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BLOOD, BULBS, AND BUNODONTS: ON EVOLUTIONARY ECOLOGY AND THE DIETS OF *ARDIPITHECUS*, *AUSTRALOPITHECUS*, AND EARLY *HOMO*

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Abstract

Beginning with Darwin, some have argued that predation on other vertebrates dates to the earliest stages of hominid evolution, and can explain many uniquely human anatomical and behavioral characters. Other recent workers have focused instead on scavenging, or particular plant foods. Foraging theory suggests that inclusion of any food is influenced by its profitability and distribution within the consumer's habitat. The morphology and likely cognitive abilities of *Ardipithecus*, *Australopithecus*, and early *Homo* suggest that while hunting and scavenging occurred, their profitability generally would have been considerably lower than in extant primates and/or modern human hunter-gatherers. On the other hand, early hominid diet modelers should not focus solely on plant foods, as this overlooks standard functional interpretations of the early hominid dentition, their remarkable demographic success, and the wide range of available food types within their likely day ranges. Any dietary model focusing too narrowly on any one food type or foraging strategy must be viewed with caution. We argue that early hominid diet can best be elucidated by consideration of their entire habitat-specific resource base, and by quantifying the potential profitability and abundance of likely available foods.

Keywords

human origins; primate behavior; hunting hypothesis; scavenging; plant foods; meat; underground storage organs; optimal foraging theory

Introduction

The Evolution of Human Diet

Anthropologists rarely agree on anything, although some may take issue with this statement. Moreover, even in a field so ripe with contentiousness, many of the most enduring controversies, particularly in biological anthropology and archeology, have involved the evolution of human diet. This is illustrated by the vast range of hypotheses relating to the ecological lifeways that could have characterized our early hominid ancestors. These include stem hominids such as *Ardipithecus*, gracile and robust *Australopithecus*, and early *Homo*

up through the initial appearance of *H. erectus*. A common theme, becoming more and more apparent as time goes on, is that arguments often gravitate toward proposing the one “key” foraging strategy and/or food type that provided the impetus for important aspects of hominization, such as the evolution or refinement of bipedal locomotion (e.g., Jolly 1970; Hunt 1994; Bramble and Lieberman 2004), marked changes in social structure or life history (e.g., Wrangham et al. 1999; Kaplan et al. 2000), and cerebral expansion or reorganization (e.g., Crawford et al. 1999; Bunn 2007). Another trend is that relatively specialized and unique diets are increasingly being described for the above hominid groups or even putative hominid species (Ungar and Sponheimer 2011; Henry et al. 2012). These efforts contrast somewhat with more traditional, “classic” accounts of early hominid foraging, possibly excepting robust australopithecines, as being strongly omnivorous and exceedingly flexible (Bartholomew and Birdsell 1953; gracile australopithecines, Robinson 1968).

Some “prime-mover” models have characterized early hominid diet as largely meat-based—or at least have emphasized the importance of this resource category—with spoils garnered from hunting (e.g., Hill 1982; Stanford 1999; Pickering and Domínguez-Rodrigo 2010), scavenging (e.g., Blumenschine 1987), or both (e.g., Bramble and Lieberman 2004). Related treatments feature invertebrates (McGrew 2014) or animal products such as honey (Crittenden 2011). Other accounts stress plant or other nonanimal foods, or particular gross categories of these, including whole fruits (Hunt 1994), seeds (Jolly 1970), fungi (McKenna 1992), and underground storage organs (Wrangham et al. 1999). The focus on plant foods has accelerated in recent years, partly due to the increasing popularity of techniques, such as phytolith and microwear analysis, that are applied exclusively or primarily to document the use of such foods. This is particularly evident in descriptions of hominid diet that mainly limit themselves to postulating only about broad physical categories of plant resources, such as those that are “hard” or “tough” (Teaford and Ungar 2000; Ungar and Sponheimer 2011).

Even given the anthropological penchant for healthy debate, this lack of consensus is somewhat surprising, given that workers should be examining essentially the same evidence, and that there now exists an incredible range of analytical techniques (study of carbon enamel isotopes, phytoliths, microwear, and finite elements, among others) that inform on the foods that our ancestors did eat, or at least could have eaten. The refinement of these techniques, however, has proved to be something of a curse as well as an inarguable blessing. Indeed, recent work (e.g., Ungar and Sponheimer 2011; Sponheimer 2013) often portrays the “reconstruction of hominid diet” as primarily or exclusively a technology-driven enterprise, being moved forward only by more sensitive instruments for detecting chemicals, more powerful microscopes, or more efficient sampling methods (and, of course, more hominid specimens on which to apply these advances). This review, while not ignoring the value (and limitations) of such technologies, takes a very different tack. We argue that dietary reconstruction—or, more properly, the reconstruction of foraging strategies—should strive to be holistic, and should not be limited to any one, or even several, analytical technologies. It should instead be rooted first and foremost in evolutionary ecology.

The holistic, ecological approach (e.g., Sept 1984, 2007; Peters 2007; Griffith et al. 2010) views an individual hominid as an agent striving to maximize its returns in a unique habitat. Ideally, it should take into consideration all of the potential food resources available,

whether plant, animal, or otherwise. It should also take into account the likely abundance and profitability of these available food types to particular hominids at differing spatiotemporal points. The documentation of the former (abundance) requires paleoecological data and modern analogue habitats. The reconstruction of the latter (profitability of potential food types, e.g., energy/handling time, see below) ideally would include considerations of the hominid's masticatory apparatus, digestive physiology, locomotor capabilities, and cognitive capacity, as well as the chemical contents of foods. Although estimating such variables is by no means an easy task, pioneering work using the ecological approach suggests that by incorporating them into realistic evolutionary models (tested with the behavior of living organisms) we can glean important insights into how our ancestors actually behaved (e.g., Griffith et al. 2010).

The purpose of this review is to take a holistic view of the foraging strategy of our hominid ancestors. By way of example, we will examine the potential role of hunting and other forms of meat-procurement in their lifeways, and in comparison to the potential role of various nonanimal foods. The emergence (*Ardipithecus*) and refinement (*Australopithecus*, early *Homo*) of bipedality, which represents the first major adaptive shift in hominid evolution, will be used as the temporal framework.

We argue that earliest human feeding strategies must be evaluated in light of those central elements paramount in the diets among extant taxa. After a historical overview of the literature on the hunting hypothesis juxtaposed against more recent scavenging and plant-based models, we introduce foraging theory, referencing a simple model that has been applied successfully to many organisms. We then utilize elements of this model, along with knowledge from the paleontological and archeological records, to examine the likely dietary strategies of early hominids. Today there exist strong theoretical tools (not just technological ones) and a large, relevant fossil record with which to examine postulated behaviors of our earliest ancestors. Although our essay does not intend to provide all of the answers concerning early hominid foraging strategies, it does, instead, intend to encourage more holistic treatments of their behavior.

The Hunting Hypothesis Versus Scavenging and Plant-Based Scenarios

If issues pertaining to the evolution of the human diet are controversial, then ideas about hunting being a primary determinant in hominid divergence are unusually so. This is striking because topics such as “hunting” and “scavenging” are, for primates and other omnivores, generally minor issues within the larger and more general questions of overall foraging strategy. Yet debates concerning this and other dichotomies (e.g., meat versus underground storage organs) make up a sizable portion of the literature on human dietary origins.

One reason for such controversy is the historical longevity of the “hunting hypothesis.” Its origins date to the famous sketch of human evolution given by Darwin ([1874] 1998). He suggested that erect posture freed the hands and arms for tool carriage related to personal defense, killing of prey, and/or other forms of food gathering. The ability to carry weapons resulted in the reduction of canine size through disuse, which Darwin paralleled with the reduction of the anterior teeth in horned ungulates. The large relative size of the human

brain was understandably linked to increased mental powers, which in turn were loosely linked with the use of weapons and other tools, as well as to complex social interactions. Virtually no fossil or archeological evidence was available to 19th-century theorists, so Darwin's assertions were contingent entirely on comparisons to living vertebrates. Although much of his output focused on demonstrating continuity between humans and other animals, he was hesitant to describe early human behaviors, including hunting, from the perspective of any particular nonhuman model (Latimer et al. 1981). Indeed, his ideas on ancestral human behaviors were heavily influenced by observations of non-European peoples (see Schrire 1980).

Raymond Dart followed Darwin with the first truly detailed hunting model, and concluded that *Australopithecus africanus* was an efficient predator that used minimally modified bones, teeth, and horns as tools for hunting and butchering (Dart 1953, 1957). His views were later popularized in Ardrey's "killer ape" scenario (1961, 1976), and it is therefore somewhat ironic that the eventual systematic examination of Dart's putative "osteodontokeratic culture" was directly responsible for the emergence of modern taphonomy (Brain 1970, 1981; Wolberg 1970; Shipman and Phillips-Conroy 1977; Wolpoff 1999), as its earliest practitioners successfully challenged the main components of Dart's scenario (although bone tools may have been used for digging, see Brain and Shipman 1993; Backwell and d'Errico 2001).

Dart also used the behavior of nonhuman primates in the development of his hunting hypothesis, although, intriguingly, in a more complex (albeit more sensationalistic; Dart 1953) fashion than some subsequent researchers (e.g., Washburn and Lancaster 1968; Stanford 1999; Pruett and Bertolani 2007), who have tended to equate chimpanzee behavior with that of early hominids. Conversely, Dart did not rely on a single nonhuman model for possible australopithecine hunting, but rather drew from many fields, including paleoanthropology, archeology, and evolutionary theory, in addition to primatology. Contrary to assertions that 1960s chimpanzee studies forced a redefinition of humankind (Leakey 1972), Dart had already accepted, based on published evidence from both nature and captivity, that certain nonhuman primates used and sometimes fashioned tools, hunted vertebrate prey, and could even understand rudimentary symbols (Dart 1953, 1957). He argued that his hypothetical osteodontokeratic industry was a specialized intensification of behaviors already found in living primates, merely requiring greater cognitive sophistication. Dart opined that hunting in wild baboons showed "that predatory behavior in a large terrestrial primate other than man was natural and...consistent with the insectivorous origin and diet of Primates..." (Dart 1963:49). Due largely to their savanna-dwelling and hunting inclinations, baboons were to become an important model for early human evolution (Washburn and DeVore 1961; Strum and Mitchell 1987), as were social carnivores (Schaller and Lowther 1969; Thompson 1975).

Among anthropologists, the hunting hypothesis reached its zenith with publication of *Man the Hunter* (Lee and DeVore 1968). This title now seems notably ironic for at least two reasons: first, it is remembered largely for documenting the importance of plant foods to modern hunter-gatherers (Hill 1982; Waguespack 2005) and, second, despite containing several chapters on human evolution, Dart received not a single citation. Perhaps as cosmic

retribution for this slight, but more probably due to its claims, the “hunting hypothesis” (written large) has fallen somewhat from the lofty perch it once enjoyed. Initially formulated as the “prime mover” of earliest human emergence, predation was viewed as explaining the most fundamental aspects of our earliest evolution (e.g., bipedality in *Australopithecus* and brain expansion thereafter; Dart 1953). Although this view still persists, some more recent scholars have taken a cue from now classic studies (e.g., Washburn 1957; Brain 1981) and have highlighted the potentially important role of predation upon, rather than hunting by, early hominids (e.g., Hart and Sussman 2005). With increasing frequency, researchers have restricted the role of hunting to later human evolutionary periods that are accompanied by a relevant lithic record, e.g., earliest *Homo* and/or *Homo erectus* (Shipman and Walker 1989), but often, again, with causal linkages to brain expansion (e.g., Krantz 1968; Bunn 2007).

Although “Man the Hunter” has lost popularity, interest in possible predatory behavior by earliest hominids has not been fully abated—indeed it remains the lynchpin of many accounts of human origins. The many differing (nonmutually exclusive) arguments that consider hunting as a significant factor in early human evolution can be summarized as follows:

1. Chimpanzee hunting represents a reasonable model for the behavior of the last common ancestor (LCA) of *Pan* and *Homo* and/or of early hominids before *Homo*. This underlies almost all research concerning chimpanzee (*Pan troglodytes*) hunting (Stanford 1999, 2001, 2003; Pruett and Bertolani 2007; Hohmann 2009; Pickering and Domínguez-Rodrigo 2010).
2. Early hominids (*Ardipithecus*, *Australopithecus*, early *Homo*) engaged in vertebrate predation either more commonly or more efficiently than do extant nonhuman primates (Stanford 2001, 2003). Evaluating this hypothesis requires examining: its profitability in nonhuman primates compared to its likelihood of success in early hominids and any actual evidence for early hominid meat-eating.
3. Hunting was a major guiding force in hominization. In some cases, hunting is argued to be a “prime mover,” and that it “elegantly and economically explain(s) a large number of the unusual aspects of hominid evolution” (Tooby and DeVore 1987:223). Predatory behavior is argued to account for anatomical changes (bipedality, brain expansion) as well as male parental investment, reciprocal exchange, home bases, and a sexual division of labor (Washburn and Lancaster 1968; Tooby and DeVore 1987). More common today are hypotheses that link hunting (and frequently scavenging) to the evolution of only one of these unique human features, such as bipedality (*Ardipithecus*, *Australopithecus*; Stanford 2003) or its supposed sequential refinement (early *Homo*; Bramble and Lieberman 2004; Lieberman et al. 2009).

Others have alternatively emphasized the possible role of scavenging. Although meat often assumes the same exalted role as in “Man the Hunter,” these workers emphasize anatomical and cognitive (including technological) constraints on early hominid behavior that may have limited hunting ability, and instead point to a “scavenging niche” for early hominids (e.g., Blumenschine 1987). This hypothesis first gained widespread attention with taphonomic

studies suggesting that hominids generally had access to carcasses following other consumers (e.g., Shipman and Philips-Conroy 1977; Shipman 1986), although these arguments created a verbal windstorm, and a monumental, oftentimes frustrating, literature has been generated by debates about whether certain archeological assemblages are best explained by hunting or by scavenging (e.g., FLK 22 *Zinjanthropus*; Bunn and Kroll 1986; Binford 1988; Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Barba 2006; Blumenschine et al. 2012; Pante et al. 2012; Domínguez-Rodrigo et al. 2014). As reliable evidence of modified stone tools does not appear until 2.6 mya (Semaw et al. 2003; claims from earlier dates are considered below), these taphonomic studies generally have little to say about *Ardipithecus* (sensu lato, *Orrorin* and *Sahelanthropus* are here considered likely congeners of *Ardipithecus*) or its likely (but uncertain) descendant, *Australopithecus*.

Although the above discussion highlights ideas concerning the role of meat in human evolution, much focus in recent decades has been placed on plant foods, particularly with regard to *Australopithecus* and earlier hominids. For early *Homo*, the predominate focus today remains squarely on vertebrate meat, with “hunting versus scavenging” being the unfortunate perennial debate but as noted below, the importance of underground storage organs is currently being stressed by a vocal minority.

The timing of this shift in emphasis cannot be pinpointed exactly, but was heavily influenced by the aforementioned *Man the Hunter* and its acknowledgment of plant foods, as well as at least several theoretical models of human evolution. The first alternative treatment of particular note was Jolly’s (1970) “seed-eater” model which utilized *Theropithecus gelada* as an analogy to some aspects of *Australopithecus* adaptation. These baboons feed heavily on grass parts and often assume an erect trunk during feeding or while moving between food patches. In addition, Jolly noted or argued some anatomical (mainly dental) convergences with early hominids, which were viewed as feeders on “small objects” such as grass seeds.

Another alternative to meat-based hypotheses was the “Woman the Gatherer” scenario (Linton 1971). As hominid brain size slowly began to increase, and periods of infant dependency slowly began to lengthen, females, according to this hypothesis, widened the scope of gathering to facilitate care for their young. The earliest important manufactured tools were containers to carry food and nets or slings to transport babies. In terms of actual diet, the earliest incarnation of this model suggested that Plio-Pleistocene hominids likely foraged for foods similar to those of modern hunter-gatherer females (plants and perhaps small game). Later interpreters (e.g., Tanner 1987), working within the same theoretical framework, emphasized potential similarities between early hominids and extant chimpanzees, which feed largely on fruits, leaves, and pith.

A third plant-focused model (Wrangham et al. 1999; Conklin-Brittain et al. 2002) of note, undoubtedly attracting the most attention in recent years, links the exploitation of plant foods, and especially underground storage organs (USOs), with elements of hominid anatomical and behavioral evolution, particularly during the transition from *Australopithecus* to *Homo*. In relation to the dietary issues at hand, it is argued that the addition of significant amounts of USOs to the menu, facilitated by digging implements,

allowed australopithecines to colonize a wide variety of habitats, and that the cooking of USOs and other plant foods facilitated the cranial expansion, stature increases, and postcanine reduction observed in *Homo erectus*.

Various technological developments which are generally utilized to inform upon the plant component of diets also worked to shift the emphasis for pre-*Homo* hominids from meat to plant-based fare. These will be reviewed in greater detail below, in addition to some components of the aforementioned plant-based theoretical models. It will suffice to state here that some of these technology-driven studies have gone to the opposite extreme of the “hunting or scavenging” focus by admitting or discussing only plant foods in relation to *Australopithecus* diet (e.g., Teaford and Ungar 2000; Dominy et al. 2008; Cerling et al. 2011; Estebaranz et al 2012). Work in evolutionary ecology over the last half century, however, suggests strongly that the focus on very general food types (hard versus tough plants, meat, fruit, and underground storage organs, among others) likely underestimates the plasticity or complexity of diets in generalized forms such as most or all early hominids, and that all available potential foods must be considered in predicting their likely foraging strategy.

Foraging Theory

Foraging theory is a branch of evolutionary ecology concerned with animal decision-making during feeding (Stephens and Krebs 1986). It involves general mathematical models aimed at (and generally succeeding in) predicting behavior using several simple variables. Although foraging theory has been utilized in discussions of early hominid dietary evolution (e.g., Gaulin 1979; Sept 1984; Kurland and Beckerman 1985; Peters 2007), and more frequently in archeological treatments of later hominids or humans (e.g., Keene 1981; Reidhead 1981; Yesner 1981; Mithen 1990; Broughton 1999; Gremillion 2002; Dusseldorp 2009), these laudable applications have been at best sporadic and have in recent years, as noted above, been eclipsed by particular technology-driven methodologies. As will be described, we argue that the latter represent a supplement to the former, and should ideally not be utilized in absence of the former. By way of example, it will be most economical here to consider the classical optimal diet or prey model (Schoener 1971; Charnov 1976). There exist very good and more complex models incorporating the concepts involved (e.g., Sept 2007; Griffith et al. 2010) but we have chosen, for simplicity, to emphasize only those fundamentals that are most important for predicting diet, whether the object of study is the aardvark or *Australopithecus*.

In practical terms, given a set of potential foods with known parameters, this model predicts those foods that are most likely to play a critical dietary role. The “known parameters” include mean energetic value, handling time (time required to capture and consume a food), and abundance (how often, over time, the food type is encountered). The model is expressed as:

$$\frac{E_n}{T} = \frac{\sum \lambda_i e_i}{1 + \sum \lambda_i h_i}$$

where E_n/T is net energy intake while foraging, λ_i is encounter rate with food type i , e_i is mean energy acquired when exploiting food type i , and h_i is the mean time spent handling food type i . Handling time includes both pursuit (e.g., chasing an antelope) and processing (e.g., butchering, transporting, preparing, and consuming an antelope). Pursuit and processing costs (including losses due to digestion or detoxification, see Whelan and Schmidt 2007; Sayers et al. 2010) can be subtracted from item-specific energy yield, and general search costs—the cost of travel between food encounters—can also be included (e.g., Paulissen 1987). The latter is referred to as cost of locomotion (CoL, kcal/min) or cost of transport (CoT, kcal/km), depending on whether it is measured by time or distance (e.g., Steudel-Numbers and Wall-Scheffler 2009).

When applying the classical prey model, food types are entered into the equation in stepwise fashion in order of their profitability, which is defined as mean energy gained divided by mean handling time (e/h). Note again that handling time includes pursuit and processing. The “profitability” of a hunted animal, for example, that must be chased, killed, butchered, and transported cannot be determined without taking all of these into consideration. In addition, unsuccessful hunts will result in a negative gain (the energetic and time costs of futile pursuits) and will reduce the mean profitability of a given prey animal. These factors are rarely applicable to immobile foods such as plants and carcasses, although any foods may have quantitative (e.g., fiber) or qualitative (e.g., toxins) factors that can also reduce value.

As each food type is entered into the equation, a differing net intake rate (E_n/T) results, and the set of foods that yields the highest E_n/T constitutes the optimal diet. This establishes a simple behavioral rule: when an animal comes upon a potential food, it should exploit it if its profitability is above the threshold E_n/T (essentially the average return rate for the habitat) but ignore it if its profitability is below it. The model yields other predictions. For example, the inclusion of food is independent of its own abundance, but dependent instead on the abundance of more profitable foods. As the environment or animal changes, so will the predicted optimal diet. All else being equal, “positive changes,” such as an increase in the abundance of valuable foods, or a reduction in their handling times or search costs (e.g., CoT), should result in a narrower diet. Conversely, “negative changes” result in diet expansion. Likely the most often-supported prediction here is that when profitable items are abundant, a forager should not waste time with those of lesser value. When profitable foods are scarce, however, those same items (often referred to as “fallback” foods) may become a dietary mainstay.

Hypotheses concerning potential fallback resources for assorted early hominids have become common in recent years (e.g., underground storage organs in *Australopithecus*; Laden and Wrangham 2005; Dominy et al. 2008), although few such efforts deal extensively with the potential energetic (or other nutritional) values, handling times, and encounter rates of the proposed fallbacks when compared with other available delicacies. Note from the above discussion that it is difficult to identify fallback foods unless the profitability and seasonal abundance of all available resources are considered. It is important to note that few environments are static (including those of early hominids; see Potts 2012) and also that geographically widespread taxa frequently inhabit markedly differing habitats. This leaves

open the very real possibility, indeed suggests the likelihood, that assorted fallback resources characterized particular hominids, and that these differed temporally and/or spatially, as they do for extant generalist primates (e.g., *Semnopithecus entellus*, Sayers and Norconk 2008; Sayers 2014; *Papio* spp., Hill and Dunbar 2002; *Macaca fuscata*, Suzuki 1965). The most constructive way to identify components of early hominid foraging strategy, including fallback foods, involves the reconstruction of particular ancient habitats and the application of foraging theory.

One practical limitation of applying the classical prey or similar models to such questions is, however, the apparent difficulty of quantifying the profitability and encounter rates of foods available to these ancient forms. Such challenges are, however, more manageable than they would at first appear. The answer partially lies in the reconstruction, at whatever level possible, of the habitats and resources available to hominids at particular sites and times, and the identification of modern environs and associated food resources that are similar (Sept 1984). This can give data about the likely abundance (encounter rates) with particular resources, nutritional characters can likewise be estimated from modern analogue foods, and likely pursuit and processing times (as well as other information) can be estimated by drawing from fossil anatomy and regressions or other statistical models based on the behavior of living forms.

For example, Griffith and colleagues (2010) utilized data from two modern analogue habitats in Kenya (Turkana and Voi) and agent-based simulations incorporating variables from the classical prey model, to predict the optimal foraging strategy of *Australopithecus boisei*. In the simulations, it was found that adding tubers to the diet (in their model, via the use of digging sticks) increased the probability of virtual robust australopithecines meeting energy requirements in Turkana and Voi-like habitats, particularly during the dry season. Note that disagreements may exist concerning the selection of analogue habitats, or how some important variables are estimated, but the overall goal should be to draw from eclectic data sets (e.g., fossils, archeological traces, extant organisms) to develop the most robust, realistic, and inclusive models possible.

The classical prey model is not the final word on foraging, of course, and factors such as nutritional requirements and purposeful encounters with patches (i.e., memory, planning, and other aspects of cognition) can result in deviations from predictions (Westoby 1978; Krebs and McCleery 1984; Sayers et al. 2010). Energy, handling time, and encounter rates are crucial, and should be considered in every detailed treatment of hominid foraging, but can and should be supplemented with the inclusion of other variables deemed important. A major component of determining what “other variables” are “deemed important” requires detailed consideration of the foraging behavior of living forms, particularly primates and nonprimate omnivores, and the explicit examination of the variables deemed crucial via tests of foraging theory.

The variables of the classical prey model, however, represent an appropriate starting point. Although relatively simple, they still retain substantial predictive power. The model is robust and often withstands violations of its assumptions (Sih and Christensen 2001). Variations from predictions are generally slight, and despite the complexity of foraging, it

has been useful in analyzing the diets of many nonprimates (Sih and Christensen 2001), modern human hunter-gatherers (e.g., Winterhalder and Smith 1981; Hawkes et al. 1982; Kaplan and Hill 1992), and monkeys (Sayers et al. 2010), as well as predicting the order in which hidden foods are recovered by chimpanzees (i.e., memory for food value and processing difficulty; Sayers and Menzel 2012). In addition, related models address certain behaviors considered particularly important in hominid evolution, such as central place provisioning (Orians and Pearson 1979; Lovejoy 1981). Surprisingly, foraging theory is not now, nor ever has been, the predominate paradigm for examining the potential diets of human ancestors, even though it is likely the single most powerful analytical tool available for predicting the diets of extinct (as well as extant) taxa. If the ecological lifeways of early hominids are ever to be reconstructed, foraging theory, with its emphasis on crucial variables and all potential food resources, will need to be an integral part of the process.

The Chimpanzee Referential Model for Diet in the Last Common Ancestor and Earliest Hominids

Although predominantly ripe fruit eaters (Conklin-Brittain et al. 2001), chimpanzees supplement their diet with leaves, pith, insects, and small-to-medium-sized vertebrates (particularly red colobus monkeys) acquired mainly via predation rather than scavenging (Teleki 1973; Stanford 1999). A commonly made assumption is that the *Pan-Homo* LCA had a diet similar to extant chimpanzees (e.g., Hohmann 2009) or that isolated foraging behaviors, such as hunting strategies, were likewise similar. These comparisons have frequently been extended to models of subsistence in early hominids, including *Ardipithecus* and *Australopithecus*.

This brings us to a major philosophical question: upon what grounds should it be assumed that earliest hominids were similar to a particular extant ape? The first (Pickering and Domínguez-Rodrigo 2010) is simple *homology*; chimpanzees and bonobos are genomically closest to our ancient forebears (Wrangham and Pilbeam 2002). The relatedness argument, however, if taken to its logical conclusion, undermines its own persuasiveness. Even chimpanzees and bonobos—far more closely related to one another than to the LCA or early hominids—differ significantly between themselves in ecology, social structure, and diet. In addition, if *Pan* were now extinct, *Gorilla* would then be “uniquely suited” to be the most appropriate genomic model, even though they in turn also differ substantially from chimpanzees and bonobos. Gorillas, for example, do not engage in vertebrate predation, and bonobos and chimpanzees differ in this activity as well (Hohmann and Fruth 2008). Pertinent to the current discussion, some early hominid anatomical features that do resemble those of apes are more similar to *Gorilla* than to *Pan* (Haile-Selassie et al. 2010; see also Duda and Zrzavý 2013), but the main point is that genetic relationships, at least in hominoids, tell us surprisingly little about broad ecological or behavioral characters.

The popularity of the chimpanzee model, in relation to homology, is therefore the stochastic result of what might be termed the “Miocene hominoid sweepstakes.” Chimpanzees are “available” and thereby selected as the most appropriate model only because they have survived (see Andrews 1981), while other late Miocene forms much closer anatomically to the earliest hominids did not (Lovejoy 2009).

The second argument for chimpanzee models of the LCA and/or early hominid foraging is *analogy*. If these forms share certain characteristics with chimpanzees they might act in the same way, at least under a given socioecological context. Pickering and Domínguez-Rodrigo (2010) have made a useful distinction between “trivial” and “nontrivial” analogies. The former and more common are essentially “if-then” statements; e.g., if chimpanzees do “x,” then *Australopithecus* also did “x.” A more useful and contrasting approach involves “linked, non-trivial chimpanzee analogies... that [are] testable using paleoanthropological data” (Pickering and Domínguez-Rodrigo 2010:109). For example, these authors suggest that studying the determinants of chimpanzee hunting, such as nutritional factors, might yield clues as to whether early hominids consumed meat or engaged in predatory behavior.

Although this is a reasonable viewpoint, a chimpanzee model can only be taken as far as these animals actually resemble their extinct referents. Not only do chimpanzees differ profoundly from early hominids in locomotor behavior, but also in dentition as well (see below) and the structure of both greatly affects the pursuit and processing required for assimilation of food. Such analogies are therefore likely to be anything but robust. It is more useful to determine those variables important to foraging in a wider range of taxa, including but not limited to chimpanzees. Once determined, these can be investigated specifically in early hominids, with full consideration of their unique anatomy and habitats as known from the fossil record. How such principles can be applied to putative hominid hunting, scavenging, and consumption of plant foods is a critical next step.

Vertebrate Hunting, Nutrition, and Profitability in Primates

At least small amounts of animal prey are included in the diets of most primates (Harding 1981). Tarsiers are faunivorous, with some species supplementing their predominantly arthropod diet with small reptiles, birds, and mammals (Niemitz 1979; Gursky 2007). Vertebrates are hunted not only by tarsiers, baboons, and chimpanzees, but by, among others, capuchins (Perry et al. 2003), marmosets and tamarins (Porter 2007), blue monkeys (Butynski 1982), macaques (Estrada and Estrada 1977), mandrills (Kudo and Mitani 1985), orangutans (Hardus et al. 2012), and bonobos (Badrian and Malenky 1984; Hohmann and Fruth 2008). Save tarsiers, plant foods still make up the overwhelming dietary bulk in most of these primates, although “bulk,” as noted above, does not necessarily equate with profitability. Some very valuable foods, if encountered sufficiently rarely, may make up only a small percentage of an organism’s diet.

Both ecological and social factors can potentially be involved in any primate’s “decision to hunt” (Stanford 1998; Mitani and Watts 2001). Our concern here is with the former, explicitly referencing optimal foraging theory. We will focus on chimpanzees and baboons, for which there are the greatest amount of comparative data. Observations about food energy, handling time, or encounter rates for these primates are, however, unlikely to accurately reflect these variables in early hominids (cf. Pickering and Domínguez-Rodrigo 2010) since they differed in anatomy, habitat, and almost certainly social structure as well. A useful and well-known corollary of the optimal diet model can help illustrate this point. This is the all-or-nothing rule, which holds that a food type, at some given level of resource abundance, should either always be taken or never be taken when encountered while

foraging (Krebs and McCleery 1984). Animals commonly show deviation from this rule, but on the whole and over a wide range of taxa, highly profitable foods (high e/h) are rarely skipped and very poor items (low e/h, the aforementioned “fallback foods”) are eaten predominantly during periods of resource scarcity (Sih and Christensen 2001).

Estimated rates of chimpanzee predation per encounter with red colobus are especially relevant. Assuming that auditory contact can be regarded as an “encounter,” red colobus vocalizations result in surprisingly low hunting rates among Tai and Gombe chimpanzees (hunting by at least one observed individual, Tai hunting season 32%, Tai nonhunting season 7%, Gombe over all seasons 7%; Boesch 1994). At Gombe, limiting encounters to situations where notebook data recorded chimpanzees within 50 meters of red colobus gives higher, but still low, hunting rate estimates (party level 69%, maximum for any one individual 46%; Gilby et al. 2006), even though such data may overestimate these frequencies (i.e., red colobus may be more likely to be noted as present when they are pursued by chimpanzees). For Kibale, the criterion of suspected visual detection of red colobus by these apes yields intermediately low hunting rates (hunting by at least one observed individual, 37%; Mitani and Watts 2001). In addition, at all sites with adequate data, vertebrate hunting appears to be somewhat seasonal (Stanford 1996; Mitani and Watts 2001).

These results suggest that red colobus predation enters and leaves a chimpanzee’s foraging strategy depending on the availability of more profitable food types. This might seem surprising, but perhaps it should not be. In addition to the uncertain outcome of hunting (Gilby and Wrangham 2007) and time/energetic costs of the chase, muscle, unlike guts and brains, requires considerable chewing time (Wrangham 2009). Conversely, various nut types, some of which are relatively common, actually provide chimpanzees with more energy or fat per gram than do red colobus (Stanford 1998) and, even discounting pursuit times, vertebrate hunting appears less profitable for chimpanzees than harvesting of their preferred fruits (Sept 1984). In addition, vertebrate carcasses are sometimes shared, which further reduces an individual hunter’s “cut” of any proceedings (Teleki 1975). Pursuit costs for such highly mobile adult prey may be curtailed somewhat by focusing instead on easier-to-acquire immature individuals, but encounters with such prey are likely to be sporadic and total energy costs would still be appreciably greater, perhaps by orders of magnitude, than are those of immobile foods.

The data from baboons present interesting comparisons and contrasts to those from chimpanzees. Baboons at many locales inhabit large home ranges with a comparatively poor flora in relation to most chimpanzee sites. Although baboon diet is still dominated by plant foods, the intake of animal matter is generally greater, but also more variable, than that of chimpanzees (Hill and Dunbar 2002). There are also some situations where certain animal foods appear to be of greater profitability than co-occurring fruits, grass seeds, flowers, or underground plant parts, although data for energy, handling time, and/or encounter rates for some or all of these resource categories are generally lacking. Chacma baboons (*Papio ursinus*), for example, specialize on certain insects, to the near exclusion of plant foods, when outbreaks occur (Hamilton et al. 1978). Also, olive baboons (*Papio anubis*) in areas with reduced populations of carnivore competitors show high vertebrate hunting rates,

indeed overlapping those of modern human foragers, with energetic return rates potentially higher than those of most plant foods (Strum 1981; Hill 1982). These are situations where ecological factors (low habitat quality, decreased pursuit times due to prey abundance, decreased pursuit costs due to competitor absence) have increased the comparative profitability of faunivory.

In addition to energetic concerns, it remains possible that vertebrate soft tissue provides critical micronutrients for chimpanzees or baboons (Tennie et al. 2009), although these same micronutrients can be found in easier-to-acquire plant foods or, as in the case of vitamin B₁₂, insects (Wakayama et al. 1984) and adverse physical effects resulting from nutrient deficiencies may appear only after many months of absolute, controlled elimination from the diet (*Macaca mulatta* and B₁₂, pathology signs after 33–45 months; Kark et al. 1974; National Research Council 2003). In addition, even incidental ingestion of insects found on normal plant foods may be adequate to cover micronutrient requirements, including B₁₂, in gorillas (Harcourt and Harcourt 1984).

The nonhuman primate data on hunting, therefore, illustrate several important points relevant to reconstructions of early hominid behavior. The first is that vertebrate hunting does not, on the whole, appear to be a particularly profitable activity for those nonhuman primates in which it has been investigated. Although the default stance of most considerations of human dietary evolution is that meat is a valuable resource regardless of how acquired and whether or not it is cooked (e.g., Bunn 2007) this clearly need not be the case. The second point is, however, that for strongly omnivorous anthropoids such as baboons, this prognosis can change based on characteristics of the environment, as predicted by foraging theory. Factors such as a change in the abundance or quality of profitable foods, anatomical or cognitive (including cooperative or technological), means to reduce pursuit or processing time for particular resources, and other factors could serve to dramatically shift the diet of an organism. Any hypothesis postulating a major shift in hominid dietary focus, at any stage in our evolution, needs to come to grips with these points. It is important to reiterate that the likelihood of any particularly subsistence activity, whether hunting, scavenging, fruit picking, or root digging, is dependent on the profitability and abundance of all potential resources, and these variables are far from being spatially or temporally static.

Early Hominids: The Fossil and Chemical Evidence of General Diet

This review, as noted, encourages a holistic view of hominid subsistence based on evolutionary ecology. Current studies generally involve investigating diet based on dental anatomy, microwear on teeth, chemical signatures, or plant phytoliths (these are discussed in more detail below). In our view, these techniques, while valuable, cannot be used in exclusion to reconstruct foraging strategy. They can, however, be used to set up parameters relative to food profitability (e.g., how does dental anatomy, in association with cranial and postcranial anatomy, likely influence pursuit and processing?) or can be used to test models of subsistence (e.g., do chemical signatures, phytoliths, and microwear agree with a particular model?). We here explore what these lines of evidence suggest regarding the feeding behavior of early hominids.

Current opinions on the question of early hominid diets, as noted at the outset, vary and can differ substantially. These include:

1. The diets of *Ardipithecus* and *Australopithecus* were sufficiently herbivorous that faunal matter need not be discussed, even when looking at data (e.g., enamel carbon isotopes, microwear) that cannot be used in isolation to discriminate animal from plant foods (e.g., *A. boisei*, Cerling et al. 2011; *A. anamensis*, Estebananz et al. 2012). A closely related viewpoint is that pre-*Homo* patterns of plant and meat-eating (acquisition and consumption) were similar to those of living chimpanzees, which are largely ripe fruit (and leaf and pith) consumers but also capable hunters (see above), and are presumptively viewed as representing the primitive LCA state (e.g., Stanford 1999, 2001, 2003; Pruettz and Bertolani 2007; Hohmann 2009). Such arguments are rarely applied to early *Homo* (but see Wrangham et al. 1999).
2. All or most early hominids (robust australopithecines being a possible exception) were characterized by diets more generalized than those of living apes, with greater omnivory (presumably reflecting the potential for a greater contribution of animal foods, e.g., *Ardipithecus ramidus*, Suwa et al. 2009; *Australopithecus*, Bartholomew and Birdsell 1953; early *Homo*, Ungar et al. 2006).
3. The consumption of vertebrate flesh was very common in early hominids, was the central component of their niche, and was indeed central to the process of hominization (e.g., Blumenschine 1987; Mann 2000, 2007).
4. Early hominid diets differed significantly among multiple taxa or adaptive grades. The robust australopithecines, for example, are classically viewed (e.g., Robinson 1968) as having evinced a largely vegetarian diet, as opposed to greater omnivory in gracile australopithecines and early *Homo*. It is common today, however, for authors to draw further distinctions between the diets of other individual hominid taxa (or putative taxa). For example, Sponheimer (2013) reviews hypotheses that postulate a more restricted, extant ape-like foraging strategy in *Australopithecus afarensis* when compared to the presumably more generalized *Au. africanus*, as well as other potential differences in general foraging strategy or fallback foods within the australopithecines.

Distinguishing between these possibilities requires a look at myriad forms of physical evidence available and also, importantly, rigorous consideration of foraging theory. As with any other aspect of early hominid ecology or behavior, bonobo and/or chimpanzee feeding behavior should not be construed as a default proxy for those of the *Pan-Homo* LCA or early hominids (Latimer et al. 1981; Cachel 2006; Sayers and Lovejoy 2008; Suwa et al. 2009; Duda and Zrzavý 2013). Hominid anatomy and physiology may impose considerably different constraints on foraging strategy than those that limit these behaviors in chimpanzees.

Anatomy reflects previous evolution and, thus, with relation to diet, the types of foods that were selectively important in the past. It may or may not reveal the routine diet of individuals that can be examined in the fossil record (Sponheimer 2013) given the speed at which conditions can change (Van Valen 1973) and the potential importance of rarely

consumed but potentially important fallback foods. Nonetheless, with both extinct forms and extant primates, anatomy can go a long way in establishing the parameters of likely diet, particularly in tandem with information on what potential foods were or are present.

The dentitions of both *Ar. ramidus* (4.4 mya, Afar Rift, Ethiopia) and *Australopithecus* spp. are characterized by generalized molar topography, with low, rounded (bunodont) cusps. Along with moderately thick enamel and lack of shearing capacity, they are closer in morphology to *Dryopithecus* (Suwa et al. 2009) than extant African apes. Chimpanzees, bonobos, and especially gorillas exhibit greater occlusal relief and much thinner enamel (Ungar 2004; Suwa et al. 2009), reflecting their known propensity for diet expansion beyond preferred fruits to fibrous, leafy foods (e.g., chimpanzee diets average 16% leaves; Conklin-Brittain et al. 2001).

In addition, *Ar. ramidus* is characterized by small incisors relative to those of *Pan* and *Pongo*, which utilize their anterior dentition to process fruit pericarp (Suwa et al. 2009). Of special note is the fact that the sectorial canine, the only hominoid tooth capable of readily penetrating flesh even in its reduced state in females, nevertheless underwent systematic restructuring so complete in early hominids as to entirely remove any such capacity, arguing against adaptation *specifically* for carnivory. The postcanine teeth, in addition, are relatively large in *Ardipithecus*, although not to the degree observed in *Australopithecus*. Early *Homo* essentially retains the signatures of a generalized, bunodont dentition with moderate to thick enamel (Beynon and Wood 1986; Ungar et al. 2006). The anatomical evidence is clearly congruent with a broad range of potential plant and animal foods for *Ardipithecus*, gracile *Australopithecus*, and early *Homo*, and less congruent with strong directional selection for the exploitation of any one broad category of resources (e.g., vertebrate meat or individual plant type/part).

The status of robust australopithecines in this respect is less clear. Although variable and including taxa and individuals of varying “robustness,” they are of course generally known for their large postcanine teeth with thick enamel, robust mandibles, flaring cheekbones, and/or sagittal crests, all part of an extensive masticatory package that has been variably interpreted as either reflecting a specialized diet of challenging foods (Robinson 1968; Beynon and Wood 1986; Cerling et al. 2011) or a potentially diverse one incorporating these, at least in times of dearth (Wood and Strait 2004; Peters and Vogel 2005).

Another line of evidence involves microwear on teeth that correlates with the physical properties of foods or extraneous particles (e.g., dust) that are or were consumed. Generally, hard and/or brittle foods (e.g., certain seeds and bones) are expected to be associated with pitting, while tough but pliable foods that require shearing (e.g., certain leaves and soft animal tissues) are expected to be associated with parallel scratches (Ungar and Sponheimer 2011). Microwear studies, however, while worthy of attention, have several limitations that help underscore why isolated analytical techniques must be considered supplementary to evolutionary ecology in the reconstruction of foraging strategy, as opposed to wholesale methods for determining diet.

The most famous limitation is that microwear turnover occurs relatively quickly—the celebrated “Last Supper Effect” (Grine 1986)—meaning that, in relation to fossil individuals, microwear only gives evidence of the physical properties of certain items that entered the mouth shortly before death. It goes without saying that this may or may not reflect the routine diet of the species, and is also prone to miss rare but selectively important foodstuffs (Sponheimer 2013). In addition, the microwear associated with feeding must be differentiated from that caused by later deposition (Teaford 1988), wear differs based on tooth areas sampled even at a micro level (Gordon 1982), and extraneous materials such as dust, dirt, and other grit may in some cases wear teeth more greatly than the actual “intended foods” being consumed. Questions concerning to what degree plant silica phytoliths or other plant components are hard enough to abrade or even rub enamel, for example, are currently under debate (Sanson et al. 2007; Lucas et al. 2013; Rabenold and Pearson 2014).

With these caveats in mind, molar wear in *Ar. ramidus* is minimal, and suggests consumption of fewer abrasive, hard-object and/or gritty food types than in later *Australopithecus* (Suwa et al. 2009), particularly the South African forms. Within *Australopithecus*, East African *Au. anamensis/afarensis* and the robust *Au. boisei* generally exhibit less complexity (pitting) and variability than *Au. africanus* and early *Homo*, although all such values are overlapping and relatively lower than would be expected by wear caused by hard, brittle objects (Ungar and Sponheimer 2011; Grine 2013). The clear outlier here is South African *Au. robustus*, which exhibits wildly variable wear complexity (again, overlapping with most of the aforementioned) but includes some specimens with extensive pitting. Excepting this specific hominid, the conclusions generally drawn from these data are essentially that if hard objects were important to early hominids, it is at least not signaled in their microwear (Ungar and Sponheimer 2011). Taking into account the anatomical evidence and the cautions raised above, however, none of these factors contradict the notion that all of these hominids exhibited broad, generalist diets that could have included such food types, especially during times of resource scarcity.

Together, the above data indicate that unlike extant African apes, early hominids, and likely the *Pan-Homo* LCA as well, were not ripe fruit specialists or especially frequent consumers of leafy or other stereotypically high-fiber resources. The latter is especially important, as leaves and pith prove key to chimpanzees, bonobos, and gorillas when more preferred foods are scarce (Laden and Wrangham 2005). This of course does not mean that these items were not sometimes consumed by early hominids (see Henry et al. 2012), but virtually all of the molar characters in early hominids (bunodonty, increasing enamel thickness, increasing size), for example, do suggest a reduced profitability of leaves/pith, with an attendant reduction in any impact on selection that their consumption would impose. Dentitions from *Ardipithecus* to *Homo* instead suggest an extremely varied diet, with “compromise” morphology. In what ways might early hominids have been dietary “generalists,” however? What foods could have generated such a significant shift away from those consumed by extant apes? Moreover, what foods are also consistent with the abundant evidence that *Ar. ramidus* (and, of course, *Australopithecus* and *Homo*) was so frequently terrestrial that it had undergone substantial modifications of the foot, leg, thigh, and hip for habitual upright walking (Lovejoy et al. 2009a,c,d)?

Two possible classes of foods sometimes suggested to be central to early hominid diets, as noted, are animal resources and low-fiber underground storage organs (Hatley and Kappelman 1980; Milton 1987; Wrangham et al. 1999; Conklin-Brittain et al. 2002; Laden and Wrangham 2005; Yeakel et al. 2007; Dominy et al. 2008). Arguing by analogy and structural similarity to living species, both can be considered likely foods in *Ardipithecus* (Suwa et al. 2009) and especially *Australopithecus*, whose postcanine teeth strongly converge on those of bears and pigs, taxa which consume both of these gross food categories and are well-known for their exceptionally generalist foraging strategy (Hatley and Kappelman 1980 and see below). The changes that likely occurred in gut morphology/physiology throughout human evolution, from at least as ancient a form as *Australopithecus*, are also consistent with, although not necessarily indicative of, exploitation of similar resources (Milton 1987; Conklin-Brittain et al. 2002; Mann 2007; Haile-Selassie et al. 2010).

In relation to the specific question of meat-eating in early hominids (USOs will be considered below), some workers have gone beyond general anatomy or microwear in attempts to answer it more directly. One potentially useful technique is the diagnosis of infectious disease linked with animal consumption. D'Anastasio and colleagues (2009) reevaluated a lumbar vertebra from an *A. africanus* partial skeleton (Stw 431) and provided evidence that associated lesions were consistent with early stage brucellosis, a disease contracted by contact with or consumption of contaminated animal tissues. Although the authors clearly favor this as evidence of vertebrate meat consumption, they note that brucellosis does not necessitate eating animals, and alternative diagnoses (including trauma, as suggested by an earlier study) are possible.

Similarly, the parietal fragments comprising Olduvai Hominid 81—from a 1.5 mya hominid child near weaning age and of uncertain taxonomic affinity—have been diagnosed with porotic hyperostosis, a nonspecific erythroid marrow hyperplasia in the cranium often linked with malnutrition or iron deficiency. One interpretation is that this reflects a “meat-deficient” diet in the mother of OH 81, which influenced the nutrient content of her milk; another is that it reflects developmental stress associated with a reduction in the availability of maternal milk, and thus to the full complement of nutrients ultimately derived from meat (Domínguez-Rodrigo et al. 2012:e46414). Although being another line of evidence suggestive of significant meat consumption, porotic hyperostosis is widespread in some hunter-gatherer skeletal populations, and is generally associated with the occurrence of postcranial periostitis, itself reflective of chronic infection (Mensforth et al. 1978). Moreover, trace minerals, including iron, are found in a wide assortment of plant and animal foods (National Research Council 2003) and the link between maternal intake of specific micronutrients and milk composition is, at the very least, more complex than a simple one-to-one correlation (e.g., Vuori et al. 1980).

The ratio of strontium to calcium (Sr/Ca) can differ in the tissues of organisms based on the trophic level they occupy, at least within regions with known soil chemistry (reviewed in Sillen 1992). Such ratios are therefore another potential means of deducing potential early hominid meat consumption. Animals preferentially assimilate dietary calcium relative to strontium, resulting in lower Sr/Ca ratios in herbivores compared to the plants that sustain

them. However, some plants and/or their parts (e.g., grasses, sedges, and rhizomes) have higher Sr/Ca than do others (e.g., woody leaves, flowers, and fruit). Thus, grass grazers average higher Sr/Ca ratios than tree browsers, and these consumer categories can often be distinguished via analysis of bone or tooth enamel. Carnivores, again preferentially assimilating calcium as opposed to strontium, are generally expected to exhibit relatively low Sr/Ca ratios, but these will also reflect the consumption patterns of their prey. Indeed, carnivore Sr/Ca ratios sometimes overlap the low values typical of browsers, and in other cases overlap those of grazers (Sponheimer et al. 2005). Due to such discrepancies, Sr/Ca ratios are often coupled with other evidence (e.g., additional chemical or morphological analyses) when ancient dietary reconstructions are being attempted.

Although Sr/Ca signals can be lost from bone during fossilization, Sillen and colleagues (Sillen 1992; Sillen et al. 1995) utilized a “solubility profile” technique that relies on distinguishing diagenetic apatites (minerals formed during fossilization) from biological ones. Using these methods, fossilized bone of *A. robustus* at Swartkrans revealed low Sr/Ca, which was interpreted as possible evidence of animal, including vertebrate meat, consumption (Sillen 1992). Contrary to classical interpretations of both “robust” *Australopithecus* and early *Homo* feeding strategies (i.e., rigid herbivory versus omnivory; Robinson 1968), the *A. robustus* Sr/Ca values were surprisingly lower than those from a small sample of early *Homo* at the same site (Sillen et al. 1995).

This picture receives at least partial clarification from results obtained by Sponheimer and colleagues (2005), who explored the Sr/Ca ratio in tooth enamel—which is less susceptible to diagenesis than bone—in both modern animals at Kruger National Park and fossils from Swartkrans and Sterkfontein. They found Sr/Ca ratios to be significantly higher in *A. africanus* than in *A. robustus*, and higher in both taxa than in papionins and browsers, although *A. robustus* did not differ significantly from these other mammals. This led them to conclude that “there is no reason to believe that... [*A. robustus*]... consumed greater amounts of animal foods than contemporaneous baboons” (Sponheimer et al. 2005:153). As noted previously, the modern baboon diet, while heavily biased toward plant foods, does in some cases overlap modern human hunter-gatherers with respect to animal foods. Sr/Ca ratios were, as noted, higher in *A. africanus* and possibly suggestive of greater grass consumption. Another option that Sponheimer and colleagues examine, and likely attractive to many students of human evolution (McGrew 2014), is insect consumption, as insectivores tend to have higher Sr/Ca ratios than do carnivores.

Coupling these results with additional data for barium/calcium (Ba/Ca) ratios may likely resolve this issue. The relatively rare combination of high Sr/Ca but low Ba/Ca (low Ba/Ca is unlike grazers; insectivores are little known with respect to this measure) is a characteristic “signature” of both warthogs (*Phacochoerus africanus*) and mole rats (*Cryptomys hottentotus*), two entirely unrelated species that rely heavily on USOs. “Thus, the consumption of underground resources seems to be a reasonable hypothesis to explain the Sr/Ca of South African hominins in general, and the very high Sr/Ca of [gracile] *Australopithecus* in particular” (Sponheimer et al. 2005:154 and see below). It is important to note, however, that values for both gracile and robust australopithecines overlapped those of at least some browsers, grazers, and carnivores in this study, and thus do not contradict

the interpretation that one or both taxa exhibited a broad, omnivorous diet. On a related note, the data deal with hominids over a limited spatial and (to a lesser degree) temporal range, and the same taxa in different habitats might of course exhibit different chemical signatures of diet. The Sillen (1992; Sillen et al. 1995) and Sponheimer et al. (2005) studies are nevertheless important for their cautioning against broad generalizations about robust versus gracile australopithecine diet, and highlighting the potential importance of underground storage organs.

By the time one gets to roughly 2.6 million years ago, the assertions about meat-eating in early hominids (likely *Australopithecus garhi* and/or early *Homo*) are no longer equivocal. Here there is direct evidence of modified stone tools that were used to butcher large animals and extract bone marrow (Bouri and Gona, Ethiopia; Heinzelin et al. 1999; Semaw et al. 2003). The questions at this point have traditionally shifted to whether these animals were acquired by hunting or some form of scavenging, and what the importance of meat was relative to another (e.g., USOs) category of food. We will return to these questions shortly.

Another widely used technique to analyze habitat and diet takes advantage of differing photosynthetic pathways in plants. Most plants, including almost all woody plants, utilize a three-carbon pathway (C_3 plants) while a smaller number use a four-carbon pathway (C_4 plants and Crassulacean acid metabolism (CAM) plants). The four-carbon systems are characteristic of plants in dry or seasonal environments, and are differentiated by whether certain steps in the photosynthetic process are separated spatially in differing cell types (C_4) or temporally (CAM) (Keeley and Rundel 2003; Yeakal et al. 2007). Fortunately for paleoanthropology, an exceptionally high percentage of African savanna grasses and sedges are C_4 , and these plants can be distinguished chemically from C_3 plants by an elevated concentration of the comparatively sparse isotope ^{13}C in relation to ^{12}C (Peters and Vogel 2005; Sponheimer et al. 2007). With some variation, the $^{13}C/^{12}C$ ratios in CAM plants, which include succulent desert forms and some tropical epiphytes, tend to overlap those of C_4 plants, but there are notable exceptions, such as aquatic CAM species (where environmental factors influence carbon ratios, Keeley and Rundel 2003; Yeakal et al. 2007). In short, the tissues of herbivores will vary in isotope composition based on the plants they have consumed, and carnivores will vary based on what their prey have consumed. Strict browsers or the predators that eat them (C_3) can be distinguished from strict grazers or their predators (C_4).

Carbon enamel isotopes, again, are not the final word on diet, and animals do not choose plants to eat based on their photosynthetic pathway, but rather based on profitability criteria. Importantly, this technique cannot be used alone to distinguish between plant and animal consumption. Another complication is that USOs can be C_3 , C_4 , or CAM. Examples of C_4 USOs are underground portions of Cyperaceae (sedges), which include the familiar papyrus (Laden and Wrangham 2005; Peters and Vogel 2005).

The known *Ar. ramidus* immediate habitat (a subdivision of the larger regional environment in the Middle Awash (Ethiopia) Pliocene; Cerling et al. 2010; White et al. 2010) has been characterized as woodland (Louchart et al. 2009; WoldeGabriel et al. 2009) and differed from those of extant apes and later hominids. Analysis of *Ar. ramidus* enamel carbon

isotopes indicates a diet high in C₃ plants and/or animals that consumed these (White et al. 2009). However, the C₄ signal was higher in *Ar. ramidus* than in sampled chimpanzees, which are close to being obligate C₃ feeders. In turn, they are much lower than in most sampled *Australopithecus* living after approximately 3.5 million years ago, both gracile and robust, and early *Homo*, which on the whole appear to have utilized a somewhat even mix of both C₃ and C₄ foods (Sponheimer et al. 2007, 2013; Ungar and Sponheimer 2011; Wynn et al. 2013).

This shift toward more C₄ resources likely reflects the steadily broadening dietary niche that appears to be a hallmark of later hominid evolution (Lee-Thorp et al. 2010, 2012), partially related to more “open country” habitation, with rough analogues in certain primates such as baboons (Sponheimer et al. 2007) that are described as “eclectic omnivores” (Altmann 1998). Particularly interesting in the context of the aforementioned suid-like, bunodont, brachydont dentition of early hominids (Hatley and Kappelman 1980), the mixed and highly variable C₃–C₄ signals of *Australopithecus* are similar to those of the living African bush pigs (*Potamochoerus* spp.)—true omnivores whose diet includes fruits, USOs, invertebrates, small vertebrates, carrion, stems/leaves, and eggs (Jones 1984; Nowak 1991; Harris and Cerling 2002; Sponheimer et al. 2007).

An extreme in the general C₃–C₄ pattern is *Australopithecus sediba* (a probable late chronospecies of *A. africanus*) from Malapa, South Africa (2 mya; Henry et al. 2012). A sampling of two teeth suggests a diet heavily reliant on C₃ resources, even more so than in *Ar. ramidus*. This study also included analyses of phytoliths, which are silica deposits that form in plants and in some cases can be utilized to identify, with varying levels of precision, the plant taxa or plant parts they came from (for a recent review of archeological applications and limitations, see Shillito 2013). The identifiable plant phytoliths (n = 24) recovered from the dental calculus (which forms over months or years; Henry 2012) of *Au. sediba* include those from fruits, sedges, leaves, and wood/bark—all of which are consumed by many extant catarrhines, and all of which have been considered possible foodstuffs for hominids prior to the use of controlled fire (based on profitability characteristics and the effects of seasonality; Peters 2007). As noted above, nothing in *Australopithecus* dentitions or postcrania is suggestive of adaptations or stabilized characters associated with folivory. As with living bush pigs (Jones 1984), leaves and bark were likely a relatively minor resource for these hominids; however, there exist considerable chemical and structural variations within such gross food categories (see Sayers 2013).

These results, again, highlight the fact that *Ardipithecus* and especially *Australopithecus* and *Homo* had broad dietary niches, and their diets at any given site, at any given time, were likely more closely linked to habitat characteristics than putative taxon-specific feeding constraints (Luca et al. 2010). This is forcefully demonstrated by the observation that *Ar. ramidus* and *A. robustus* are more closely aligned on the C₃–C₄ spectrum than *A. robustus* is to *A. boisei* (Sponheimer et al. 2007; van der Merwe et al. 2008; White et al. 2009; Lee-Thorp et al. 2010; Cerling et al. 2011). In other words, there is no firm anatomical, chemical, or microwear evidence demonstrating that any known early hominid (potentially even robust australopithecines, see Peters and Vogel 2005) was particularly specialized (i.e., exhibited narrow dietary niche breadth), and suggestions that this might be the case (e.g., those based

largely on microwear) must be viewed with caution, as they sidestep several known tenants of foraging theory. Given that gracile *Australopithecus*, for example, ranged at least from Chad to South Africa (Brunet et al. 1995), it is probable that their diets at particular sites/times differed at least as greatly as those in most other wide-ranging primates or nonprimate omnivores, or most probably even more so, given their markedly generalized dentitions (see also Wynn et al. 2013). Their remarkable demographic success (Lovejoy 1981) is not compatible with narrow niche breadths—their most likely “specialization” was that they were not specialized.

In this context, it is again particularly important to consider the limitations of using only a small number of current technologies and techniques for reconstructing diet. It has been suggested, for example, that *A. boisei* subsisted on copious amounts of “low-quality” foods, as evidenced by high C₄ signatures and some aspects of microwear (Cerling et al. 2011:9337). It has been noted (Sponheimer 2013) that the isotopic evidence here would compare favorably with a *Theropithecus*-like diet as first proposed by Jolly (1970). Carbon enamel isotopes, however, do not even distinguish between plant and animal foods, and microwear analysis, even if accurate, reflects only the gross physical properties of certain items that enter the mouth (intended foods or otherwise) shortly before death. Even in the case of robust *Australopithecus*, alternative hypotheses involving marked omnivory, while debated, are also able to readily explain available evidence (Peters and Vogel 2005).

In the literature, the importance of gross food types is often framed as a dichotomous choice: e.g., for a particular phase of human evolution, was it the consumption of USOs or meat (or insert other food categories) that provided the greatest selective advantage (e.g., Bunn 2007)? Similar “either/or” presentations are often applied to the “hunting or scavenging” debates (e.g., Shipman 1986; Dominguez-Rodrigo and Barba 2006). Unless all early hominid habitats were identical (certainly not the case) and the associated return rates and patterns of seasonality for gross food types were equally identical (certainly not the case)—or anatomy suggests selectively important reliance on certain food categories (generally not the case, with gracile/robust differentiation being one possible exception)—these are unnecessary dichotomies. Coupled with habitat selection—which is determined not only by food presence, but also by factors such as competition (Rosenzweig 1981) and predation danger (Gilliam and Fraser 1987)—a forager’s diet is determined by the specific resources available, as well as the seasonal densities, associated handling times, and nutritional characteristics of these elements. A particular type of potential food that is passed over in a habitat of abundance, as noted previously, may be regularly eaten in poor habitats or during lean seasons (Schoener 1971).

Craniodental and alimentary characteristics, and even postcranial and cognitive ones, place constraints on diet by influencing how valuable a resource will be to a given animal. Colobine monkeys, for example, with their extensive shearing crests and compound, microbe-infested stomachs, are likely able to derive more energy from high-fiber leaves than cercopithecines or hominoids (e.g., Kay and Davies 1994), and their anatomy presumably reflects a long history of having done so. Leaves are therefore not necessarily “low-quality” from the perspective of a colobine monkey (Sayers et al. 2010; Sayers 2013). So it goes with our immediate ancestors: the habitat of emergent hominids, as with all other animals,

determined their diet, as did the anatomical “equipment” they had to rely on to extract its nutrients. It is true that certain aspects of ancient habitats or the anatomical equipment involved (particularly, soft tissue characters and physiology) may be hidden from view, but even here data exist to make reasonable assumptions about such variables (e.g., Conklin-Brittain et al. 2002; Griffith et al. 2010). The potential role of meat-eating, USO consumption, or the exploitation of any other gross food category must be examined within a holistic context. Given the lack of evidence in *Ar. ramidus* and *Australopithecus* for the evolutionarily significant folivory (i.e., folivory which is reflected in morphology) that plays such an important role in the natural history of extant African apes, in addition to the bear/pig analogy, the likelihood that animal foods or USOs would enter their optimal diet must be considered comparatively high.

As noted, the evidence for animal consumption includes some archeological (insectivory; Backwell and d’Errico 2001) and morphological evidence (vertebrate consumption; Mann 1981), and evidence for USO exploitation, although controversial (Bunn 2007), continues to accumulate. In addition to traditional morphological arguments (Hatley and Kappelman 1980), the isotopic signature of modern mole rats and their fossil counterparts, which feed heavily on USOs, compare favorably with *A. africanus* and *A. robustus* (Yeakel et al. 2007). Modern humans, in addition, have approximately three times the number of functional salivary amylase genes (AMY1) than chimpanzees and bonobos do (Perry et al. 2007). Salivary amylase is involved in one of six steps that result in the degradation of “gelatinized” or “raw” starch to glucose in the small intestine, while other “resistant starches,” aided by microbes, are used to produce short-chain fatty acids in the large intestine. Cooking greatly aids the assimilation of some starches in the body (Ao et al. 2012:S42) and although the degree to which uncooked starches are utilized is still little understood in a quantitative sense, uncooked, high-starch foods are exploited by Old World monkeys (e.g., Perry et al. 2007; Sayers et al. 2010) and some human hunter-gatherers (e.g., Schoeninger et al. 2001; Marlowe and Berbesque 2009).

In modern humans, AMY1 copy number positively correlates with salivary amylase protein levels (which are also high in Old World monkeys; McGeachin and Akin 1982) and is greater in populations with a high-starch diet, and “high-starch” characterizes many types of USOs (Perry et al. 2007). It is unknown how far back into hominid evolutionary history such adaptations date, but even into the Pliocene would not be surprising and would complement certain anatomical data. Indeed, some workers have utilized morphology and the mechanical properties of underground resources to link the divergence of gracile and robust australopithecines to differing “fallback” USO types being exploited during periods of resource scarcity (gracile: C₄ corms and C₃ tubers; robust: C₄ bulbs; Dominy et al. 2008). Such a hypothesis deserves to be explored further, ideally with habitat data and optimality models, along with plausible alternative interpretations (e.g., Peters and Vogel 2005).

Some discussions concerning the diet of early hominids have noted that overall biological productivity (biomass) decreases from tropical forests to woodlands to open habitats (e.g., Baccini et al. 2008). In the context of the classical optimal diet model, this decrease in overall abundance of foods (lower E_n/T of the habitat) would promote the adoption of an increasingly generalist feeding strategy (Gaulin 1979). To this it can be added that an

increasing commitment to terrestrial, bipedal locomotion would tend to have a similar effect via the reduction of access to arboreal resources (Lovejoy 1981, 2009), again making habitats more marginal per unit area, all else being equal. This is fully consistent with an increase in the likelihood of exploitation of foods atypical of extant apes, of which USOs and certain animal foods represent possibilities, in *Ardipithecus*. If it is assumed that biological productivity was comparatively reduced in certain later hominid habitats, and/or that the commitment to terrestrial bipedality was greater, it is also consistent with an even wider gamut of potential foods (e.g., hard objects that require significant processing) in *Australopithecus* and/or early *Homo*.

The relative contribution of specific resources to the diet, again, would be wholly dependent on their availability and variables related to profitability, such as nutritional value and handling time. These are not static and, as noted above, will be influenced by myriad factors, including habitat-specific features as well as the social and technological innovations of these foragers (which, again, will change over time). The technologies and techniques reviewed in this section give clues as to what early hominids ate, and in some cases even direct evidence for certain foods, but this does not equate to reconstructing their *foraging strategy*. Arguments concerning “gross food type A” (e.g., meat) versus “gross food type B” (e.g., fruits, USOs, insects) being more important are of limited value. In the future, whenever possible, increased attention should be given to reconstructing ancient habitats, and the likely profitability of all resources available to the hominids that lived in them (see for example, Sept 1984; White et al. 2009).

How Profitable Would Vertebrate Hunting and Scavenging Have Been For Early Hominids?

Ar. ramidus lived in a habitat where potential analogs to chimpanzee prey species, such as colobus monkeys, also existed, and chimpanzees have been argued to represent a potential model for early hominid hunting behavior (e.g., Boesch and Boesch 1989; Stanford 1995; Pickering and Domínguez-Rodrigo 2010). The potential value of vertebrate prey can be assessed with the three variables utilized to calculate profitability: potential dietary energy, pursuit time, and processing time. All foods with profitability above the habitat E_n/T can be expected to be exploited whenever encountered while foraging (Schoener 1971).

It is unlikely that the energy derived from vertebrate carcasses would be greater for most pre-*Homo* hominids than for extant primates, or that there would be appreciably less required processing time. The processing time associated with meat and bone marrow was likely reduced by the utilization of stone tools in East African hominids living roughly two-and-a-half million years ago. In addition, evidence of large mammal exploitation, as opposed to the small vertebrates eaten by extant primates, is found at the Bouri, Ethiopia, site that has yielded such early evidence (2.5 mya; Heinzelin et al. 1999), and also at nearby Gona (2.6 mya; Semaw et al. 2003). This would increase energy available per carcass considerably, although to what degree would depend on the state of the carcasses when acquired, and whether or not they needed to be defended from competitors. *Au. garhi* is currently the only hominid known from this time/area and may be the toolmaker (Heinzelin et al. 1999), although this contention must be tested against future evidence (Klein 2000). At

Hadar, Ethiopia, a mandible (A.L. 666-1) associated with modified stone tools provides evidence for similar behavior in early *Homo* at 2.3 mya (Kimbel et al. 1996).

At present, however, there is no evidence for butchery by *Ardipithecus* and only limited evidence for earliest *Australopithecus* (see Panger et al. 2002 for discussion). The latter includes one ungulate rib and one bovid femur that exhibit purported stone tool cut marks, from Dikika, Ethiopia (McPherron et al. 2010). Similar markings, however, have been experimentally produced by trampling (Domínguez-Rodrigo et al. 2010) and these essentially isolated samples are surface recoveries. At present, therefore, arguments for butchery in early australopithecines remain unsubstantiated. There is also essentially no evidence of controlled use of fire or cooking in *Australopithecus* or earlier hominids, which could potentially increase the amount of energy available to a forager by reducing processing costs and/or time (particularly if including postconsumptive handling, Darwin ([1874] 1998; Engels ([1876] 1953); Oakley 1961; Leopold and Ardrey 1972; Clark and Harris 1985; Wrangham et al. 1999; Whelan and Schmidt 2007). The lack of shearing surfaces on *Ardipithecus* and *Australopithecus* molars (Ungar 2004; Suwa et al. 2009) actually would make the chewing of fresh vertebrate muscle, unmodified by cooking, somewhat more challenging than for extant apes (Teaford and Ungar 2000). Their dentitions, however, while not representative of pure carnivores (Gaulin 1979) are clearly a compromise allowing many possible foodstuffs, including meat.

The foregoing discussion makes no distinction of whether vertebrate meat might have been acquired by hunting or by scavenging. In all known pre-*Homo* hominids, hunting mobile prey would likely be associated with longer expected pursuit times and lower success rates than for extant chimpanzees. Any successful hunting of highly mobile and arboreal prey, such as red colobus, can be almost entirely ruled out for *Ar. ramidus*, short of postulating highly advanced social organization, which has not yet even been argued to have been present in *Au. afarensis*. In such hunts, chimpanzees rely heavily upon their arboreal and climbing skills, which are both highly honed and were, to the contrary, much more limited in *Ar. ramidus*. Chimpanzees possess enhanced pedal-grasping abilities, heavily buttressed lumbar columns, shortened hindlimbs, greatly lengthened forelimbs and metacarpals, and fully reinforced central joint complexes in the wrists that greatly enhance their arboreal agility, all of which *Ar. ramidus* lacked.

The preceding indicates that arboreal hunting of mobile prey such as monkeys, likely of only borderline profitability even in chimpanzees, would be virtually profitless for *Ar. ramidus*. Although possessing a grasping great toe, *Ar. ramidus* was a slow climber and far less-suited to rapid arboreal movements than are extant or extinct cercopithecoids or apes (Lovejoy et al. 2009a; Lovejoy et al. 2009b). Indeed, given the probable body mass of the species, and its heavily modified pelvis and still primitive lumbar spine, the arboreal environment was probably most important for nesting, protection of offspring from predators, and occasional low canopy feeding. Terrestrial hunting variations exhibited by chimpanzees on small mammals such as bushbucks and bushpigs would also be associated with longer pursuit times, lower success rates, and lower profitability in *Ar. ramidus*, which exhibits sufficient adaptations to upright walking to assure that its primary means of terrestrial travel was bipedality. Its skeleton is therefore indicative of a form of cursorial locomotion that was far

more restricted in speed and agility than that of *Australopithecus*, and certainly inferior to the highly specialized knuckle-walking of living African apes (Lovejoy et al. 2009d).

Australopithecus lacked the arboreal adaptations of *Ar. ramidus*, and its postcranium indicates a history of intense selective pressures favoring long-term habitual terrestrial bipedal locomotion (Latimer 1991; Lovejoy et al. 2009d; Simpson 2010). For this reason, arboreal hunting for these hominids would have been both unprofitable and dangerous, and can essentially be removed from consideration (Sayers and Lovejoy 2008). This includes virtually all variations of arboreal hunting reported in extant chimpanzees, whether tool-assisted (Pruetz and Bertolani 2007) or otherwise (Stanford 1998). When on the ground, *Australopithecus*, with an adducted great toe, arched and essentially rigid foot, valgus knee, and greatly reduced hamstrings and adductors, would have been a considerably more agile biped than its likely predecessor, and certainly capable of more sustained walking and running than *Ardipithecus* (Lovejoy et al. 2009d). The capture of any running animal, however, would have still been considerably difficult for *Australopithecus* from a biomechanical perspective when compared to a more agile quadruped such as a chimpanzee (Lovejoy 1982). Thus even terrestrial hunting of such prey would be associated with almost debilitating pursuit time and costs compared to those in extant apes, and saving some as-yet-undefined property, would be of lower profitability for them. This contrasts markedly with assumptions made in the virtual entirety of the ape literature, and some of the paleodietary literature as well, which presumes that chimpanzee hunting techniques or diet represent the primitive LCA condition, retained through at least the time of *Australopithecus* (Stanford 1999, 2001, 2003; Pruetz and Bertolani 2007; Hohmann 2009).

These limitations point to the conclusion that neither *Ardipithecus* nor *Australopithecus* systematically engaged in almost any form of chimpanzee-like pattern of vertebrate predation. This is not to say, however, that all modes of vertebrate hunting observed in modern chimpanzees were unavailable to these hominids. In rare cases, for example, Gombe chimpanzees will seize young mammals with only limited pursuit or essentially no chase at all (Goodall 1986). It is certainly possible that this form of opportunistic ambush hunting was within the capacities of emergent hominids. The most likely animal prey would have included small reptiles and amphibians, the young or weak of larger vertebrates, eggs, fledglings, helpless fish, invertebrates, and burrowing mammals, of course coupled with other resources typical of forest floor/riparian omnivores, e.g., fruits, berries, nuts, USOs, fungi, vegetative plant parts, shoots, honey (Bartholomew and Birdsell 1953; Mann 1981; Lovejoy 1993).

Thus, although it is true that thoughtful studies of chimpanzees or other particular nonhuman primates can yield information relevant to the question of early hominid meat consumption or hunting (e.g., Pickering and Wallis 1997), it is nonetheless a dubious practice to posit the chimpanzee or any other extant animal as a model for LCA or early hominid foraging strategy, any more (and probably even less) than white-faced saki monkeys can be used as a model for the behavior of bearded sakis (e.g., Norconk 1996) or chimpanzees can be used as a model for bonobos (see Sayers et al. 2012). It also does not follow that potentially rare predatory behaviors held any particular selective importance for early hominids, or that chimpanzee hunting and faunivory, outside the context of overall diet, should be considered

a separate and singularly relevant topic in chimpanzee behavioral ecology. In other words, in extinct or extant primates, studies of foraging strategy should be the rule, and studies of niche topics such as hunting, scavenging, or insectivory, even if tool-aided, the exception.

There are potential behavioral means for reducing the pursuit time or costs associated with hunting larger or more mobile game, although few authors have granted exceptional abilities of this nature to earliest hominids. Evidence that brain organization in *Australopithecus* differed from extant apes, however, has been presented and associated with increased skills related to communication, memory, problem solving, and dexterity (Dart 1925; Holloway et al. 2004; Carlson et al. 2011), abilities that are already substantial in living nonhuman primates (E. Menzel 1971, 1973, 1974; Putney 1985, 2007; C. Menzel 1999). Any such advances, which are to date only vaguely articulated, could serve to improve the profitability of certain types of hunting.

Nonetheless, it is unlikely from our perspective that any such advantages from this modification, such as increasingly complex social foraging or throwing ability, would be sufficiently advanced in *Ardipithecus* or *Australopithecus* to compensate substantially for their almost laborious modes of locomotion (Lovejoy 1982; Lovejoy et al. 2009d). Again, all available evidence suggests that hunting would be largely limited to easily acquired forms. Omnivores with constrained mobility—although admittedly not as constrained as early hominids—such as equatorial or temperate bears and pigs, provide a rough rubric for the amount of animal foods that may have been consumed by *Ardipithecus* or *Australopithecus*. For these taxa, animal prey (including insects, small vertebrates, and carrion) make up from about 2 to 36% of the diet, with variation likely dependent on habitat characteristics and seasonal encounter rates (Hatley and Kappelman 1980; Hill 1982; Jones 1984; Bull et al. 2001).

As noted above, for at least some hominids after 2.6 million years ago, large vertebrates were unquestionably on the menu. Although frequently assumed to be a “high-quality” food for early *Homo*, it is currently unclear how profitable even sizable carcasses would have been when compared to other foods—this is entirely contingent on the likely pursuit and processing time and costs. The question of pursuit raises the perennial debate concerning whether these prey were predominately hunted or scavenged. Most archeological work has focused on whether early hominids had early or late access to carcasses, gauged by the location and juxtaposition of carnivore tooth marks versus stone tool cut marks (Shipman and Phillips-Conroy 1977; Shipman 1986). Early access would suggest hunting or prompt “confrontational (power) scavenging” (chasing predators from their kills; Bunn and Ezzo 1993) and late access would suggest some form of passive scavenging. Four decades of concerted work at Olduvai Gorge (e.g., FLK *Zinjanthropus*, 1.8 mya) has scarcely helped the problem, as the same evidence is viewed in diametrically opposed fashion by different workers (early access emphasis reviewed in Domínguez-Rodrigo et al. 2014; late access emphasis reviewed in Pante et al. 2012).

Without wishing to encourage more of this old debate, there is little evidence suggesting that locomotor ability in early *Homo* would reduce the pursuit time or costs of rapid, mobile hunting when compared with earlier hominids, as these forms largely retain the slow and

injury-prone bipedality of their *Australopithecus* ancestors (a contrasting hunting model, the persistence hunting or “endurance running” hypothesis, which emphasizes pursuit over very long periods, is considered below). As a result, “early access” models that emphasize hunting, beyond ambush of especially vulnerable prey, likely need to invoke substantial cognitive mechanisms for reducing pursuit costs if this is to be considered to have been a major component of foraging strategy.

The differences in the communication abilities of modern humans, for example, when contrasted with early *Homo* are likely profound. Consider the characteristic of human language termed “displacement” (Hockett 1960) that involves the referencing of objects or events remote in time and/or space. This faculty is used by modern humans extensively, including foraging groups deciding where to go to collect game (and plants) and discussing past or anticipated future strategies (e.g., the Aché; Hill and Hawkes 1983). Along with other aspects of modern cognition (see below) it is likely crucial to hunting success. Nonhuman primates can pick up very subtle pieces of information from the behavior of others (e.g., E. Menzel 1971, 1974; C. Menzel 1996) and can engage in quite complex nonverbal communication when given the means to do so (e.g., lexigrams; Rumbaugh 1977). In naturalistic settings, the information picked up from the behavior of others, while impressive, appears limited to events of the very recent past and anticipatory of actions to be engaged in the immediate future (e.g., chimpanzees; Menzel 1971). Symbol-proficient chimpanzees—again, probably because they have been given the means to do so—demonstrate somewhat exaggerated displacement abilities and can “comment” on events observed hours or days earlier (e.g., Menzel 1999). The vocal output of nonhuman primates, in contrast, is generally quite constrained even by vertebrate standards (cf. birds and marine mammals) and characterized by emotionally triggered cries that are produced from infancy (Owren et al. 2011).

According to most students of language evolution, the displacement abilities present in early *Homo* were only modestly more pronounced than those of nonhuman primates (see also Kurland and Beckerman 1985), at least when juxtaposed against the supreme abilities of modern humans in this regard. It is generally argued that comparatively advanced communication abilities in the form of “protolanguage” (whether gestural or vocal) was not evident until at least *Homo erectus*, based on factors such as brain size, range expansion, and archeological indicators of potential cognitive ability. Most reconstructions of the hypothetical protolanguage reveal increased powers of displacement but, again, quite truncated from the modern human standpoint (reviewed in Fitch 2010). Especially when considering the other uses or correlates of communication (e.g., teaching, cooperation, joint attention) and general cognition (e.g., episodic memory, planning, associating prey with their signs) this would put early *Homo* at a distinct disadvantage (high pursuit time or costs, low success rates) when hunting large and/or mobile game, especially in a social context. This is especially true if projectile weapons were not utilized by these forms, a question on which the archeological record is silent. Passive or power scavenging scenarios are less constrained by these limitations, but the locating or defense of carcasses would still be conducted with comparatively reduced cognition (cf. modern human power scavenging; Silberbauer 1981) and an almost certainly poor olfactory sense.

As noted previously, in relation to processing, chewing, and digesting vertebrate muscle that has not been cooked exacts definite difficulties, although such costs might be slightly curtailed with certain types of tool use such as pounding. Some authors have used largely morphological arguments (e.g., postcanine size reduction) to argue for the importance of cooking from the initial appearance of *Homo erectus* (Wrangham et al. 1999), although the archeological evidence of controlled use of fire before about 800,000 years ago (Goren-Inbar et al. 2004) is much debated (see Clark and Harris 1985; comments in Wrangham et al. 1999; Luca et al. 2010). Other tissue (such as brains, digestive organs, and bone marrow) would be associated with lower costs; for example, estimates of the energetic yield of bone marrow and the processing time required to extract it have led to suggestions that early hominids should have exploited it whenever encountered, at least in the form of safe carcasses (Blumenshine and Pobiner 2007), although it is unlikely to have been as valuable to prefire hominids as to those coming after (Speth 1989). Thus, although the archeological evidence suggests reductions in processing time and costs associated with foods (including meat) due to advancements in technology, these reductions would have been constrained by the factors outlined above.

Taken together, the most reasonable interpretation is that vertebrate meat, whether hunted or scavenged, would have been of lower profitability to early *Homo* when compared to modern humans in comparable habitats. This extends arguments first made cogently in the “Woman the Gatherer” hypothesis (Linton 1971). A simplistic reading of the evidence would be to assume that vertebrates made up less of the diet than in modern hunter-gathers. Ultimately, however, this would be influenced by habitat-specific characteristics, including the seasonal abundance and value of all potential foods. The progression of cognitive capacities in *Homo*, including technological strides and extremely generalist niche, likely led to increasingly divergent specializations in different habitats, and not always involving the same foods (e.g., fruit, seeds, underground storage organs, vertebrate meat, insects, and honey, among others).

Locomotor Efficiency, Foraging, and the Origins of Bipedality

Although general ecological models have only sporadically been applied to early hominid foraging, considerable attention has been given to the narrow subject of search costs—only one of many variables that impact feeding behavior. Indeed, most foraging theorists consider search costs a sufficiently minor consideration that, perhaps too cavalierly, they are often ignored when calculating predicted optimal diets (Stephens and Krebs 1986; Lifjeld and Slagsvold 1988; Sih and Christensen 2001). Despite this, one of the broadest presumptions in early hominid modeling is that search costs—specifically, the cost of transport (CoT; Steudel-Numbers and Wall-Scheffler 2009) or locomotor “efficiency”—has been a primary target of natural selection (Rodman and McHenry 1980), and/or that such economy emerged from a need for tracking and hunting (Krantz 1968; Carrier 1984; Bramble and Lieberman 2004).

Despite its frequent tacit acceptance (see Leakey and Lewin 1992; Stanford 2003), the hypothesis that CoT played a principal role in the evolution of bipedality is a presumption for which, to our knowledge, no systematic justification has ever been provided. Travel costs certainly can influence behavior and represent a possible selective pressure for many

animals, including hominids. Yet this is only one factor in animal locomotion, and is constantly being weighed against many competing evolutionary demands, including time costs. This can be stated succinctly as follows: locomotor efficiency does not necessarily equate to foraging efficiency, nor does it equate to efficiency in social behavior or predator avoidance (e.g., Pontzer 2012).

In fact, “animals do not necessarily use their cheapest gaits when moving during their predominant field activity. Rather,... the output of organismal locomotor decision making...is driven more by what the animal needs to do (e.g., foraging, escape, social interactions) and evolutionary constraints...than the need to optimize locomotor economy” (Reilly et al. 2007:286). The most recent demonstration of this fact can be found in the assessment of CoT in the gliding by colugos (Byrnes et al. 2011). Direct comparison of the cost of gliding and traveling the same distance quadrupedally shows the latter to be more economical, thereby rejecting the presumptive “dogma” that gliding in these animals evolved to lower CoT. Instead, it appears to have been a means of increasing foraging efficiency (e.g., time savings during between-patch travel) and avoiding predators, a lesson that should strike home to any interested in the relationships among social behavior, diet, and locomotion in early hominids.

Even in cases where CoT declines in a lineage over evolutionary time, the primary reason for such a decline may be unrelated to an organism’s overall “energy budget.” Indeed, many of the highly complex social interactions that play a central role in species fitness are probably energy costly, but are not restrained by such costs lest the individual’s reproductive success would otherwise suffer. The mammalian locomotor system exhibits a plethora of self-protective mechanisms, each favored not only as a means of preventing catastrophic musculoskeletal failure, but also to ameliorate progressive hard tissue degradation, as the latter eventually accentuates the likelihood of the former. Because soft tissues are the principal means by which locomotor systems can generate negative work—a task that cannot be performed by cartilage, which has a favorable elastic modulus but too little volume, and not by bone, which is too stiff—soft-tissue integrity is crucial, but nevertheless is degraded and nullified by fatigue.

Simply demonstrating that one mode of locomotion is energetically advantageous compared to another is therefore not a test of the central problem, which is whether energy consumption has been minimized in order to lower the animal’s CoT or has instead been generated by the likely more critical need to reduce soft tissue fatigue during high or prolonged loading (Carrier et al. 2011). The connective tissue component of the longitudinal pedal arch in hominid bipeds serves as an energy-storing spring and its capacity to do so will thereby reduce the CoT, but the arch’s intrinsic musculature simultaneously generates eccentric joint-protective work. Which was the target of selection? Almost certainly the latter, although there are, at present, no direct data with which to answer this question.

We do have, however, observations of living primates that bear indirectly on the issue, at least with respect to bipedality. A relatively simple answer to the question is provided by CoT studies of living primates whose musculoskeletal systems were most similar to those of the earliest hominids. The limb proportions and ample lumbar spines of Japanese macaques

make them more suitable for comparison to early hominids than are chimpanzees (e.g., Sockol et al. 2007) because the latter's extreme specializations include a stiffening of the pelvis and thorax so substantial as to prevent systematic hindlimb extension during upright walking. These specializations have never been present in hominids (Lovejoy and McCollum 2010; McCollum et al. 2010; Sayers et al. 2012).

Bipedal CoT was found to be 120 to 130% that of "normal" quadrupedality in two specially trained individuals (Nakatsukasa 2004). Although a small sample, these data nevertheless provide no support for the hypothesis that early hominids adapted upright walking as a CoT strategy, and inasmuch as they represent a direct test of hypothesis, they clearly supplant those derived from broad, indirect, and highly presumptive calculations (e.g., Rodman and McHenry 1980). These data highlight what appears to be the most reasonable view of early hominid locomotion—that emergent bipedality would be less efficient than the more refined locomotion of *Australopithecus* or *Homo*. As a corollary, it suggests that: the selective drive for upright walking in early hominids was socioecological and not locomotor and that selective advantage for bipedality was sufficient despite its likely elevation of CoT.

This brings into question the frequent argument that major modifications in the hominid locomotor skeleton occurred for increasing locomotor efficiency during general foraging (Rodman and McHenry 1980) or hunting (e.g., early *Homo*; Bramble and Lieberman 2004). It also provides no evidence that either the adoption of bipedal locomotion, or its refinement, was causally and specifically linked with scavenging efficiency (Shipman 1986; Bramble and Lieberman 2004). As noted, emergent bipedality was unquestionably more awkward and less efficient than in extant *Homo sapiens* (e.g., Lovejoy 2009d). This is one reason why comparing locomotor efficiency in modern humans and chimpanzees will not yield answers to questions on the origins of bipedality. Another is that chimpanzees likely differ profoundly in anatomy from the LCA (Sayers and Lovejoy 2008; Lovejoy et al. 2009c; Sayers et al. 2012). Most important, however, are the numerous striking disadvantages of bipedality that must be countered in any reasonable explanation of its origin or evolution. Even in its more advanced incarnations, bipedality reduces speed and agility, curtails access to arboreal resources, and increases risks of injury (Lovejoy 1981, 1988; Latimer 1991, 2005). Any explanation where the benefits do not outweigh the substantial costs—whether it involves questionable energetic savings (Rodman and McHenry 1980; Bramble and Lieberman 2004), standing up for visual display (e.g., Dart and Craig 1959), fruit picking, or wading, or increased throwing ability (reviewed in Niemitz 2010)—is unlikely to account for bipedality's defining features, whether they appeared in *Ardipithecus*, *Australopithecus*, or early *Homo*.

The advanced adaptations to bipedality seen in *Homo* have been argued by some to have been adaptations to "persistence hunting" (Krantz 1968), today repackaged as "endurance running" (which may or may not include a scavenging component; Carrier 1984; Bramble and Lieberman 2004). In persistence hunting, which is rare even in modern ethnographic populations, a pursued animal is chased for long periods until it collapses. Such a practice is a prime example of an activity characterized by excessive pursuit requirements (time and energy spent on the chase) and processing costs (time and energy spent on defending, butchering, and transporting a carcass, along with any other handling). How profitable

would persistence hunting/ endurance running be in comparison to other forms of food acquisition, especially in the likely absence of later *Homo*'s profoundly hypertrophied social and logistical planning?

The energetic value of the carcass itself is immaterial unless the pursuit and processing time and energy costs are considered. It has been estimated that running for the average duration of a modern persistence hunt would constitute 72–84% of the daily energy expenditure for a *Homo erectus* male (KNM-WT 15000; Steudel-Numbers and Wall-Scheffler 2009), and elsewhere argued that thermoregulatory considerations would essentially limit such behavior to hominids with the musculoskeletal, glandular, and hirsuteness profiles of modern humans (Ruxton and Wilkinson 2011). In addition, unless potential game animals were kept in constant perceptual (especially visual) contact, which is very unlikely, persistence hunting via endurance running would require extensive tracking abilities. The following of animal prey through signs is a sophisticated skill that was likely severely truncated, if not virtually absent, in early *Homo* when compared to modern humans, and would have been performed in less-than-optimal (for tracking) savanna-woodlands (Pickering and Bunn 2007; Bunn and Pickering 2010). The extraordinarily high potential yields cited for persistence hunting/ endurance running (Lieberman et al. 2007) are likely exaggerated by orders of magnitude, as they do not consider the *highly negative returns* that would have characterized unsuccessful hunts. Even modern humans, with the advantages of unparalleled cognition and refillable water bottles, show fairly low success rates in persistence hunting (Pickering and Bunn 2007). Moreover, to some extent such modern human hunting behavior is a “dietary luxury,” in that its frequent failure does not seriously impact food supply that is largely maintained by simple gathering. Indeed, modern human hunting is as much a social behavior as a dietary one.

Scenarios such as the persistence hunting/ endurance running hypothesis, which attempt to explain major anatomical changes in human evolution with little regard for the fitness consequences of the alterations, must therefore be considered largely fanciful from the point of view of foraging theory.

It has also been suggested, as noted above, that endurance running could have been used in the context of locating carcasses, such as moving toward the sight of circling vultures (Bramble and Lieberman 2004; Lieberman et al. 2007). An analysis of the scavenging opportunities for early hominids, based on conservative spatial models and the distribution and behavior of extant animals, suggests that running would provide little advantages in the context of vulnerable hominids (i.e., those that could not usurp or dominate carcasses), but that running relatively short distances (those traversed in under 30 minutes) might provide a selective advantage if hominids could defend themselves from large carnivore competitors (Ruxton and Wilkinson 2013). This scenario differs considerably from earlier proposals (e.g., Bramble and Lieberman 2004) and the costs of usurpation and defense would need to be considered to evaluate the potential profitability of such an activity. The idea that meat was a valuable resource for early hominids is an assumption that is often stated without evidence, but clearly needs to be tempered with information concerning habitat-specific factors, other available resources, and handling time and costs.

Conclusion

The goal of paleoanthropologists should not be to opine hunting or scavenging behavior in our ancestors, or to wax poetic about underground storage organs or honey, but ultimately to reconstruct their overall foraging strategy. Fossil anatomy provides information as to the foods that a given animal likely exploited, i.e., our greatest ally in reconstructing the past is almost always natural selection and its effects on the skeleton (*sensu lato*). Fossil anatomy also helps delineate, at least partially, the fundamental dietary niche (Hutchinson 1957; Sept 1984; Peters and Vogel 2005; Shipley et al. 2009), which is the total range of foods that an organism can consume based on chemical, mechanical, or other considerations. The realized dietary niche contains the foods that are actually eaten (Hutchinson 1965; Shipley et al. 2009), and can be addressed to some degree by examination of phytoliths, enamel element and isotope data, and microwear. These methods have their limitations, and it is likely that ancient “diet” cannot be reconstructed without invoking evolutionary ecology, or without detailed consideration of the particular habitats in question. After all, you cannot eat what you cannot find. In relation to human dietary evolution, a future goal should be to reconstruct the fundamental and realized niches for individual hominids at particular sites at the highest resolution possible (White et al. 2009). In the long run, it is far more informative to establish any particular fossil’s habitat through exhaustive excavation and collection of data, than to place its hominid contents within overarching and often vague taxonomic hierarchical trees. Questions such as hunting and scavenging and underground storage organs will not sort themselves out until such contextual data are more forthcoming than current “standard” practices provide. Indeed, the answers to these questions, even at low taxonomic levels, may differ based on the time and/or site being studied.

Even a cursory evaluation of the literature reveals that observed diets of primates vary considerably even within species (human, Winterhalder and Smith 1981; nonhuman, Campbell et al. 2007). At some locations, for example, stereotypically “folivorous” howler and leaf monkeys are predominately fruit eaters. From a foraging theory perspective, diet is expected to vary by location based on the availability of profitable foods, with “profitability” based on both the chemical characteristics of the resources and the physical characteristics of the animal. A holistic study of early hominid diet could be considered analogous to reconstructing specific habitats, estimating pertinent variables (e.g., available foods, their likely chemical characteristics, ease of procurement, physiology of digestion) and actually calculating optimal resource use.

Is such an approach feasible? We maintain that the answer is yes and, indeed, a number of workers have been moving profitably along these lines (see especially Sept 1984, 2007; Stahl 1984; Peters 2007; Griffith et al. 2010). Studies related to ancient paleoenvironments (Reed and Rector 2007; Dominy et al. 2008; Louchart et al. 2009; White et al. 2009) along with modern analogue habitats can provide information concerning the rate at which particular foods were likely encountered by hominids (Peters 2007; Sept 2007). Primate nutritional ecology (Conklin-Brittain et al. 1998; Norconk and Conklin-Brittain 2004) provides useful information about their relative value, although much work remains to be done on the physiology of digestion in uncooked (and cooked) foods. Work regarding the time costs of foraging (Nakagawa 2009) coupled with data on body mass and anatomy, can

provide estimates of the pursuit or processing costs associated with individual resources (Sullivan 1988; Sayers and Menzel 2012). Based on what is known from modern evolutionary ecology (Sih and Christensen 2001), these are all the data one needs in order to have a fairly sound grasp on an animal's diet.

The assumption that vertebrate soft tissue or bone marrow represent high-quality resources, for example, is common in early hominid paleoecology, and indeed remains a predominate explanation for brain expansion in our family (e.g., Mann 2007). Although this idea has elsewhere been challenged from a nutritional perspective (Speth 1989), more striking is that a large proportion of this literature has virtually ignored 50 years of work in foraging theory, and 80 years in Skinner boxes, which both demonstrate unequivocally that the time and other costs spent acquiring and processing resources are absolutely central to determining their value, and thus their utility, to an animal. Even modern Aché hunter-gatherers who utilize guns and bows and arrows exploit large amounts of plant foods, and when time factors are considered, this can be largely explained via the simple optimal diet model outlined above (Hawkes et al. 1982; Kaplan and Hill 1992). Any early hominid “aware” of the high energetic content of bone marrow can almost certainly have been expected to have harvested any that it encountered and could easily bring to hand. There is no requirement, however, that a highly valued food necessarily became a *primary target* of foraging behavior (e.g., that it guided ranging patterns) and, in any event, such a proposition cannot be made without knowing (or at least estimating) the profitability and abundance of other potential foods. The fact that we can find archeological evidence of marrow consumption is very likely to be a case of searching for lost keys under a streetlight at midnight.

Current evidence suggests that hunting ability in *Ardipithecus* and *Australopithecus*, due largely to constraints placed on them by postcranial anatomy, was limited to easily acquired animal prey that could be collected with only very limited pursuit. For this set of resources, the anatomical and ecological evidence reviewed above suggests that these, and/or vertebrate carcasses, may have frequently entered the optimal diet. Both genera, however, lacked the speed and agility of chimpanzees or baboons, and return rates for highly mobile vertebrate prey would have been significantly lower than in their extant anthropoid relatives. Even with the commonly accepted increases in cognitive abilities in early *Homo*, the question of hunting remains a matter of debate and, as noted above, it is unlikely that refinements in the hominid locomotor skeleton before or at this point reflect changes specifically associated with tracking game or carcasses. Although increases in hominid brain size and/or intellectual capacities have traditionally been associated with an increasingly meat-based diet or activities such as hunting, the strong signals for wide niche breadth—including dietary—actually lends more credence to more domain-general neurophysiological processes and behaviors being at work (Genovesio et al. 2014).

Taken in the overall perspective of evolutionary time, neither the dental nor postcranial character progression that occurs within the broad taxonomic milieu of *Ardipithecus* or *Australopithecus* → *Homo* (sensu lato) implies any modification that would have increased hunting efficiency—indeed most would have substantially reduced it—and these long-ranging effects of selection provide compelling evidence against the hypothesis that hunting was a central, singularly significant activity during the emergence of earliest hominids. If we

are indeed “killer apes,” which is doubtful, we did not become so until social cooperation and cohesion, along with at least major advancements in communication and tool-making skills, became sufficient to overcome the inherent disadvantages of the early hominid phenotype. But this criticism should not be limited to the hunting hypothesis. Models that focus intensely on scavenging or gross plant categories are also missing key aspects of the Plio-Pleistocene picture. Given the generalist leanings of most early hominids, any dietary model that focuses too strongly on any single particular food type or foraging strategy should be viewed with caution.

These issues, while pertinent to current anthropological debates, are nonetheless tangential to the central point of this paper: the percentage of the diet that was composed of any particular food in any early hominid depended on the rate at which sufficiently accessible forms (considering pursuit and processing time and cost) were encountered, based soundly on what is known from foraging theory. The importance of these cannot be determined without considering the entire habitat at particular places and times, and all available foods, both plant and animal. This requires a holistic, interdisciplinary approach that goes beyond merely what we can observe chemically or through a microscope, and draws from ecology, anatomy and physiology, cognitive science, and behavior. Just as early hominid foraging strategies should not be pigeonholed, nor should the lines of evidence deemed appropriate to reconstruct them.

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References

- Altmann, SA. Foraging for Survival: Yearling Baboons in Africa. Chicago (Illinois): University of Chicago Press; 1998.
- Andrews, P. Species diversity and diet in monkeys and apes during the Miocene. In: Stringer, CB., editor. Aspects of Human Evolution. London (United Kingdom): Taylor and Francis; 1981. p. 25-61.
- Ao Z, Quezada-Calvillo R, Nichols BL Jr, Rose DR, Sterchi EE, Hamaker BR. The nature of raw starch digestion. *Journal of Pediatric Gastroenterology and Nutrition*. 2012; 55:S42–S43. [PubMed: 23103655]
- Ardrey, R. African Genesis. New York: Atheneum; 1961.
- Ardrey, R. The Hunting Hypothesis: A Personal Conclusion Concerning the Evolutionary Nature of Man. New York: Atheneum; 1976.
- Baccini A, Laporte N, Goetz SJ, Sun M, Dong H. A first map of tropical Africa’s above-ground biomass derived from satellite imagery. *Environmental Research Letters*. 2008; 3:045011.
- Backwell LR, d’Errico F. Evidence of termite foraging by Swartkrans early hominids. *Proceedings of the National Academy of Sciences of the United States of America*. 2001; 98:1358–1363. [PubMed: 11171955]
- Badrian, N.; Malenky, RK. Feeding ecology of *Pan paniscus* in the Lomako Forest, Zaire. In: Susman, R., editor. The Pygmy Chimpanzee: Evolutionary Biology and Behavior. New York: Plenum Press; 1984. p. 275-299.
- Bartholomew GA, Birdsell JB. Ecology and the protohominids. *American Anthropologist*. 1953; 55:481–498.

- Beynon AD, Wood BA. Variations in enamel thickness and structure in East African hominids. *American Journal of Physical Anthropology*. 1986; 70:177–193. [PubMed: 3090891]
- Binford LR. Fact and fiction about the Zinjanthropus floor: data, arguments, and interpretations (with reply by Bunn and Kroll). *Current Anthropology*. 1988; 29:123–149.
- Blumenschine RJ. Characteristics of an early hominid scavenging niche (and comments and reply). *Current Anthropology*. 1987; 28:383–407.
- Blumenschine, RJ.; Pobiner, BL. Zooarchaeology and the ecology of Oldowan hominin carnivory. In: Ungar, PS., editor. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford (United Kingdom): Oxford University Press; 2007. p. 167-190.
- Blumenschine RJ, Stanistreet IG, Njau JK, Bamford MK, Masao FT, Albert RM, Stollhofen H, Andrews P, Prassack KA, McHenry LJ, Fernández-Jalvo Y, Camilli EL, Ebert JI. Environments and hominin activities across the FLK Peninsula during *Zinjanthropus* times (1.84 Ma), Olduvai Gorge, Tanzania. *Journal of Human Evolution*. 2012; 63:364–383. [PubMed: 22440745]
- Boesch C. Chimpanzees-red colobus monkeys: a predator-prey system. *Animal Behaviour*. 1994; 47:1135–1148.
- Boesch C, Boesch H. Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*. 1989; 78:547–573. [PubMed: 2540662]
- Brain CK. New finds at the Swartkrans australopithecine site. *Nature*. 1970; 225:1112–1119. [PubMed: 5418243]
- Brain, CK. *The Hunters or the Hunted?: An Introduction to African Cave Taphonomy*. Chicago (Illinois): University of Chicago Press; 1981.
- Brain, CK.; Shipman, P. The Swartkrans bone tools. In: Brain, CK., editor. *Swartkrans: A Cave's Chronicle of Early Man*. Pretoria (South Africa): Transvaal Museum; 1993. p. 195-215.
- Bramble DM, Lieberman DE. Endurance running and the evolution of *Homo*. *Nature*. 2004; 432:345–352. [PubMed: 15549097]
- Broughton, JM. *Resource Depression and Intensification During the Late Holocene, San Francisco Bay: Evidence from the Emeryville Shellmound Vertebrate Fauna*. Berkeley (California): University of California Press; 1999.
- Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam D. The first australopithecine 2,500 kilometres west of the Rift Valley (Chad). *Nature*. 1995; 378:273–275. [PubMed: 7477344]
- Bull EL, Torgersen TR, Wertz TL. The importance of vegetation, insects, and neonate ungulates in black bear diet in northeastern Oregon. *Northwest Science*. 2001; 75:244–253.
- Bunn, HT. Meat made us human. In: Ungar, PS., editor. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford (United Kingdom): Oxford University Press; 2007. p. 191-211.
- Bunn HT, Ezzo JA. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *Journal of Archaeological Science*. 1993; 20:365–398.
- Bunn HT, Kroll EM. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania (and comments and reply). *Current Anthropology*. 1986; 27:431–452.
- Bunn HT, Pickering TR. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running-hunting and passive scavenging by early Pleistocene hominins. *Quaternary Research*. 2010; 74:395–404.
- Butynski TM. Blue monkey (*Cercopithecus mitis stuhlmanni*) predation on galagos. *Primates*. 1982; 23:563–566.
- Byrnes G, Libby T, Lim NTL, Spence AJ. Gliding saves time but not energy in Malayan colugos. *Journal of Experimental Biology*. 2011; 214:2690–2696. [PubMed: 21795564]
- Cachel, S. *Primate and Human Evolution*. Cambridge (United Kingdom): Cambridge University Press; 2006.
- Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK. *Primates in Perspective*. Oxford (United Kingdom): Oxford University Press; 2007.
- Carlson KJ, Stout D, Jashashvili T, de Ruiter DJ, Tafforeau P, Carlson K, Berger LR. The endocast of MH1, *Australopithecus sediba*. *Science*. 2011; 333:1402–1407. [PubMed: 21903804]

- Carrier DR. The energetic paradox of human running and hominid evolution (and comments and reply). *Current Anthropology*. 1984; 25:483–495.
- Carrier DR, Anders C, Schilling N. The musculoskeletal system of humans is not tuned to maximize the economy of locomotion. *Proceedings of the National Academy of Sciences of the United States of America*. 2011; 108:18631–18636. [PubMed: 22065766]
- Cerling TE, Levin NE, Quade J, Wynn JG, Fox DL, Kingston JD, Klein RG, Brown FH. Comment on the paleoenvironment of *Ardipithecus ramidus*. *Science*. 2010; 328:1105. [PubMed: 20508112]
- Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, Sponheimer M, Uno KT. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences of the United States of America*. 2011; 108:9337–9341. [PubMed: 21536914]
- Charnov EL. Optimal foraging: attack strategy of a mantid. *American Naturalist*. 1976; 110:141–151.
- Clark JD, Harris JWK. Fire and its roles in early hominid lifeways. *African Archaeological Review*. 1985; 3:3–27.
- Conklin-Brittain, NL.; Knott, CD.; Wrangham, RW. The feeding ecology of apes. *The Apes: Challenges for the 21st Century; Conference Proceedings; Brookfield (Illinois): Brookfield Zoo; 2001. p. 167-174.*
- Conklin-Brittain, NL.; Wrangham, RW.; Smith, CC. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar, PS.; Teaford, MF., editors. *Human Diet: Its Origin and Evolution*. Westport (Connecticut): Bergin & Garvey; 2002. p. 61-76.
- Conklin-Brittain NL, Wrangham RW, Hunt KD. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology*. 1998; 19:971–998.
- Crawford MA, Bloom M, Broadhurst CL, Schmidt WF, Cunnane SC, Galli C, Gehbremeskel K, Linseisen F, Lloyd-Smith J, Parkington J. Evidence for the unique function of docosahexaenoic acid during the evolution of the modern hominid brain. *Lipids*. 1999; 34:S39–S47. [PubMed: 10419087]
- Crittenden AN. The importance of honey consumption in human evolution. *Food and Foodways*. 2011; 19:257–273.
- Daegling DJ, Judex S, Ozcivici E, Ravosa MJ, Taylor AB, Grine FE, Teaford MF, Ungar PS. Viewpoints: Feeding mechanics, diet, and dietary adaptations in early hominins. *American Journal of Physical Anthropology*. 2013; 151:356–371. [PubMed: 23794331]
- D’Anastasio R, Zipfel B, Moggi-Cecchi J, Stanyon R, Capasso L. Possible brucellosis in an early hominin skeleton from Sterkfontein, South Africa. *PLoS ONE*. 2009; 4:e6439. [PubMed: 19649274]
- Dart RA. *Australopithecus africanus*: the man-ape of South Africa. *Nature*. 1925; 115:195–199.
- Dart RA. The predatory transition from ape to man. *International Anthropological and Linguistic Review*. 1953; 1:201–218.
- Dart, RA. *The Osteodontokeratic Culture of Australopithecus prometheus*. Pretoria (South Africa): Transvaal Museum; 1957.
- Dart RA. The carnivorous propensity of baboons. *Symposia of the Zoological Society of London*. 1963; 10:49–56.
- Dart, RA.; Craig, D. *Adventures with the Missing Link*. New York: Harper and Brothers; 1959.
- Darwin, C. *The Descent of Man, and Selection in Relation to Sex*. Amherst (New York): Prometheus Books; 1874. [1998 reprint.]
- Domínguez-Rodrigo M. Hunting and scavenging by early humans: the state of the debate. *Journal of World Prehistory*. 2002; 16:1–54.
- Domínguez-Rodrigo M, Barba R. New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore-hominid-carnivore hypothesis falsified. *Journal of Human Evolution*. 2006; 50:170–194. [PubMed: 16413934]
- Domínguez-Rodrigo M, Bunn HT, Yravedra J. A critical re-evaluation of bone surface modification models for inferring fossil hominin and carnivore interactions through a multivariate approach: application to the FLK Zinj archaeofaunal assemblage (Olduvai Gorge, Tanzania). *Quaternary International*. 2014; 322–323:32–43.

- Domínguez-Rodrigo M, Pickering TR, Bunn HT. Configurational approach to identifying the earliest hominin butchers. *Proceedings of the National Academy of Sciences of the United States of America*. 2010; 107:20929–20934. [PubMed: 21078985]
- Domínguez-Rodrigo M, Pickering TR, Díez-Martín F, Mabulla A, Musiba C, Tranco G, Baquedano E, Bunn HT, Barboni D, Santonja M, Uribealarea D, Ashley GM, del Sol Martínez-Ávila M, Barba R, Gidna A, Yravendra J, Arriaza C. Earliest porotic hyperostosis on a 1.5-million-year-old hominin, Olduvai Gorge, Tanzania. *PLoS One*. 2012; 7:e46414. [PubMed: 23056303]
- Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evolutionary Biology*. 2008; 35:159–175.
- Duda P, Zrzavý J. Evolution of life history and behavior in Hominidae: towards phylogenetic reconstruction of the chimpanzee-human last common ancestor. *Journal of Human Evolution*. 2013; 65:424–446. [PubMed: 23981863]
- Dusseldorp, GL. *A View to a Kill: Investigating Middle Palaeolithic Subsistence Using an Optimal Foraging Perspective*. Leiden (The Netherlands): Sidestone Press; 2009.
- Engels, F. *The Part Played by Labour in the Transition From Ape to Man*. Moscow (Russia): Foreign Languages Publishing House; 1876. [1953 reprint.]
- Estebarez F, Galbany J, Martínez LM, Turbón D, Pérez-Pérez. Buccal dental microwear analyses support greater specialization in consumption of hard foodstuffs for *Australopithecus anamensis*. *Journal of Anthropological Sciences*. 2012; 90:1–24.
- Estrada A, Estrada R. Patterns of predation in a free-ranging troop of stump-tail macaques (*Macaca arctoides*): relations to the ecology II. *Primates*. 1977; 18:633–646.
- Fitch, WT. *The Evolution of Language*. Cambridge (United Kingdom): Cambridge University Press; 2010.
- Gaulin SJC. A Jarman/Bell model of primate feeding niches. *Human Ecology*. 1979; 7:1–20.
- Genovesio A, Wise SP, Passingham RE. Prefrontal-parietal function: from foraging to foresight. *Trends in Cognitive Sciences*. 2014; 18:72–81. [PubMed: 24378542]
- Gilby IC, Eberly LE, Pintea L, Pusey AE. Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*. 2006; 72:169–180.
- Gilby IC, Wrangham RW. Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology*. 2007; 61:1771–1779.
- Gilliam JF, Fraser DF. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*. 1987; 68:1856–1862.
- Goodall, J. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge (Massachusetts): Belknap Press of Harvard University Press; 1986.
- Gordon KD. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *American Journal of Physical Anthropology*. 1982; 59:195–215. [PubMed: 7149017]
- Goren-Inbar N, Alperson N, Kislev ME, Simchoni O, Melamed Y, Ben-Nun A, Werker E. Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. *Science*. 2004; 304:725–727. [PubMed: 15118160]
- Gremillion KJ. Foraging theory and hypothesis testing in archaeology: an exploration of methodological problems and solutions. *Journal of Anthropological Archaeology*. 2002; 21:142–164.
- Griffith CS, Long BL, Sept JM. HOMINIDS: an agent-based spatial simulation model to evaluate behavioral patterns of early Pleistocene hominids. *Ecological Modelling*. 2010; 221:738–760.
- Grine FE. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *Journal of Human Evolution*. 1986; 15:783–822.
- Grine, FE. Molar microwear, diet and adaptation in a purported hominin species lineage from the Pliocene of East Africa. In: Reed, KE.; Fleagle, JF.; Leakey, RE., editors. *The Paleobiology of Australopithecus*. New York: Springer; 2013. p. 213–223.
- Gursky, SL. *The Spectral Tarsier*. Upper Saddle River (New Jersey): Pearson/Prentice Hall; 2007.

- Haile-Selassie Y, Latimer BM, Alene M, Deino AL, Gibert L, Melillo SM, Saylor BZ, Scott GR, Lovejoy CO. An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proceedings of the National Academy of Sciences of the United States of America*. 2010; 107:12121–12126. [PubMed: 20566837]
- Hamilton WJ III, Buskirk RE, Buskirk WH. Omnivory and utilization of food resources by chacma baboons, *Papio ursinus*. *American Naturalist*. 1978; 112:911–924.
- Harcourt AH, Harcourt SA. Insectivory by gorillas. *Folia Primatologica*. 1984; 43:229–233.
- Harding, RSO. An order of omnivores: nonhuman primate diets in the wild. In: Harding, RSO.; Teleki, G., editors. *Omnivorous Primates: Gathering and Hunting in Human Evolution*. New York: Columbia University Press; 1981. p. 191-214.
- Hardus ME, Lameira AR, Zulfa A, Atmoko SS, de Vries H, Wich SA. Behavioral, ecological, and evolutionary aspects of meat-eating by Sumatran orangutans (*Pongo abelii*). *International Journal of Primatology*. 2012; 33:287–304. [PubMed: 22467998]
- Harris JM, Cerling TE. Dietary adaptations of extant and Neogene African suids. *Journal of Zoology*. 2002; 256:45–54.
- Hart, D.; Sussman, RW. *Man the Hunted: Primates, Predators, and Human Evolution*. New York: Westview Press; 2005.
- Hatley T, Kappelman J. Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of belowground food resources. *Human Ecology*. 1980; 8:371–387.
- Hawkes K, Hill K, O'Connell JF. Why hunters gather: optimal foraging and the Aché of eastern Paraguay. *American Ethnologist*. 1982; 9:379–398.
- Heinzl J, Clark JD, White T, Hart W, Renne P, WoldeGabriel G, Beyene Y, Vrba E. Environment and behavior of 2.5-million-year-old Bouri hominids. *Science*. 1999; 284:625–629. [PubMed: 10213682]
- Henry AG. Recovering dietary information from extant and extinct primates using plant microremains. *International Journal of Primatology*. 2012; 33:702–715. [PubMed: 22707809]
- Henry AG, Ungar PS, Passey BH, Sponheimer M, Rossouw L, Bamford M, Sandberg P, de Ruiter DJ, Berger L. The diet of *Australopithecus sediba*. *Nature*. 2012; 487:90–93. [PubMed: 22763449]
- Hill K. Hunting and human evolution. *Journal of Human Evolution*. 1982; 11:521–544.
- Hill, K.; Hawkes, K. Neotropical hunting among the Aché of Eastern Paraguay. In: Hames, RB.; Vickers, WT., editors. *Adaptive Responses of Native Amazonians*. New York: Academic Press; 1983. p. 139-188.
- Hill RA, Dunbar RIM. Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology*. 2002; 16:579–593.
- Hockett CF. The origin of speech. *Scientific American*. 1960; 203:88–96. [PubMed: 13683472]
- Hohmann, G. The diets of non-human primates: frugivory, food processing, and food sharing. In: Hublin, J-J.; Richards, MP., editors. *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. New York: Springer; 2009. p. 1-14.
- Hohmann G, Fruth B. New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatologica*. 2008; 79:103–110.
- Holloway RL, Clarke RJ, Tobias PV. Posterior lunule sulcus in *Australopithecus africanus*: was Dart right? *Comptes Rendus Palevol*. 2004; 3:287–293.
- Hunt KD. The evolution of human bipedality: ecology and functional morphology. *Journal of Human Evolution*. 1994; 26:183–202.
- Hutchinson GE. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*. 1957; 22:415–427.
- Hutchinson, GE. *The Ecological Theater and the Evolutionary Play*. New Haven (Connecticut): Yale University Press; 1965.
- Jolly CJ. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man*. 1970; 5:5–26.
- Jones MA. Seasonal changes in the diet of bushpig, *Potamochoerus porcus* Linn., in the Matopos National Park. *South African Journal of Wildlife Research*. 1984; 14:97–100.

- Kaplan, H.; Hill, K. The evolutionary ecology of food acquisition. In: Smith, EA.; Winterhalder, B., editors. *Evolutionary Ecology and Human Behavior*. New York: Aldine de Gruyter; 1992. p. 167-201.
- Kaplan H, Hill K, Lancaster J, Hurtado AM. A theory of human life history evolution: diet, intelligence, and longevity. *Evolutionary Anthropology*. 2000; 9:156–185.
- Kark JA, Victor M, Hines JD, Harris JW. Nutritional vitamin B₁₂ deficiency in rhesus monkeys. *American Journal of Clinical Nutrition*. 1974; 27:470–478. [PubMed: 4207339]
- Kay, RNB.; Davies, AG. Digestive physiology. In: Davies, AG.; Oates, JF., editors. *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge (United Kingdom): Cambridge University Press; 1994. p. 229-249.
- Keeley JE, Rundel PW. Evolution of CAM and C₄ carbon-concentrating mechanisms. *International Journal of Plant Sciences*. 2003; 164:S55–S77.
- Keene, AS. *Prehistoric Foraging in a Temperate Forest: A Linear Programming Model*. New York: Academic Press; 1981.
- Kimbel WH, Walter RC, Johanson DC, Reed KE, Aronson JL, Assefa Z, Marean CW, Eck GG, Bobe R, Hovers E, Rak Y, Vondra C, Yemane T, York D, Chen Y, Evensen NM, Smith PE. Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *Journal of Human Evolution*. 1996; 31:549–561.
- Klein RG. Archeology and the evolution of human behavior. *Evolutionary Anthropology*. 2000; 9:17–36.
- Krantz GS. Brain size and hunting ability in earliest man. *Current Anthropology*. 1968; 9:450–451.
- Krebs, JR.; McCleery, RH. Optimization in behavioural ecology. In: Krebs, JR.; Davies, NB., editors. *Behavioural Ecology: An Evolutionary Approach*. 2. Sutherland (Massachusetts): Sinauer Associates; 1984. p. 91-121.
- Kudo H, Mitani M. New record of predatory behavior by the mandrill in Cameroon. *Primates*. 1985; 26:161–167.
- Kurland JA, Beckerman SJ. Optimal foraging and hominid evolution: labor and reciprocity. *American Anthropologist*. 1985; 87:73–93.
- Laden G, Wrangham R. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. *Journal of Human Evolution*. 2005; 49:482–498. [PubMed: 16085279]
- Latimer, B. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Coppens, Y.; Senut, B., editors. *Origine(s) de la Bipedie Chez les Hominidés*. Paris (France): Editions du CNRS; 1991. p. 169-176.
- Latimer B. The perils of being bipedal. *Annals of Biomedical Engineering*. 2005; 33:3–6. [PubMed: 15709701]
- Latimer BM, White TD, Kimbel WH, Johanson DC, Lovejoy CO. The pygmy chimpanzee is not a living missing link in human evolution. *Journal of Human Evolution*. 1981; 10:475–488.
- Leakey, LSB. Facts instead of dogmas on man's origin. Transcript of a symposium sponsored by the Wenner-Gren Foundation for Anthropological Research in 1965. In: McCown, TD.; Kennedy, KAR., editors. *Climbing Man's Family Tree: A Collection of Major Writings on Human Phylogeny*. Englewood Cliffs (New Jersey): Prentice-Hall; 1972. p. 386-399.
- Leakey, R.; Lewin, R. *Origins Reconsidered: In Search of What Makes Us Human*. New York: Doubleday; 1992.
- Lee, RB.; DeVore, I. *Man the Hunter*. Chicago (Illinois): Aldine Publishing Company; 1968.
- Lee-Thorp J, Likius A, Mackaye HT, Vignaud P, Sponheimer M, Brunet M. Isotopic evidence for an early shift to C₄ resources by Pliocene hominins in Chad. *Proceedings of the National Academy of Sciences of the United States of America*. 2012; 109:20369–20372. [PubMed: 23150583]
- Lee-Thorp JA, Sponheimer M, Passay BH, de Ruiter DJ, Cerling TE. Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2010; 365:3389–3396.
- Leopold AC, Ardrey R. Toxic substances in plants and the food habits of early man. *Science*. 1972; 176:512–514. [PubMed: 5032351]

- Lieberman DE, Bramble DM, Raichlen DA, Shea JJ. The evolution of endurance running and the tyranny of ethnography: a reply to Pickering and Bunn (2007). *Journal of Human Evolution*. 2007; 53:439–442. [PubMed: 17767947]
- Lieberman, DE.; Bramble, DM.; Raichlen, DA.; Shea, JJ. Brains, brawn, and the evolution of human endurance running capacities. In: Grines, FE.; Fleagle, JG.; Leakey, RE., editors. *The First Humans: Origin and Evolution of the Genus Homo*. New York: Springer; 2009. p. 77-92.
- Lifjeld JT, Slagsvold T. Effects of energy costs on the optimal diet: an experiment with pied flycatchers *Ficedula hypoleuca* feeding nestlings. *Ornis Scandinavica*. 1988; 19:111–118.
- Linton, S. Woman the gatherer: male bias in anthropology. In: Jacobs, SE., editor. *Women in Cross-Cultural Perspective*. Urbana (Illinois): University of Illinois Press; 1971. p. 9-21.
- Louchart A, Wesselman H, Blumenschine RJ, Hlusko LJ, Njau JK, Black MT, Asnake M, White TD. Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat. *Science*. 2009; 326:66e1–66e4.
- Lovejoy CO. The origin of man. *Science*. 1981; 211:341–350. [PubMed: 17748254]
- Lovejoy CO. Models of human evolution. *Science*. 1982; 217:304–306. [PubMed: 17791500]
- Lovejoy CO. Evolution of human walking. *Scientific American*. 1988; 259:118–125. [PubMed: 3212438]
- Lovejoy, CO. Modeling human origins: are we sexy because we're smart, or smart because we're sexy. In: Rasmussen, DT., editor. *The Origin and Evolution of Humans and Humanness*. Sudbury (Massachusetts): Jones and Bartlett; 1993. p. 1-28.
- Lovejoy CO. Reexamining human origins in light of *Ardipithecus ramidus*. *Science*. 2009; 326:74e1–74e8.
- Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science*. 2009a; 326:72e1–72e8.
- Lovejoy CO, McCollum MA. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip-bent-knee gait. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2010; 365:3289–3299.
- Lovejoy CO, Simpson SW, White TD, Asfaw B, Suwa G. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science*. 2009b; 326:70e1–70e8.
- Lovejoy CO, Suwa G, Simpson SW, Matternes JH, White TD. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science*. 2009c; 326:100–106. [PubMed: 19810199]
- Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. *Science*. 2009d; 326:71e1–71e6.
- Luca F, Perry GH, Di Rienzo A. Evolutionary adaptations to dietary changes. *Annual Review of Nutrition*. 2010; 30:291–314.
- Lucas PW, Omar R, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Thai LA, Watzke J, Strait DS, Atkins AG. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *Journal of the Royal Society Interface*. 2013; 10:20120923.
- Mann, AE. Diet and human evolution. In: Harding, RSO.; Teleki, G., editors. *Omnivorous Primates: Gathering and Hunting in Human Evolution*. New York: Columbia University Press; 1981. p. 10-36.
- Mann N. Dietary lean red meat and human evolution. *European Journal of Nutrition*. 2000; 39:71–79. [PubMed: 10918988]
- Mann N. Meat in the human diet: an anthropological perspective. *Nutrition and Dietetics*. 2007; 64 (Supplement 4):S102–S107.
- Marlowe FW, Berbesque JC. Tubers as fallback foods and their impact on Hadza hunter-gatherers. *American Journal of Physical Anthropology*. 2009; 140:751–758. [PubMed: 19350623]
- McCollum MA, Rosenman BA, Suwa G, Meindl RS, Lovejoy CO. The vertebral formula of the last common ancestor of African apes and humans. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*. 2010; 314B:123–134.
- McGeachin RL, Akin JR. Amylase levels in the tissues and body fluids of several primate species. *Comparative Biochemistry and Physiology Part A: Physiology*. 1982; 72:267–269.

- McGrew WC. The 'other faunivory' revisited: insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution*. 2014;10.1016/j.jhevol.2013.07.016
- McKenna, TK. *Food of the Gods: The Search For the Original Tree of Knowledge: A Radical History of Plants, Drugs, and Human Evolution*. New York: Bantam Books; 1992.
- McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, Geraads D, Bobe R, Bérart HA. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*. 2010; 466:857–860. [PubMed: 20703305]
- Mensforth RP, Lovejoy CO, Lallo JW, Armelagos GJ. Part two: the role of constitutional factors, diet, and infectious disease in the etiology of porotic hyperostosis and periosteal reactions in prehistoric infants and children. *Medical Anthropology: Cross-Cultural Studies in Health and Illness*. 1978; 2:1–59.
- Menzel CR. Spontaneous use of matching visual cues during foraging by long-tailed macaques (*Macaca fascicularis*). *Journal of Comparative Psychology*. 1996; 110:370–376. [PubMed: 8956507]
- Menzel CR. Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. *Journal of Comparative Psychology*. 1999; 113:426–434. [PubMed: 10608566]
- Menzel EW Jr. Communication about the environment in a group of young chimpanzees. *Folia Primatologica*. 1971; 15:220–232.
- Menzel EW Jr. Chimpanzee spatial memory organization. *Science*. 1973; 182:943–945. [PubMed: 17737534]
- Menzel EW Jr. A group of young chimpanzees in a one-acre field. *Behavior of Nonhuman Primates*. 1974; 5:83–153.
- Milton, K. Primate diets and gut morphology: implications for hominid evolution. In: Harris, M.; Ross, EB., editors. *Food and Evolution: Toward a Theory of Human Food Habits*. Philadelphia (Pennsylvania): Temple University Press; 1987. p. 93-115.
- Mitani JC, Watts DP. Why do chimpanzees hunt and share meat? *Animal Behaviour*. 2001; 61:915–924.
- Mithen, SJ. *Thoughtful Foragers: A Study of Prehistoric Decision Making*. Cambridge (United Kingdom): Cambridge University Press; 1990.
- Nakagawa N. Feeding rate as valuable information in primate feeding ecology. *Primates*. 2009; 50:131–141. [PubMed: 19205830]
- Nakatsukasa M. Acquisition of bipedalism: the Miocene hominoid record and modern analogues for bipedal protohominids. *Journal of Anatomy*. 2004; 204:385–402. [PubMed: 15198702]
- National Research Council. *Nutrient Requirements of Nonhuman Primates*. 2. Washington (DC): National Academies Press; 2003.
- Niemitz, C. Outline of the behavior of *Tarsius bancanus*. In: Doyle, GA.; Martin, RD., editors. *The Study of Prosimian Behavior*. New York: Academic Press; 1979. p. 631-660.
- Niemitz C. The evolution of the upright posture and gait—a review and a new synthesis. *Naturwissenschaften*. 2010; 97:241–263. [PubMed: 20127307]
- Norconk, MA. Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanus*) in Guri Lake, Venezuela. In: Norconk, MA.; Rosenberger, AL.; Garber, PA., editors. *Adaptive Radiations of Neotropical Primates*. New York: Plenum Press; 1996. p. 403-423.
- Norconk MA, Conklin-Brittain NL. Variation on frugivory: the diet of Venezuelan white-faced sakis. *International Journal of Primatology*. 2004; 25:1–26.
- Nowak, RM. *Walker's Mammals of the World*. 5. Baltimore (Maryland): Johns Hopkins University Press; 1991.
- Oakley, KP. On man's use of fire, with comments on tool-making and hunting. In: Washburn, SL., editor. *Social Life of Early Man*. Chicago (Illinois): Aldine Publishing Company; 1961. p. 176-193.
- Orians, GH.; Pearson, NE. On the theory of central place foraging. In: Horn, DJ.; Stairs, GR.; Mitchell, RD., editors. *Analysis of Ecological Systems*. Columbus (Ohio): Ohio State University Press; 1979. p. 155-177.

- Owren MJ, Amoss RT, Rendall D. Two organizing principles of vocal production: implications for nonhuman and human primates. *American Journal of Primatology*. 2011; 73:530–544. [PubMed: 21509789]
- Panger MA, Brooks AS, Richmond BG, Wood B. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology*. 2002; 11:235–245.
- Pante MC, Blumenschine RJ, Capaldo SD, Scott RS. Validation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. *Journal of Human Evolution*. 2012; 63:395–407. [PubMed: 22192864]
- Paulissen MA. Optimal foraging and intraspecific diet differences in the lizard *Cnemidophorus sexlineatus*. *Oecologia*. 1987; 71:439–446.
- Perry GH, Dominy NJ, Claw KG, Lee AS, Fiegler H, Redon R, Werner J, Villanea FA, Mountain JL, Misra R, Carter NP, Lee C, Stone AC. Diet and the evolution of human amylase gene copy number variation. *Nature Genetics*. 2007; 39:1256–1260. [PubMed: 17828263]
- Perry, S.; Panger, M.; Rose, LM.; Baker, M.; Gros-Louis, J.; Jack, K.; MacKinnon, KC.; Manson, J.; Fedigan, L.; Pyle, K. Traditions in wild white-faced capuchin monkeys. In: Fragaszy, D.; Perry, S., editors. *The Biology of Traditions: Models and Evidence*. Cambridge (United Kingdom): Cambridge University Press; 2003. p. 391-425.
- Peters, CR. Theoretical and actualistic ecobotanical perspectives on early hominin diets and paleoecology. In: Ungar, PS., editor. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford (United Kingdom): Oxford University Press; 2007. p. 233-261.
- Peters CR, Vogel JC. Africa's wild C₄ plant foods and possible early hominid diets. *Journal of Human Evolution*. 2005; 48:219–236. [PubMed: 15737391]
- Pickering TR, Bunn HT. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *Journal of Human Evolution*. 2007; 53:434–438. [PubMed: 17720224]
- Pickering TR, Domínguez-Rodrigo M. Chimpanzee referents and the emergence of human hunting. *Open Anthropology Journal*. 2010; 3:107–113.
- Pickering TR, Wallis J. Bone modifications resulting from captive chimpanzee mastication: implications for the interpretation of Pliocene archaeological faunas. *Journal of Archaeological Science*. 1997; 24:1115–1127.
- Pontzer H. Relating ranging ecology, limb length, and locomotor economy in terrestrial animals. *Journal of Theoretical Biology*. 2012; 296:6–12. [PubMed: 22138093]
- Porter, LM. *The Behavioral Ecology of Callimicos and Tamarins in Northwestern Bolivia*. Upper Saddle River (New Jersey): Pearson/Prentice Hall; 2007.
- Potts R. Evolution and environmental change in early human prehistory. *Annual Review of Anthropology*. 2012; 41:151–167.
- Pruetz JD, Bertolani P. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology*. 2007; 17:412–417. [PubMed: 17320393]
- Putney RT. Do willful apes know what they are aiming at? *Psychological Record*. 1985; 35:49–62.
- Putney, RT. Willful apes revisited: the concept of prospective control. In: Washburn, DA., editor. *Primate Perspectives on Behavior and Cognition*. Washington (DC): American Psychological Association; 2007. p. 207-219.
- Rabenold D, Pearson OM. Scratching the surface: a critique of Lucas et al. (2013)'s conclusion that phytoliths do not abrade enamel. *Journal of Human Evolution*. 2014.10.1016/j.jhevol.2014.02.001
- Reed, KE.; Rector, AL. African Pliocene paleoecology: hominin habitats, resources, and diets. In: Ungar, PS., editor. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford (United Kingdom): Oxford University Press; 2007. p. 262-288.
- Reidhead, VA. *A Linear Programming Model of Prehistoric Subsistence Optimization: A Southeast Indiana Example*. Indianapolis (Indiana): Indiana Historical Society; 1981.
- Reilly SM, McElroy EJ, Biknevicius AR. Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. *Zoology*. 2007; 110:271–289. [PubMed: 17482802]
- Robinson, JT. The origin and adaptive radiation of the australopithecines. In: Kurth, G., editor. *Evolution and Hominsation: Papers to the Theory of Evolution as well as Dating, Classification, and Abilities of Human Hominids*. 2. Stuttgart (Germany): Gustav Fischer Verlag; 1968. p. 150-175.

- Rodman PS, McHenry HM. Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology*. 1980; 52:103–106. [PubMed: 6768300]
- Rosenzweig ML. A theory of habitat selection. *Ecology*. 1981; 62:327–335.
- Rumbaugh, DM. *Language Learning by a Chimpanzee: The LANA Project*. New York: Academic Press; 1977.
- Ruxton GD, Wilkinson DM. Thermoregulation and endurance running in extinct hominins: Wheeler's models revisited. *Journal of Human Evolution*. 2011; 61:169–175. [PubMed: 21489604]
- Ruxton GD, Wilkinson DM. Endurance running and its relevance to scavenging by early hominins. *Evolution*. 2013; 67:861–867. [PubMed: 23461334]
- Sanson GD, Kerr SA, Gross KA. Do silica phytoliths really wear mammalian teeth? *Journal of Archaeological Science*. 2007; 34:526–531.
- Sayers K. On folivory, competition, and intelligence: generalisms, overgeneralizations, and models of primate evolution. *Primates*. 2013; 54:111–124. [PubMed: 23263563]
- Sayers, K. High altitude primates, extreme primates, and anthropological primatology: or, there is more to human evolution than tool use, culture, or African apes. In: Grow, NB.; Gursky-Doyen, S.; Krzton, A., editors. *High Altitude Primates*. New York: Springer; 2014. p. 325-350.
- Sayers K, Lovejoy CO. The chimpanzee has no clothes: a critical examination of *Pan troglodytes* in models of human evolution (and comments and reply). *Current Anthropology*. 2008; 49:87–114.
- Sayers K, Menzel CR. Memory and foraging theory: chimpanzee utilization of optimality heuristics in the rank-order recovery of hidden foods. *Animal Behaviour*. 2012; 84:795–803. [PubMed: 23226837]
- Sayers K, Norconk MA. Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: diet, activity patterns, and resources. *International Journal of Primatology*. 2008; 29:509–530.
- Sayers K, Norconk MA, Conklin-Brittain NL. Optimal foraging on the roof of the world: Himalayan langurs and the classical prey model. *American Journal of Physical Anthropology*. 2010; 141:337–357. [PubMed: 19844998]
- Sayers K, Raghanti MA, Lovejoy CO. Human evolution and the chimpanzee referential doctrine. *Annual Review of Anthropology*. 2012; 41:119–138.
- Schaller GB, Lowther GR. The relevance of carnivore behavior to the study of early hominids. *Southwestern Journal of Anthropology*. 1969; 25:307–341.
- Schoener TW. Theory of feeding strategies. *Annual Review of Ecology and Systematics*. 1971; 2:369–404.
- Schoeninger MJ, Bunn HT, Murray SS, Marlett JA. Composition of tubers used by Hadza foragers of Tanzania. *Journal of Food Composition and Analysis*. 2001; 14:15–25.
- Schrire C. An inquiry into the evolutionary status and apparent identity of San hunter-gatherers. *Human Ecology*. 1980; 8:9–32.
- Semaw S, Rogers MJ, Quade J, Renne PR, Butler RF, Domínguez-Rodrigo M, Stout D, Hart WS, Pickering T, Simpson SW. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution*. 2003; 45:169–177. [PubMed: 14529651]
- Sept, J. PhD diss. University of California; Berkeley: 1984. Plants and early hominids in East Africa: a study of vegetation in situations comparable to early archaeological site locations.
- Sept, J. Modeling the significance of paleoenvironmental context for early hominin diets. In: Ungar, PS., editor. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford (United Kingdom): Oxford University Press; 2007. p. 289-307.
- Shillito LM. Grains of truth or transparent blindfolds? A review of current debates in archaeological phytolith analysis. *Vegetation History and Archaeobotany*. 2013; 22:71–82.
- Shiple LA, Forbey JS, Moore BD. Revisiting the dietary niche: when is a mammalian herbivore a specialist? *Integrative and Comparative Biology*. 2009; 49:274–290. [PubMed: 21665820]
- Shipman P. Scavenging or hunting in early hominids: theoretical framework and tests. *American Anthropologist*. 1986; 88:27–43.
- Shipman P, Phillips-Conroy J. Hominid tool-making versus carnivore scavenging. *American Journal of Physical Anthropology*. 1977; 46:77–86.

- Shipman P, Walker A. The costs of becoming a predator. *Journal of Human Evolution*. 1989; 18:373–392.
- Sih A, Christensen B. Optimal diet theory: when does it work, and when and why does it fail? *Animal Behaviour*. 2001; 61:379–390.
- Silberbauer, G. Hunter/gatherers of the central Kalahari. In: Harding, RSO.; Teleki, G., editors. *Omnivorous Primates: Gathering and Hunting in Human Evolution*. New York: Columbia University Press; 1981. p. 455–498.
- Sillen A. Strontium-calcium ratios (Sr/Ca) of *Australopithecus robustus* and associated fauna from Swartkrans. *Journal of Human Evolution*. 1992; 23:495–516.
- Sillen A, Hall G, Armstrong R. Strontium calcium ratios (Sr/Ca) and strontium isotopic ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) of *Australopithecus robustus* and *Homo* sp. from Swartkrans. *Journal of Human Evolution*. 1995; 28:277–285.
- Simpson, SW. The earliest hominins. In: Larsen, CS., editor. *A Companion to Biological Anthropology*. West Sussex (United Kingdom): Wiley-Blackwell; 2010. p. 314–340.
- Sockol MD, Raichlen DA, Pontzer H. Chimpanzee locomotor energetic and the origin of human bipedalism. *Proceedings of the National Academy of Sciences of the United States of America*. 2007; 104:12265–12269. [PubMed: 17636134]
- Speth JD. Early hominid hunting and scavenging: the role of meat as an energy source. *Journal of Human Evolution*. 1989; 18:329–343.
- Sponheimer, M. Some ruminations on australopith diets. In: Reed, KE.; Fleagle, JF.; Leakey, RE., editors. *The Paleobiology of Australopithecus*. New York: Springer; 2013. p. 225–233.
- Sponheimer M, Alemseged Z, Cerling TE, Grine FE, Kimbel WH, Leakey MG, Lee-Thorp JA, Manthi FK, Reed KE, Wood BA, Wynn JG. Isotopic evidence of early hominin diets. *Proceedings of the National Academy of Sciences of the United States of America*. 2013; 110:10513–10518.
- Sponheimer M, de Ruiter D, Lee-Thorp J, Späth A. Sr/Ca and early hominin diets revisited: new data from modern and fossil tooth enamel. *Journal of Human Evolution*. 2005; 48:147–156. [PubMed: 15701528]
- Sponheimer, M.; Lee-Thorp, J.; de Ruiter, D. Icarus, isotopes, and australopith diets. In: Ungar, PS., editor. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford (United Kingdom): Oxford University Press; 2007. p. 132–149.
- Stahl AB. Hominid dietary selection before fire (and comments and reply). *Current Anthropology*. 1984; 25:151–168.
- Stanford CB. Chimpanzee hunting behavior and human evolution. *American Scientist*. 1995; 83:256–261.
- Stanford CB. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist*. 1996; 98:96–113.
- Stanford, CB. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Cambridge (Massachusetts): Harvard University Press; 1998.
- Stanford, CB. *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. Princeton (New Jersey): Princeton University Press; 1999.
- Stanford, CB. A comparison of social meat-foraging by chimpanzees and human foragers. In: Stanford, CB.; Bunn, HT., editors. *Meat-eating and Human Evolution*. Oxford (United Kingdom): Oxford University Press; 2001. p. 122–140.
- Stanford, CB. *Upright: The Evolutionary Key to Becoming Human*. Boston (Massachusetts): Houghton Mifflin; 2003.
- Stephens, DW.; Krebs, JR. *Foraging Theory*. Princeton: Princeton University Press; 1986.
- Studel-Numbers KL, Wall-Scheffler CM. Optimal running speed and the evolution of hominin hunting strategies. *Journal of Human Evolution*. 2009; 56:355–360. [PubMed: 19297009]
- Strum, SC. Processes and products of change: baboon predatory behavior at Gilgil, Kenya. In: Harding, RSO.; Teleki, G., editors. *Omnivorous Primates: Gathering and Hunting in Human Evolution*. New York: Columbia University Press; 1981. p. 255–302.

- Strum, SC.; Mitchell, W. Baboon models and muddles. In: Kinzey, WG., editor. *The Evolution of Human Behavior: Primate Models*. Albany (New York): State University of New York Press; 1987. p. 87-104.
- Sullivan KA. Age-specific profitability and prey choice. *Animal Behaviour*. 1988; 36:613–615.
- Suwa G, Kono RT, Simpson SW, Asfaw B, Lovejoy CO, White TD. Paleobiological implications of the *Ardipithecus ramidus* dentition. *Science*. 2009; 326:94–99. [PubMed: 19810195]
- Suzuki A. An ecological study of wild Japanese monkeys in snowy areas—focused on their food habits. *Primates*. 1965; 6:31–72.
- Tanner, N. The chimpanzee model revisited and the gathering hypothesis. In: Kinzey, WG., editor. *The Evolution of Human Behavior: Primate Models*. Albany (New York): State University of New York Press; 1987. p. 3-27.
- Teaford MF. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. *Scanning Microscopy*. 1988; 2:1167–1175. [PubMed: 3399851]
- Teaford MF, Ungar PS. Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Sciences of the United States of America*. 2000; 97:13506–13511. [PubMed: 11095758]
- Teleki, G. *The Predatory Behavior of Wild Chimpanzees*. Lewisburg (Pennsylvania): Bucknell University Press; 1973.
- Teleki G. Primate subsistence patterns: collector-predators and gatherer-hunters. *Journal of Human Evolution*. 1975; 4:125–184.
- Tennie C, Gilby IC, Mundry R. The meat-scrap hypothesis: small quantities of meat may promote cooperative hunting in wild chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology*. 2009; 63:421–431.
- Thompson PR. A cross-species analysis of carnivore, primate, and hominid behaviour. *Journal of Human Evolution*. 1975; 4:113–124.
- Tooby, J.; DeVore, I. The reconstruction of hominid behavioral evolution through strategic modeling. In: Kinzey, WG., editor. *The Evolution of Human Behavior: Primate Models*. Albany (New York): State University of New York Press; 1987. p. 183-237.
- Ungar PS. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *Journal of Human Evolution*. 2004; 46:605–622. [PubMed: 15120268]
- Ungar PS, Grine FE, Teaford MF. Diet in early *Homo*: a review of the evidence and a new model of adaptive versatility. *Annual Review of Anthropology*. 2006; 35:209–228.
- Ungar PS, Sponheimer M. The diets of early hominins. *Science*. 2011; 334:190–193. [PubMed: 21998380]
- van der Merwe NJ, Masao FT, Bamford MK. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *South African Journal of Science*. 2008; 104:153–156.
- Van Valen L. A new evolutionary law. *Evolutionary Theory*. 1973; 1:1–30.
- Vuori E, Mäkinen SM, Kara R, Kuitunen P. The effects of the dietary intakes of copper, iron, manganese, and zinc on the trace element content of human milk. *American Journal of Clinical Nutrition*. 1980; 33:227–231. [PubMed: 7355796]
- Waguespack NM. The organization of male and female labor in foraging societies: implications for early Paleolithic archaeology. *American Anthropologist*. 2005; 107:666–676.
- Wakayama EJ, Dillwith JW, Howard RW, Blomquist GJ. Vitamin B₁₂ levels in selected insects. *Insect Biochemistry*. 1984; 14:175–179.
- Washburn SL. *Australopithecines: the hunters or the hunted?* *American Anthropologist*. 1957; 59:612–614.
- Washburn, SL.; DeVore, I. Social behavior of baboons and early man. In: Washburn, SL., editor. *Social Life of Early Man*. Chicago (Illinois): Aldine Publishing Company; 1961. p. 91-105.
- Washburn, SL.; Lancaster, CS. The evolution of hunting. In: Lee, RB.; DeVore, I., editors. *Man the Hunter*. Chicago (Illinois): Aldine Publishing Company; 1968. p. 293-303.
- Westoby M. What are the biological bases of varied diets? *American Naturalist*. 1978; 112:627–631.

- Whelan, CJ.; Schmidt, KA. Food acquisition, processing and digestion. In: Stephens, DW.; Brown, JS.; Ydenberg, RC., editors. *Foraging: Behavior and Ecology*. Chicago (Illinois): University of Chicago Press; 2007. p. 141-174.
- White TD, Ambrose SH, Suwa G, et al. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. *Science*. 2009; 326:87–93. [PubMed: 19810193]
- White TD, Ambrose SH, Suwa G, Woldegabriel G. Response to comment on the paleoenvironment of *Ardipithecus ramidus*. *Science*. 2010; 328:1105.
- Winterhalder, B.; Smith, EA. *Hunter-Gatherer Foraging Strategies: Ethnographic and Archeological Analyses*. Chicago (Illinois): University of Chicago Press; 1981.
- Wolberg DL. The hypothesized osteodontokeratic culture of the Australopithecinae: a look at the evidence and the opinions (and comments and reply). *Current Anthropology*. 1970; 11:23–37.
- WoldeGabriel G, Ambrose SH, Barboni D, Bonnefille R, Bremond L, Currie B, DeGusta D, Hart WK, Murray AM, Renne PR, Jolly-Saad MC, Stewart KM, White TD. The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. *Science*. 2009; 326:65e1–65e5.
- Wolpoff, MH. *Paleoanthropology*. 2. Boston (Massachusetts): McGraw-Hill; 1999.
- Wood B, Strait D. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution*. 2004; 46:119–162. [PubMed: 14871560]
- Wrangham, R.; Pilbeam, D. African apes as time machines. In: Galdikas, BMF.; Briggs, NE.; Sheeran, LK.; Shapiro, GL.; Goodall, J., editors. *All Apes Great and Small, Volume I: African Apes*. New York: Kluwer Academic/Plenum Publishers; 2002. p. 5-17.
- Wrangham, RW. *Catching Fire: How Cooking Made Us Human*. New York: Basic Books; 2009.
- Wrangham RW, Jones JH, Laden G, Pilbeam D, Conklin-Brittain NL. The raw and the stolen: cooking and the ecology of human origins (and comments and reply). *Current Anthropology*. 1999; 40:567–594. [PubMed: 10539941]
- Wynn JG, Sponheimer M, Kimbel WH, Alemseged Z, Reed K, Bedasoe ZK, Wilson JN. Diet of *Australopithecus afarensis* from the Pliocene Hadar Formation, Ethiopia. *Proceedings of the National Academy of Sciences of the United States of America*. 2013; 110:10495–10500. [PubMed: 23733965]
- Yeakel JD, Bennett NC, Koch PL, Dominy NJ. The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet. *Proceeding of the Royal Society B: Biological Sciences*. 2007; 274:1723–1730.
- Yesner, DR. Archeological applications of optimal foraging theory: harvest strategies of Aleut hunter-gatherers. In: Winterhalder, B.; Smith, EA., editors. *Hunter-Gatherer Foraging Strategies: Ethnological and Archeological Analyses*. Chicago (Illinois): University of Chicago Press; 1981. p. 148-170.