# Chapter 4
# Subsistence and Stress

## 4.1  Introduction

Long-standing methods for reconstructing the feeding habits of fossil species include the study of jaw function along with tooth size, shape, and structure. However, this work is largely limited to foods that *could* have been eaten. More recently developed methods indicate the kinds of food that were *actually* eaten (Teaford et al. 2023). One such method is the study of dental microwear—microscopic scratches and pits caused by the foods consumed. Stable isotopes, extracted from teeth and bones, provide additional information about food, as well as inferences about the environment that provided the food.

The vital element carbon illustrates stable isotope analysis. Three isotopes of carbon vary in atomic weight due to different numbers of neutrons in the nucleus of the atom. Carbon-14 (used in dating fossils and other items) is unstable, resulting in radioactive decay. Carbon-12 and carbon-13 are stable and maintain a constant ratio in the atmosphere, which is absorbed by plants. That ratio is changed within different plants by alternative processes of photosynthesis. Plants using these processes are grouped as $C_3$, $C_4$, and CAM (the last stands for crassulacean acid metabolism). The altered ratios are preserved in animals (bones, teeth, hair) and provide information about what the animals ate. That in turn implies the kind of environment that the animals were exploiting.

Each of these methods entails complexities and ambiguities, which argues for a "multi-proxy" approach (Teaford et al. 2023). Addition of baboon analogies to this comprehensive approach can provide more detailed hypotheses concerning issues such as which plants were eaten, which parts of the plants were eaten, and what foraging behaviors were needed to obtain them. In discussing models for hominin dietary reconstruction, Paine and Daegling (2023:5) noted that extant papionins occur in a variety of habitats "that are generally associated with ancient hominins"

G. E. King, *Baboon Perspectives on Early Human Ancestors*,

and that both taxa "have been faced with the specific ecological challenges these habitats present."

## 4.2  Dietary Variation and Trends

A major feature of early hominin evolution was a series of dietary shifts, apparently related to both variation across habitats and long-term changes in the environment. Paleoanthropology follows several lines of evidence that trace these variations in broad terms. Baboon analogies suggest important details.

### 4.2.1  Hominin Dietary Shifts

The earliest hominins, represented by *Ardipithecus*, have been characterized as "nearly pure" $C_3$ feeders. This indicates that they subsisted on the products of trees and shrubs in relatively closed woodlands (Martin et al. 2020). *Australopithecus anamensis* may have undergone relatively little change from *Ardipithecus*, adding some variety to the diet of $C_3$ foods with occasional forays into open areas (Bobe and Reynolds 2022; Bobe et al. 2020; Bobe et al. 2022; Martin et al. 2020). However, Quinn (2019) recalculated isotope values for some *A. anamensis* and postulated that the species added a substantial amount of $C_4$ food by foraging across diverse habitats in a mosaic setting. She argued this view to be more consistent with dental features (tooth structure and microwear) that indicate consumption of tough and/or hard foods. Roughly contemporary with *A. anamensis*, an *Australopithecus* species in Chad (classification still somewhat controversial) had a diet that was "predominantly" $C_4$ (Bobe and Reynolds 2022).

Whatever the earlier situation, there is general agreement that the $C_4$ component was significantly expanded in later hominin stages. After about 3.5 mya, multiple hominin taxa in eastern Africa (Martin et al. 2020; Quinn et al. 2021) and southern Africa (Grine et al. 2020; Sewell et al. 2022) began incorporating more $C_4$ foods into their diets. Isotopic evidence and tooth microwear suggested that *A. africanus* was a mixed feeder that may have "effectively straddled different ecotones" (Grine et al. 2020). Carbon isotope analysis from Sterkfontein indicated "a high proportion" of $C_4$ foods in the diet by 2.6 mya if not earlier (Sewell et al. 2022). Phytoliths extracted from the teeth of *A. sediba*, dating to about 2 mya, also provided evidence for a significant amount of $C_4$ food (Reynolds 2022). These developments are thought to be associated with increasing exploitation of "savannas" (recall that savanna is a broad term that can include any habitat with significantly reduced tree cover).

The diet of earliest *Homo* in South Africa resembled that of *A. anamensis* until a significant increase in $C_4$ took place after 1.7 mya, which was about a million years after the genus first appeared (Bobe and Reynolds 2022; Patterson et al. 2019). It

seems that subsistence analogies from baboons can be useful in reconstructing early *Homo*, as well as its predecessors. This view is consistent with a gradual transition from *Australopithecus* to *Homo*, as postulated by Kimbel and Villmoare (2016; see Chap. 1). The shift after 1.7 mya was probably influenced by increased consumption of animal foods, which will be discussed at length in Chap. 5.

### *4.2.2   Generalists and Specialists*

All of the hominin situations postulated in the preceding section are paralleled by variations in behavioral ecology across baboon populations. One of the most important points that emerges from comparative study is that baboons tend to favor forest and woodland habitats like those that have been postulated for *Ardipithecus* and its predecessors. The yellow baboons of Tana River in Kenya provide an example. The forest there covers less than 9% of the area that the baboons regularly use, but 42% of food consumption observations were made in the forest. Similarly, forest components of habitat were used more than predicted by chance by olive baboons in Ivory Coast (Kunz and Linsenmair 2008) and Guinea baboons in Senegal (Zinner et al. 2021). Some baboons are described simply as "forest dwelling" (Johnson et al. 2012). Forest and woodland baboons make extensive use of $C_3$ foods such as fruits and flowers, but most of them spend a significant amount of time foraging in various kinds of savannas. Thus, baboons can provide analogies and scenarios for various early hominins that pertain to details of their subsistence behavior.

Paleoanthropology demonstrates hominin expansion into more open habitats with different food resources. Baboon analogies suggest how the hominins managed the change. According to researchers who carried out a 5-year study of yellow baboons in Mikumi National Park, Tanzania, "Eclectic feeding and selectivity are a powerful combination; together they probably go a long way toward explaining the baboons' success over a large part of a continent with diverse ecosystems" (Norton et al. 1987:115). This is a scenario that is readily transferred to the expansion of the hominins.

Codron et al. (2008) analyzed the feeding ecology of chacma baboons in South African savannas and found that they were like "australopiths" in consuming substantial amounts of $C_4$ foods. Attributing this to parallel shifts from wooded habitats to open savannas, they cautiously inferred that "there is some benefit in an analogous comparison." However, they posited that differences between hominins and baboons, rather than similarities, might provide valuable information. For example, they found baboons to be less isotopically variable than *Australopithecus*, which suggested to them that the hominins were even more generalist than the baboons.

This is an important difference with regard to the *total* diets of hominins and baboons. However, it allows for useful similarities in their *basic* foods or food categories. Furthermore, many or most modern baboons are probably at least as generalist as "nearly pure" $C_3$ feeders such as *Ardipithecus* and perhaps *A. anamensis*. Comparative study of extant baboons can probably help us to understand the stages

by which earlier hominins increased the breadth of their diets. Different extant baboon populations suggest the changes that took place as hominins expanded from woodlands into more open areas or were confronted by more open habitats resulting from aridification.

Norton et al. (1987) pointed out that the breadth of baboon diet was easily underestimated because of studies that were too short or focused on other matters. For example, a distinguished primatologist listed 65 plant species eaten by the baboons that he studied; then increased the number to 94 after 1 more year of research. Norton and colleagues identified 185 species of baboon foods in one locality after 5 years of study. Long-term fieldwork at Amboseli has led to the conclusion that baboons can subsist on almost any plants (Alberts and Altmann 2007). This kind of flexibility must have been necessary for hominins to survive in diverse habitats from eastern to southern Africa (Paine et al. 2019) and in diverse localities within those regions (Henry et al. 2019).

Selectivity is the complementary dimension of subsistence in both baboons and early hominins. Paine et al. (2019) posited that many early hominins were probably selective feeders, eating particular plants and plant parts depending on habitat and season. The baboon evidence strongly supports this view. In the study by Norton et al. (1987), 185 food species exploited by the baboons were selected from at least 700 possibilities. Furthermore, in consuming approximately 80% of their food species, the baboons ate only one or two parts of the plant. They ignored other parts or removed them by stripping or peeling. In the Budongo Forest of Uganda, olive baboons strongly emphasized a few species out of the 51 food plants identified in a 6-month study (Okecha and Newton-Fisher 2006). Forest dwelling baboons at Kibale in Uganda ate some parts and discarded others (Johnson et al. 2012).

Norton et al. (1987) summed up the baboon pattern in this way: baboons are adapted to consuming a wide array of foods and make choices among them in the context of "an ever-changing mosaic" of possible foods in combinations that satisfy their energetic and nutritional needs. Such a suite of adaptations could well have propelled early hominins on the way to their expansion throughout most of Africa in the context of diverse and changing environments. Within this broad framework, extant baboons provide more specific analogies for early hominin selection and treatment of particular food species.
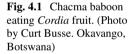
## 4.3  Food Sources

Stable isotopes, carbon and others, provide only a first approximation to the ecology and behavior of subsistence. A variety of foods can account for each of the isotopes. Some reasonable hypotheses and guesses can be provided by paleoenvironments and chimpanzee analogies. Baboon evidence can add more detail for a wider variety of contexts.

### 4.3.1  Fruit

Hominins apparently originated as $C_3$ feeders in woodlands and forests, where fruits can provide a large portion of such a diet. Given the hominin phylogenetic relationship with chimpanzees, the latter often termed "fruit specialists," hominins probably derived an emphasis on this source from the Common Ancestor. Most baboon populations are consistent with this scenario (Fig. 4.1, Table 4.1). The chacma exception in the table is probably due to the colder and drier conditions at the southern tip of Africa.

In an example from West Africa (Ivory Coast), two troops of olive baboons of different sizes were observed in a savanna-forest mosaic (Kunz and Linsenmair 2008). Population density was lower than expected for this kind of habitat (1.2 baboons per km$^2$), which was hypothesized to be related to the "highly frugivorous" diet. The baboons spent about 50% of their feeding time on the fruits and seeds of many plant species and devoted relatively little time to more abundant but lower quality foods. Both troops, though very different in size, had comparatively large home ranges. This allowed them to cope with the irregular availability of fruit as compared with other plant foods. They used the forest more often than expected by chance, presumably to pursue the fruit diet.

Across the continent, in Ethiopia, another population of forest-living olive baboons also demonstrated a preference for fruit (Mullu and Solomon 2016). Fruit was the largest portion of their diet (about 28%), followed by leaves (about 20%). Figs of a sweet tasting variety provided a variety of nutrients. In contrast to

**Fig. 4.1** Chacma baboon eating *Cordia* fruit. (Photo by Curt Busse. Okavango, Botswana)

**Table 4.1**  Food preferences of forest/woodland baboons

| Species | Olive baboons *Papio anubis* | Olive baboons | Olive baboons | Olive baboons | Hamadryas baboons | Chacma baboons *P. ursinus* |
|---|---|---|---|---|---|---|
| Location | Comoé Park Ivory Coast | Kibale Park Uganda | Arba Minch Ethiopia | Budongo Forest Uganda | Borena-Sayint Ethiopia | Tokai Forest South Africa |
| References | Kunz and Linsenmair (2008) | Johnson et al. (2012) | Mullu and Solomon (2016) | Okecha and Newton-Fisher (2006) | Ibrahim et al. (2023) | Johnson et al. (2013) |
| Method | Feeding time | Feeding events | Total scans | Feeding time | Scan of activities | Focal subject |
| Favored foods | Fruit 29% Grass 29% Seeds 18% Flowers 6% Leaves 5% | Fruit 46% Stems 33% Tubers 7% Leaves 7% Seeds 4% | Fruit 28% Leaves 20.5% Grass 15.5% Bark 15% Roots 9.7% | Fruit 34% Leaves/ Grass 17% Seeds 13% Garbage 17% Misc. 19% | Fruit 32% Graminoid blades[a] 21% Young leaves 13% Cereals 9% Flowers 6% | Leaves 58% Seeds and nuts 15% Mushrooms 15% USOs 9% Fruit 2% |

The preponderance of olive baboons is an artifact of the literature that lists food preferences. Relevant material from other baboon species is discussed in the text
[a]Graminoids are herbaceous plants with grass-like leaves

hamadryas baboons in arid lowland habitats, a hamadryas population with access to "large areas of natural forest" in the Ethiopian highlands had a diet in which fruit was the leading component (Ibrahim et al. 2023).

Fruit trees were of special significance in a study of competition between humans and kinda baboons on the fringe of a national park in the D.R. Congo (Kazaba et al. 2020). The kinda baboons ate fruit in all nine of the tree species that they exploited, especially the wild loquat tree (*Uapaca kirkiana*) and the monkey orange tree (*Strychnos cocculoides*). The researchers recommended domestication of these species in order to alleviate the competition.

The taste for fruit in wild baboons is illustrated by their response to the intrusive prickly pear cactus (*Opuntia stricta*). The fruits, with sweet low-acid pulp, became a baboon favorite (Schoeninger et al. 2019). Experiments with olive baboons demonstrated that they were "among the most sugar-sensitive nonhuman primates tested so far" (Laska et al. 1999:25). The researchers inferred that this might be a criterion for food selection. Since baboons share this taste with humans, it seems likely that their responses are analogous to those of early hominins.

An important point related to this food choice is that baboons generally prefer forest habitats when available. This bears on an old controversy about whether hominins expanded into savannas to take advantage of new opportunities or were forced to do so by changing conditions. The fact that baboons prefer forests despite their success in savannas suggests that early hominins were forced to adapt to savannas.

### 4.3.2   High-Protein Plants

Early hominins in mosaic environments, despite a preference for forest or wood-land, probably used the savanna components to add $C_4$ foods to the diet (Bobe et al. 2022; Martin et al. 2020; Quinn 2019). Baboons are consistent with this scenario and indicate that proteinaceous plants were an important factor. Bentley-Condit and Power (2018) reported on the food of yellow baboons in a partially forested habitat. Comparing forest to savanna samples, they found the savanna items to be higher in crude protein and minerals. Applying a narrower focus to the typically eclectic diet, they examined the top 15 foods. The savanna items had significantly higher crude protein, ash (an indicator of mineral content), magnesium, and manganese. Forest items were higher in gross energy.

Johnson et al. (2017) studied olive baboons in a "heterogeneous forested habitat" and found a pattern of "protein prioritization." They followed individual females and quantified nutrient intake from both feeding observations and nutritional analy-sis. The baboons maintained a 5:1 kilocalorie ratio of nonprotein energy to protein, based on annual intake. As food availability changed seasonally, the baboons main-tained protein intake while exploiting energy sources where possible. The savanna baboon diet contains a greater proportion of protein-rich foods than is the case of sympatric ungulates (Codron et al. 2006).

Protein prioritization is also displayed by humans, with kilocalorie/protein ratios comparable to the baboons. This suggests an evolved ecological strategy that allowed both lineages to exploit energy in multiple environmental contexts (Johnson et al. 2017). In modern human populations, with a different pattern of food avail-ability, protein prioritization seems to cause some humans to overconsume energy as they try to maintain protein intake (Johnson et al. 2017). It is considered a central factor in obesity and associated cardiometabolic disease.

### 4.3.3   Savanna Plants

Another evaluation of potential hominin foods was developed with reference to chimpanzees, but is also relevant to baboons. Copeland (2009) noted the evidence that early hominins occupied relatively more open and arid savannas than those in which any chimpanzees live. She compared plant foods at savanna chimpanzee sites with those in semiarid savannas that are not inhabited by chimpanzees but are potentially similar to environments occupied by some early hominins. In the semi-arid savanna, trees that produce fleshy fruits are manifested in fewer species and lower densities. The most abundant potential hominin plant foods are seasonally available *Acacia* flowers and seeds/pods, grass seeds, and the underground parts of marsh plants. Copeland explicitly cited baboon diets as demonstrating the value of these foods.

### 4.3.4    Underground Storage Organs

Underground Storage Organs (USOs) are starchy underground organs in which many plants retain carbohydrates and water during periods that are unfavorable for growth (Dominy et al. 2008). USOs are often classified and named according to their structure and orientation in the ground, which can be confusing. Most are stems of some kind. *Corms* are swollen and compacted stems. *Rhizomes* are horizontal stems that can produce roots and shoots. *Tubers* are generally thickened roots or swellings on roots. *Bulbs* are modified shoots. Some plants with USOs use the $C_3$ pathway and others use the $C_4$ pathway. Regardless of category, the USOs of many plants are rich in starches that the body can convert into sugars that are essential for brain development and maintenance (Macho 2016).

Dominy et al. (2008) evaluated the various USOs as to their suitability for consumption by early hominins. Rhizomes are too tough to have been a useful food for hominins under most circumstances, although the rhizomes of some aquatic plants are an exception. Tubers are more plausible, but few tuberous plants use the $C_4$ pathway. Corms and bulbs are the most likely hominin foods and conform to previous authors' hypotheses in this respect. They are widespread, low in fiber, more likely to be found in $C_4$ plants, and are sought by very few other animals. They are also gritty, which is consistent with wear on hominin teeth. Bulbs are the tougher and more elastic of these two forms, leaving corms as the most valuable for the subsistence of most hominins.

Direct evidence for USO consumption by early hominins comes from Kanjera South, where use-wear on the tools of early *Homo* in a savanna environment indicate the processing of tubers. Dense patches of tubers in this location offered a significant source of food (Bishop et al. 2022). Preparation with tools explains the use of tubers, which are tougher than corms or bulbs.

USOs occur in the diets of forest and woodland baboons, but with limited significance. They occur among the top listed foods for three of the five populations in Table 4.1, but as relatively minor components. In the savannas of eastern Africa, USOs were more important. Grass USOs were a rich source of nutrients, as well as water, during the dry seasons (Altmann and Altmann 1970; DeVore and Washburn 1963).

Macho (2016) emphasized the significance of USOs for the spread of *Australopithecus* into more open and fragmented habitats with greater seasonality. USOs made up for the decreased supply of fruit by offering "energy-dense" foods that were also high in nutrients and water content. She compared hominins with baboons as to the benefit of this source: eclectic feeders in a similar range of environments, needing USOs to compensate for less fruit as a supply of glucose necessary for the growth and maintenance of relatively large brains. Most animals break down starches through the action of salivary amylase and baboons have a concentration of the enzyme that is greater than twice that of modern humans (Macho 2016). Hominins might have evolved to a similar level if they had not begun to use tools and fire to process USOs.

### 4.3.5  Grasses and Sedges

Fruit may not have been the only attraction in forests and woodlands. Henry et al. (2019) collected plant samples from several localities in South Africa in order to explore the implications for early hominin use of similar habitats. One of their important findings was that woodland habitats were more nutritionally valuable than anticipated. Grasses from these wooded environments were generally good resources with relatively high protein content and low in chemical and mechanical contents that interfered with feeding. This could have been particularly important in the dry season, when protein content among all of the sampled plants was lower. Despite strong temperature and rainfall variation between seasons, most nutritional properties other than protein remained relatively constant.

Hominins in East Africa around 3 mya inhabited a vegetational mosaic in which grasslands were becoming more common (Bobe et al. 2022). By 2 mya some early *Homo* were living in open savannas where grass was the predominant vegetation (Bishop et al. 2022). At about the same time, South Africa underwent increasing aridity that led to a regional expansion of grasslands. Strontium/carbon ratios suggest a higher level of either insectivory or "grazing" (Sewell et al. 2022). Baboon analogies support both insects (Chap. 5) and grasses as hominin foods (Figs. 4.2 and 4.3).

Paine et al. (2018) agreed with previous writers that early hominins almost certainly paralleled baboons in making grass seeds part of their broad dietary repertoire. However, noting the limited seasonal availability of grass seeds, they focused



**Fig. 4.2** Yellow baboon foraging in grass. (Photo by Oliver Paine. Amboseli National Park, Kenya)

**Fig. 4.3** Yellow baboon eating the base of a grass stem. (Photo by Oliver Paine. Amboseli National Park, Kenya)

on grass *leaves* as potential hominin food. Grass leaves are the single most abundant $C_4$ resource in modern African savannas. Analysis of savanna grass leaves for their nutrient value and physical characteristics showed that species differed significantly with regard to traits that would have been favorable for the hominin diet. Some grass blades would have been good food sources because they were less tough, lower in fiber, and higher in protein.

Paine et al. (2018) were explicitly encouraged in their work 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 (DeVore and Washburn 1963). 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 (Macho 2015).

The grass-like sedges that grow in watered localities have also been proposed as important food sources for hominins (Lombard 2022; Paine et al. 2018). At Kanjera South in Kenya, early *Homo* lived in an arid savanna and the use-wear on their tools indicates the processing of herbaceous plants such as sedges (Bishop et al. 2022). The high protein content of grasses and sedges in the wetlands of Amboseli in Kenya during the dry season may be one reason that baboons have done relatively well there, even during some periods of severe drought (Alberts and Altmann 2007; Paine et al. 2018). Grasses with bulbs and sedges with corms are likely to use the $C_4$ pathway. They are common over much of eastern and southern Africa, the areas where most hominin fossils have been found (Dominy et al. 2008).

Schoeninger et al. (2019) doubted the significance of grasses for baboons and, therefore, the relevance of baboons to early hominins in this context. They cited references compiled by Crowley et al. (2010) for isotope analysis of baboon teeth that showed little or no $C_4$ intake. Schoeninger and colleagues accounted for the

small amounts of $C_4$ evidence as coming from intrusive sources: consumption of crops or fruit of the intrusive prickly pear cactus. On the other hand, isotype analyses by Codron et al. (2008) found that baboons eat substantial amounts of $C_4$ foods, comparable to the $C_4$ proportion of the *Australopithecus africanus* diet.

Most behavioral studies, especially in eastern Africa, have reported grasses to be an important part of the baboon diet (e.g., Altmann and Altmann 1970; DeVore and Washburn 1963). They stripped the seeds with their fingers or mouths, exploiting a highly nutritious food during dry seasons. Baboons ate grass blades after wet seasons, when the blades were young and green.

### 4.3.6   More About Plant Foods

The varied ecologies of baboon populations suggest ways in which hominins might have augmented the basic foods. As eclectic feeders, baboons are able to include valuable but rarer food sources when they become available. Seeds from fruits and grasses are important in the diet of baboons (Table 4.1) and presumably in the diet of early hominins. However, some are more valuable than others. On the Laikipia Plateau in Kenya, baboons consumed *Acacia* seeds with protein/fiber ratios almost five times higher than those assessed for other plants by Paine et al. (2019). That is, they were highly nutritious and very easy to digest. These seeds constituted only about 3% of the diet, but this may underrate their seasonal nutritional value.

Yellow baboons in Amboseli National Park spent long periods of time feeding on exudates from fever trees (*Acacia xanthophloea*) and, exemplifying baboon selectivity, paid little attention to the umbrella trees of the same genus (*A. tortilis)* (Hausfater and Bearce 1976). Fever trees produce greater quantities of exudate, and chemical analysis indicated that it is probably composed of a complex polysaccharide that contains at least four sugar constituents—potentially nutritious for baboons and other animals. In contrast, low solubility and apparently low carbohydrate content suggest that umbrella tree exudate has little nutritional value. Furthermore, its taste (which is unpleasant to humans) suggests that it contains toxic compounds. Fever tree gum is tasteless and odorless for humans. Early hominins could presumably have distinguished between these two potential foods as readily as baboons and humans.

Bark stripping by primates and other animals was investigated with regard to its commercial significance, but the results have implications for baboon ecology and its relationship to early hominin subsistence behavior. Thirteen primate species have been recorded stripping bark from trees of commercial value worldwide, but three species are responsible for most of the damage in large-scale plantations (Di Bitetti 2019). The two Old World species are Sykes monkeys (*Cercopithecus albogularis*) and chacma baboons. Yellow baboons are also implicated, but in fewer reports. Actions to mitigate this problem, including the massive killing of primates, have proven ineffective in the long term, which seems to suggest that there is some compelling reason for the behavior.

The most frequently cited hypothesis for primate bark stripping is that they eat soft bark when or where their natural food is scarce. However, this hypothesis is not generally supported by empirical evidence. Instead, *Eucalyptus* bark may be sought for its high sodium content. Pines are apparently bark stripped to consume the sugary phloem during their growing season (when bark is presumably more easily peeled off) (Di Bitetti 2019). This evidence suggests that bark stripping can be valuable for subsistence whether other foods are scarce or not.

### 4.3.7  Toxic Plants

In concluding their comparative analysis of protein/fiber ratios, Paine et al. (2019) noted that hominins might have been influenced by other important nutrients, including lipids and water. Codron et al. (2006) reported chacma baboon consumption of the succulent but toxic species *Euphorbia ingens* and they cited other accounts of baboons in various localities consuming the same species or at least the same genus. The baboons might be immune, but this would raise the question of why immunity would have evolved. Codron and colleagues noted that these succulents are high in lipids and water. Since water was plentiful for the baboons in question (as it would have been for many woodland hominins), they concluded that lipids were the most plausible factor for consuming these toxic plants.

Yellow baboons in Mikumi Park, Tanzania, occasionally fed from the cassod tree (*Senna siamea*), which contains a variety of toxic compounds, including a trypsin inhibitor that causes severe digestive distress in humans and other mammals. The baboons ate seeds from the tree, but no other parts. The quantity was small, being consumed by individuals during less than 1% of follows (Kitegile 2022). However, consumption was concentrated during the latter part of a long dry season (5–6 months). The tree increased seed production during this time when other foods became scarce, that is, a fallback food.

To interpret the behavior of these baboons, Kitegile referred to the work of Altmann (1999) on yellow baboon consumption of *Vachellia tortilis*, another tree that contains a trypsin inhibitor. In both cases adult females and subadults processed the seeds before eating, while adult males rarely did. Removal of the seed coat reduced the toxin but also reduced the available protein. Males were able to tolerate the toxin because of their greater body size and longer digestive tract. The molecule of the trypsin inhibitor, which is a protein, may split during a long enough period in the digestive tract and allow the absorption of more amino acid and less toxin. Early hominins were larger than extant baboons and might have been more able to take advantage of such fallback foods.

## 4.4  Ingestion of Other Substances

Baboons ingest substances other than plants or animals, perhaps for certain nutrients and perhaps for other health reasons. Early hominins, living in similar environments, are likely to have had similar problems and might have responded in the same way.

### *4.4.1  Geophagy*

Geophagy, the consumption of soils and clays, is common among humans and other primates (Pebsworth et al. 2018). Pebsworth et al. (2011) continually monitored the largest and most frequently visited geophagy sites in their study area with camera traps and recorded visits by baboons on almost half of 545 days. During 3500 baboon visits, camera traps captured almost 60 h of geophagy. The baboons spent more time ingesting white alkaline soils with high percentages of clay and fine silt, which contained higher concentrations of sodium, than acidic soils that contained higher concentrations of iron. Pregnant females spent more time in consuming soil than baboons of any other age class, sex, or reproductive state. The soils in question would be effective at alleviating gastrointestinal distress and possibly supplementing minerals for all age/sex classes, but might also have met more specific age/sex requirements. The full distribution of geophagy in baboons is unknown but reports include other chacma populations as well as olive and yellow baboons (Pebsworth et al. 2018).

### *4.4.2  Medicinal Plants*

Chimpanzee consumption of medicinal plants is well known. Some baboon evidence augments the hypothesis that such behavior may have benefitted early hominins. Scientists studying hamadryas baboons at the Awash Falls in Ethiopia noted that although the desert date tree (*Balanites aegyptiaca*) grew all around the falls, only the baboons living below the falls ate the tree's fruit. These baboons were exposed to a parasitic worm found in water snails and the desert date fruit can repel these snails. Baboons living above the falls were not in contact with the water snails and therefore had no need of the presumably medicinal fruit (Admassu et al. 2013).

## 4.5  Foraging and Stress

Life in forests and woodlands might have been relatively easy for hominins, though there must have been some stresses, including seasonal scarcity of some foods (and danger from predators, see Chap. 6). To the extent that they foraged in savannas,

hominins would have encountered new sources of stress resulting from changes in diet and more exposure to the sun. Baboons demonstrate solutions that hominins might have found.

### 4.5.1  Dietary Stress

Paine et al. (2019) reviewed a history of studies leading to the conclusion that many hominin habitats were "characterized by stark seasonality and mosaic habitats, just as modern African savannas are today." They followed Copeland's (2009) comparative study of chimpanzee habitats to the conclusion that early hominins could not have depended on fruit to the extent that their hominoid ancestors did, and probably shifted to a diet more like that of most baboons. This led Paine and colleagues to perform nutritional analyses of plants growing in eastern and southern savannas across both wet and dry seasons. They discovered a general decline in protein/fiber ratios during dry seasons. Most important for this discussion, they found dry season increases in the protein levels of foods like those that are often heavily consumed by baboons: sedges, grasses, and underground plant organs.

The role of feeding problems in stress is suggested by a seminatural experiment resulting from food made available by humans. Lodge et al. (2013) measured hormonal levels in two troops of olive baboons in the same population. The troops faced similar ecological challenges, but differed in that one troop augmented its diet by raiding crops. Based on detailed feeding observations and nutritional analysis of food samples, the crop-raiding troop experienced 50% higher energy intake rates and 50% lower glucocorticoid levels (indicating stress), compared to the troop that did not exploit crops. Energetic stress in the non-raiders was associated with elevated progesterone levels and lower reproductive output. Variation from richer to poorer natural food sources, either geographic or temporal, might have had similar effects on hominin populations.

### 4.5.2  Heat Stress

To the extent that early hominins spent time in open areas rather than shaded woodland, they would have been subjected to heat stress. Hominins evolved distinctive adaptations for coping with this problem, the most obvious being perspiration. Humans have by far the highest eccrine sweat gland density among primates, resulting from multiple interacting mutations (Aldea et al. 2021).

How might early hominins have coped with heat stress before distinctively human adaptations appeared? Wheeler (1991) posited that bipedalism provided relief from heat. The major benefit would have been reduction in the surface area of the body directly exposed to the sun. In addition, windspeeds are higher and air temperatures lower away from the ground, both increasing the rate of heat

dissipation. Wheeler argued that the drastic adaptation of bipedalism would have been essential for a large-brained primate under such conditions.

Baboons remained quadrupedal (and furred) while becoming the most successful primates in colonizing the African savannas (Mitchell et al. 2009), which casts some doubt on Wheeler's hypothesis. The baboon analogy can be questioned on the basis of the fact that baboon brains are much smaller than those of early hominins. On the other hand, a key feature in favor of the comparison is that baboon brains are like human brains in that they lack special mechanisms (such as are found in other animals) to cool them (Hill 2006; Maloney et al. 2007).

The presence of heat stress, and successful adaptation to it, are both represented in a study by Gesquiere et al. (2008). Measurement of hormone levels in female baboons confirmed seasonal heat stress, yet they were able to reproduce throughout the year. Baboons cope with heat by means of behavior patterns that are simple and could easily have been discovered and adopted by early hominins. They rest in shade as much as possible (cf. Wheeler 1994), especially during midday , when they also engage in a drinking session that facilitates evaporative cooling (Hill 2006). Even in savanna habitats, some shade trees are available and are incorporated into the ranging pattern of a troop (Fig. 4.4). Baboons occasionally sleep in caves (Hamilton 1982; McGrew et al. 2003), which may provide thermoregulation. Measured by scientists, the temperature in one cave remained steady and mild



**Fig. 4.4**   Chacma baboons resting in the shade under a tree at midday. (Photo by Glenn King. On the road near Mkhuzi, South Africa)

compared to outside conditions (Barrett et al. 2004). Chacma baboons seem to be more prone than other *Papio* species to enter caves, which may be due to more extreme temperature variation in southern Africa.

### 4.5.3   Dehydration

Humans and other terrestrial animals must maintain a tight balance of water gain and water loss each day in order to survive (Pontzer et al. 2021). Pontzer and colleagues designed a comparative study to investigate the phenomenon in humans. It measured water turnover in five human populations (including hunter-gatherers in semiarid savanna) and all three genera of great apes (housed in zoos and rainforest sanctuaries). Controlling for external factors, the researchers found that water turnover was 30–50% lower in humans than in apes despite the loss of water through sweating. Water stress apparently led to previously unknown water conservation adaptations in hominin physiology.

Pontzer and colleagues turned to baboons to expand their perspective with naturalistic information. They characterized water sources as "an ecological tether" for savanna baboons that constrains daily travel (they noted that the same seems true of "savanna" chimpanzees). This implies that at some point hominins began to evolve mechanism(s) for reduced water demand. The researchers related this to the appearance of the external nose in early *Homo* at about 2 mya. This structure reduces water loss and has been proposed as a water conservation adaptation. The hypothesis is consistent with increasing association between early *Homo* fossils and dry, open paleoenvironments.

The hypothesis of Pontzer and colleagues suggests two phases in the comparison of hominins with baboons. The first phase is defined by four million years or more (during which external noses had not yet evolved) when hominins were presumably "tethered" to water sources. In the second phase, beginning about 2 mya, hominins evolved one or more unique mechanisms for water retention as they penetrated farther into open environments and evolved a human-like hunting and gathering adaptation.

Like baboons (and chimpanzees) in woodland habitats such as Gombe National Park in Tanzania, early hominins could drink water from a variety of sources while moving around in response to food availability (Ransom 1981). With expansion into more open areas, water must have become a more limiting resource. However, the "tether" would vary in strength from time to time and place to place. Yellow baboons at Amboseli, for example, went without drinking on 3 of 19 days and drank only once on 11 days (Altmann and Altmann 1970).

Variations in water availability are associated with variations in baboon behavior that suggest further analogies with early hominins. Where water is scarce, for example, troops may converge on water sources and conflicts sometimes occur (Altmann and Altmann 1970). Another response to scarcity (and perhaps to pollution) is to dig holes to obtain water (also done by some chimpanzees).

In more recent work at Amboseli (Paietta et al. 2022), the baboon response to artificial wells indicates an intense need for water. They accessed the wells during dry periods and extended their range to encompass new wells when older ones had dried up. The baboons continued use of the wells, despite danger from pastoralists and their dogs (over a period of years, one-third of all adult deaths were linked to these encounters).

## 4.6   Summary and Conclusions

Feeding habits of fossil species can be reconstructed in several ways. Visible features of the teeth and chewing apparatus show what kind of foods the animals *could* have eaten. Two approaches provide evidence for the general types of food that they *actually* ate. Microwear analysis examines the marks that food left on fossil teeth. Stable isotope analysis reveals the chemical evidence of food types left in the teeth and bones. The latter depends on stable ratios between variants of elements such as carbon. These are absorbed by plants and altered by the processes of photosynthesis. For example, the $C_3$ photosynthetic pathway usually represents foods such as fruits. Grasses are often indicated by the $C_4$ pathway. However, there are overlaps (e.g., grasses may be $C_4$ or $C_3$) and these are still rather broad categories of food. Baboon analogies can suggest specifics about the particular foods that were exploited and how they were obtained.

The earliest hominins, inhabiting forests and woodlands, depended almost entirely on $C_3$ foods. Later hominins, such as *Australopithecus*, incorporated more $C_4$ foods into the diet as they expanded into savannas, or the environment around them changed into savanna. Paleoanthropologists have postulated that this transition was possible because hominins could choose from a wide variety of foods and could select the most nutritious parts of those items. Some have alluded to the fact that baboons, spanning very similar environments, are also eclectic and selective feeders. Baboons are like humans in that they tend to adjust their food intake to maximize protein, so this almost certainly was a key feature of early hominin diets as well.

Fruit must have played a large role in the diets of early hominins. This inference from chimpanzee ecology is strongly supported by baboon analogy. Fruit is the preferred type of food for all baboons wherever it is available in any significant quantity. However, the baboon evidence indicates important changes that took place as hominins expanded into more open and fragmented environments. Grass probably became more important. Baboons eat grass seeds and blades. They also eat the underground storage organs (USOs) of grasses and other plants. These are structures in which plants retain water, starch, and other nutrients when conditions are not right for the use of these substances for growth. Hominins were probably like baboons in excavating these plant organs, especially during dry season. The starch from USOs can turn into sugars that support the growth and maintenance of large brains.

Some baboon populations consume less common foods, and early hominins might have augmented their diets with comparable items. These include acacia seeds with unusually high protein content; tree exudates that may contain polysaccharides with diverse sugar components; and soft tree bark that might be high in sodium. Some baboons eat toxic items that may supply them with important nutrients such as lipids.

Baboons, other primates, and many extant human populations ingest various clays and soils. These items might provide sodium and/or some essential minerals. Some might also have medicinal properties. The latter may also be true of some of the plants that baboons consume. Possible functions of such ingesta include relief of gastric distress and resistance to parasites. Early hominins might not have eaten the same items, but might well have had comparable ones in their diets.

Foraging animals encounter various stresses as they seek food. Stresses would certainly have increased as hominins dealt with more open and fragmented habitats, culminating in savannas with only scattered trees. Baboons demonstrate the stresses in this range of environments and some of the ways in which early hominins might have coped with them.

Food is and was less readily available in savannas, especially during dry seasons. The flexibility of the eclectic/selective subsistence adaption, as seen in baboons, would have helped to alleviate the problem. One specific solution to dry seasons, underground storage organs, was probably available to most hominin populations.

With minimal tree cover, heat would have been a major stress, especially dangerous for brains without the defensive mechanisms evolved by other savanna mammals. Baboons adjust with behavioral patterns that could easily have been adopted by early hominins: use of shade whenever available, midday rest, and occasional sheltering in caves.

In dry seasons water would have been a "tether" for early hominins, as it is for baboons. Baboons illustrate the results of this constraint on behavior. One concomitant is reduced foraging due to limitations on travel. Another is the convergence of separate social groups at water sources, potentially resulting in complex social interactions, some hostile, that could be avoided during other times of the year.

Two vital topics have been left out of this chapter. One is the role of animal prey in the expansion of $C_4$ foods. This extensive subject is covered in the next chapter. The other topic is the stress caused by predators while baboons are foraging and even when they are sleeping above the ground. This is the subject of Chap. 6.

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