Chapter 3
Conceptual Frameworks and Criticisms

3.1 Introduction

Various attempts have been made to introduce intellectual concepts or systems that provide the hominin–baboon comparison with a rationale and consistency of approach. Most or all of these can be subsumed by the concepts of *model*, *analogy*, and *scenario*. Each of these will be examined in the following sections as to its applicability to hominin–baboon comparison.

Some critics have completely rejected baboon perspectives while others have argued that other primates are better sources. Discussion of these criticisms leads into a closer comparison of baboons with other primates with regard to reaching a better understanding of early hominins. The final part of the chapter discusses strengths and shortcomings in the criticisms and asserts that baboons offer more to reconstruction of early hominin behavior than any other primate except for chimpanzees. In some ways baboons are even more significant for that purpose than chimpanzees.

3.2 Models

The word "model" has been used widely but loosely, creating uncertainty about its meaning. Moore (1996) listed and discussed numerous synonyms, many of which have been employed in the study of primate behavior (Table 3.1). He distinguished between those that are potentially useful, if applied carefully, and those that contribute little or actually mislead. Boldfaced terms in Table 3.1 are those that are treated as useful in the present discussion. On the negative side, "just-so story" is a term frequently used by critics of models for behavior in extinct species. Derived from the title of children's stories by Rudyard Kipling, it implies that the model it maligns

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Table 3.1 Meanings of the word "Model" in comparative studies (Based on Moore 1996)

Meanings for "Model"	Explanation/Example
Analogy	A relation based on similarity between attributes of two things
Model (noun)	Known member of an analogous pair
Model (verb)	Process of constructing an aspect of the unknown member of an analogous pair
Scenario	A broad, internally consistent "story" about a specific extinct taxon
A set of formal instructions	For example, mathematical representation of an idea or system
Sketch	Deliberately self-effacing term (intended to provoke thought without criticism[a])
Overview	Similar to sketch
Hypothesis	An idea amenable to testing; narrower than a scenario
Reconstruction (noun)	Synonymous with scenario, but sounds more precise (misleading, to be avoided)
Reconstruction (verb)	Process of using contemporary sources to hypothesize about aspects of the past[a]
Metaphor	Figure of speech intended to evoke a feeling of similarity; not analytically useful
"Theory"	Often, a formal-sounding synonym for "idea" or "suggestion"
"Just-so story"	A fairy tale; someone else's model with which one disagrees
A body of theory	For example, natural selection
A set of ideas with a central focus	For example, role of carnivory in human evolution
A direct analogy	For example, arborealism in hominins and apes
A world view	For example, scientific knowledge

[a] My interpretation of Moore and/or of the concept

is a fairy tale. Moore's addition of "someone else's model" to the definition is an apt dig at the rancor in some discussions of the topic. Perhaps the greatest problem with models is the word itself, because it seems to imply a comprehensive picture of the referent. This can lead to unrealistic expectations of numerous and detailed similarities.

Two kinds of models have been presented as relevant to reconstructing early hominin behavior through comparison with extant primates: *referential* and *conceptual*. Mathematical models (e.g., Dunbar 2001) can be considered a form of conceptual model because they conform to Moore's definition of a "set of formal instructions." Such models, however, are beyond the scope of this book.

3.2.1 Referential Models

Moore (1996) described referential models as using "real phenomena" to illuminate others that are more difficult to study. In this context, the "real phenomena" are extant primates; early hominins are the problematic target. Moore was most interested in chimpanzees as the extant model for hominins, but his general concepts apply equally well to baboon perspectives. This includes the ways in which referential models can be used:

1. Demonstration of behaviors that might have been possible for the problematic subjects, such as tool use by chimpanzees with materials that would leave no archeological remains.
2. Facilitating the incorporation of demographic factors into reconstruction. An example is the dispersal (migration) of individuals from one community to another, typically one sex or the other.
3. Suggesting important new ideas. For instance, Moore hypothesized that male–female differences in chimpanzee insectivory might be a model for the evolution of the sexual division of labor in hominins.
4. Generating detailed scenarios as a basis for testable hypotheses. This is illustrated by a scenario in which hominin females form kinship-based units for shared protection, child care, and food-getting (Swedell and Plummer 2019; Chap. 9 in this book).

I would add that referential models can provide evidence for both general patterns and particular activities. An example of such a general pattern is the scenario of an omnivorous diet, based on dental traits of extant species that might be found in the teeth of fossils. An example of a particular activity is digging up roots for food, which is performed by both chimpanzees and baboons (Chap. 4).

Following Susman (1987) and Potts (1987), Moore (1996) advocated a referential approach that is based on intraspecific variability in order to model diachronic change in the hominin lineage. He compared "forest" and "savanna" chimpanzees for this purpose. At the time he wrote, this was largely limited to framing questions to be answered. Much more is known now, including information about limits on chimpanzee exploitation of savanna biomes (Marchant et al. 2020). Baboons, in contrast, encompass the full range of environments experienced by hominins (this important point has been noted previously and will be noted again). As for using variation, as in Moore's modeling, this can be derived from the differences among the six baboon species as well as variation within each of the species. Even Guinea baboons, found in a relatively small region, have populations in forests and in the arid Sahel (Zinner et al. 2021; Chap. 1 in this book).

There is no single baboon model (King 2022), except in the most general terms (e.g., terrestriality, sexual dimorphism). This became apparent early in the development of field research, with reports of baboons in gallery forests and woodlands rather than savannas (Ransom 1981; Rowell 1966). Now we have six different species of baboons living in an even wider range of environments, including, for example, chacma baboons in the swampy Okavango Delta in Botswana (Cheney and Seyfarth 2007) and hamadryas baboons in the semideserts of lowland Ethiopia (Schreier and Swedell 2012).

Whatever referential model one may bring to bear, it is vital to specify its characteristics and to be clear about the specific behavior pattern(s) under study (cf. Moore 1996). Given the variation among baboons, it is also important to specify the particular baboon species or group of species that is the basis for the model. Throughout this book, an attempt has been made to name the baboon species that were the subjects of each cited study or set of studies.

3.2.2 Conceptual Models

Conceptual models are constructed very differently from referential models and are held by some to be superior (Tooby and DeVore 1987). They are based on theoretical analysis rather than specific real-life subjects. Conceptual models draw on general principles from behavioral ecology and other fields in order to specify theoretical relationships pertinent to a particular situation. The process is based on the following premises: (1) the gene is the unit of selection, and (2) animals act like strategists promoting their *inclusive fitness* (Tooby and DeVore 1987). This concept refers to the idea that animals behave in ways that support their relatives, a phenomenon caused by the probability that relatives share the same genes for the same kind of "altruistic" behavior.

Conceptual models tend to be very speculative, which heightens the risk of being refuted by new evidence (Stanford 2012). Tooby and DeVore (1987), for example, made the theory-based assumption that social animals must emigrate from their natal groups in order to avoid inbreeding depression. Subsequent fieldwork demonstrated that neither sex consistently emigrated in a number of primate species (Moore 1996).

Though placed in opposition by some scientists, the conceptual and referential approaches overlap and can be complementary (Stanford 2012). Strum and Mitchell (1987) created a conceptual model for early hominins that concluded with a description that sounded very much like baboon behavior (King 2001). They acknowledged that looking at baboons was a good "first step" toward reconstructing early hominin behavior. An approach that includes both referential and conceptual models is likely to be the most effective, because reciprocal refinement can result in a better understanding of the problem at hand (Moore 1996).

Some primatologists and others continue to denigrate and reject referential models, including baboons. Others continue to use them effectively, as did many of the sources for this book. Referential models have derived new life from recently developed knowledge of diversity in the genus *Papio*. Recent findings about baboons and hominins present us with a series of challenging choices rather than a unitary model.

3.3 Analogies

Analogies provide a flexible framework for dealing with specific behavior patterns that have been chosen for investigation. Though analogies in a general sense are sometimes considered a kind of model (Moore 1996; Table 3.1), it is best to distinguish them because analogies can be defined in relatively rigorous way. Analogy in the strict sense refers to a likeness of relationship rather than a simple resemblance (Jolly 2013). 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 a simple but 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 (Jolly 2013). The analogy in question is limited to the predator–prey relationship. It can be narrowed further to relations with particular types of predators, such as terrestrial mammals or raptors (Chap. 6). This use of analogies falls into the “referential” category, but it does not exclude amplification by the principles associated with conceptual models.

The concept of strict analogy provides useful guidelines for hominin-baboon comparisons, but there is no reason to be rigidly bound by it. More general analogies (the looser, more common usage of the term) can also provide useful ideas. For example, baboons and hominins are distinctive among primates in combining the status of medium-sized mammals and a high level of sociality with life in diverse habitats in Africa. Given these parallels, diversity in the social organization of baboons suggests alternative possibilities for patterns of social organization in early hominins, such as the nature of long-term relationships between particular males and females (Chap. 8). Such loose analogies are heuristic and do not in themselves produce conclusions with any degree of probability. However, they can stimulate the formation of testable hypotheses.

The emphasis in this book is on carefully selected analogies rather than comprehensive models. Increasing knowledge of variation among baboons (Fischer and Zinner 2020) makes this approach both necessary and profitable. The basis for selection of particular analogies is the need to address particular problems in understanding early hominin ecology and behavior.

3.3.1 Scenarios

Productive thought can also come from broader and more dynamic settings of the kind often termed *scenarios*. These might be considered extended analogies of the loose variety (i.e., without precisely delimited boundaries). In the explication by Greene (2017), scenarios summarize evolutionary patterns and processes in a phylogenetic context. They are constructed by (1) describing *phenotypes*, the physical characteristics of an organism, *including behavior*; (2) inferring the evolutionary processes that produced those characteristics; and (3) integrating those components with ecological and other ancillary data.

At their best, such evolutionary scenarios are "factually dense narratives" with the following characteristics: they (1) contain no known falsehoods; (2) are transparent as to their empirical and methodological shortcomings; (3) can be rejected based on new discoveries, and (4) their potential ideological pitfalls are flagged for scrutiny. If constructed carefully and regarded skeptically, such scenarios can synthesize knowledge, inspire research (Greene 2017), and lead to testable hypotheses (Moore 1996).

Strum (2019) described a scenario for the social behavior of male troop-living olive baboons that she observed. They did not have a stable dominance hierarchy and some displayed social intelligence by using nonaggressive strategies in competition with other troop members. Bonds with females and infants were part of this suite of behaviors. Strum emphasized that recognition of this complex system (only partially described here) required the integration of her quantitative data with long-term qualitative observations. This is a "factually dense narrative" that can be expanded into a phylogenetic origin and applied to early hominins, taking account of "ancillary data" for baboon ecology and hominin paleoecology.

3.4 Criticism and Papiophobia

During the 1960s Sherwood Washburn inspired many people to study baboons as a source of hypotheses about hominin adaptations to living on the ground and in the relatively open habitats loosely called savannas (DeVore and Washburn 1963; Washburn and Devore 1961). The resultant "baboon model" once pervaded accounts of hominin evolution and then, subjected to severe criticism, its influence declined. Some pronounced its demise. By the year 2000 a popular textbook said that the model was seldom used and that baboons are only of interest for illustrating the variability of primate behavior. This conclusion has been overturned by abundant information from recent research on both baboons and early hominins, as well as increasingly incisive thought about how the baboon data pertain to early hominins. In the following discussion of criticisms, the term "model" will be used loosely because the subjects of the discussion have used the term in various ways.

Some objections to the baboon model were never valid, while others were resolved by increasing knowledge of both baboons and early hominins. It is worth considering some longstanding arguments for two reasons. One is to warn against perpetuation of past errors. Though overt criticism seems to have subsided, baboons are now ignored in some contexts where they are obviously relevant (e.g., Newson and Richerson 2021, discussion in Chap. 9). The other reason to consider criticisms is to distinguish those that raise valid issues and learn from them. These reasons correspond roughly to a division of critical arguments into two general categories: absolutist (baboons are irrelevant) and relativist (other species are better). Some absolutist arguments are so strained that I think of them as *papiophobia*. The relativist category is the one that contains useful critiques.

3.4.1 Absolutist Arguments

According to these arguments, baboon perspectives are useless or misleading and should be entirely dismissed. Some absolutist arguments were based on logical confusions of one kind or another, such as the unwarranted alignment of baboons with other models for human evolution. In one version of this fallacy, baboons were conflated with human hunter-gatherers. A writer described the “basic formula” of the baboon model as a “baboon type” society with hunting added (Fedigan 1982). The author then listed and criticized 15 alleged traits of the “hunting way of life” before returning to baboons. Although baboon and hunter-gatherer models have sometimes been used in conjunction, there is no logical necessity for doing so. The two models have distinct sources and apply to different stages of hominin evolution.

Some critiques of baboon–hominin comparison confused models with inferences: baboon analogies were rejected because perceived conclusions were considered wrong. One such text asserted that the baboon model should be dismissed because there was no evidence that a terrestrial primate in open country is subject to greater predator pressure. Assessment of predator pressure in open country (or any other habitat) is an inference drawn from a model; it is not part of the method itself. The fact is that ongoing research shows that open country is more dangerous and that baboons respond in highly patterned ways (Chap. 6).

Another example of a misused inference is the idea that any baboon model is wrong because males do not always defend the troop. Specifically, the report by Rowell (1966) was cited as to the fact that the presence of predators resulted in male baboons outrunning others for the trees. Not mentioned by the critics was the fact, also reported by Rowell, that the only large predators that approached baboons in her study area were humans. Most baboons will run from humans, who have hunted them for decades or centuries or millennia (depending on the area in question). Male baboons, however, often confront other large predators such as leopards and cheetahs (Altmann and Altmann 1970; Chap. 6 in this book). The baboon model required modification, not rejection.

According to Tanner (1981:19–20), “the earlier picture of savanna baboon social life was so incomplete as to be misleading.” A footnote informed the reader that this was because the importance of females was neglected. Some absolutist objections were more overtly based on ideology. For example, the baboon model was criticized as “androcentric” (Martin and Voorhies 1975). If androcentrism means a form of prejudice that distorts the data, then the problem is in the researchers rather than the subjects. The remedy is better research rather than rejection of the model. If objections are raised because of distaste for established facts (such as male dominance or male aggression against females), this is not science.

The criticism about neglecting females had some validity with regard to early research on baboon behavior. However, decades of fieldwork by more diverse investigators have provided us with an enriched understanding of baboons that accords females a key role in social life and ecology (e.g., Strum 1987). This has led to more sophisticated models of early hominin behavior (e.g., Strum 2019; Swedell and Plummer 2019).

In some cases, critics contradicted each other. The first comparisons between baboons and early hominins emphasized savanna adaptations, so some critics portrayed baboons as forest animals that occasionally ventured into grasslands (Martin and Voorhies 1975). Put simply, hominins were savanna animals while baboons were forest animals. When paleoanthropology provided evidence that early hominins engaged in arboreal locomotion in wooded habitats, baboon analogies were dismissed because they could only tell us about "adapting to open country" (Susman 1987). Hominins were forest animals while baboons were savanna animals. In short, the baboons were too forest for some critics and too savanna for others.

Both formulations were simplistic with regard to both baboons and early hominins (Chap. 2). The earliest hominins may have lived in relatively closed woodlands, but never in dense rainforest or "jungle." Their successors occupied mixed habitats that included deciduous woodlands and more open areas. Expanding across Africa, hominins encountered major geographic variation as well as diverse local habitats. During millions of years of existence, they were subjected to major environmental fluctuations and a general drying trend. Baboons, also living in Africa, though later in time, experienced much the same conditions.

Some critics contradicted themselves. Tanner (1981) rejected the baboon model because it had allegedly not been compared to other "savanna" monkeys. Her example was patas monkeys, which deal with predators by hiding or running. This is the opposite of the chimpanzee model that she favored, from which she inferred that both male and female hominins deterred predators by throwing things at them. Baboons, like chimpanzees, are capable of active defense against predators. Baboons, like chimpanzees, live in relatively large groups that make this possible. Patas monkeys live in smaller groups with a single adult male in each one. Furthermore, while Tanner rejected the baboon model because of "extreme" sexual dimorphism, the same degree of sexual dimorphism is found in patas monkeys.

The argument about sexual dimorphism, setting aside spurious comparisons, actually had some potential validity. As discussed in Chap. 2, sexual dimorphism in body mass is substantial in all baboon species, and males can be twice the size of females in one or two species. Human size dimorphism, on the other hand, is relatively minor. Some researchers consider early hominins to be comparable to modern humans in this regard, but many view the fossil record as showing much greater dimorphism in early hominins than in modern humans.

It is also relevant that there is significant variation in sexual dimorphism among baboon species. The ratio of male to female mass can be as little as 1.5 (for modern humans the figure is about 1.15). Explanations for variation among baboon species may shed light on factors in early hominin evolution. Evolutionary *changes* in hominin sexual dimorphism might be modeled by variation across baboon species (cf. Moore 1996).

Finally, some absolutists belabored the obvious—that baboons are not close relatives of the hominin lineage. Such assertions refuse to recognize the importance of both homology and analogy in evolution. Without going into theoretical complexities, these concepts refer to the fact that some similarities between species are related to their common ancestry and other similarities are due to adaptation to similar circumstances. A classic example of the latter is the structurally different wings that allow both bats and birds to fly.

3.4.2 Relativist Arguments

Relativist critiques are more important than absolutist because they are more likely to lead to constructive discussions of the best strategies for understanding early hominins. Relativists argued that other primates were equal to or better than baboons for the reconstruction of early hominin behavior. In examining these alternatives, it should be borne in mind that inferences from different primates are not always in conflict with one another. In some cases, they are mutually reinforcing, pointing to the same or similar conclusions. In other instances, they are complementary, providing different components of the answer to a question about early hominins.

Chimpanzees
Many referential models and analogies for early hominins are based on chimpanzees, because of the common ancestry of the two lineages. This includes two approaches. One considers the possibility of homologies shared by chimpanzees and humans, derived from the LCA. Chimpanzees, for instance, provide important suggestions regarding the origin of vital human features such as tool use and culture (Boesch 2012). Such models postulate that hominins and chimpanzees retained the same ancestral traits and/or evolved in the same direction because of those traits (Andrews 2020; Moore 1996). Chimpanzees are certainly of interest in the reconstruction of early hominin ecology due to the phylogenetic connection and also the similarity in brain size. This is a sound approach and baboon perspectives on hominins must continuously adjust to its findings.

Less compelling is the argument that some chimpanzee populations are models for early hominins because they are “savanna” dwellers (Moore 1996). The term is sometimes used loosely and may simply suggest that the habitat of a given population is not dominated by forest cover (Marchant et al. 2020). Recent studies and reviews have attempted to treat the subject with more rigor. Van Leeuwen et al. (2020) reviewed 43 chimpanzee field research sites across equatorial Africa. Nine of these were characterized as “savanna” sites, based on the terminology of the researchers or their description of the vegetation cover of the landscape. These habitats are described as “hot, dry and open, dominated by woodland and grassland vegetation types, and with minimal forest cover.” The common quantified features that separated all of these sites from forests were annual rainfall of less than 1360 mm/year and forest cover of less than 12.5%.

As noted by Hunt and McGrew (2002), such habitats may include woodland with the grassland and are often labeled mosaic. Fongoli, for example, is a “savanna-mosaic” (Wessling et al. 2018b) or “savanna-woodland mosaic” (Wessling et al. 2018a). Semliki is simply a “mosaic” that includes forest, wooded grassland, and open grassland (Hamilton et al. 2019). Chimpanzees in these habitats display low population densities and may spend relatively little time in the most open parts of their range. The more open habitats represent some of the extremes of where chimpanzees can persist—occupying the biogeographical edges of the species’ distribution (Wessling et al. 2020). Many of these groups show signs of environmental stress in relation to heat and dehydration, and at least some of these chimpanzees seem reluctant to exploit the grassland parts of their habitats. One indication of stress is the frequency of thermoregulatory behaviors such as cave use in the hottest and driest landscapes (Lindshield et al. 2021).

Observations at Semliki “indicate that even in open or mosaic habitats … chimpanzees remain forest primates, utilizing primarily forest resources and only a minor subset of savanna resources” (Hamilton et al. 2019: 560). These chimpanzees harvest fruits from open areas close to the forest edge, but they are “uneasy and fearful” when they do so. Olive baboons were also observed at Semliki, by the same researchers, and the baboons did not display the same “aversion” to the open parts of the environment as did other monkeys and the chimpanzees.

Baboons have gone beyond grasslands to survive in deserts and semideserts. Table 3.2 compares the extremes of chimpanzee “savanna” environments with some

Table 3.2 Chimpanzees and baboons in arid habitats

Species	Location	Rainfall	Dry season(s)	Temperature	Vegetation
Chimpanzees	9 locations	Lowest mean annual 750 mm	Longest 7 months	Highest mean/ ann. 29 °C	Savanna-forest mosaic
Olive baboons	Laikipia Plateau Kenya	Mean annual ~42 mm	Two seasons total 7 months	Highest daily temp 34 °C	Dry savanna with gallery forests
Chacma baboons	Tsaobis Namibia	Mean annual ~123 mm	Approaches 8 months	Highest *shade* temp ~ 40 °C	Riparian woodland and desert scrub
Hamadryas baboons	Filoha Ethiopia	?	?	Mean daily (1y) 31.5 °C high ~35 °C	*Acacia* scrub, open grassland

This table compares the extremes of “savanna” chimpanzee habitats (Van Leeuwen et al. 2020) with figures from two studies of baboons in arid habitats: olive baboons (Musyoki and Strum 2016), chacma baboons (King et al. 2011), and hamadryas baboons (Schreier and Swedell 2012). The available figures are not strictly comparable, but they strongly suggest the adaptive gap between “savanna” chimpanzees and baboons that have penetrated more arid habitats. The text provides more detail selected examples of baboons in open country. A much more detailed comparison of baboon ecologies can be found in Zinner et al. (2021).

In relation to open country and early hominins, an important parallel between chimpanzees and baboons is susceptibility to predation despite their size. This issue provides an example of complementary hypotheses from the two sources. Male baboons have large canine teeth, which can be used to fight predators, but early hominins did not have such dentition. Nevertheless, our ancestors could have become effective defenders by substituting weapons for teeth. Chimpanzee evidence shows that they might have used clubs and spear-like sharpened sticks (Chap. 6).

This last point brings up the assertion by Tanner (1981:19) that “the transitional hominins of both sexes could doubtless throw branches and leaves at potential predators at least as effectively as chimpanzees today.” First, this statement is unreferenced and unlikely, especially as regards deterring a predator like a leopard by throwing leaves. Second, this is an ideological response to the idea that males defend females. Female chimpanzees may be just as good at throwing things as males, but the idea that this applies to early hominins depends on the assumption that hominin sexual dimorphism in body mass was no greater than the relatively small difference in chimpanzees. To most paleoanthropologists the fossil record tells a different story (Chap. 2).

Other Apes

Several scientists have suggested analogies for early hominins from gorillas. Macho (2018), for example, drew on contrasts between gorilla populations. The reliable vegetation available to mountain gorillas allows for accelerated development of the young, which seems to be related to relatively small brains. Lowland gorillas feed mainly on fruit, which is a rich but unreliable source nutrition. A slower rate of growth reduces the risk of starvation (presumably because the smaller body requires less). The brain continues to grow after weaning and is ultimately larger than that of a mountain gorilla. Gorillas are even more terrestrial than chimpanzees and more like hominins in that respect. However, as discussed earlier, body mass has a powerful effect on many aspects of life and gorillas are far larger than chimpanzees or early hominins. The size of gorillas imposes very different limits on their biology.

Following Elton (2006), Macho acknowledged that baboons are good ecological models for early hominins because they are eclectic omnivores that live in large groups, some of which are multilevel societies. Along with hominins, snub-nosed monkeys, and Japanese macaques, baboons are the only (relatively) large-bodied primates to survive at higher latitudes where environments are more seasonal and demanding (northern Asia in the case of macaques).

Orangutan facility with tools may represent homologies among the great apes (including humans). However, ecological relevance to early hominins is limited because these abilities are mainly displayed in captive and rehabilitant settings. In their natural lives, most orangutans are more arboreal than early hominins are likely to have been. They also tend toward a relatively solitary existence, especially adult males. Orangutans are pertinent to the hypothesis of arboreal bipedalism in hominins (Crompton et al. 2010), but this tells us little or nothing about the functions and/or selective influences on terrestrial bipedalism. The other Asian apes, the gibbons, live in small groups that have been compared to human families. However, these groups tend to be territorial and lack the larger community that is characteristic of humans, presumably early hominins, and baboons (Chap. 7).

Monkeys Other Than Baboons

Monkeys other than baboons have also been proposed as models for early hominins. The case of the patas monkeys was discussed above. Geladas (*Theropithecus gelada*) are a more appropriate model for hominins (e.g., Jolly 1970). They are relatively large, ground-foraging primates that associate in large groups. However, in contrast to baboons, geladas are limited to highland regions of northeastern Africa. They provide some analogies for the reconstruction of early hominin traits; however, many of these, such as multilevel societies and consumption of grasses, are also found in baboons.

Another genus that has been compared to hominins is *Chlorocebus*, which includes the well-known vervet and closely related species. Baboons and early hominins both differ from *Chlorocebus* in spanning diverse environments, including very open ones. Vervets and their kin are creatures of the forest and woodland fringes. According to Altmann (1998), baboons differ from these taxa in that baboons "stride unhesitatingly into the open from the cover of the woodland." They walk long distances, often without shade or water, with "relative immunity" to predators. As one result of these capabilities, they consume a much wider variety of foods than vervets. These and other characteristics of baboons are related to their size. While baboons fall short of hominin size, vervets are far behind both with a maximum weight of about 6 kg. Alberts and Altmann (2007) reported a crisis at Amboseli, Kenya, in which baboons responded well to deteriorating conditions while vervets experienced a substantial population decline.

Comparison with All Primates

The order Primates, containing hundreds of species, offers many possibilities for comparison with hominins. For some purposes, the whole order can be considered (Strier 2001). 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 almost all primate species do today.

On the other hand, generalizations that encompass the entire primate order can tell us little or nothing about the consequences of living on the ground in relatively open habitats as our ancestors eventually did and baboons do. This is because the great majority of primates are forest dwellers and primarily arboreal.

3.5 Summary and Discussion

Baboons have often been characterized as a "model" for early hominin behavior, a term that has caused some confusion because of multiple definitions and theoretical disagreements. The most commonly used kind of model has been, and continues to be, the referential model. It uses a real phenomenon (in this case, baboon behavior) to illuminate another phenomenon that is more difficult to study (early hominins). Referential models can demonstrate the possibility of certain behaviors, facilitate the use of demographic factors in reconstruction, suggest important new ideas, and generate scenarios.

Conceptual models are more theoretical and complex. They postulate that animals behave like strategists to maximize their inclusive fitness. Inclusive fitness refers to behavior that promotes the survival and reproductive success of relatives as well as the individual. Conceptual models produce more sophisticated results, but tend to be more speculative than referential models and more subject to empirical contradictions. The two types of models are not mutually exclusive and can be used to check on one another. There is no single baboon model. Six different species, and variation within the species, provide many possibilities.

Analogies provide a flexible framework for dealing with specific behavior patterns that are chosen for investigation. Analogy can be defined rigorously as a likeness of relationship, that is, parallel functional connections in two different cases. Here, the analogies have to do with understanding the factors connected with a selected behavior pattern in extant primates and the possible application of these relationships to particular early hominins. More loosely formulated similarities can be useful for heuristic purposes and may be the first step toward constructing testable hypotheses.

Scenarios are broader than analogies but more constrained than comprehensive models. If constructed carefully, with assumptions made explicit, they can be useful for the organization and synthesis of knowledge and as an inspiration for further research. They should integrate behavior with underlying evolutionary processes and with ecological data.

Criticisms of the hominin–baboon comparison can be roughly divided into two categories. Absolutists have completely rejected the idea, while relativists have postulated that other primates are better sources of information and hypotheses. Some absolutist arguments were based on logical confusions and misused inferences. In some instances, the critics contradicted each other or themselves.

Many relativist critiques offered constructive criticism of baboon perspectives and the possibility of coordinated effort. Chimpanzees are often cited as the best model for early hominins, especially with reference to their common ancestry. This is a sound approach and baboon perspectives must be adjusted to its findings. Ecological comparison of chimpanzees with early hominins is also of value, but more limited in possibilities. This is because "savanna" chimpanzees are mostly occupants of mosaic habitats in which they may minimize their use of open areas and may suffer stresses not found in other chimpanzees. In contrast, baboons have successfully colonized the full range of environments that are manifested in the early hominin record. This includes habitats that are hotter and drier than any that chimpanzees are known to occupy.

Other apes are also close relatives of hominins and can provide some useful analogies. However, the possibilities are more limited. Gorillas are huge, and body mass has a powerful effect on many aspects of life. Orangutans are found only in Asian biomes, tend to be more arboreal than baboons or early hominins, and tend to be solitary rather than social (especially adult males). Gibbons are highly arboreal Asian apes. They live in small groups with a superficial resemblance to human families, but which lack the community context that is characteristic of baboons, chimpanzees, and hominins.

Monkeys other than baboons are sometimes compared to early hominins. The most noteworthy are geladas and the *Chlorocebus* group (vervets and closely related species). However, geladas are limited to the highlands of northeastern Africa. Vervets and their relatives are much smaller than baboons and, like chimpanzees, are only tentative users of open areas.

Chimpanzees are the only primates that rival baboons with regard to providing information relevant to reconstruction of early hominin behavior. Chimpanzees have the vital status of having the last common ancestor with hominins. However, baboons have many advantages over chimpanzees in helping us to understand the problems and possible adaptations of early hominins as they expanded into hotter, drier, and increasingly open habitats.

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