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Baboon perspectives on the ecology and behavior of early human ancestors

Glenn E. King[a,1,2]

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For more than 70 y researchers have looked to baboons (monkeys of the genus *Papio*) as a source of hypotheses about the ecology and behavior of early hominins (early human ancestors and their close relatives). This approach has undergone a resurgence in the last decade as a result of rapidly increasing knowledge from experimental and field studies of baboons and from archeological and paleontological studies of hominins. The result is a rich array of analogies, scenarios, and other stimuli to thought about the ecology and behavior of early hominins. The main intent here is to illustrate baboon perspectives on early hominins, with emphasis on recent developments. This begins with a discussion of baboons and hominins as we know them currently and explains the reasons for drawing comparisons between them. These include occupation of diverse environments, combination of arboreal and terrestrial capabilities, relatively large body size, and sexual dimorphism. The remainder of the paper illustrates the main points with a small number of examples drawn from diverse areas of interest: diet (grasses and fish), danger (leopards and crocodiles), social organization (troops and multilevel societies), social relationships (male–male, male–female, female–female), communication (possible foundations of language), cognition (use of social information, comparison of self to others), and bipedalism (a speculative developmental hypothesis about the neurological basis). The conclusion is optimistic about the future of baboon perspectives on early hominins.

baboons | hominins | ecology | social behavior | cognition

As part of the Ancient Human Studies series, this paper intends to provide a broad audience with some up-to-date illustrations of an important approach to understanding human ancestors. This is the use of perspectives derived from living baboons (monkeys of the genus *Papio*) for reconstructing the behavior and ecology of early hominins (members of the evolutionary group from which *Homo sapiens* arose). The approach has been used for more than 60 y (1) but is undergoing a resurgence due to progress in research on both baboons and hominins (see refs. 2–4 for reviews). Some older hypotheses have been supported by ongoing research and new hypotheses have emerged. These developments are represented by selected examples in this brief review.

A Closer Look at Hominins

To be somewhat more precise, *hominin* refers to any species in the taxonomic group that contains *Homo*, technically the tribe hominini (4). Hominins are an evolutionary lineage with many branches (also called lineages) that include ourselves, our presumptive ancestors, and their closest (extinct) relatives. The hominin linage originated from the last common ancestor shared with the genus *Pan* (chimpanzees and bonobos). Separation of the *Pan* and *Homo* lineages took place between 12 and 6 Ma according to varying estimates based on the fossil record (5, 6) and molecular comparisons of living species (7). Early hominins are represented by the relatively well-studied fossil genera *Ardipithecus* (8) and *Australopithecus* (9, 10), dated to a period from about 5 to 2 Ma. Evidence for earlier forms, such as *Sahelanthropus*, is sparser and their hominin status is subject to more controversy (5).

A Closer Look at Baboons

The term *baboon* as used here is limited to the genus *Papio*. Extant baboons can be divided into six species on the basis of morphological and behavioral traits that are unambiguous and homogeneous over large geographic distances (11). Baboon species are united by the common ancestry of the genus and also, as recent research shows, by substantial interbreeding at the margins and by repeated introgressions of genes from one species to another (11). All species share important features such as relatively large body size and a tendency to live in unusually large social groups, as well as wide within-species variation in habitat features such as terrain and rainfall (12, 13).

The Conceptual Framework for Baboon–Hominin Comparisons

Direct evidence for early hominin ecology and behavior comes from the paleoanthropological record provided by archeology and paleontology (e.g., ref. 10). This information has been augmented by studies of living nonhuman primates (hereafter, NHPs). First, NHP studies contribute

Author affiliations: [a]Department of History and Anthropology, Monmouth University, West Long Branch, NJ 07764

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[1] Email: gking@monmouth.edu.

[2] Retired.

to interpretations of available paleoanthropological data. Second, they suggest hypotheses about behavior and ecology of hominins where direct evidence is meager or lacking. The latter applies to gaps in the record and to the earliest period of hominin evolution in which there is no archeological record and fossils are sparse and highly controversial (14, 15).

Modes of Comparison between NHPs and Early Hominins. Comparisons can be made in terms of various frameworks (the examples given here are expanded in the discussions below). Analogy in the strict sense refers to a likeness of relationship rather than a simple resemblance (16). It postulates that a functional connection in one case parallels a functional connection in the other. In reconstructing the prehistoric past the extant case is used to formulate a predictive hypothesis about the past case. The functional connection between predation and escape is an important example. The presence of dangerous predators (A) leads extant primates (e.g., baboons) to climb trees to escape them (functional connection B), from which we hypothesize that the presence of dangerous predators in the paleontological record (C) caused prehistoric primates (e.g., hominins) to seek refuge in trees (functional connection D). This example illustrates another aspect of strict analogies: They delimit the boundaries of comparison. The analogy is limited to the predator–prey relationship. It may be further limited to relations with particular types of predators, such as terrestrial mammals rather than raptors.

More general analogies (the looser, more common usage of the term) can also provide information leading to useful hypotheses. For example, baboons and hominins are distinctive among primates in combining medium size and a high level of sociality with life in diverse habitats outside the tropical rain forest in Africa. Diversity in the social organization of baboons suggests alternative possibilities for the social organization of hominins. Productive thought might also come from broader and more dynamic settings of the kind often termed *scenarios* (16, 17). One prominent example derived from baboons describes a transition in social organization from undifferentiated social groups to tiered multilevel societies in which tightly knit female groups benefit from mutual aid (18).

Which Hominins? Baboon–hominin comparisons are most often directed toward hominin taxa that occupy an intermediate position in the evolution of possible human ancestors (from about 5 to 2 Ma), mainly the genera *Ardipithecus* and *Australopithecus*. Some inferences may be directly applicable to early members of the genus *Homo* as well as to earlier hominins. While Swedell and Plummer (17, 18) focused on *Homo erectus* (in a broad sense), a taxon that follows the earliest representatives of the genus, they suggested that their baboon–hominin comparisons could be applied to any point in hominin evolution. This interpretation is consistent with the view of some paleoanthropologists that the transition to *Homo* was not as sharp as has been commonly thought. It has been argued that a number of key *Homo* attributes may have been amplifications or extensions of features already present in some species of *Australopithecus* (19). If this is the case, then at least some analogies derived from extant species for *Australopithecus* should also be applicable to early *Homo*.

Which NHPs? The order primates, containing hundreds of species, offers many possibilities for comparison with hominins. For some purposes, the whole order can be considered (20). Common features at this level are very generalized but nonetheless important. For example, hominins probably lived in social groups from the beginning of their evolution as virtually all NHP species do today. Common ancestry on a smaller scale is also important in comparing hominins with other NHPs, especially with regard to the great apes in general and the *Pan* species in particular. Chimpanzees, for instance, provide important suggestions regarding the origin of vital human features such as tool use and culture (21, 22). Various monkey species provide diverse analogies for hominins (23). However, among the monkeys, baboons have long played an especially prominent role because of numerous parallels with hominins (1, 16, 17, 24).

Which Baboons? Recent research offers an increasing number of choices for inference from baboons to hominins. As noted above, all baboons share certain important morphological and behavioral features that set them apart from most other NHPs. These common traits include resemblances to hominins that argue in favor of a search for analogies and other perspectives. With regard to the genus as a whole, baboons resemble hominins in being relatively large-bodied, largely terrestrial, highly intelligent primates that have adapted to a wide variety of environments in Africa (16, 24).

For some comparisons a focus on species is necessary, or at least the most informative approach. For example, Elton and Dunn (25) inferred a relationship between body size and aggressive mate competition from such an analogy: The largest baboon species (*Papio ursinus* and *Papio anubis*) display the highest levels of overt competition, while smaller species (*Papio hamadryas* and *Papio papio*) are characterized by greater male tolerance. In the smallest species (*Papio kindae*) the pattern of competition seems to differ from any of the others (26), which shows that distinctive features of a single species are of special interest.

Finally, some intraspecies variation seems to follow parallel patterns in different species (12, 13). A recently developed example is the relationship between day path length, or DPL (distance traveled in 24 h) and several ecological variables for 47 baboon troops across 23 different populations of 4 species (27). In the significant relationships found in the study, DPLs were shorter in habitats with higher mean monthly rainfall and with anthropogenic influences (hypothetically related to food availability) and DPLs were surprisingly longer in hotter habitats despite potentially debilitating effects of the heat (the temperatures are hypothesized to cause arid environments that are less productive and provide less surface water) (27). Such findings suggest that analogies with hominins based on functional connections can be built from variation within baboon species as well as between them.

Significance of Baboons for Comparison with Early Hominins

The rationale for comparison between baboons and hominins has been strengthened by recent research in various ways. Some of these developments have been indicated above. These and others are discussed in more detail below.

Occupation of Diverse Environments. Hominin evolution involved an expansion (not a transition, as is sometimes erroneously stated or implied) from primarily woodland habitats to encompass a greater variety of environments. These included increasingly open and dry habitats (22, 30). Among NHPs, baboons are the best match for the range of habitats ultimately occupied by early hominins (1, 12, 15). This includes highland habitats documented in recent archeological research on *Australopithecus* (28), which can be compared to the mountains occupied by some South African baboons (29).

Cyclical aridification on local and regional scales and general aridification on a continental scale resulted in larger areas of grassland within and adjacent to hominin habitats (22, 30). The cyclical environmental shifts experienced by both hominins and ancient baboons probably resulted in some form of “variability selection” for the ability to respond to short-term and long-term fluctuations (31, 32). Extant baboons display the kind of flexibility predicted by variability selection hypotheses (33). For example, they are like humans and unlike most other primates in showing little or no seasonality in their reproductive behavior, which allows the pattern of reproduction to respond to changing conditions (33).

Combination of Arboreal and Terrestrial Capabilities. Bipedalism is a fundamental trend in the evolution of the hominins that ultimately indicates terrestrial adaptation. Bipedal posture and/or locomotion in hominins may have originated in trees, a theory based on poor grasping ability in the *Ardipithecus* foot and comparison with the differentiation of hands and feet in extant orangutan locomotion (34). However, the continuing evolution of anatomical structures for bipedalism indicates that movement on the ground became more frequent and eventually habitual. For example, fossil bones and footprints provide evidence for a stride that is pushed off by a hallux (big toe) aligned with the other toes and ends in a strong heel strike supported by a human-like calcaneus (35). Recent analysis of an *Australopithecus* calcaneus indicates an elongated Achilles tendon that would have contributed to the stride (36). Since baboons are quadrupedal, the analogy with hominins in this case is entirely functional/ecological, having to do with the amount of time spent on the ground.

At the same time early hominins probably retained considerable ability for arboreal locomotion, though there is controversy about the mode. Relatively long arms persist through *Australopithecus* to early *Homo*, which could have facilitated slow climbing, suspensory behavior, or assisted arboreal bipedalism. Based on phylogenetic comparison and morphometric analysis of skeletal material, the *Ardipithecus* hand was capable of vertical climbing and suspensory behavior (37). Foot and arm morphology of at least one late *Australopithecus* species (*Australopithecus sediba* at about 2 Ma) display features consistent with climbing and/or suspensory behavior. The legs of this species were shorter than those of *Homo*, which suggested limits on terrestrial bipedality to the researchers (38).

This combination of positional patterns raises major questions about ecological issues such as foraging behavior and responses to predators. It may also bear on social matters, such as cosleeping. Analogies with baboons can suggest answers to some of these questions because they engage in a broadly similar daily cycle of activities. As noted above, baboons differ from most other NHPs and parallel early hominins in spending most of their daylight time on the ground and yet they are agile in the trees and on cliffs (1, 2, 33).

Body Size and Sexual Dimorphism. Body size, usually considered in terms of weight or mass, is a basic feature of animals that affects almost every aspect of their biology, including (for example) locomotion, diet, energy requirements, social organization, and life history (39, 40). Early hominins probably weighed about 30 to 45 kg, though some individuals in one population may have been significantly larger (41, 42). Baboons are significantly smaller, most falling into the range of 10 to 30 kg (2), but they are among the few NHPs that approximate the size of the hominins and also occupy a comparable range of environments.

Sex difference in early hominin size is the subject of a long-running debate. This is because sexual dimorphism has important social and/or ecological implications for a wide variety of animal species (43). One common explanation is aggressive competition among males for mates (44). An important alternative is niche partitioning for access to resources, especially food (43). A long-standing hypothesis that combines ecological and social factors is that male baboons defend females and young against predators (1). Another such hypothesis is that males defend mothers and young against infanticide by immigrant males, which is explained in terms of male competition for reproductive success (45). Whatever hypotheses are favored, there is general agreement that sexual dimorphism in body mass is important.

There is also general agreement that body mass dimorphism in early hominins was significant, with males larger than females, but the degree is controversial. Some experts think that it was much greater than in modern humans with a male-to-female ratio as high as 2.0 (46, 47). Others argue that the difference was much more like that of modern humans at about 1.15 (48). If the majority view of greater dimorphism is correct, then baboons are a better match for early hominins than chimpanzees. Male/female ratios among baboons vary from 1.55 to 2.20 (2); among the *Pan* species the range is 1.11 to 1.36 (table 19.2, p. 324 of ref. 49). Recent work on hominins suggests that interpretation may be complicated by variation across the fossil record. *Ardipithecus* seems to show minimal size dimorphism, while *Australopithecus* species vary from modest to strong dimorphism (50). The increase in *Australopithecus* indicates that the relatively slight dimorphism in *Pan* and *Homo* is derived in both (50). Cautious use of comparison between baboons and hominins seems to be appropriate with close attention to variation among baboon species.

Baboon Perspectives on Hominin Ecology

Feeding on Grasses. There is growing interest in grasses and grass-like sedges as possible food sources for early hominins. Paine et al. agreed with other researchers that early hominins almost certainly paralleled baboons in making grass seeds part of their broad dietary repertoire (51). However, noting the limited seasonal availability of grass seeds, they focused on grass leaves as potential hominin food. Grass leaves are the single most abundant C_4 resource in African savannas. Paine et al. analyzed the leaves of savanna grasses for their nutrient value and physical characteristics. They found that species differed significantly with regard to traits that would have been favorable for the hominin diet. Some were less tough, lower in fiber, and higher in protein.

Paine et al. were explicitly encouraged by numerous studies showing that grasses are a major source of food for baboons in savanna environments. Grass is the most important single food for at least some savanna baboons, with bulk intake up to 40% and as high as 90% during dry seasons for some populations (52). Baboons demonstrate how grasses can be an important year-around food. Depending on the season they shift their attention to different parts of the grasses: seeds, thick lower stems, and rootlike underground rhizomes (53).

The grass-like sedges that grow in watered localities have also been proposed as important to hominins (51). The high protein content of grasses and sedges in the wetlands of Amboseli in Kenya during the dry season may account for the fact that baboons have done relatively well there, even during some periods of severe drought (33, 51).

Feeding on Fish. The proximity of early hominins to various bodies of water raises the possibility that they fed on fish as well as land vertebrates. Lakes in the time of early hominins were stocked with fish (54). Stewart (55) suggested that obtaining fish in early hominins was at first inadvertent and then progressed successively to opportunistic hand-catching, deliberate hand-catching, and tool-catching. Baboon analogies are consistent with the speculation about fish eating and with the first two stages of the sequence proposed by Stewart. Baboons at two sites have been observed eating dead or dying fish in dry conditions (56, 57). Hand catching was observed at one of these sites (57). The baboons walked into pools and groped around to collect larger dead fish that had sunk to the bottom and captured live fish as they floundered in shallows or when they surfaced. Occasionally the baboons patrolled the edges of pools and reached out to slap the water surface, stunning fish. Some baboons entered larger pools and seized active fish beneath the surface, especially under boulders. Large fish, some more than 30 cm long, were captured in this way. Baboons show that hand catching of fish was a possibility for hominins and might have become a profitable source of food.

Danger from Carnivores. Early hominins coexisted with numerous predatory species, including ancient forms of cats and hyenas. Some taxa became extinct, but modern leopards and lions evolved (58, 59). Baboon analogy suggests that felids among the many carnivores were a major threat to hominins. Leopards are the most likely to attack baboons (1, 60) and similar cats probably preyed on hominins. Ongoing progress in the study of baboons (and other NHPs) is exemplified by the use of Global Positioning Systems. Isbell et al. (60) used this method to study collared leopards, baboons, and vervet monkeys. They found that the two monkey species are equally vulnerable to leopards, but in very different ways. Vervets are vulnerable on the ground but safe in trees at night because they are small enough to roost at the ends of flexible branches that leopards cannot negotiate. Baboons are vulnerable at night because they are too large to occupy terminal branches and/or hide in dense vegetation. During the day baboons are not attacked by leopards, presumably because of their propensity for preemptive attacks and counterattacks (60). In this respect they confirmed long-standing observations and inferences (1).

Body size figures prominently in this comparison of baboons and hominins. Isbell et al. hypothesized that the size of early hominins, as with baboons discussed above, would have limited their ability to take refuge in trees at night but would have facilitated defense on the ground during the day (60). An additional factor that they mention is that baboons are within range of prey size preferred by leopards. This is also true of early hominins. An extensive survey determined that leopards prefer prey in the range of 10 to 40 kg with strongest preference about 25 kg (61). Vervets are much smaller at about 2.8 to 5.6 kg (62).

Crocodiles. The lakes where hominins probably found food were commonly inhabited by crocodiles, potential enemies for which hominins would presumably have no defense, and hominin bones are claimed to display the marks of crocodile teeth (63). However, doubts have been raised about the statistical approach used to distinguish crocodile marks from others. Applying an alternative method, McPherron et al. concluded that the original results are indistinguishable from a null model based on random data (64).

The controversy lends additional weight to baboon evidence supporting the plausibility of crocodile predation on hominins. Baboons also exist in proximity to bodies of water in which crocodiles are common. In the Okavango Delta of Botswana baboons become extremely vigilant when crossing water and their perception of danger may be reflected in the pattern of their alarm calls and other responses: The bark for a mammalian predator caused a dash for trees while the putative crocodile bark resulted in the baboons running a short distance from the water and then stopping to watch (65). On three occasions a crocodile was observed to leap out of shallow water to attack adult male baboons (65).

Baboon Perspectives on Hominin Social Life

Grouping. A recent conference of archeologists approached consensus on three points regarding the social organization of prehistoric hominins (66). Although the archeologists mainly referenced recent human hunter-gatherers, the three points also articulate with baboon analogies. First, the archeologists agreed that prehistoric groupings of 20 to 50 individuals were common. Second, these groups were probably not rigidly separated from one another. Third, group size was a dynamic phenomenon varying from small bands to large aggregations for various functions and purposes, two of which were subsistence and predator defense. The presence of similar patterns in baboons suggests that such organization could have existed in small-brained early hominins as well as in later hominins (18) and recent hunter-gatherers (66).

The Troop. In the context of recent archeological thought the well-known phenomenon of baboon social organization takes on new significance. Most baboons live in groups that typically include multiple members of all age–sex categories, commonly called a troop. Troop size varies from roughly 10 to 200, but many troops fall into the 20 to 50 range postulated by the archeologists (67). Troop organization is often somewhat flexible and allows for groupings of various sizes. A troop usually moves as a unit but in some circumstances, especially food scarcity, subgroups forage independently and then reunite (68, 69). Intertroop relationships vary from hostility to avoidance to tolerance to occasional brief associations that give rise to supratroop groupings (70, 71). Predator defense, as described above, is a potential function at all levels. The troop occurs among baboons across nearly all of their habitats and may have been adaptive for early hominins in parallel circumstances.

Multilevel Societies. Hamadryas baboons and Guinea baboons differ from the others in forming multilevel societies. In these societies smaller groups are nested in larger ones to form tiers of social organization. Students of the two species have used different terminologies for the two species. For hamadryas these are the *one-male unit* (OMU), the *clan*, the *band*, and (confusingly) the *troop* (which is nothing like the troop in other baboons) (72, 73). The nested units of the Guinea baboons are the *reproductive unit*, the *party*, the *gang*, and the *community* (74, 75).

Despite the differing terminology, there are significant correspondences between the species and the units have been equated by students of both species (75, 76), beginning with use of the same term (one-male unit or OMU) for the basic unit of both hamadryas and Guinea baboons. They go on to equate *party* with *clan*, and *gang* with *band*. Though not mentioned, that leaves *community* and *troop* as the top level in each system. The relationships within and across units are manifested in proximity, grooming, and joint travel.

In both hamadryas and Guinea baboons the OMUs can forage separately, but they usually belong to a larger group (clan/party) that sometimes travels and forages as a unit. This second-level group often includes “bachelor” males that may not be affiliated with females or with any OMU. Further affiliation takes place at third and fourth levels of organization. The functions of fourth-level aggregations are limited: In Guinea baboons their home ranges largely overlap with little conflict; in hamadryas baboons they usually tolerate each other at the same sleeping cliffs at night (74, 76).

The nesting structure and function of these societies, as described by Swedell and Plummer for hamadryas, for example (17, 18), is consistent with the archeologists’ view of nonexclusivity and the functions of foraging and predator defense (see above). First- and second-level groups are reproductive and foraging units. Second-level groups tend to contain 20 to 30 individuals with a range of perhaps 10 to 40, thus fitting well with the archeologists’ formulation of 20 to 50. Larger groups at all levels mean more effective predator defense. A study of hamadryas, for example, 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 (76). These subjects remained in larger aggregations before morning departure after predators were heard in the vicinity.

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. The latter interpretation is in accord with an evolutionary scenario developed by Jolly (77) in which troop organization was the foundation for the evolution of multilevel systems in some populations (this complex hypothesis addressed demographic changes that may have affected both baboons and hominins as the taxa expanded across Africa and adapted to new conditions).

Chapais (78) also postulated two such stages at the beginning of hominin social evolution. The first of these stages was a “promiscuous” multimale–multifemale group that he compared to the chimpanzee community, using a description that also applies to the baboon troop. The next stage, inferred from hamadryas and other primate data, was a “multiharem” group. Chapais saw this as the foundation for the multifamily community as the modal pattern for humans. He argued that later hominins were largely constrained to monogamy when weapons increased the risks of male–male competition.

Male–Male Association. Tiger surveyed all-male groups across diverse human 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 (79; see also ref. 80). Since Tiger’s work, much more has been learned about male–male association in baboons. Comparison with baboons suggests that male bonding originated in early hominin evolution and that the basis was largely kinship. In the multilevel societies of hamadryas and Guinea baboons, males at the comparable levels of band and gang, respectively, are more closely related to each other than to males in other such units (81, 82). Close associations are more likely to occur in the next lower level of social organization (clan/party). Hamadryas prefer association with male relatives within the clan rather than those in other clans (81). In Guinea baboons preferred partners are almost always found within the same party even though there is no significant difference in relatedness within and across parties in the same gang (82). These strong bonds are differentiated, equitable, and stable for up to 4 y or more and form the basis for coalitions in the (rare) agonistic interactions (74). Such male–male associations were presumably facilitated by a shift from female to male philopatry (i.e., males were more likely than females to remain close to the area of their birth), the central focus of Jolly’s scenario above (77).

An OMU in hamadryas or Guinea baboons commonly includes an additional male, termed a *follower* for hamadryas (75) and a *bachelor* for Guinea baboons (82). In hamadryas the central male and follower are maternal relatives more often than expected by chance (83). In Guinea baboons central males maintain strong bonds with bachelors as well as other central males, and relatedness in both cases is significantly higher than in any other dyads (74).

Hamadryas and Guinea baboons differ in some ways that may offer alternative or complementary analogies for early hominins. In Guinea baboons every bachelor male is affiliated with an OMU and many of them are associated with multiple primary males (82). This seems to suggest that the bachelor males function as reinforcement for cohesion of OMUs. In hamadryas each follower is typically affiliated with only one OMU and not every OMU has a follower. The functions of hamadryas followers seem more focused on relations within the OMU. In the hamadryas system, where females are mainly acquired by coercion, leaders with followers have longer tenures as leaders, acquire more females, and sire more infants than males without followers (84). Follower relationships with OMU females may encourage the females to adhere to the leader as long as possible (84). This variation between the two baboon species applies across different levels of social integration, OMU and higher levels. As early hominin societies became more complex, parallels to both baboon species might have occurred.

Greeting Rituals. Male baboons in troops and multilevel societies maintain relatively peaceful and cooperative relationships with affiliative behaviors called greeting rituals (85–87). These nonaggressive signals are widespread among animal species but the repertoire of *Papio* is exceptional, involving potentially harmful behaviors such as touching or grasping one another's genitals (86). Similar social communication, including genital manipulation, occurs in some traditional human societies. These actions imply trust, tolerance, and willingness to cooperate. Comparison among baboons shows that the complexity and risk of greeting rituals increase with the degree of male–male tolerance and cooperation.

Male–Female Association. Across all cultures and time periods, the typical human mating relationship is a relatively long-term association between one male and one to three females (78). Demography dictated that monogamy was most common, but polygyny was allowed in the majority of societies and desired by many men, if not most. Though submerged by larger kinship groups in the complex societies of recent times, these personal associations probably have an ancient evolutionary origin (16, 78). A crucial point with regard to comparison with NHPs is that human mating relationships always exist within a community of some kind (78). This limits the usefulness of "pair-bonded" species (e.g. gibbons) in which the male–female group is more or less an isolate (16).

Baboons in troops display long-term relationships of particular males and females that could have been the basis for differentiation of families (81) early in hominin evolution. These "special friends" can be identified by elevated rates of proximity and grooming (88, 89). The female receives protection from harassment by competing females that may result in infant death (90, 91), as well as protection from infanticide by immigrant males (45). The male may gain mating access and/or the opportunity to care for his own infant (91). An individual male or female may have several such friends. If early hominins had such relationships, a narrower focus (linking just two or three individuals) would have resulted in a unit similar to the human family (a division of labor might have been the precipitating factor).

The OMUs of hamadryas and Guinea baboons might represent the next stage in the evolution of the family. In these species the family-like unit is a universal feature and is always nested within larger social entities. However, there are differences in dynamics. Hamadryas females have been accumulated by the male and the relationship is largely maintained by coercion (92). The females are strongly oriented toward the leader male and sometimes fight over grooming access to him. Male–female relationships in Guinea baboons seem more similar to the special friendships in troops. The stability of these relationships varies considerably and females play an active role (74). A female maintains a social and mating relationship with one primary male, but she may transfer at any time without interference. This possible analogy for early hominins suggests that the origin of the family in a multilevel society does not require rigidly male-dominated OMUs.

Female Associations with Other Adults. Baboon studies also suggest foundations for female social relationships in early hominins and humans. In addition to their connections with adult males, females in troops can form enduring social relationships with each other that are close, equitable, and supportive (93). There is a strong preference for close relatives, especially mothers and daughters. Females also form strong attachments to others who are close to their own age, possibly paternal half-sisters.

In some baboon field studies female relationships with other adults of both sexes are correlated with offspring survivorship, an effect that is unrelated to dominance rank or ecological conditions (94). According to social network analysis, reproductive success is further enhanced by having partners that themselves have extensive social connections (95). Complementary work focused on longevity (96). Females with social connections to either males or females live longer than isolated individuals. Females with strong connectedness to individuals of both sexes live the longest.

Other research concluded that female–female bonds enhance offspring survivorship independent of connections with specific males (97). Females with the strongest social bonds to other adult females have the highest survivorship among both daughters and sons. Benefits persist into offspring adulthood, are unrelated to female dominance rank, and increase quantitatively with the strength of female–female bonds.

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 (94, 96). Experimental studies in humans suggest that social integration is the cause and not the consequence of improved health outcomes (94).

Analogy with baboons suggests relevant stresses for early hominins and relief provided by social relationships. First, females with stronger and more secure social bonds may be less spatially peripheral while feeding during the day and in sleeping trees at night, resulting in less vulnerability to predators for themselves and their offspring. Second, females with allies may be better shielded from social conflicts and therefore able to feed more efficiently, benefitting themselves and the offspring that they nurse (94).

Other baboon analogies suggest the continuation of such female relationships during a transition from troop-like communities to multilevel societies. This is particularly striking in the case of hamadryas baboons where female kin are separated from one another by males that coerce females into OMUs, usually one at a time (18). 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 and that at least a third of these maternally related dyads are mother–daughter pairs (83). It may be that the baboons can recognize maternal kin and can find a way to express choice in at least some takeover situations (18). Together, these results imply that an ancestral maternal kin bias has been retained in hamadryas society (83), 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 (18).

These developments reinforced a scenario for later hominin evolution based on changes in ecological conditions, subsistence patterns, and costs of reproduction for females. It postulated female subgrouping into small social units in which females assisted one another with food procurement as well as care and provisioning of offspring (17, 18). Kinship bonds would have strengthened such groups, which might have led to multiple generations of related females.

Baboon Perspectives on Hominin Mental Processes

Most hominin–baboon comparisons are functional in a broad sense: They hypothesize about overt relationships between behavior and the environment or the relationships between various patterns of social behavior. However, baboons may offer some insights into possible mental processes of early hominins. Some behaviors in the wild and in captivity suggest hypotheses while recent experiments have explicitly addressed baboon–hominin comparisons.

General Cognition. In the latest of a long series of experiments on baboon cognition, Anikaev et al. (98) compared captive hamadryas baboons and rhesus macaques (*Macaca mulatta*) in performance on seven tests that the researchers deemed measures of general cognitive capacities. Specifically, they tested exploratory activity and learning ability in naïve subjects. More baboons than rhesus were active in the tasks and they were less likely to decrease activity as the tasks became more complex. The result was significantly greater overall success for the baboons. The researchers noted that this was in agreement with earlier findings on manipulative ability and concluded that hamadryas baboons possess a higher level of cognitive ability than rhesus macaques. They attributed the difference to behavioral plasticity and adaptability and postulated that these qualities contributed to the evolutionary success of baboons. Similar qualities could have meant evolutionary success for early hominins as they evolved under conditions much like those facing baboons.

Object Manipulation. Wild baboons display sporadic object manipulations, some of which suggest precursors to tool use. Some chacmas selectively overturn rocks to feed on underlying invertebrates (99). They tend to move medium-sized rocks, a trade-off between the effort needed for larger rocks and insufficiency of prey under smaller ones. They reduce effort by flipping flatter rocks along the shortest axis and by moving rocks downslope (100). While interesting in themselves, these recent accounts provide a new perspective on earlier reports of baboons using stones as weapons.

Sporadic accounts of baboons defending themselves by “throwing” stones came from questionable sources until primatologists reported that chacmas dropped and threw stones at them from the tops of cliffs on numerous occasions (101). Escape movements and vocalizations indicated that the baboons regarded the humans as a threat and positioning in relation to the observers indicated intent. This report from southern Africa elicited accounts from other scientists about similar incidents in Sudan (102) and Kenya (103). Critics of the original report argued that the humans were too far away to be struck by the stones, and they pointed out that some baboons throw sticks during displays without understanding their potential as weapons (65). However, Pettet (102) stated that his baboons displayed good aim much of the time. Nevertheless, all reports make clear that the baboons were agitated; thus, errant throws may have resulted from arousal overshadowing cognitive control. Inference of intent in this behavior is made more plausible by the recent observations of chacmas moving stones for feeding, including the downslope orientation.

Social Cognition. Classification of relationships is an important aspect of social cognition, providing a guide to differentiated behavioral patterns. Comparison of two baboon species demonstrated this ability in a way that could be pertinent to early hominin society (104). The researchers recorded grunt vocalizations from two baboon species with very different social systems and played them back to the baboons. In all baboons grunts are deep rhythmic sounds that convey various positive meanings, from contact maintenance to friendliness to cooperation. Playbacks in this field experiment simulated affiliative interactions with the potential of females transferring from one male to another or one group to another. The reactions of male Guinea baboons were mild, presumably because little is at stake for them in a society in which females are free to choose their affiliations. Male chacma baboons, living in a troop where competition for females is intense, responded more strongly to the same grunts. The experiment suggests that the value of social information varies with the degree of competition in a baboon society. These results have potential implications for the evolution of social cognition in hominins, since either kind of society might have been characteristic of hominins at some stage. Viewed narrowly, this experiment might be relevant to the cognitive dimension of male–female relationships in early hominins. More generally, the results combine with other studies to suggest that the earliest hominins were capable of classifying social relationships.

Comparison of self to others is an important characteristic of human social life and may have been a component of social organization in early hominins. An experiment used a computerized task presented in a social context to explore the psychological mechanisms of social comparison in humans and baboons (105). The two species responded in comparable ways, depending on whether the other individual was similar or dissimilar to the subject and whether the other was better or worse off. The researchers inferred that humans and baboons shared similar social comparison mechanisms. Like many contemporary French experimenters with captive baboons, they interpreted the similarity as representing a very ancient homology derived from the common ancestor of monkeys and apes. However, it is at least equally plausible that such similarities are functional analogies resulting from parallel evolution of baboons and hominins.

Components of Language. Baboons, especially in experimental settings, contribute to discussion of language origins. Human language can be viewed as resulting from an assemblage of multiple cognitive and anatomical components, some of which are present in other species (106). Fagot et al. argue that baboons and humans share many cognitive or brain mechanisms that are essential to the construction of language (106). Some of these have to do with vocal production (see below). Others are involved with gestural production, which has been observed and trained in captive baboons. More broadly, baboons display rudimentary cerebral lateralization and some domain-general functions that are related to language. The capabilities of baboons suggest the cognitive components that may have existed in early hominins and that in hominins became integrated into the first language systems.

Other researchers agree that baboons may provide clues to the origins of language. One such study proceeded from the premise that the extent to which NHP vocalizations are amenable to modification through experience is relevant for understanding the substrate from which human speech evolved (107). In the multilevel society of Guinea baboons, grunts (described above) were determined to have an acoustic structure that varied with party and gang membership. These acoustic similarities did not correlate with genetic relatedness of the individuals involved, which suggests that the frequency of social interaction within these groups promotes vocal convergence. The researchers considered this convergence a result of sensory–motor integration and suggested it is an implicit form of vocal learning shared with humans.

Neurology of Bipedalism. Bipedal locomotion occasionally occurs in baboons and a baboon analogy suggests an evolutionary pathway from quadrupedalism to bipedalism in hominins. When captive infant baboons engage in spontaneous bipedal walking, hindlimb coordination improves during the same developmental stage as interlimb coordination in quadrupedal walking. Observers inferred that the same neural networks were involved in both changes (108). They postulated that a secondary locomotor mode that was a by-product of infant development might lead to evolutionary innovation under appropriate selection pressure.

Summary and Discussion

Sources of Hypotheses. Hypotheses derived from the study of living baboons can augment the paleoanthropological record by facilitating interpretation of the data and by making suggestions about what the record does not show. Baboons are particularly apt for this purpose because they resemble early hominins in a number of key features, including adaptability, variety of environments occupied, intelligence, relative size, and possibly sexual dimorphism. This does not make baboons a substitute for chimpanzees or any other NHP source of information. Rather, they can reinforce and complement some hypotheses derived from other species and in other cases they can provide competing and alternative hypotheses. The strongest inferences from baboons to hominins are based on analogies in the strict sense, i.e., similar functional connections within limited pairs of phenomena. However, observations and experiments on baboons have led to other kinds of hypotheses as well, some inspired by simple resemblances and others involving scenarios combining several elements.

The approach by analogy (still less the hodgepodge of other perspectives) does not lend itself to elegant synthesis or integration. It is a piecemeal approach that addresses particular questions and fills in particular gaps in knowledge derived from other sources. For example, the paleoanthropological record juxtaposes hominins with bodies of water containing fish. This leads to the question of whether hominins could have added fish to their diet and speculation about how they might have done it. Baboons show how even the earliest small-brained hominins could have obtained fish by a variety of hand-capture methods. The origin of family-like units poses a more complex question that requires sifting of analogical possibilities. Pertinent relationships in early hominins might have resembled long-term relationships in baboon troops or in one or the other of the multilevel species.

Other kinds of hypotheses are inspired by particular observations and experiments with baboons. Druelle et al. (108) noted certain developmental patterns in baboon locomotion, studied them systematically, and used the information to formulate a hypothesis about a possible neurological basis for the evolution of bipedalism in hominins. That developmental pattern might occur in many other NHPs; however, it might be specific to the terrestrial adaptation of baboons and therefore provide a real analogy with very early hominin evolution.

Some Scenarios. Coordination of baboon perspectives with the paleoanthropological record suggests that the earliest hominins lived in mosaic habitats and subsisted on an omnivorous diet that included relatively soft products of forest and woodland. They used bipedal postures and locomotion on the ground, but arboreal capability allowed them to forage and sleep in trees. Trees (and perhaps cliffs) may have been the refuge from very large (now extinct) predators because the trees were close and the predators large enough to detect at a distance. The community may have been a troop much like those of most baboons today.

Major environmental trends over millions of years resulted in populations of both hominins and baboons expanding into increasingly open and seasonal environments with more heterogeneous components. This must have encouraged and/or required changes in diet that may have included increased consumption of grasses and addition of fish, along with more meat and exploitation of underground storage organs of plants. Hominins in more open habitats were more exposed to predators as the composition of the carnivore guild shifted to extant species. Most important to hominins was the leopard, smaller than its predecessors but stealthy and powerful. Foraging in relatively large groups, hominins probably discouraged leopards with their willingness to engage in aggressive cooperative defense. The earliest manipulation of stones may have involved turning over heavy rocks to find food. This could have been the foundation for the use of stones as weapons against predators where the conditions were right.

The earliest hominin societies were probably troops encompassing multiple males and females, but multilevel societies might have emerged at an early date. The latter would have entailed male–male relationships more like those of modern humans with increased tolerance and cooperation based mostly on kinship bonds. Both troops and multilevel societies display male–female bonds that may be analogous to the foundation of the hominin and human family. However, multilevel societies contain relatively stable OMUs that are more like human families. A more complex social environment could have selected for cognitive capabilities such as classification of relationships and comparison of self to others. Communication may have been elaborated to the point of laying the foundations for language.

One of the most important findings of the last few years is the clarification of similarities and differences between the multilevel species of baboons. For example, coercion of females is a major factor in the formation of hamadryas OMUs, while Guinea baboon females are freer to move from one male to another. Nevertheless, female choice occurs in both species even if to different degrees, which argues for continuity with troop-living ancestors. This is a fertile area for comparisons with humans and reconstruction of stages in hominin social evolution.

The baboon perspective on hominins has been invigorated by recent discoveries about both taxa. This paper has tried to illustrate the approach by sampling recent developments. If the last few decades are any indication, continued cross-fertilization between paleoanthropology and the study of baboons (as well as other NHPs) will produce more insights into possible and probable hominin behaviors.

Data, Materials, and Software Availability. There are no data underlying this work.

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