distillations (Evans et al. 2022; Swedell and Plummer 2019) of a long history of research by many primatologists, especially the seminal work of Hans Kummer (1968). The unimale group of hamadryas baboons is commonly called the "one-male unit," abbreviated OMU. The core of each OMU is a "leader" male (central male) who has a close social relationship with one or more females that may last for years. These females are also his sexual partners when they are available, but the social relationship continues through anestrus periods, including infant care. The OMU may also contain one or more "follower" males that have social but not sexual access to the females. The OMU is the most stable group in hamadryas social organization and is the minimal foraging group.

A distinctive feature of the hamadryas OMU is that it is formed by successive takeovers of females by various means: (1) a subadult male "recruits" a juvenile

female from her natal group; (2) a follower "inherits" one or more females from his leader; (3) a male challenges a leader for his females; (4) a male opportunistically obtains a female when her leader can no longer defend her.

The next tier in hamadryas multilevel organization is the *clan*. This is an association based on kinship among males (Städele et al. 2015). A clan may be as small as 2 OMUs or as large as 13 or more (Schreier and Swedell 2009). In addition to OMUs a clan contains "bachelor" males that are not affiliated with any OMU. Though capable of dispersing into its constituent OMUs, the clan tends to be spatially cohesive within larger groups and as a separate foraging unit. It also provides for defense against predators. Clan males have been observed forming a shield against hyenas while other members retreated. Clan males also groom each other more often than they do nonmembers. The clan is fully documented in just one hamadryas population, located at the Filoha area in Ethiopia.

The *band* has been equated with the COKY troop because of its spatial and functional unity, composition, and size. It is a multi-male/multi-female group that combines several OMUs along with bachelor males, and several clans if they are present. Most bands probably have 50–100 members, though some contain 200 or more. The largest bands likely result from unusual resources in certain regions. Each band has its own area on the sleeping cliff. In the morning friendly bands often travel for a short distance together, though they always split apart and go in different directions for the rest of the day. Eventually, as the day goes on, each band fragments into its OMU components, though it often reassembles at a waterhole around midday. One study found that a band was more likely to break up into OMUs where general food availability was low and into clans when preferred resources were not available (Schreier and Swedell 2012).

The largest grouping of hamadryas baboons has been called the "troop." This is confusing because it is nothing like the troop in COKY baboons. The term maximum social group or MSG (coined above) will be used here. The hamadryas MSG may consist of hundreds of individuals, most of which have very limited social relationships with each other. It is an aggregation of bands that tolerate each other at the same sleeping cliffs at night. This allows for the use of a vital and limited resource in a desert region where trees are scarce. During daytime activity the hamadryas MSG has no significance.

7.4.2 Multilevel Society in Guinea Baboons

The social life of Guinea baboons is so far known from just one locality in a fairly rich environment (Zinner pers. comm.). The basic multilevel structure of this society is similar to that of hamadryas baboons, but there are major differences in behavior and social dynamics. These differences, especially those that characterize male–female relationships, make Guinea baboons an alternative model for the social behavior of early hominins.

Unimale groups of Guinea baboons, the fundamental units within the multilevel society, have been called "reproductive units" or just "units" (Dal Pesco et al. 2022). Each is composed of one "primary" male and 1–6 females. A primary (central) male has largely exclusive affiliative and sexual relationships with the females in his group. Females maintain exclusive social and mating relationships with one male at a time.

Unimale groups of Guinea baboons differ sharply from hamadryas OMUs with respect to the status and role of females. First, in contrast to accumulation of females by male hamadryas, female Guinea baboons play an active role in forming and maintaining relationships with males (Goffe et al. 2016). Second, a female Guinea baboon, though usually close to her central male, spatially and socially, has freedom of movement. Third, a female is free to leave the relationship at any time and affiliate with another male. *Male-focal Unit* (MFU) might be an appropriate term for these flexible groups.

Guinea baboons also differ from hamadryas with regard to secondary males or followers. These males can be identified in both species as associating with unimale groups and having social but not sexual relationships with the females (Goffe et al. 2016). However, in Guinea baboons a single bachelor is often associated with several unimale groups (in roughly 67% of cases) (Dal Pesco et al. 2021).

Two higher levels of social organization can be compared to those of hamadryas baboons in structural terms, but functional equivalence is dubious. A Guinea baboon "party," which is composed of several unimale groups and their secondary males, is the equivalent of the hamadryas clan. Two or three of these Guinea baboon clans regularly aggregate into "gangs" that can be compared with hamadryas bands. However, it seems that there is little to identify them other than overlapping home ranges (Patzelt et al. 2014). Guinea baboon clans vary in size from about 10–40 members and the Guinea baboon band averages about 70 (Fischer et al. 2017). The maximum social groups of the species are barely social, being identified by a common home range.

7.4.3 Possible Societies of Early Hominins

The troop and the multilevel society in baboons can be considered two alternative sources for reconstructing the social organization of early hominins. They can also be viewed as representing two stages in the social evolution of hominins. Chapais (2008) postulated two such stages at the beginning of hominin social evolution. The first of these stages was a "promiscuous" multimale-multifemale group. Chapais compared this postulated group to the chimpanzee community, but his description also applies to the baboon troop. The next stage, inferred from hamadryas baboons and other primate data, was a "multiharem" group. Chapais saw this as the foundation for the multifamily community that became the modal pattern for humans. Others have also inferred such a sequence in hominin evolution (e.g., Swedell and Plummer 2012, 2019).

7.5 Male Philopatry

An important feature of human and animal societies is the movement of maturing individuals from one group to another. Primate group size and composition are maintained in large part by emigration and immigration. The typical situation is that one sex usually or almost always leaves and the other stays in the birth group. The tendency of one sex to stay is called *philopatry* and departure from the natal group is often termed *dispersal.* Comparison of baboon societies suggests that philopatry shifted from females to males in early hominin evolution.

7.5.1 Male Philopatry in Humans and Baboons

In the majority of human societies, recent and past, male philopatry was the predominant pattern of residence. That is, most men lived their lives in the communities to which they were born while women left when they married. This is opposite to the pattern of troop-living baboons, in which males leave their natal groups. However, both of the multilevel *Papio* species resemble humans in that females leave their natal groups to enter a sociosexual relationship with a male in another group. For example, adult females in one hamadryas baboon study transferred between clans nineteen times while only one adult male transfer was seen. This is broadly analogous to exogamy in most traditional human societies and may represent an early hominin origin of the practice.

7.5.2 The Frontier Hypothesis

Jolly (2020) described and elaborated a hypothesis about baboon expansion and social organization that he and others suggested as a model for hominins (e.g. Fischer et al. 2017; Swedell and Plummer 2012). Male philopatry is a crucial factor in this "Frontier Hypothesis," which suggests that a population norm of male philopatry evolved in the common ancestor of hamadryas and Guinea baboons. It was a response to a demographic context peculiar to the frontier of a rapidly expanding population with repeated group fission (fission in this context refers to permanent separation between a group and one or more daughter groups). Jolly's emphasis on demography distinguishes this scenario from other hypotheses, most of which revolve around ecological factors.

According to the Frontier Hypothesis, the common ancestor of the two multilevel baboon species was probably similar to extant Guinea baboons, including male philopatry. Other social features evolved to accommodate male philopatry: one-male units, multilevel society, male–male tolerance, and some degree of female dispersal. The larger context for these events goes back to a southern origin for the

genus *Papio*. The genetic population structure of living baboons preserves evidence of the initial expansion of *Papio* from the south. Immediately after the expansion, male-philopatric, multilevel populations with a general physical and behavioral resemblance to Guinea baboons occupied the whole northern range of the genus. Hamadryas baboons presumably changed further in response to less productive habitats in the Horn of Africa. Subsequently, olive and yellow baboons shifted to female-philopatric systems and replaced most of the northern populations as males moved from one troop to another.

The Frontier Hypothesis is based on established patterns of papionin population structure and demography, as well as more general evolutionary theory and models related to dispersal, invasive expansion, and frontier effects on population structure and evolution (Jolly 2020). It seems to be an example of a referential model embedded in the framework of a conceptual model (Chap. 3).

According to Jolly, the Frontier Hypothesis has far-reaching implications for the reconstruction of early hominin evolution. First, it brings a baboon model more in line with chimpanzee evidence. The behavior of extant chimpanzees and humans suggests that their Last Common Ancestor was male-philopatric, and the Frontier Hypothesis posits a similar origin for *Papio*. Second, the sequence of evolutionary events in the Frontier Hypothesis contradicts the scenario of baboon troops giving rise to multilevel societies through increasing fission–fusion and strengthened male–female bonds (see Chap. 8). The result is two mutually exclusive theories explaining major changes in hominin social organization: troop to multilevel society or the reverse. Finally, the Frontier Hypothesis seems to render the behavior of olive and yellow baboons as having little relevance to reconstructing early hominin behavior. These implications are all highly debatable, but they must be considered in future work. For the present, I will continue with more conventional comparisons that encompass hominins and all the baboon species.

7.6 Male–Male Relationships in Troops

Relationships between adult males are one important component of social organization in humans and other primates. The behavior of baboons in troops provides several important analogies for male–male relationships in early hominins. These involve aggression, dominance, cooperation, and tolerance. More complicated relationships in multilevel societies will be discussed in the next section.

7.6.1 Aggression and Dominance Among Males

The evolution of male–male aggression in hominins and its implications for the behavioral tendencies of modern humans have been the subject of bitter conflict in scientific and popular publications. The focus often has been on the most extreme

forms of aggression: injurious and lethal violence. As a result, reconstructions of early hominin behavior have been plagued by controversies about male aggressiveness and levels of violence.

Some early descriptions of baboon behavior (in some cases captives in poor conditions) emphasized male dominance, achieved by aggression. This was one stimulus for the backlash in which many writers rejected any baboon model for early hominin behavior (Chap. 3). However, extensive research on wild baboons has developed a more complex and varied picture of conflict and conflict resolution among males. Thus, the baboon perspective can address questions about both causes and limits on aggression in the diverse habitats occupied by early hominins. How much violence was likely to occur in large troops and how much could be sustained in the face of external dangers? To what extent might it have been mitigated by stable dominance relationships? Which resources were involved in the competition?

Fighting between male baboons quickly draws attention from observers because it is noisy, may involve vigorous chases (Fig. 7.1), and occasionally results in serious injuries inflicted by large canine teeth. However, baboons have less spectacular ways to regulate male interactions. Threats are usually sufficient to maintain status differences and simple displacements (forcing another individual to move away

Fig. 7.1 An adult male olive baboon chases another male after a fight. In many such chases the fleeing individual is never caught. In some, the roles are reversed at some point. (Photo by Glenn King, Tarangiri, Tanzania)

Fig. 7.2 A male chacma baboon with a typical fight wound. (Photo by Curt Busse. Okavango, Botswana)

from a spot) are daily reminders. This is the case because aggression is not an "instinct," but a set of tactics in pursuit of social advantage.

This explains the pattern reported by Kitchen et al. (2005) in which most chases and fights, including those that led to injuries, were between males of similar rank, that is, those that were involved in serious competition for dominance. Opponents of disparate ranks clashed most frequently in contests that involved resources of high fitness value: meat, estrous females, and endangered infants. Results of the study suggested that competitive encounters among male baboons follow patterns predicted by evolutionary game theory (Kitchen et al. 2005). Given similar social structure and environmental circumstances, there is no reason to think that hominin aggression was any more intense or common (Fig. 7.2).

7.6.2 Coalitions

A male coalition, consisting of two and occasionally three individuals, can play a major role in mating effort in a troop. Male baboons strive to establish *consort relationships* in which they more or less monopolize mating opportunities with females when they are fertile. In a study of yellow baboons, coalitions succeeded in causing a consort turnover in 35 of 55 attempts (Alberts et al. 2003). This was the main cause of deviations from the system of access to females based on individual dominance. Selection of a coalition partner seems to be based mainly on fighting ability (Bercovitch 1988). Having an affiliative relationship may be a factor in forming a coalition, but it can also be explained as cementing an existing partnership (Noë and Sluijter 1995). Recurrent partners rarely spend extra time in affiliative behavior and

their spatial proximity can be explained by the common focus of the coalition. It may be that coalitionary behavior is each partner's opportunistic response to a situation, and only appears to be cooperative. This interpretation avoids anthropomorphism, but seems to be undercut by the occurrence of preliminary recruiting behaviors. Signals exchanged by prospective partners include head flagging, staccato grunting, and mounting. The baboons seem to anticipate the cooperative relationship.

Low cost is an important factor in coalitionary behavior. Comparative evidence indicates that the behavior requires little time (usually less than 30 min) and energy (mostly threatening with occasional short bursts of running and fighting) and that wounds are rare and usually slight. In short, joining a coalition is a low-cost behavior with the prospect of a substantial benefit. This suggests the possibility that the behavior was favored by natural selection in a way that could also apply to early hominins.

7.6.3 The Kinda Baboon Alternative (?)

The Kinda species provides an alternative model for male–male relationships in baboon troops and possibly for early hominins (Petersdorf et al. 2019). Living in relatively large groups and displaying less sexual dimorphism than the other species, Kinda male dominance is organized by *queuing* rather than contest, that is, waiting in a metaphorical line for an opportunity to reproduce. New males entering a troop accept a place at the end of the line rather than fighting with resident males. Alpha males have long tenures.

An important factor in the Kinda system is *sperm competition*, which means that reproductive advantage over other males comes from fertilizing as many females as possible with large quantities of high-quality sperm. The hallmark of this adaptation is large testis in proportion to body mass. Kinda baboons outdo all other baboon species in this regard. This feature tends to negate the relevance of Kinda baboon behavior to early hominins. Lacking evidence of testis size in early hominins, we have to look to the evolutionary end result in humans. Humans have not evolved a comparable adaptation. Relative testis size in proportion to body mass is average for primates (Dixson 2012).

7.7 Male–Male Affiliation in Multilevel Species

In troops, coalitions are often situational and temporary (although partners in some cases may display a degree of affiliative behavior). Baboons in multilevel societies have more organized and longer-term alliances, especially between leader and follower. Males develop enduring relationships with other males that are characterized by general tolerance, friendly interaction, and occasional coalitionary behavior.

These male–male associations link the central males of unimale groups with each other and with their followers. Kinship accounts for some but perhaps not all of these relationships. Within this common framework, hamadryas and Guinea baboons differ in some ways that may offer alternative or complementary analogies for early hominins.

7.7.1 Male–Male Relationships in Hamadryas Baboons

Hamadryas baboons have a complicated system of ongoing male–male relationships (Evans et al. 2022). One aspect is the takeover of females by one central male from another. In some cases, a younger and/or healthier male takes females from another who can no longer defend them. This may be a cost to the losing male, but there is little or no aggression. In other takeover attempts, one fit male challenges another and serious fights may result.

Takeovers are sporadic events and most of the time central males seem to "respect" one another's possession of females (Evans et al. 2022). This state of affairs seems to depend on recurring communication between males in the form of *notifications*, that is, a set of ritualized signals that seem to convey mutual trust (see Chap. 11 for details). Another possible factor is that leader males who limit aggression toward other males may be more successful in attracting followers, who contribute to maintaining females. In sum, the hamadryas system entails occasional aggression between males to obtain females and restraint of aggression between males at most times (mediated by notifications) (Fig. 7.3). Evans et al. (2022) argue that this combination of tactics was favored by natural selection and provides an analogy for social relationships in early hominins.

In hamadryas baboons, each follower is affiliated with only one OMU, and not every OMU has a follower. The functions of hamadryas followers seem to be focused on relations within the OMU. In a system where females are mainly acquired by coercion, hamadryas leaders with followers had longer tenures as leaders, acquired more females, and sired more infants than males without followers (Choudhury et al. 2015). Follower relationships with OMU females may encourage the females to adhere to the leader as long as possible. A central male may be aware of this function, but a follower male is readily tolerated because he belongs to the same clan as the leader and is likely to be a relative. Leaders and followers are maternal relatives more often than expected by chance (Städele et al. 2016).

Kinship is also a factor in the hamadryas clan, a group in which males prefer to associate with relatives (Städele et al. 2015). Two anecdotes suggest the strength of clan ties (Colmenares et al. 2006). First, a juvenile male stayed with his father when his mother was abducted into another clan. Second, an infant of an abducted female returned to his natal clan on his own when he reached the age of 3 years. Closer kinship is illustrated by the case of a captive colony in which maternal brothers had the most cohesive relationship among males.

Fig. 7.3 Tolerance among three male hamadryas baboons in the Alexandria Zoo. (Photo by Hatem Moushir. Resized for publication. Wikimedia license: https://creativecommons.org/licenses/by-sa/4.0/)

7.7.2 Male–Male Relationships in Guinea Baboons

Kalbitzer et al. (2015) compared male chacma and Guinea baboons with regard to competition, aggression, and dominance. Chacmas were more frequently involved in agonistic interactions and displayed consistent dominance relationships. Although theory predicts that the intensity of male competition is higher if many males compete for access to few females, differences in the ratio of males and cycling females could not explain the species difference in agonistic behavior. In a study of Guinea baboons, "agonistic interactions were generally rare and largely restricted to a few dyads" (Patzelt et al. 2014).

Male chacmas of high rank and those engaged in sexual activity showed elevated levels of stress hormones (glucocorticoids) and also tended to show elevated testosterone levels. There were no such effects in Guinea baboons. In related contrasts with chacma baboons, male Guinea baboons in a group do not form linear dominance hierarchies and dominance relationships between individuals are less consistent than in chacmas. An attempt to quantify dominance relations found that a clear male dominance hierarchy could not be established due to the high degree of uncertainty in individual rank scores. The only clear tendency was that bachelor males were more likely to be found at the low end of the scores (Dal Pesco et al. 2021).

Male Guinea baboons in the same "party" (the equivalent of the hamadryas clan) are tolerant and friendly toward one another. In one study, 80% of dyads displayed greeting interactions (comparable to hamadryas notifications) and a third of them engaged in affiliative behaviors such as sitting in close proximity (Patzelt et al.

2014). However, most males have a small number of "preferred partners," usually two or three, said to have a "strong bond" (Dal Pesco et al. 2022). These are friendly and enduring relationships characterized by high spatial tolerance, support in agonistic interactions, and occasional grooming sessions (Fischer et al. 2017; Fig. 7.4). Continuing research showed that these bonds could be stable for at least 4 years (the full length of the study) and were not affected by the males' relationships with females (Dal Pesco et al. 2021).

Dal Pesco et al. (2021) pursued the issue of relatedness between males with strong bonds. They confirmed that these relationships are differentiated, equitable, and stable over time, and that there are no clear dominance patterns between partners. Relatedness was assessed with genetic material obtained from fecal samples. The evidence demonstrated that average relatedness was significantly higher between strongly bonded males, suggesting that kin bias contributes to the social preferences of males

Dal Pesco et al. (2022) tested the evolutionary significance of male bonding in Guinea baboons with behavioral and paternity data collected over 45 months. Strong bonds did not lead to reproductive success. Instead, males that spent less time socializing with other males were associated with a higher number of females and sired more offspring. Reproductively active males still maintained bonds with other males, but adjusted their time budgets. They may have maintained strong bonds with the most intense ritualized greetings, such as mounting and genital manipulation

It is not clear why males maintained these relationships at some cost or risk, since they did not contribute to reproductive success. Two possible factors are the effect of close kinship (Dal Pesco et al. 2021) and the benefit of occasional

Fig. 7.4 A male Guinea baboon grooms another male. (Photo by Dietmar Zinner. Niokolo Koba National Park, Senegal)

coalitionary support (Patzelt et al. 2014). The absence of reproductive success means that any analogy with hominins would not be based on natural selection. Perhaps similar social contexts resulted in parallel development of strong bonds with male kin.

Bachelor males among Guinea baboons play a different role than hamadryas followers (Dal Pesco et al. 2021). Most central males among Guinea baboons have at least one associated bachelor, and a majority have more than one. A bachelor is likely to associate with several unimale groups and he interacts with the central males as well as their female associates. Average relatedness between a central male and associated bachelors is higher than in any other relationship except for central males who are closely bonded to each other.

The kinship bond between primary and secondary male parallels the hamadryas baboon. However, the social functions seem to differ. While the hamadryas follower focused on his leader, the multiple ties of Guinea baboon bachelors seem to contribute more to social solidarity within and across unimale groups.

7.7.3 Men in Groups

Tiger (1969) surveyed all-male groups across diverse cultures. He characterized this behavioral tendency as male bonding and hypothesized that it had an evolutionary basis, which he attributed to the need for cooperation among men in hunter-gatherer societies. Since Tiger's work, much more has been learned about male–male association in primates, including baboons. This work supports and modifies Tiger's ideas. Developments include information about dominance and aggression, and about coalitions and bonds. Dominance, aggression, and coalitions are important in male–male relations in most baboon troops. These features are modified in a human-like direction in the multilevel societies, suggesting what the transition in early hominins might have been like.

Rodseth (2012) set forth similar arguments. Humans live in modular societies with a minimum of two levels of organization, the conjugal family and the local community. Yet any human community is likely to contain at least one other social unit, a same-sex association such as a men's "club" or "brotherhood." What has been called "bachelor threat" in other mammalian species is also a problem in human societies, but tensions between married men and bachelors are often eclipsed by the need for warriors to defend the local community. The ethnographic record includes many cases in which fraternal security takes precedence over conjugal bonds, resulting in the physical segregation of the sexes, including husbands and wives. At the extreme, a husband usually sleeps at a men's house while making regular visits to his conjugal family. Though this pattern is classically associated with tribal Amazonia and Melanesia, Rodseth sees it as part of a continuum of variation in small-scale societies worldwide.

The two multilevel baboon species suggest an early hominin foundation for these associations, long before they became culturally elaborated and differentiated. In

both baboon species, male–male bonds pervade social entities beyond the unimale groups. These relationships include kinship among many of the males, friendships where there is no kinship, and dominance-subordination between primary and secondary males. Control of mating is often considered a motivation and/or function of these male associations in humans and this seems to be anticipated by the exclusion of secondary males in both baboon species.

Male–male relationships in Guinea baboons form a network that seems to be a possible model for the beginning of the human pattern of all-male groups, as expounded by Tiger and Rodseth. However, further research that focused on the adaptive benefits of these relationships cast doubt on the hypothesis that they were favored by natural selection. If this result applies to hominins, "men in groups"was either selected for in later hominins (hunting parties?) or originated as a cultural phenomenon for reasons educed by cultural anthropologists.

7.8 Summary and Discussion

Baboons provide diverse options for hypotheses about early hominin social organization, pertaining to variation and change. Based on recent human hunter-gatherers, members of an archeological conference came to some agreement about probable early human societies. Groupings of 20–50 were common, but not rigidly separated from one another. Size changed with various functions and purposes. Larger groups were especially important for defense and cooperation when technology was limited. These inferences from human hunter-gatherers articulate well with baboon evidence, suggesting deep evolutionary roots for basic features of hominin social organization.

The original hominin society might have been much like the baboon troop. This is a multi-male/multi-female social entity found in four of the six baboon species. Medium-sized troops fit into the 20–50 range. Larger troops may be important for defense against predators or other troops. Competition for resources may lead to fighting, but displays and avoidance are more common. Occasionally tolerance allows the brief formation of a super-troop. When a troop is too large for its resources, it has two ways to compensate. It can fission temporarily into smaller foraging subgroups, or it can fission permanently into two groups. The flexibility of the troop suggests that it could have been the social unit of early hominins as they expanded from their woodland base to encompass increasingly diverse habitats. Some archeological evidence suggests that the hominin troop could have persisted for millions of years, until major changes in the hominin way of life took place around 2 mya.

Variation among baboon species provides a series of potential models or sources of analogy for early hominins. Chacma baboons in southern Africa may represent the original troop organization of *Papio*. Olive and yellow baboons to the north display some more complex forms of social organization, such as the formation of coalitions to achieve mating success. Kinda baboon troops are unusually large,

often including more than 200 members. Kinda baboons also differ from the other species in that reproductive competition is carried out through sperm competition rather than aggression.

Hamadryas and Guinea baboons are organized into multilevel societies. The basic unit in each of these systems is a unimale group that is composed of a single central adult male affiliated with one or more adult females. This group can forage separately, but it is integrated into larger social groups. The higher levels of social organization manifest numbers consistent with the archeological model from hunter-gatherers and include units for travel, foraging, and predator defense.

Common features of the multilevel baboons can be summarized as follows: (1) Unimale groups, each composed of one central male, one or more affiliated females who are social and reproductive partners, and one or more followers. (2) Often one or more secondary males with social but not sexual access to the females. (3) One or two higher levels of social organization, identifiable by groups with consistent membership. (4) An ephemeral maximum social group, defined by mutual tolerance among constituent groups with regard to a sleeping places and/or home range overlap. (5) Male philopatry: males tend to stay in one group while females leave (the circumstances of female departure are very different in the two species).

Baboon troops and multilevel societies can be considered alternative models for early hominin social organization. Alternatively, they can be linked as two stages in hominin evolution. The latter view has been advanced by some social anthropologists. Male philopatry and female dispersal have been predominant characteristics of human society and similar patterns distinguish the multilevel baboon societies from the troops.

An influential scenario called the "Frontier Hypothesis" suggests that male philopatry was a key development in the expansion of both baboons and hominins to occupy a wide range of habitats. The hypothesis further suggests that male philopatry was a causal factor in the origin of unimale groups and multilevel society. The postulated *Papio* phylogeny casts doubt on the relevance of olive and yellow baboons for analogies to early hominins. While accepting this as a subject for future debate, this work continues with the application of all baboon species to the goal of reconstructing early hominin behavior patterns.

One such topic is the evolution of male–male relationships, which have been the subject of bitter debate about the role of aggression in the human evolutionary heritage. Early descriptions of baboons in troops, especially popular accounts, tended to focus on injurious violence. However, even among chacma baboons, reputed to be the most aggressive baboon species, disputes are more often settled by displays or by established dominance relations. Much the same is true of olive and yellow baboons, with the added feature of coalitions for cooperation in aggressive confrontations.

Aggression is a tool to obtain status and resources, including mating opportunities. Kinda baboons suggest an alternative in which sperm competition largely substitutes for direct competition and aggression. However, the relevance of this pattern to hominins is questionable because of the difference in the main physical correlate.

Sperm competition is represented by relatively large testis in proportion to body mass, a trait found in Kinda baboons but not in humans.

Male philopatry could have set the stage for new long-term relationships among male hominins. While cooperation in troops takes the form of temporary coalitions, multilevel societies display long-term relationships among central males and between them and secondary males. These affiliations are often based on kinship. Peace and solidarity are maintained in part through the exchange of ritualized communication. Secondary males may have social but not sexual relationships with females in unimale groups.

Within this general framework, there are important differences between hamadryas and Guinea baboons that suggest alternative models for early hominins. Hamadryas males control females and sometimes acquire them in aggressive confrontations with other males; Guinea baboon females choose their affiliations with males and are free to change them without interference. Central males among hamadryas "respect" each other's possession of females; Guinea baboon males have strong bonds with a few others and are "tolerant" of most other males. Hamadryas followers each associate with one unimale group; Guinea baboon bachelors have multiple connections. Hamadryas followers seem to contribute to the tenure and female holdings of the central male; Guinea baboon bachelors seem to function as a network that contributes to the solidarity of the larger social unit.

Stronger bonds among males, in association with more complex and ongoing forms of cooperation, suggest an early evolutionary foundation for patterns of male bonding and group formation in human societies. Culturally elaborated forms in recent humans have been characterized as "men in groups"and attributed to cooperative hunting. While hunting and other recently developed human patterns may well have contributed to the phenomenon, baboons show us that it could have originated in early hominins.

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