Chapter 5
Animal Foods and the Origins of Meat Eating

5.1 Introduction

Faunivory is a convenient term for the consumption of all forms of animal food, including invertebrates, vertebrates, and eggs. The expansion of C_4 resources in hominin diets was probably due in part to increased consumption of animals that fed on C_4 plants (Martin et al. 2020). Living primates provide clues to the particular kinds of prey animals involved and how they were obtained. Chimpanzee evidence is highly relevant, but has its limitations, especially due to the emphasis on arboreal prey. Baboon analogies augment the chimpanzee evidence in some cases and provide alternative possibilities in others.

Meat can denote the flesh and organs of vertebrates, though another common usage limits it to mammals. Meat, especially from mammals, has played a major role in theories of hominin evolution. Compared to other sources of animal food, many mammals are larger and/or more elusive. Like early hominins and unlike most chimpanzees' faunivory, baboons hunt mammalian prey on the ground.

5.2 Invertebrates

Baboons are like many other primates in consuming a variety of invertebrate animals. Most of them are terrestrial arthropods, including insects and spiders. Some baboons and a few other monkeys are able to access shellfish. These are all food sources that could have been used by early hominins, but would leave little or no evidence after millions of years. The great shell middens beloved by archeologists came later in hominin evolution.

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5.2.1 Arthropods

Insects and other arthropods are consumed by most primates and in many human cultures around the world (Lesnik 2017, 2018). The use of arthropods for food is unlikely to be represented in the paleoanthropological record, but primate evidence suggests that this contributed to hominin subsistence. Chimpanzees are famous for their use of probing tools to obtain a variety of insects such as termites, ants, and bees. A baboon analogy suggests at least one source of insect food that did not necessitate the use of tools or require ground penetration of any kind. Baboons differ from many other primates in their exploitation of swarming insects such as locusts, dragonflies, and caterpillars, which are captured by hand. These sometimes provide a group with food for hours or even days (Altmann and Altmann 1970; Schreier et al. 2019).

Three chacma troops were under observation in the Namib desert when they were presented with an outbreak of large grasshoppers (Hamilton et al. 1978). Baboons in one troop ate these insects as an almost exclusive diet while they were available. Various vegetative food items, especially *Acacia* seeds, added some diversity, but troop movements were not oriented to these alternatives. Instead, the baboons remained in the vicinity of a waterhole and one nearby sleeping cliff and moved only a few hundred meters per day. In contrast, in the absence of grasshoppers, their day routes averaged several kilometers and ended at various alternative roosts. At the time of the grasshopper swarm, fecal material under the sleeping cliffs of the two baboon troops upriver established that they too were concentrating on those insects. Yellow baboons at Amboseli also fed on swarming grasshoppers with a capture rate of 75% (Altmann and Altmann 1970).

When parasitic scale insects attacked mopane trees in the home ranges of five chacma troops, the insects became their main food during the outbreak (Hamilton et al. 1978). One troop ignored abundant alternative foods such as seed pods and palm nuts, which were heavily utilized during other times. Baboons in a troop a few kilometers away, with only a few scattered mopane trees in their range, maintained a diet that was nearly animal-free.

Hamadryas baboons at Filoha ate locusts and dragonflies when they swarmed, chasing and jumping up to catch them (Schreier et al. 2019). The majority of attempts were successful and the baboons spent 30–60 min in these feeding sessions. Most of the 200 members of the study group participated. Monthly insect consumption rose to 2% of the monthly diet during peak periods. The researchers noted that this pattern was consistent with observations of other hamadryas baboons and other *Papio* species.

Baboons can also obtain non-swarming insects for food. In at least one population, chacma baboons overturned rocks to feed on underlying invertebrates (Mare et al. 2019). That prey were the goal of the behavior was indicated by the fact that the baboons selected some rocks to turn over while ignoring others. Concentration on medium-sized rocks maximized the balance between food energy obtained and

effort expended. Early hominins may well have obtained insects from such terrestrial sources as well as from swarms.

5.2.2 Aquatic Invertebrates

From their earliest appearance, hominins were associated with bodies of water of various kinds: lakes, rivers, streams, and wetlands (Andrews 2020). This suggests that aquatic resources may have been of some importance to them. De Chevalier et al. (2022) maintained that exploitation of aquatic food sources is an issue of particular significance for understanding human evolution. Their thinking was that hominins are the primate group with the highest degree of adaptedness to aquatic environments and the only group in which true coastal and maritime adaptations have evolved.

Lakes in the time of *Australopithecus anamensis* were stocked with diverse mollusks and fish (Van Bocxlaer 2020). Baboons have obtained such foods from lakes and also from marine sites. Chacma baboons of Cape Peninsula in South Africa took advantage of intertidal organisms, such as shellfish and the remains of crabs. Crustaceans and mollusks are rich in protein and some provide energy (Lewis and O'Riain 2019). Congruence between observation-based estimates of diet composition and those generated by isotope-based models, using baboon hair and feces, confirmed that these chacmas consumed small amounts of marine foods on a seasonal basis (Lewis et al. 2017). Marine foods were also part of the diet in a population of yellow baboons in Somalia (P. Messeri 1978, cited by Lewis and O'Riain 2019).

5.3 Vertebrates: Fish

Stewart (2010) suggested that early hominins caught fish, a process that advanced from inadvertence to opportunistic hand-catching to deliberate hand-catching. Baboon evidence supports this scenario. Matsumoto-Oda and Collins (2016) reported two cases of fish eating by olive baboons, at sites in Kenya and Tanzania. In both instances the consumers were adults (rather than exploring juveniles) that ate recently dead or dying fish. The opportunity for fish eating occurred by chance, suggesting that it would be difficult for the baboons to eat fish regularly. These researchers noted comparative evidence from orangutans and Japanese macaques, indicating that fish-eating occurred when fruits or other foods were scarce. They viewed this as evidence that fish are favored as a fallback food. Chacma baboons observed in Namibia, like the olive baboons in East Africa, ate dead or dying fish in dry conditions (Hamilton and Tilson 1985).

Supporting Stewart's scenario, the Namibian chacma baboons also captured live fish by hand (Hamilton and Tilson 1985). A river at this desert site periodically dried

and left waterholes containing fish. Baboons walked into pools and groped around to collect larger dead fish from the bottom. Live fish were captured as they floundered in shallows or when they surfaced. Occasionally baboons slapped the water surface, stunning fish that they then grabbed. Some individuals 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. This baboon analogy suggests that hand capture of live fish was a possibility for early hominins.

Two factors suggest some doubts about the relevance of the Namibian case to early hominins. First, the fish were made available by unrelated human activities upstream. Second, the extent of baboon fishing may have been related to the absence of competition from piscivorous birds such as herons in this very dry environment. Acknowledging these caveats, the analogy still implies that early hominins might have added fish to their diet wherever and whenever conditions were favorable.

5.4 Terrestrial Vertebrates

Meat can be defined as the flesh and viscera of vertebrates, and may include eggs (Watts 2020). The emergence of regular meat consumption, especially the distinctive exploitation of meat from mammals, is regarded as a major development in hominin evolution. Three hypotheses have been proposed for the adaptive significance of meat eating in primates (Watts 2020). Compared to plant foods, meat (1) is denser in calories, (2) provides higher quality protein, and/or (3) provides essential micronutrients such as vitamins. These hypotheses apply as much to hominins and baboons as they do to other primates.

Baboon data are pertinent to several interrelated questions about meat eating in early hominins. How did the behavior begin? How did it develop to the point of leaving remains detectable by archeology? What kind of behavior was necessary to obtain meat? The sections below consider the evidence for meat eating in early hominins and baboons; baboon analogies for the methods by which early hominins might have obtained meat; and hints from baboons as to the motivational basis for meat eating and procurement in early hominins.

5.4.1 Meat Eating

On current evidence, consumption of mammals seems to have become well established by the time of early *Homo*. Ferraro et al. (2013) critically examined archeological sites dating to more than 3 mya that yielded remains of mammals that were apparently butchered with tools. The sites were isolated in time and space and the data limited, leaving open the question of how important meat was to hominins during that period. Comparison with evidence from three large and well-preserved faunal assemblages dating to about 2 mya led the researchers to infer a fundamental

shift in subsistence patterns around that time. They concluded that these hominins transported and ate numerous individuals of small bovid species. They defined "small bovid" broadly as comparable to extant Grant's gazelles, which may weigh anywhere from 35 to 80 kg. Archeology shows that butchery became "more prevalent" in East Africa shortly after 2 mya (Patterson et al. 2019). Calcium isotope analysis supports the implication that a major expansion of faunivory took place after the appearance of *Homo* (Martin et al. 2020).

Comparative evidence from baboons and other primates strongly implies that consumption of animal matter was part of the hominin diet from the beginning of the lineage. It would have consisted mainly of invertebrates and small vertebrates such as birds and lizards. This tendency would have provided the platform for a more distinctive orientation to mammalian prey. Three groups of primates stand out as consumers of meat: chimpanzees, baboons, and the capuchin monkeys of the Americas (Watts 2020). Chimpanzees and baboons demonstrate vertebrate capture in African habitats similar to those occupied by early hominins. Together, they support the view that early hominins ate meat, probably from some early time in the evolution of the lineage.

More distinctively, and more pertinent to the major innovation in hominin subsistence, consumption of mammal flesh is relatively prominent in chimpanzee and baboon diets. The genus *Papio* stands apart from other monkey genera with respect to the breadth of vertebrate species that they exploit, and because mammals are eaten by every baboon species for which relevant data exist (Sommer et al. 2016; Table 5.1), except for the (so far) less-studied Kindas. Baboons eat 21 wild mammal species belonging to 5 different taxonomic orders, as well as immature domestic sheep and goats (Watts 2020).

Papio meat eating spans the geographic and environmental distribution of the genus from the chacma baboons of the Namibian desert (Davies and Cowlishaw 1996) to olive baboons in the Nigerian forest (Sommer et al. 2016) to Guinea baboons in Senegal (Goffe and Fischer 2016) to hamadryas baboons in Ethiopia (Schreier et al. 2019). Particulars differ significantly from one environment to another, with different implications for various aspects of hominin evolution.

Data from olive baboons were gathered in Nigeria at the wettest and most forested site studied to that date (Sommer et al. 2016). Despite abundant wildlife, meat eating was rare compared to many other baboon sites. Mammals were killed at a rate of one during 1291 h of observation. The rarity of meat eating in that location probably reflects the difficulty of acquiring prey animals when vegetation cover is dense. Olive baboons associated with a Ugandan forest ate a prey animal every 30 h (Rowell 1966). Early hominins may have begun to expand the exploitation of land mammals while still closely associated with some forests or woodlands.

Chacma baboons in a mountainous habitat ate vertebrates at a rate of one every 78.5 observation hours (Allan et al. 2022; Table 5.1). A key meat source was young antelopes, particularly bushbuck, which were consumed once every 115 h. The relatively high rate of meat eating suggests that the behavior may have been stimulated when early hominins penetrated the higher altitudes documented in recent archeological findings (Chap. 2). Anecdotal reports on chacma baboons note some of the

same prey elsewhere (e.g. Davies and Cowlishaw 1996), but add domestic fowl and goats (Ade n.d.; Jackson 1978; McKee 1992).

Meat seemed to be virtually absent from the diet of hamadryas baboons until they were studied at Filoha, a somewhat richer habitat than most of those occupied by the species (Schreier et al. 2019; Table 5.1). These baboons maintained a small amount of animal matter in the diet throughout the year, alternating between insects and vertebrates. They were seen to eat vertebrates 38 times in a year of observation. The difference between Filoha and other hamadryas sites seems likely to be due to availability in a habitat that is slightly more abundant than the deserts occupied by other populations of the species. Prey availability and the availability of feeding time shaped vertebrate predation (Schreier et al. 2019).

Schreier et al. (2019) addressed a hypothesis of meat eating that may also be relevant to early hominins: Seasonal variation in plant food availability has been suggested to motivate dietary flexibility in a range of species and thus primates may seek more prey when key plant resources are unavailable. They found no relationship between faunivory (either insect or vertebrate) and either rainfall or the consumption of staple plant foods. Thus, in this case at least, faunivory seems to be independent of the supply of plant foods.

Table 5.1 Baboon prey

Prey type	Total (%)	Olive	Yellow	Chacma	Guinea	Hamadryas
Ungulates	135 (40%)	113	11	8 [+39][a]	1	1 [+15][b]
Hares	84 (25.5%)	57	20	1	2	4 [+7][b]
Birds	41 (12.5%)	16	17	7 [+7][a]	4	1 [+11][b]
Primates	30 (9.1%)	0	25	6	0	0
Rodents	18 (5.5%)	1	4	13 [+3][a]	0	0
Herpetofauna	15 (4.6%)	4	10	[4][a]	1	[3][a]
Mammals (?)	5 (1.5%)	3	2	0	0	0
Other	1 (0.3%)	1 bat	0	1 hyrax[a]	0	1 hyrax[b]
All	329 (100%) [+91]	196	88	35 [+54][a]	4	6 [+37][b]

Abridged with gratitude from Sommer et al. (2016), where references for all figures can be found. In a few cases the exact number of prey animals were unknown, so these were counted as one individual in the summaries. Herpetofauna included lizards, a snake, and frogs. In five cases the prey could be identified as a mammal, but not as any particular species. Data from more recent papers are added in brackets

[a]Allan et al. (2022): Chacma baboons in a montane environment. Two cases of scavenging were not counted as predation. Fifteen failed attempts were recorded

[b]Schrier et al. (2019): Hamadryas in scrubland/grassland typical of the species. Of 38 meat-eating episodes, 11 kills were observed. In the other instances, the meat was so fresh that the researchers inferred that it was a recent kill. These data were not broken down by taxa

5.4.2 *Foraging and Hunting*

Ferraro et al. (2013) concluded from their analysis of archeological sites (see above) that hominins (presumably early *Homo*) engaged in regular hunting of small bovids. This was based on the quantities of the animal bones and the evidence that had been transported to the places where they were discovered. Baboon behavior suggests earlier meat-getting patterns that provided the foundations for such archeologically visible sites.

Both chimpanzees and baboons provide hints as to the earlier faunivorous practices of hominins. Baboon analogies augment chimpanzee evidence in some respects, but provide alternative possibilities in others. Chimpanzees' favored prey are arboreal monkeys (Bugir et al. 2021) that they hunt with the kind of arboreal skill that may never have been in the repertoire of vertically climbing hominins (Chap. 1). Hominin climbing skills may have persisted for a long time, but any approximation to ape-like agility in the trees would have been greatly diminished by the time of early *Homo* (Chap. 1). Baboons find all of their animal foods on the ground (or in adjacent waters). In this respect baboon analogies are more relevant to hominin behavior than chimpanzee patterns.

The simplest and most common way that baboons obtain meat is to happen across a helpless animal, most often an infant antelope hidden in the grass (DeVore and Washburn 1963; Sommer et al. 2016). Such discoveries can be considered an aspect of foraging. However, baboons sometimes engage in higher levels of activity to obtain prey. They hunt some animals in the sense of stalking and/or pursuit. Yellow baboons chase hares and sometimes groups of almost all age/sex classes participate (Hausfater 1976). Also, adult males "definitely hunted or stalked young vervet monkeys in the strict sense of these words" (Hausfater 1976:48). Goffe and Fischer (2016) described Guinea baboons as stalking and chasing prey (although dense vegetation prevented any estimate of the distance covered by chases). Captures included a hare and seven antelopes (three of the latter identified as bushbuck).

A survey of baboon meat acquisition (Sommer et al. 2016) found that 60% of prey animals were simply "grabbed" in a chance encounter. However, 40% were "spotted and then chased." About 90% of the prey animals were immature and all of the ungulate prey were immature. However, immatures ranged in size, strength, and speed from neonates to subadults. Baboons at Gashaka struggled to maintain control of young antelopes (Sommer et al. 2016). Cases like these represent hunting, as opposed to foraging.

The most intense and elaborate hunting practices of any baboons were recorded at Gilgil, Kenya (beginning with Harding 1973; summarized by Strum 1981). Individual olive baboons altered their movements to engage in "active searching." They left the troop to walk through gazelle herds or detoured into thickets to find dik-diks. A pursuit could last for almost 10 min and take the baboon almost 300 m away from the troop.

"Complex" hunts, always directed at Thomson's gazelles (Fig. 5.1), involved more than one baboon and lasted more than 10 min. Searching, stalking, and pursuit

Fig. 5.1 Thomson's gazelle, a prey animal of some baboons. Fawns are easily killed, but hunting larger animals is difficult. (Photo by Glenn King, Ngorongoro Crater, Tanzania)

in some cases totaled as much as 2 h. The direct distance from start to capture could be as much as 1600 m, but the actual distance covered by an individual could be 4000 m. Some cases seemed to suggest intentional coordination of two types: one baboon chased a gazelle in the direction of another hunter, or several baboons pursued the same prey in sequence. A baboon's top speed seemed to be limited to a duration of about 5 min.

The significance of this behavior is subject to a major caveat: there were no other large predators at Gilgil to compete with or endanger the baboons (Strum 1981). This is a situation that would rarely if ever have been encountered by early hominins (Chap. 6). However, the behavior does suggest hunting capabilities available to early hominins when they found ways to deal with other predators, presumably with the development of weapons.

5.4.3 Hunting and Scavenging

Another way to obtain meat is by scavenging, that is, taking it from the carcasses of animals killed by predators or dead from other causes. Archeological evidence and primate analogies support the view that hunting was more common than scavenging in early hominins. Three archeological sites dated to about 2 mya were interpreted as the result of hunting rather than scavenging (Ferraro et al. 2013; see above).

Evidence of butchery indicated that carcasses were acquired in a relatively complete state, providing the hominins with primary access to the flesh and organs. Bovid fossils displayed few or no carnivore tooth marks (see also Parkinson et al. 2021).

Domínguez-Rodrigo et al. (2021) argued for hominin scavenging at a site that they investigated. Baboons scavenge, but the behavior is rare (Watts 2020). Several instances of scavenging were seen at Gilgil, where there were no other predators to compete with the baboons for carcasses (Strum 1981). One report from another site described a single instance of baboons appropriating a bushbuck that a leopard had killed and cached in a tree (Allan et al. 2022). On the other hand, the same study reported a high level of predation by baboons. It also alluded to the absence of baboon encounters with numerous potential prey species, suggesting that the baboons were a key component of several species' "landscapes of fear." Thus, baboon evidence indicates that early hominins obtained most of their meat by means other than scavenging, including foraging and hunting.

An argument that hominins depended on scavenging for meat is that, being bipedal, they could not have chased animals with the speed and agility of baboons. However, baboons demonstrate hunting practices that would have been possible for early hominins. One is the relay chase, such as was practiced by the olive baboons of Gilgil (Strum 1981). Bipedal hominins might have been successful with this tactic against juvenile animals that were mobile but lacked the speed and endurance of adults.

Another possibility is the surround. This has not been reliably reported for hunting by baboons, but the pattern occurs in the mobbing of leopards: if baboons are able to isolate a leopard, "they immediately surround it, alarm calling, and lunging at it, seemingly without fear" (Cheney and Seyfarth 2007:46). Leopards are sometimes injured or killed in such incidents (Altmann and Altmann 1970; see Chap. 6). Leopards are dangerous carnivores and most adult leopards weigh between 40 kg and 90 kg. If baboons can kill a leopard in a surround, early hominins could certainly have used the tactic to kill small or even medium-sized antelopes.

Oliver et al. (2019) added more archeological evidence by comparing bovid mortality profiles at sites located at Kanjera and Olduvai Gorge. The remains of prime adults dominated the bovid profile from the heterogeneous woodland habitat at Olduvai, leading to the inference that the hominins used cover to ambush their prey. On the other hand, juvenile bovids were predominant in the remains from the grassland of Kanjera. In those circumstances, limited cover presumably necessitated opportunistic emphasis on more vulnerable prey, some probably captured after short chases (Oliver et al. 2019). Acquisition of juveniles could have originated in baboon-like behavior of the earliest hominins. Even ambush (Bunn and Gurtov 2014) might have been anticipated by early hominins, according to a baboon analogy. In predation on sheep, goats, and domestic fowl, "the typical hunting strategy involves sitting still until the potential prey is close enough so that it can be leapt at and caught" (Sommer et al. 2016: 74). When two small antelopes ran past an adult male "sitting quietly on a log," he jumped at them (but missed) (Altmann and Altmann 1970).

5.4.4 Meat: Costs and Motivation

In many instances baboons procure meat with relatively little effort, especially in the fortuitous discovery of hidden antelope fawns. However, other lines of evidence indicate significant costs in hunting for meat. This in turn contributes to the inference that baboons are strongly motivated to obtain meat. Along with similar evidence from chimpanzees, this suggests the hominin foundation for elaboration of hunting and scavenging.

Chasing prey can cost baboons significantly in energy expenditure and time away from foraging for plant foods and engaging in social behavior. The ultimate examples are the complex hunts by olive baboons at Gilgil (Strum 1981). Pursuit involved considerable energy expenditure and capture was not necessarily easy. Gazelles that could elude baboons for any length of time were older than infants and almost certainly subadults in some cases.

Prey size is important because hunting entails some degree of control over animals that may struggle and/or flee. The study of Guinea baboons by Goffe and Fischer (2016) provides more specific information. The researchers estimated weights ranging from 10 kg to 14 kg for young antelopes killed by the baboons. Since male Guinea baboons weigh a maximum of about 26 kg, the best case for the hunters was that they were about 2.5 times the size of their prey. This seems to suggest some difficulty in wrestling the prey down. Such difficulties were explicit in the report on the olive baboons at Gashaka that struggled to control young antelopes (Sommer et al. 2016).

Persistence in hunting despite failure is another indicator of motivation. Where pursuit is necessary, unsuccessful chases take up additional time and energy. In the montane chacma baboon study (Allan et al. 2022), 4 of 12 hunts were unsuccessful, 2 of which targeted antelopes. Persistence has another dimension in the case of baboons at Gashaka (Sommer et al. 2016). The very low rate of meat eating may be due to the difficulty of finding prey in the wet forest. The fact that it occurs at all under these circumstances suggests that there is a predisposition to the behavior.

Persistence in the face of cost took a different form in at least one case arising from passive defense by prey rather than flight. Chacmas in the De Hoop Reserve fed on tortoises six times in 13 months, but failed in ten attempts to break the carapaces (Hill 1999).

Motivation for meat eating is further evidenced by baboon behavior in response to possession of a fresh carcass. The interest of others is sometimes expressed passively in the "vulture response" of sitting near the possessor and staring at him (Altmann and Altmann 1970; Sommer et al. 2016). These individuals might be rewarded by scraps left behind. In some of these situations, scraps are taken while the meat possessor is distracted (Allan et al. 2022).

Possessors of carcasses usually resist sharing. Females sometimes groom a male in order to get some meat or an entire carcass (Sommer et al. 2016). Voluntary sharing takes place between individuals with special connections, most often in male–female relationships (Goffe and Fischer 2016; Schrier et al. 2019; Strum

1981). In at least one case an adult female shared with her juvenile son (Sommer et al. 2016).

There are also attempted and successful appropriations. In one case there was "much fighting among the adult males" over an infant gazelle (Altmann and Altmann 1970: 154). In another case two coalition partners obtained a carcass from a third adult male (Sommer et al. 2016).

5.5 Summary and Discussion

Baboon and chimpanzee evidence leads to a strong hypothesis that hominins consumed invertebrate animals from the time of their origin from the LCA. Insects would have been foremost among terrestrial prey. Baboon analogies demonstrate that the earliest hominins could have obtained insects without using tools or otherwise penetrating nests or the ground. Swarming insects, such as grasshoppers and dragonflies, could be snatched from the air with high rates of success, or could be taken from trees. In at least one population, baboons turned over rocks to prey on invertebrates beneath them. These analogies suggest that terrestrial invertebrates could have provided early hominins with a small and probably irregular part of the faunivorous diet. However, this might have had disproportionate significance with regard to protein and/or other nutrients that plants did not provide with the same value, or at all.

Closely associated with lakes and other bodies of water from their beginnings, hominins would have had access to aquatic animals for food. Baboons (and a few other primates) take prey from both fresh and salt waters. Some, such as shellfish, were more difficult to process than insects, but baboons and other primates show that this was possible for early hominins. Baboons also show that fish could be obtained from ponds and the shallow edges of lakes. Some of the fish, dead or dying, are merely gathered by baboons. However, baboons can enter the water to hand-capture live fish.

Baboons also hand-capture terrestrial vertebrates, such as various species of hares and antelopes. Here again, combined with chimpanzee data, baboons provide evidence that the earliest hominins engaged in such behavior without leaving identifiable archeological remains. With regard to the further development of hominin faunivory, there is a key difference between chimpanzees and baboons. The main prey animals of chimpanzees are arboreal monkeys, while baboons find virtually all of their prey on the ground (and occasionally in adjacent waters). In this respect baboons are a better model for early hominin faunivory. Though still capable of some effective arboreal behavior, probably vertical climbing, the hominins would not have had the acrobatic agility of chimpanzees that allows them to capture monkeys in the trees or harass them to the point of falling to the ground. The decline in arboreal capability was probably related to increasing adaptation to terrestrial bipedalism.

Early hominins displayed a variety of bipedal adaptations, none of which were as efficient or speedy as the modern human gait. Even modern humans find it difficult to run down many species of animals. Early hominins could not have pursued prey in the same way as the typical baboon chase. However, baboons display several meat-getting behaviors that could have been used by early hominins. First, the bulk of the meat obtained by baboons comes from accidental encounters with small and helpless immatures, such as infant antelopes in grassy hiding places. Second, relay chases could have brought down fast but quickly tiring animals. Third, early hominins could have surrounded their prey. Finally, they might have learned to ambush their prey.

Potential for ambush is represented in baboons only by rare and rudimentary responses to potential prey. Surrounds are not reliably reported for hunting, but sometimes occur when baboons attack leopards. Relay hunts occur in baboons. It is not clear that the apparent cooperation is conscious, but the behavior pattern is there and available for elaboration, as it might have been for early hominins.

Some mammalian prey of baboons, such as subadult antelopes and sheep, approach 15 kg in weight. This is presumably the limit for baboons, since they struggle to bring these animals down. It is likely to be analogous to the last stage of hominin faunivory before weapons and social coordination made hunting a regular feature of hominin behavior. From that point on, increasingly large animals were taken and archeological evidence for hunting became clear-cut. By about 2 mya the marks of butchery show that hominins ate from the carcasses and the fact that they underlie the marks of carnivore teeth (if any) show that the hominins were there first. Scavenging might have become more important from that point on because weapons and social coordination facilitated competition with large carnivores.

Several lines of evidence indicate the motivational importance of meat to baboons (as well as chimpanzees): (1) They hunt even though it sometimes involves considerable expenditure of time and energy. (2) They persist in hunting despite failures. (3) Individuals show great interest in meat possessed by others, including the vulture response and attempts at appropriation. (4) Meat possessors resist sharing, sometimes taking evasive actions such as climbing trees. (5) Voluntary sharing only takes place within special relationships, such as a long-term affiliation between a particular male and female.

It seems likely that early hominin diets increasingly resembled those of savanna baboons as the hominins underwent two processes: expansion into more open habitats and adaptation to long-term aridification (Chaps. 1 and 2). Eventually the hominins built on that foundation with quantitative changes in their protein sources: more fish, more aquatic invertebrates, more and larger land mammals. The addition of big game hunting, probably by *Homo erectus*, was one of the markers of the end of the early hominin phase of human evolution.

A frequent topic of controversy is the role of females in the kind of hunting society that has just been described. Whenever hunting began to gain importance

among early hominins, it was probably practiced largely by males as is the case among baboons. Some females probably engaged in some hunting, but most females would have been slowed by larger and more helpless offspring than those that characterized their ancestors. However, females could have obtained meat as part of their foraging activities, and bipedalism might have allowed them to accumulate and carry foods such as USOs in sufficient quantities to exchange with males for meat.

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