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Citation	Wrangham, Richard, Dorothy Cheney, Robert Seyfarth, and Esteban Sarmiento. 2009. Shallow-water habitats as sources of fallback foods for hominins. The Importance of Fallback Foods in Primate Ecology and Evolution. Special Issue. American Journal of Physical Anthropology 140(4): 630–642.
Published Version	doi:10.1002/ajpa.21122
Accessed	April 17, 2018 3:35:23 PM EDT
Citable Link	http://nrs.harvard.edu/urn-3:HUL.InstRepos:8947970
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Shallow-water habitats as sources of fallback foods for hominins.

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pages: Text 28, Literature Cited 16, + 3 Tables, 3 Figures.

Short title: 'Hominin fallback foods in shallow-water habitats.'

Keywords: Wet savanna, delta, baboon, USOs, seasonality.

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For P. Constantino and B. Wright (eds), special issue of *AJPA* on the evolutionary significance of fallback foods.

Abstract

Underground storage organs (USOs) have been proposed as critical fallback foods for early hominins in savanna, but there has been little discussion as to which habitats would have been important sources of USOs. USOs consumed by hominins could have included both underwater and underground storage organs, i.e. from both aquatic and terrestrial habitats. Shallow aquatic habitats tend to offer high plant growth rates, high USO densities, and relatively continuous USO availability throughout the year. Baboons in the Okavango delta use aquatic USOs as a fallback food, and aquatic or semi-aquatic USOs support high-density human populations in various parts of the world. As expected given fossilization requisites, the African early to mid Pleistocene shows an association of *Homo* and *Paranthropus* fossils with shallow-water and flooded habitats where high densities of plant-bearing USOs are likely to have occurred. Given that early hominins in the tropics lived in relatively dry habitats, while others occupied temperate latitudes, ripe, fleshy fruits of the type preferred by African apes would not normally have been available year round. We therefore suggest that water-associated USOs were likely to have been key fallback foods, and that dry-season access to aquatic habitats would have been an important predictor of hominin home range quality. This study differs from traditional savanna chimpanzee models of hominin origins by proposing that access to aquatic habitats was a necessary condition for adaptation to savanna habitats. It also raises the possibility that harvesting efficiency in shallow water promoted adaptations for habitual bipedality in early hominins.

Inhabiting areas with low rainfall and temperate climates, early to mid Pleistocene African hominins would have needed to find plant foods year-round but would have found difficulty in obtaining them during periods of low plant productivity. During some periods of the annual cycle fruits tend to be unpredictable or scarce (Peters et al., 1984). Nuts and seeds are often then available, but like fruits are too seasonal to be relied on (Peters 1987). In savanna[1], during periods of fruit scarcity, the herbaceous foliage that forest-living African apes tend to eat as a fallback is also scarce (Remis, 1997; Tutin, 1997; Wrangham 2005). Some primates including orangutans *Pongo pygmaeus* utilize inner bark during periods of fruit shortage (Knott, 1998), and bark-eating could in theory be important for savanna chimpanzees (Pruetz 2006). However extensive bark-eating has not yet been recorded by chimpanzees in savanna: the density of suitable trees may be insufficient outside rainforest. Meat has been proposed as a possible fallback food, though Speth (1989) argued that during dry seasons the fat content of meat would have been so low that protein poisoning would have been induced by a diet of more than about 30% meat. By contrast, plant underground storage organs (USOs) tend to be nutritionally adequate and predictably available during low-growth seasons, features USOs owe to their primary function of storing nutrients and/or water (Andersen, 1987; Laden and Wrangham, 2005). USOs have therefore been proposed to be important components of the hominin diet (Hatley and Kappelman, 1980; Brain and Shipman, 1993; O'Connell et al. 1999; Wrangham et al. 1999). An increase in USO consumption may have even facilitated the hypothesized hominin shift from forest to more open habitats (Laden and Wrangham, 2005).

Ecological, archaeological, dental, nutritional and comparative data all support the proposed dietary importance of USOs in hominin evolution (Hatley and Kappelman, 1980; Laden and Wrangham, 2005). Edible USOs are much more abundant in savanna than rainforest habitats and there is little competition among mammals for USOs, since their underground location makes them unavailable to most species. USOs are widely eaten by human hunter-gatherers, hominid fossil sites characteristically sample habitats rich in USOs, and early hominin remains exhibit stable isotope signals with values similar to those of the USO-eating mole-rats (Bathyergidae) (Yeakel et al., 2007). Humans and early hominins all have jaws and teeth that appear well adapted for eating USOs (Hatley and Kappelman, 1980; Ungar et al., 2006). Thus Ungar et al. (2006) find that habiline teeth are adapted to crushing hard and brittle objects, while Dominy et al. (2008) conclude that USOs such as corms show low toughness but are hard and brittle. Hominin dental adaptations for processing USOs are consistent with the strong selective pressures that fallback foods are expected to place on an organism's food-processing structures (Marshall and Wrangham, 2007). USOs are a valuable human staple because they have a low concentration of fiber (Schoeninger et al., 2001; Conklin-Brittain et al., 2002) and may have sufficient nutritional quality to be significant dietary components for most human populations (Peters and Vogel, 2005; Laden and Wrangham, 2005). Finally chimpanzees have the cognitive ability to find and extract tubers using tools (Hernandez-Aguilar et al., 2007) or with their bare hands (Lanjouw, 2002), indicating that the last common ancestor of chimpanzees and humans (LCA) and early hominins probably also shared these abilities.

USOs are thus well-supported candidates as fallback foods for early hominins. However their proposed importance in hominin evolution has been challenged. For instance some USOs need to be cooked by humans to be edible, and there is little direct evidence for control of fire in the Lower Paleolithic (e.g. Plummer, 2004). Furthermore, the caloric value of some wild tubers is so low that their nutritional significance is questionable (Schoeninger et al., 2001). In addition, micro-wear studies of early *Homo* reveal fewer pits than expected for a hard-object specialist, and early *Homo* is argued to have had too much occlusal relief to be well adapted to eating USOs (Ungar et al., 2006). Moreover, African hunter-gatherer populations where USOs are reported to be most important in the diet (Hadza and San) are believed to be "demographic sinks". Living in marginal environments, these groups export few genes outside of their population and have thus been argued to be evolutionarily irrelevant (Peters and O'Brien, 1994; Plummer, 2004). Against these challenges, not all USOs have low caloric value or need to be cooked to be edible; USOs are not uniformly hard and brittle (Dominy et al., 2008); and USOs are eaten in many different environments.

Resolving the importance of USOs as hominin fallback foods may be aided by consideration of the mechanical and nutritional characteristics of different USO types (e.g. Dominy et al., 2008), and of food productivity in different habitats, the latter of which we focus on. While savannas are known to produce more edible USOs than rainforests, variability in USO production among different types of savanna habitats has not yet been examined in any detail. Here we propose that localized aquatic habitats would have been particularly productive of USOs during seasons when preferred hominin foods were scarce (cf. Wrangham, 2005). This hypothesis is in accord with evidence that hominins utilized C_4 food items such as sedges (van der Merwe et al. 2008), and more generally with the proposed importance of aquatic habitats as food sources based on paleoecology (Copeland, 2007). It also suggests that aquatic habitats would have been a valuable focus of hominin foraging during seasons of food scarcity, and that these habitats would have had important implications for hominin range use and population distribution. Our food-derived hypothesis thus conforms to prior suggestions that aquatic habitats have been important in hominin ecology (e.g. Jolly, 1970; Verhaegen et al., 2002).

We first examine whether plants growing in aquatic habitats tend to be especially productive of USOs. We then present data on baboon (*Papio cynocephalus ursinus*) diet in the Okavango Delta (Botswana) in order to test the hypothesis that a catarrhine with access to shallow water habitats surrounded by relatively arid land uses aquatic USOs as fallback foods. The Okavango baboon data together with data on USO ingestion in modern human populations is further used to assess the hypothesis that USOs would have been a likely fallback foods for hominins living in shallow water habitats. Although baboon diets are not appropriate analogues for the specific composition of hominin diets (Codron et al. 2008), the fact that baboons and modern humans consume USOs suggests that early hominins might do so also. Finally, we review the depositional habitats of early fossil hominins (i.e. *Paranthropus* and *Homo*), to test if the hominin fossil record is in accord with the use of shallow water USOs as fallback foods.

Are aquatic habitats especially productive of USOs?

Because light and water are principal factors limiting plant growth, tropical and sub-tropical shallow-water habitats tend to produce a high biomass of plant material compared to terrestrial habitats (Westlake, 1982). Aquatic habitats might therefore be unusually productive of USOs. Accordingly we consider USO productivity in the three main macrophyte types known to grow in shallow water: (1) fully aquatic macrophytes with floating leaves; (2) semi-aquatic or emergent macrophytes, i.e. plants with roots anchored below water but leaves and stems largely above water; and (3) floodplain herbs, which have roots submerged in water only seasonally.

(1) Aquatic macrophytes usually occur in still or slowly moving water. Their flat floating leaves facilitate maximal absorption of incoming light and high productivity. The high specific heat and low heat conductivity of water offer these plants stable thermal conditions and hence a longer growing season than experienced by neighboring terrestrial plants (Wetzel, 1988). Potentially, therefore, they are highly productive. They achieve maximal growth in seasonally flooded or slowly moving waters, whereas in stagnant swamps growth is usually reduced due to nutrient deficiency, especially low nitrogen (Breen et al., 1988).

The most common aquatic macrophytes are water-lilies of the family Nymphaeaceae. Nymphaeaceae are found worldwide and include three dominant genera, i.e, white water-lilies *Nymphaea* (the main African aquatic machrophyte), yellow water-lillies *Nuphar*, and water-lotuses *Nelumbo*. All produce abundant USOs that make up a large proportion of plant biomass. For instance the rhizome of *Nuphar* spp. accounts for about 80% of the plant’s biomass (den Hartog and van der Velde, 1988). The rhizomes have maximal nutrient quality at the end of the high-growth season (Brock et al., 1983).

USOs of *Nymphaea, Nuphar* and *Nelumbo* include corms, tubers and/or rhizomes, all of which are eaten both raw and cooked in every continent, by both farmers and hunter-gatherers (Brand-Miller et al., 1993; Jones and Meehan, 1989; Tull, 1999; Chawanje et al., 2001). The USOs of *Nymphaea* appear to be fallback foods in the Okavango Delta, Botswana. There the seeds, stems and USOs of *Nymphaea nouchali* are eaten by at least four modern human populations. Ingestion of raw corms and stems is especially common when food is scarce (Campbell, 1986; Ellery and Ellery, 1997; Roodt, 1998).

(2) Semi-aquatic or emergent macrophytes are found in shallow water along the edges of lakes, rivers and streams. Prominent examples include papyrus *Cyperus papyrus,* cattails *Typha* spp., and swamp potatoes or arrowhead *Sagittaria* spp. Like aquatic macrophytes, semi-aquatic macrophytes also show very high natural productivity thanks to their efficient canopies and unlimited water supply. For instance papyrus has one of the highest biomass growth rates known (up to 125 metric tons dry weight per ha per year, compared to 20-85 for grasslands and crops: Westlake, 1982). Like aquatic plants emergent macrophytes tend to invest heavily in USOs, e.g. around half of the biomass of tropical *Typha* is in USOs (Westlake, 1982). Their USO nutrient quality is high (e.g. *Cyperus papyrus*, van der Merwe et al., 2008) and like water-lilies is maximal during the dry (low-growth) season (Garver et al., 1988). These plants allow easy harvesting because they are found in large accessible patches (e.g. *Scirpus*, *Typha*; Copeland, 2007).

Cattails *Typha* spp., a wild semi-aquatic macrophyte, are so productive that their effect on human settlement patterns can be akin to that of an agricultural crop (Mitchell, 1839; Gott, 1999). According to historical accounts, cattail rhizomes were a main plant food, eaten year-round by aborigines inhabiting the lower Murray region of south-eastern

Australia (Gott, 1999). Given this rhizome's abundance in the well-watered parts of this region, these hunter-gatherers enjoyed a sedentary lifestyle. At the time of European contact population densities here were higher than anywhere else in Australia (Pate, 2006; Humphries, 2007). In fact, the population size, density and mobility was so similar to that of agricultural people that the aborigines living there were subject to pathologies similar to those associated with agriculture (Pate, 2006).

Sagittaria spp. also produce abundant tubers. Edible raw though preferably cooked, they were a staple for North American hunter-gatherers (Richardson 1981). These examples show that semi-aquatic macrophytes have a high potential for producing USOs that are eaten extensively, at all times of year.

(3) Floodplain herbs are found in seasonally flooded areas adjacent to lakes, rivers and streams. When water is available these plants store nutrients and water in USOs that enable them to lie dormant through periods of low growth and re-emerge when growth is once again optimal. Australian aborigines heavily exploit floodplain herbs such as corms of *Cyperus rotundus* and *Eleocharis dulcis*, which they may eat raw or cooked (Isaacs, 1987). For instance, Tindale (1974: 97) described *C. rotundus* corms as "an important standby item of diet… so widespread that there is little thought of it as being a clan possession; anyone may eat at will" even though "those who feed on it for long periods develop swollen bellies." Hillman et al. (1989) showed that *C. rotundus* USOs were the staple food of Paleolithic hunter-gatherers along the Nile (cited by van der Merwe, 2005). In the absence of agriculture, floodplain herbs can evidently be a highly productive source of edible USOs.

Thus the three major types of shallow-water macrophyte include dominant plants of high natural productivity. These all produce USOs year-round, which are abundant, edible and have a high nutrient quality during dry seasons, which are times of low plant growth. The USOs of all three are recorded as plant remains in archaeological sites (e.g. *Nymphaea, Typha, Cyperus rotundus*: van der Merwe, 2005). Notably, Copeland (2007) found that herbaceous USOs from shallow-water habitats are more likely to be edible than those from drier habitats, and many can be eaten raw. All these plants can be easily located and harvested by humans. We propose, therefore, that shallow-water habitats may have served as an important source of USOs for hominins during periods of food shortage.

MATERIALS AND METHODS

As a test of whether USOs in tropical aquatic habitats are eaten as fallback foods we analyzed data on baboons in the Okavango.

Dietary data for baboons were collected from June 2006 to June 2007, from a group of 70-85 free-ranging chacma baboons (*Papio cynocephalus ursinus*) occupying about 5 sq km of the Moremi Game Reserve in the Okavango Delta of Botswana (23°02'E, 19°31'S). The study site was described by Cheney and Seyfarth (2007). It floods annually from approximately June through October, leaving only islands above water, i.e. elevated tree-lined areas ca. 1 to >100 ha in extent. Observed subjects consisted of 29-31 adult females, which were evenly sampled in 10-minute focal animal observations (Altmann, 1974; Cheney et al., 2004; Cheney & Seyfarth, 2007). Observers scored feeding activity at the end of every 10-minute focal observation, assigning foods eaten to one of 33 categories. Feeding data were compiled from a total of 5365 focal observations (mean 412.7 feeding records per month, SD 190.4). Foods were unidentified in 3.1% of records. Data were collected primarily in the morning hours, before 1 p.m.

To assess which items were used as fallback foods we classified the original 33 categories into four major groups, i.e. Fruits, Foliage, USOs , and Other Foods. "Foliage" included grass blades, and the leaf, shoots and pith of various identified and unidentified herbs. "Other Foods" included insects, *Acacia* products, flowers, snails, seeds, items extracted from elephant (*Loxodonta africana)* feces and various uncommon animal and plant items. Feeding records for each of the four major food groups including USOs were tabulated monthly as a percent of feeding records for all four major food groups. Feeding records of unidentified foods were reported monthly as a percentage of total feeding records (Table 1). Fallback foods were defined as those whose consumption was negatively correlated with the fruit component of the diet (Marshall and Wrangham, 2007).

With respect to early hominin habitats we considered only those African hominin fossil localities between 1.4 and 2.5 my old. This is the time interval in which *Homo* appears (Leakey et al, 1964; Leakey, 1973; Feibel et al., 1989; Hay and Kyser, 2001), many of the anatomically unique human specializations develop (Sarmiento, 1998), and the East and South African climate purportedly turns drier (deMenocal and Bloemendal, 1995). Considering the strong commitment of the unique human anatomy (see Sarmiento, 1998), the selective pressures that brought it about must have occurred over a prolonged period of hominin evolution and justify examining such a long history in the middle third of our lineage's geologic record. Temperature and rainfall data come from meteorological records and pertain to current conditions at each fossil locality, rather than conditions when fossils were deposited. Because African land mass position relative to the equator and oceans would have changed only negligibly in the last 2.5 million years, and relatively little mountain building in eastern and southern Africa has taken place since then, it is unlikely that the climate at any locality would have been drastically different than it is today.[2] Latitude, longitude and elevation data presented come from the literature and one of the authors' notes (EES). Data are summarized in Tables 2 and 3, and in Results. A review of the flora and fauna of East African alkaline lakes and South African flooded grasslands and glades is included in the discussion. Because fossil deposition is often dependent on water a discussion as to how taphonomy may bear on our results is included.

RESULTS

The use of USOs as fallback foods by baboons.

Table 1 summarizes the Okavango baboon diet. The rhizomes or roots of *Nymphaea nouchali* provided most of the USOs consumed, on average 79.3% of USO feeding records. Baboons ate *N. nouchali* roots and rhizomes from the water's edge, wading to a depth of a few centimeters to pull them from soft mud. The remaining USOs in the diet included various unidentified corms, tubers and roots.

Fruits were the food type eaten most frequently (Table 1). If seeds were included as fruits (cf. Hill and Dunbar, 2002), the monthly mean for fruit-eating rose from 37.8% to 43.6%. Important fruits in the diet included those of the sausage-tree *Kigelia* sp. (averaging 45.1% of fruit-records per month), a strangling fig eaten by humans as well as baboons (*Ficus thoningii*, 21.0%), jackalberry (*Diospyros mespiliformis*, 17.3%), and palm-nuts (*Hyphaene petersiana*, 8.0%). We assumed that fruits were a preferred food because they appeared to be eaten in proportion to their availability, as was the case for baboons and cercopithecines in other studies (Hill and Dunbar, 2002; Marshall and Wrangham, 2007).

Across the months there was no significant correlation between the proportion of time spent eating fruit and the proportion of time spent eating Foliage (n = 13 months, r^2 = 0.08, P n.s.), or Other Foods (r^2 = 0.01, P n.s.). Foliage and Other Foods were therefore not fallback foods. By contrast, the proportion of time spent eating USOs was negatively correlated with the proportion of time spent eating fruits (n = 13, r^2 = 0.61, P < .01; Fig. 1). When fruit and Foliage were combined into a single category a similar negative correlation occurred with USOs (n = 13, r^2 = 0.78, P < .0001), but again not with Other Foods (n = 13, r^2 = 0.01, P n.s.). USOs were therefore concluded to be a fallback food for Okavango baboons, whereas foliage and Other Foods were not a fallback food. Foliage was possibly a preferred food, since USOs were eaten more often when less foliage was eaten (n = 13, r^2 = 0.41, P < .02).

**** TABLE 1 AND FIGURE 1 ABOUT HERE ****

Hominin fossil sites.

Data on African hominin fossil sites are collated in Tables 2 and 3. Sites range beyond tropical Africa from slightly north of 11°N to slightly beyond 26°S. Nearly all hominin fossil localities have a relatively dry climate with marked rainfall seasonality restricted to a single wet season. Konso, Chesowanja and Chemeron are exceptions. Slightly north of the equator, Chesowanja and Chemeron may occasionally show two rainfall seasons (i.e. a long and a short one) and a much wetter climate.[3] Konso more commonly exhibits two rainy season, but shares a relatively dry climate with the other hominin fossil sites.

With the exception of the South African caves, most of the fossils are associated with floodplain or lake margin depositional habitats reflecting lake shores or flooded grasslands (Table 2). For example, the Shungura formation which shows a considerable percentage of high-energy depositional habitats (i.e. rivers and stream beds) yields its most complete hominins (e.g. the associated OMO 323-1976 skeleton; Alemseged, et al. 2002) principally in floodplains. The majority of water-lain deposits are associated with alkaline lakes (8 out of 11) three of which (i.e. those pertaining to Konso, Olduvai, and Peninj) were strongly alkaline at the time of deposition (Suwa et al, 2003; Hay and Kyser, 2001; Lind and Morrison, 1974).

**** TABLES 2 AND 3 ABOUT HERE ****

Fauna and flora at the majority of the fossil deposits reflect relatively dry climates, but with nearby water availability. Notably, although all the South African early hominin sites are cave deposits, the majority of them are in close proximity to streams or flooded glades. None of the flora, fauna or current climatic variables associated with any of the hominin deposits is indicative of tropical forests. Climatic, and fauna and flora data indicates surrounding scrubland or grassland habitats at most fossil sites. The exceptions are Chemeron and Chesowanja which suggest bushland and/or woodlands with a precipitation close to the lower limits necessary for forests.

Analysis of sand grain angularity and ratios of chert to quartz in breccia from Sterkfontein, Swartkrans, and Makapansgat caves suggests that these deposits were slightly drier during the time of deposition than they are today (Brain, 1958). Kromdraii B is the only exception, indicating a climate somewhat wetter than the current one, i.e. ~1000 mm of precipitation (Brain, 1958). However, the possibility of stream alluvium contaminating the Kromdraii B breccia makes this rainfall estimate uncertain. Micromammal studies of South African early hominin fossil sites confirm a slightly drier climate and presence of grasslands dating back at least to 3 my (Avery, 2001). In Shungura members G-H and Koobi Fora's Okote member the presence of desert jerboa (*Jaculus*) suggest nearby desert, barren land, or at best only scattered vegetation during the time those members were deposited. The remaining Shungura and KBS fauna further confirm a climate as dry or drier than exists there today (Feibel et al., 1991). Overall, paleoenvironmental studies are more or less in accord with current temperatures and precipitation data at each of the fossil localities.

REVIEW AND DISCUSSION

Our hypothesis that aquatic habitats produce sufficiently predictable, abundant and high-quality USOs to have provided potential fallback foods for early hominins is supported by evidence from the three major types of herbaceous macrophyte in aquatic habitats (water-lilies, semi-aquatic emergents and floodplain herbs). These three types of plant all produce large amounts of USOs edible by humans, and their USOs have high nutrient quality during seasons of low growth when preferred foods are expected to be scarce. Aquatic habitats once occupied by hunter-gatherers have mostly been taken over by farmers, but in two cases where hunter-gatherers persisted (i.e. Botswana river peoples and aborigines living at high density in south-east Australia) aquatic USOs are recorded as fallback foods and staples respectively. Whether foods eaten as staples are also fallback foods depends on whether their consumption correlates inversely with the availability of preferred foods (Marshall and Wrangham, 2007). This means that without knowing the availability of preferred foods it cannot be determined if USOs were fallback foods for south-east Australian aborigines. However, the potential of non-agricultural wetland habitats to be important sources of USOs is clear. The USOs could be fallback foods, staples, or both.

Our analysis showed that Okavango baboons exploit this wetland potential. Within the single baboon population examined, aquatic USOs comprised the majority of USOs eaten and USOs were more abundantly eaten during months of low fruit consumption. No plant or animal items other than USOs could be shown to provide our baboon population with fallback foods. Our observations agree with those of previous studies. Across 15 reported baboon populations USO consumption is negatively correlated with fruit-eating, suggesting that baboons routinely use USOs as fallback foods (Hill and Dunbar, 2002). See also Alberts et al. (2005, p. 172), who concluded that grass corms were fallback foods because they “were the focus of intensive foraging activity only during the dry season, when key preferred foods (notably green grass blades and fruit) were scarce.”

Okavango is a particularly rich habitat for baboons (Johnson, 2003). Hundreds of troops occupy the delta at a higher population density (17-43 individuals per sq km) than recorded by Hamilton et al. (1976) for any other wild baboons (n = 10 populations). Elsewhere, baboon populations vary in their use of USOs. Thus in 4 of the 15 baboon populations reviewed by Hill and Dunbar (2002) USOs comprised less than 3% of the annual diet. Even in the Okavango, USOs may not always act as fallback foods, given that our data come from only one annual cycle. Furthermore, in tropical savannas the dry season is not necessarily the period when fruits are most scarce (Pruetz, 2006). USOs, therefore, are not expected to be a universal source of fallback foods. But the fact that in Okavango USOs provide fallback foods for a population of baboons living at relatively high densities in shallow water habitats surrounded by semiarid land with a strongly seasonal climate supports the hypothesis that aquatic habitats may have had a similar function for hominins living in similar conditions.

East Africa alkaline lakes and the flooded grassland and glades adjacent to the South African caves

The strong association of early hominin fossils with slow moving and shallow-water habitats where aquatic USOs would often have been abundant supports our hypothesis that aquatic USOs could have served as fallback foods for early hominins. Considering the bone preserving qualities of a high pH, it is not surprising that many of the hominin fossil deposits are associated with alkaline lakes. These lakes are situated along the East African rift, tend to have relatively dry climates with a single rainy season, are usually shallow with very gradually descending bottoms, and are surrounded by a sizable area of flat low-lying terrain that seasonally floods and dries (Ross, 1955; Feibel, et al. 1991: Hay and Kyser, 2001; Carney et al, 1971; Table 2). Trees and shrubs tolerant of saline soils grow at the lake margin where their roots are exposed to repeated flooding and drying, such as gum myrrh (*Commiphora*), salt cedar (*Tamarix*), miswak (*Salvadora*), seepweed (*Suaeda*), bush willow (*Combretum*) and willow (*Salix*). Because solutes in these lakes may be highly concentrated, non-saline tolerant trees when present occur mainly along the larger permanent feeding streams, which if large enough may give rise to riverine forest. The latter is composed mainly of colonizing (secondary growth) trees (e.g. *Albizia, Celtis, Ficus, Macaranga, Myrianthus, Solanum, Polyscias, Fagara, Sterculia etc*.) with a relatively short lifespan. Doum (*Hyphaene*) and African fan palm (*Borassus*) may also occur around permanent or seasonal feeding streams that flood surrounding grassland in areas with high underground water-tables. Flooded during the wet season, the land surrounding such lakes supports grasses, sedges, numerous herbs *(e.g. Abutilon, Crotalaria*, *Hermannia*, *Hibiscus*, *Jasminum*, *Leonotis*, *Polygala*, *Tephrosia)*, and occasionally small shrubs (*Capparis, Tarenna, Grewia, Rhus* etc.). The seasonal availability of water through flooding of what is otherwise relatively dry ground creates periods of high and low growth that benefits plants with USOs (Lind and Morrison, 1974).

In lakes that are not harshly alkaline, papyrus (*Cyperus papyrus*), other sedges *(*e.g. *Cyperus disperma*), and cattails (*Typha*) grow densely in submerged lakeshore forming reedbeds in shallow and slow moving water. These appear as a belt of vegetation around the lake's perimeter and produce an abundant crop of USOs. Shallow coves accumulating decaying plant material may transition over time into swamp forests supporting *Raphia* and a variety of trees (e.g. *Cathormium, Celtis, Cola, Croton, Garcinia, Grewia, Linociera, Syzygium etc.*) some of which (e.g. *Cathormium*) seldom grow outside of swamps. Very highly alkaline lakes (e.g. Magadi, Manyara, Natron, Eyasi etc.) are devoid of dense cattail and papyrus growth around their perimeter, at best showing only specialized sedges growing thinly at water's edge. Probably they would not have provided as rich a source of USOs as less alkaline lakes.

In lakes that are not excessively alkaline and support reedbeds, fusiform-shaped rope fish (*Polypterus*), African arowanas (*Heterotis*), African knifefish (*Gymnarchus niloticus*) and a number of catfish (*Clarias*, *Auchenoglanis*) (all with the ability to breathe air) inhabit the still, murky water.[4] Found throughout such lakes, adult carps (*Labeo*), catfish (*Bargus*) and Nile perch (*Lates*) are more common in the deeper water, but as fry they are found principally in the reedbeds. The latter form a nursery for many lake fish. Otherwise, such lakes are habitat to a number of fish that have evolved reproductive and migratory strategies for colonizing flooded terrain (e.g. *Alestes*, *Barbus*, *Hydrocynus*, *Hyperopisus* etc.). Spiny soft-shelled turtles (*Trionyx*) and terrapins (*Pelusios*) burrow in the muddy bottoms. Hippos (*Hippopotamus*) inhabit the reed beds around the lake margin. Crocodiles feed and hunt in the water, using the shoreline for rest and shelter. The seasonally flooded grassland surrounding lakes provide graze for white rhinoceros (*Ceratotherium*), cape buffalo (*Syncerus*), water-loving antelopes (*Kobus*, *Kob*, and *Tragelaphus spekei*) and rodents (*Thryonomys*). Hundreds of species of birds also use alkaline lakes for food and shelter. Increased alkalinity directly curtails the variety of plants and animals each lake supports and the food that would have been available to hominins. Even the most alkaline lakes (Magadi and Natron), however, may support fish (e.g. *Tilapia*) and invertebrates, the latter of which some birds are specialized to feed on (e.g. flamingos *Phoenicopterus*). All of the flora and fauna listed above may be found in the early hominin fossil deposits of alkaline lakes and a large part may have served the diet of hominins throughout the time they occupied these areas. The variety of life-forms attests to the richness of lake-shore, shallow-water habitat, an effect based in large part on USO-bearing macrophytes. Prior to hominin emphasis on hunting and fishing these shallow-water habitats would have provided abundant USOs during times of food shortage, and afforded a foothold in shallow-water habitats for the subsequent development of hunting and fishing techniques.

As noted, all the South African early hominin cave sites are associated with glades or flooded terrain. Swartkrans, the site with the densest accumulation of hominins (Watson, 1993a) is about 200 m west and above a meander in the Blaaubank (Rietspruit) river that floods approximately 5 hectares of its valley during the rainy season supporting *Typha* and promoting dense grass growth (Fig. 2). East of Swartkrans, Sterkfontein is about 700 m from this glade. Downstream, Kromdraii is 500 m south of an even larger patch of seasonally flooded land (the downstream continuation of the flooded land adjacent to Swartkrans). Drimolen at slightly higher elevations is about 400 meters from a one-hectare glade supporting tall grasses. Gladysvale, likewise, is proximal to an oxbow in a stream (Skeerpoort river) that at one time may have entered the cave. Makapansgat is between numerous streams that flood small patches of grassland where the streams meander and converge. Situated in river valleys, the flooded land is rich with organic peat and stream alluvium. Even in the dry season, when crossing these areas a person may sink in mud knee-high or higher.

**** FIGURE 2 ABOUT HERE ****

Like the edaphic grasslands surrounding alkaline lakes, the South African glades are seasonal with water levels and grass growth peaking in the wet season. Strong rain and temperature seasonality compounded by occasional freezing temperatures in the months of July-September promotes growth of plants with USOs. Submerged soil supports a dense growth of cattails and a large variety of grasses and herbs including members of the *Liliaceae* family. The latter produce large edible tubers which have been proposed as early hominin food (Brain and Shipman, 1993). High altitudes, cold winters, long dry seasons and bush fires are strong deterrents to tree growth, so transitions to swamp woodlands are not as common as they are in tropical climates. Although human populations have long ago extirpated most endemic large mammals that occurred at the South African hominin localities, in nearby game-farms with similar terrain these glades are always sites of animal aggregation, especially in the dry season.[5] They attract more or less the same mammalian genera found along the shores of East African alkaline lakes. Although the exact size of the South African glades during the time *Paranthropus* and early *Homo* inhabited the South African sites still needs to be worked out, dolomite faulting and terrain contours leaves no doubt that these glades existed during fossil deposition.

As in East Africa, in South Africa early hominins would have endured long dry seasons within range of shallow-water habitats with abundant USO production. The low food productivity of non-watered land during the dry season in both East and South African habitats supports the likelihood that nearby shallow-water habitats with abundant food production would have been used by hominins, and USOs would have served as a fallback food especially prior to hominins emphasizing hunting and fishing. The location of early hominin fossil remains and the nearly complete preservation of many fragile skeletal parts during deposition leaves no doubt that shallow-water habitats would have been part of the hominin range.

Hominin habitat preferences, bipedality, wading and the fossil record

The evidence that hominins ranged into shallow-water habitats and may have used USOs as fallback foods raises questions as to how hominins would have harvested USOs. We suggest that emphasis on USOs could have favored bipedal wading. Specifically, we propose that: (1) the LCA (last common ancestor of humans and *Pan*) and the earliest hominins could have waded bipedally rather than quadrupedally to collect aquatic USOs and other edible parts of aquatic and semi-aquatic macrophytes; (2) bipedal wading gave significantly increased access to these fallback foods; (3) foraging while wading bipedally would have prolonged the duration of bipedal bouts; and (4) as a result, wading could have helped select for fulltime bipedal adaptations. We assume that such a process would have been part of the origin of the hominins.

Admittedly using the fossil record to infer past behaviors and habitat preferences is fraught with difficulties. Fossilization and deposition are often associated with water so that consistently finding fossil ancestors in lake shore, mudflats, everglades, swamplands, deltas, floodplains or river bend habitats does not prove that these ancestors ate USOs, practiced wading behaviors, or would have preferentially inhabited these areas. In fact shallow-water habitats are also sites of low energy deposition, and with some exceptions are mainly the deposit types where vertebrate fossil preservation is complete enough to allow for certain identification. Because the likelihood an animal will be fossilized decreases with increases in its distance to the deposition site, fossil density ratios of our ancestors compared to those of animals with known habitat preferences from the same deposits may divulge relative distances from the deposition habitat and whether our ancestors commonly ranged into and exploited these habitats. Unfortunately, fossil collection is usually a biased endeavor and actual representative ratios of animals at any one deposit are not commonly known (Bobe et al, 2002). Moreover, hominoids typically occur at relatively low densities (Sarmiento, 2003) so that density estimates based on fossil finds may have a large degree of error, and comparisons of density ratios for habitat preference are unlikely to yield statistically significant results.

Further complicating matters a generalized ape may be expected to range into a wide variety of habitats including shallow-water habitats. Finding fossils of generalized apes in either wading or non-wading habitats would not show whether they underwent selective pressures for wading or preferentially consumed foods found in these habitats.

Nevertheless, the circumstantial evidence for hominins having been committed to lake-margin, flooded grassland and/or glade resources in the arid areas they inhabited is strong considering that 1) even in those depositional habitats where fossilization is not dependent on standing water (i.e. South African caves) flooded grasslands and glades can always be found nearby the deposits, and 2) prior to the appearance of the Homininae such habitats are practically devoid of hominoids of any kind, but with the appearance of Homininae only hominin fossils but no other hominoids are consistently found there. Given the strength of this evidence, therefore, it is relevant to ask how hominins would have obtained aquatic USOs. We suggest that in these habitats, hominins would have been prone to bipedal wading behaviors given their great ape heritage and climbing ancestry (Sarmiento, 1995, 1998).

Feeding behaviors seem to be the most logical choice to explain habitual bipedality, since in primates feeding behaviors are known to force postures that over time shape the animal's movements (Prost, 1965; Rose 1974). The most commonly accepted and often cited behavior in this respect is terrestrial feeding from lower tree limbs and/or around large shrubs (Rose, 1976; Wrangham, 1980; Hunt, 1994). Evidence for the unique importance of such low-standing plants as sources of food, especially during seasons of food scarcity when selective consequences are expected to be particularly intense, has yet to be found.

Foraging and feeding in swamps, flooded grasslands, lake-shores or glades in habitats where food is otherwise scarce offers an alternative hypothesis why habitual bipedality would have been adopted. Baboons, chimpanzees, gorillas and orang-utans wade in water if necessary, and great apes characteristically do so bipedally (Hornaday. 1910; Kortlandt, 1995; Niemitz, 2002). Bipedal wading provides access to deeper water and deeper USOs that would otherwise be unreachable (Fig. 3). Moreover, keeping more of the body above water as is done during bipedal wading reduces the cooling effect of water enabling animals to endure colder water for longer periods. Foraging in waist-high water or higher could have selected for prolonged bipedal behaviors. On the one hand, once the individual is foraging in water at this depth it can no longer breathe if it reverts to quadrupedal postures, and must walk bipedally to shallower areas to be able to effect such postures and hold its head above water. On the other hand, most visible food would be at the water surface or above and USOs could be easily attainable by pulling on the emergent parts of the plants. Wading in very deep waters would not necessarily sacrifice USO collection. When foraging for *Sagittaria* Native Americans were sometimes observed to wade up to their necks using their feet to release tubers from the stem (Lewis, 1961). The tubers floated to the surface and could then be collected. Similar foraging styles, with the use of feet to dislodge USOs, could also have been important for early hominins foraging in deeper water. The significance of aquatic USOs for hominins could therefore extend beyond being a critical food source during periods of nutritional stress. As they have in other primates, fallback foods may be expected to have placed strong selective pressures on early hominins. These may be directed not only at the jaws and teeth, but also at the locomotor and postural adaptations (i.e bipedality) which facilitate USO collection.

**** FIGURE 3 ABOUT HERE ****

Implications for models of hominization.

Our review shows that early fossil hominins are almost always associated with aquatic or flooded habitats and strongly seasonal climates with periods of relatively low rainfall. *Homo, Paranthropus* and their common ancestor, therefore, are likely to have gravitated towards shallow water habitats during dry seasons in search of food. Here they would have had regular access to aquatic USOs.

We suggest that a similar access may have applied to earlier australopithecines and other members of the hominoid stock. In fact, many of the very earliest unambiguous hominoid fossils (i.e. *Oreopithecus*, *Sahelanthropus* and *Dryopithecus*), and other fossils claimed to be members of our lineage (*Orrorin, Ardipithecus, Australopithecus annamensis, A. afarensis and A. africanus*) all come from depositional habitats representing swamp forests, lake shores, or seasonally flooded grasslands or were found close to such shallow-water habitats (this study; Hurzeler, 1958; Vignaud et al., 2002; Kazmer, 1990; Wynn, 2000; Pickford and Senut, 2001; WoldeGabriel et al., 2001; Bonnefille et al., 2004).

Considering the wading behaviors of living chimpanzees, bonobos and gorillas (Kortlandt, 1995, Niemitz, 2002), it is likely that prior to human divergence the common human African ape ancestor waded bipedally and used shallow-water habitats opportunistically (Fig. 3). With hominin divergence and shifts to more open habitats commitment to shallow-water habitats increased to the point of dependency in the driest habitats.

Our analysis suggests that aquatic habitats would have predictably provided USOs as fallback foods for early hominins when food was scarce in the surrounding grasslands and scrublands. This idea conforms to Copeland's (2007) reconstruction of habitats in Bed II of the Olduvai Gorge, indicating that river-side habitats were important sources of food. It also conforms to the conclusion that a strong C_4 signal found regularly in hominins (including *Australopithecus*, *Paranthropus* and *Homo*) comes partly from wetland sedges Cyperaceae (Sponheimer et al., 2005; van der Merwe, 2005; van der Merwe et al., 2008).

The possibility that sedges were responsible for the C_4 signal in hominins is admittedly debatable. It has been argued (Sponheimer et al., 2005) that aquatic habitats may have been too rare in South Africa to be important sources of sedge foods. We agree that aquatic habitats in South Africa were probably as rare during early hominin times as they are today. Hominin home ranges, however, would have covered a mosaic of habitats including aquatic ones (Copeland, 2007). Within the latter, we suggest that hominins would have heavily exploited shallow-water habitats, i.e. the edges of slowly moving rivers, deltas, marshes, glades and lakes. Different social groups and populations would have differed in their access to such aquatic habitats. Those with greater access would be expected to have survived better in dry seasons and times of food scarcity, presumably at higher population density, than those with less. We suggest that the best home ranges would have been those that included sufficient aquatic habitat to provide adequate fallback USOs during times of food scarcity.

How early hominins made the ecological shift to open habitats is an unsolved problem. The savanna chimpanzee model is a much discussed ecological solution. It suggests that the first hominins originated when they successfully occupied dry savannas on the fringes of the equatorial rainforest, a habitat-shift which has been more recently repeated by some modern chimpanzee populations (Moore, 1996; Hunt and McGrew, 2002; Hernandez-Aguilar et al., 2007). It argues that adaptation to these arid habitats occurred partly through behavioral innovations such as the use of digging tools, hunting weapons and new thermo-regulatory strategies (Hernandez-Aguilar et al., 2007; Pruetz and Bertolani, 2007; Pruetz, 2007). It also implies that the foods and habitats exploited by early hominins were similar to those used by dry-country chimpanzees.

In contrast to the savanna chimpanzee model, an aquatic-habitat scenario suggests that the LCA and/or early hominins made the shift to more open arid areas as a result of being able to exploit areas of shallow water that were not necessarily close to riverine forests or rainforest fringes (Wrangham 2005). The ability to reach such habitats may have depended on unusual biogeographical events. Once there, we propose, hominin ancestors were able to flourish partly by exploiting a new suite of foods, including underwater USOs. This aquatic-habitat scenario conforms to the notion advanced by Sponheimer and Lee-Thorp (2003), based on stable isotope data, that hominins and forest apes would have eaten different foods even if their ranges overlapped. Our analysis thus suggests that hominins exploiting aquatic USOs, something neither chimpanzees nor gorillas are known to routinely do, would have relied importantly in seasonal habitats on access to this novel food supply.

Acknowledgements

Cheney and Seyfarth acknowledge the Office of the President of the Republic of Botswana and the Botswana Department of Wildlife and National Parks for permission to study baboons. They thank L. Moscovice for data collection and logistical help in the field. Research was supported by NIH grant MH62249, an NRSA fellowship, the Leakey Foundation, and the University of Pennsylvania. All research conducted in Botswana complied with the laws of the country and followed all regulations of the Botswana Department of Wildlife and National Parks. This research was reviewed and approved by the Animal Care and Use Committee at the University of Pennsylvania. Thanks to Vanessa Woods for her bonobo photograph, to Kayo Burmon for technical assistance, to Martin Muller and Maryellen Ruvolo for comments, and to Christopher Ruff and three anonymous reviewers for extensive constructive advice.

Literature Cited

Aguirre E. 1970. Identification de "*Paranthropus*" en Makapansgat. Cronica de XI Congr Natl de Arquilogie Merido 1969:98-124.

Alberts SC, Hollister-Smith J, Mututua RS, Sayialel SN, Muruthi PM, Warutere JK, and Altmann J. 2005. Seasonality and long-term change in a savannah environment. In: Brockman DK, and van Schaik CP, editors. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. New York: Cambridge University Press. p 157-196.

Alemseged Z, Coppens Y, and Geraads D. 2002. Hominid cranium from Omo: description and taxonomy of Omo-323-1976-896. Am J Phys Anthrop 117:103–112.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

Andersen DC. 1987. Below-ground herbivory in natural communities: a review emphasizing fossorial animals. Q Rev Biol 62:261-286.

Asfaw B, Beyene Y, Suwa G, Walter RC, White TD, WoldeGabriel G, and Yemane T. 1992. The earliest Acheulean from Konso-Gardula. Nature 360:732–735.

Avery DM. 2001. The Plio-pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. J Hum Evol 41:113-132.

Bobe R. 1997. Hominid environments in the Pliocene: An analysis of fossil mammals from the Omo Valley, Ethiopia. University of Washington, Seattle: Ph.D. dissertation.

Bobe R, Behrensmeyer AK, and Chapman RE. 2002. Faunal changes, environmental variability and late Pliocene hominin evolution. J Hum Evol 42:475-497.

Bonnefille R. 1976. Palynological evidence for an important change in the vegetation of the Omo basin between 2.5 and 2 million years ago. In: Coppens Y, Howell FC, Isaac GL, and

Leakey REF, editors. Earliest Man and Environments in the Lake Rudolf Basin. Chicago: University of Chicago Press. p 421-431.

Bonnefille R, Potts R, Chalie F, Jolly D, and Peyron O. 2004. High-resolution vegetation and climate change associated with Pliocene Australopithecus afarensis. Proceedings of the National Academy of Sciences 101:12125–12129.

Bonnefille R, and Riollet G. 1987. Palynological spectra from the upper Laetolil Beds. In: Leakey MD, and Harris JM, editors. Laetoli: A Pliocene Site in Northern Tanzania Oxford: Oxford University Press. p 52-61.

Brain CK. 1958. The Transvaal ape-man-bearing cave deposits. Transvaal Museum Memoir no. 11, 131 pp.

Brain CK. 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. Chicago: University of Chicago Press.

Brain CK. 1993. Swartkrans. A Cave's Chronicle of Early Man. Transvaal Mus Monogr 8:195-218.

Brain CK. 1994 The Swartkrans palaeontological research project in perspective: results and conclusions. S Afr J Sci 90:220-223.

Brain CK, and Shipman P. 1993. The Swartkrans bone tools. In: Brain CK, editor. Swartkrans: A Cave's chronicle of early man. Transvaal Mus Monogr 8. p 195-218.

Brand-Miller J, James KW, and Maggiore P. 1993. Tables of Composition of Australian Aboriginal Foods. Canberra: Aboriginal Studies Press.

Breen CM, Rogers KH, and Ashton PJ. 1988. Vegetation processes in swamps and flooded plains. In: Symoens JJ, editor. Vegetation of Inland Waters. Dordrecht: Kluwer. p 183-222.

Brock TCM, Arts GHP, Goossen ILM, and Rutenfrans AHM. 1983. Structure and annual biomass production of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquatic Botany 17:167-188.

Bromage TG, Schrenk F, and Juwayeyi YM. 1995a. Paleobiogeography of the Malawi-Rift: age and vertebrate palaeontology of the Chiwondo-Beds, northern Malawi. J Hum Evol 28:37-58.

Bromage TG, Schrenk F, and Zonneveld FW. 1995b. Paleoanthropology of the Malawi-Rift: an early hominid mandible from the Chiwondo Beds, northern Malawi. J Hum Evol 28:71-108.

Campbell A. 1986. The use of wild food plants, and drought in Botswana. Journal of Arid Environment 11:81-91.

Carney J, Hill A, Miller JA, and Walker A. 1971. Late Australopithecine from Baringo District, Kenya. Nature 230:509-514.

Chawanje CM, Barbeau WE, and Grun I. 2001. Nutrient and antinutrient content of an underexploited Malawian water tuber *Nymphaea petersiana* (Nyika.). Ecology of Food and Nutrition 40(4):347-366.

Cheney DL, and Seyfarth RM. 2007. Baboon Metaphysics. Cambridge: Cambridge University Press.

Cheney DL, Seyfarth RM, Fischer J, Beehner JC, Bergman TJ, Johnson SE, Kitchen DM, Palombit RA, Rendall D, and Silk JB. 2004 Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. International Journal of Primatology 25:401–428.

Codron D, Lee-Thorp JA, Sponheimer M, de Ruiter D, and Codron J. 2008. What insights can baboon feeding ecology provide for early hominin niche differentiation? . International Journal of Primatology 29:757-772.

Conklin-Brittain N, Wrangham RW, and Smith CC. 2002. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar P, and Teaford M, editors. Human Diet: Its Origin and Evolution. Westport, Connecticut: Bergin & Garvey. p 61-76.

Copeland SR. 2007. Vegetation and plant food reconstruction of lowermost Bed II, Olduvai Gorge using modern analogs. Journal of Human Evolution.

Curnoe D, Grun R, Taylor L, and Thackeray JF. 2001. Direct ESR dating of a Pliocene hominin from Swartkrans. J Hum Evol 40:379-391.

de Heinzelin J, Clark JD, White TD, Hart W, Renne P, WoldeGabriel G, Beyene Y, and Vrba E. 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284:325-329.

Deino AL, and Hill A. 2002. 40 Ar/39 Ar dating of the Chemeron Formation strata encompassing the site of hominid KNM-BC 1, Tugen Hills, Kenya. J Hum Evol 42:141–151.

deMenocal PB, and Bloemendal J. 1995. Plio-Pleistocene subtropical African climate variability and the paleoenvironment of hominid evolution: a combined data-model approach. In: Vrba E, Denton G, Burckle L, and Partridge T, editors. Paleoclimate and Evolution With Emphasis on Human Origins. New Haven: Yale University Press. p 262-288.

den Hartog C, and van der Velde G. 1988. Structural aspects of aquatic plant communities. In: Symoens JJ, editor. Vegetation of Inland Waters. Dordrecht: Kluwer. p 113-154.

Dominy NJ, Vogel ER, Yeakel JD, Constantino P, and Lucas PW. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. Evolutionary Biology 35:159-175.

Ellery K, and Ellery W. 1997. Plants of the Okavango Delta: A Field Guide. Durban, South Africa: Tsaro Publishers.

Feibel CS, Brown FH, and McDougall I. 1989. Stratigraphic context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. Am J Phys Anthrop 78:595-622.

Feibel CS, Harris JM, and Brown FH. 1991. Palaeoenvironmental context for the late neogene of the Turkana basin. In: Harris JM, editor. Koobi Fora Research Project. Oxford: Clarendon press, . p 321–370.

Garver EG, Dubbe DR, and Pratt DC. 1988. Seasonal patterns in accumulation and partitioning of biomass and macronutrients in *Typha* spp. Aquatic Botany 32:115-127.

Gott B. 1999. Cumbungi, Typha species: a staple Aboriginal foods in southern Australia. Australian Aboriginal Studies 1:33-50.

Hamilton WJ, Buskirk RE, and Buskirk WH. 1976. Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. Ecology 57:1264-1272.

Harris JKW, Gowlett JAJ, Walton D, and Wood BA. 1981. Palaeoanthropological studies at Chesowanja. Unpublished manuscript.

Hatley T, and Kappelman J. 1980. Bears, pigs, and plio-pleistocene hominids: a case for the exploitation of belowground food resources. Human ecology 8:371-387.

Hay RL, and Kyser TK. 2001. Chemical sedimentology and paleoenvironmental history of Lake Olduvai, a Pliocene lake in northern Tanzania. GSA Bulletin 113(12):1505-1521.

Hernandez-Aguilar RA, Moore J, and Pickering TR. 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. Proceedings of the National Academy of Sciences 104:19210-19213.

Herries AIR. 2003. Magnetostratigraphic seriation of South African hominin palaeocaves. Ph.D Thesis, Geomagnetism Laboratory, Department of Archaeology, University of Liverpool.

Herries AIR, Adams JW, Kuykendall KL, and Shaw J. 2006. Speleology and magnetobiostratigraphic chronology of the Gondolin hominin palaeocave, S. Africa. J Hum Evol 51:617-631.

Hill RA, and Dunbar R. 2002. Climatic determinants of diet and foraging behaviour in baboons. Evolutionary Ecology 16:579 –593.

Hillman GC, Madeyska E, and Hathor J. 1989. Wild plant foods and diet at Late Paleolithic Wadi Kubbaniya: the evidence from charred remains. In: Wendorf F, Schild R, and Close AE, editors. The prehistory of Wadi Kubbaniya, vol2: stratigraphy, paleoeconomy, and environment. Dallas: Southern Methodist University Press. p 162–242.

Hornaday WT. 1910. Two Years in the jungle. New York: C. Scribner and Sons.

Howell FC, Haesaerts P, and de Heinzelin J. 1987. Depositional environments, archaeological occurrences and hominids from Members E and F of the Shungura formation (Omo basin, Ethiopia). J Hum Evol 16:665-700.

Humphries P. 2007. Historical indigenous use of aquatic resources in Australia's Murray-Darling Basin, and its implications for river management. Ecological Management and Restoration 8:106-113.

Hunt KD. 1994. The evolution of human bipedality: ecology and functional morphology. Journal of Human Evolution 26:183–202.

Hunt KD, and McGrew WC. 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, and Marchant L, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press. p 35-51.

Hurzeler J. 1958.§. *Oreopithecus bambolii* Gervais: a preliminary report. Verh Natur Ges Basel 69:1-48.

Isaac GL. 1967. The stratigraphy of the Peninj Group: Early Middle Pleistocene formations west of Lake Natron, Tanzania. In: Bishop WW, and Clark JC, editors. Background to Evolution in Africa. Chicago: Chicago University Press, pp. . p 229-257.

Isaacs J. 1987. Bush Food: Aboriginal Food and Herbal Medicine. Sydney, Australia: New Holland.

Johanson DC, Taeib M, and Coppens Y. 1982. Pliocene hominids from the Hadar formation, Ethiopia (1973-1977): stratigraphic, chronologic, and paleoenvironmental contexts with notes on hominid morphology and systematics. Am J Phys Anthrop 57:373-402.

Johnson SE. 2003. Life history and the competitive environment: trajectories of growth, maturation, and reproductive output among chacma baboons. American Journal of Physical Anthropology 120:83–98.

Jolly CJ. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5:1–26.

Jones R, and Meehan B. 1989. Plant foods of the Gidjingali: ethnographic and archaeological perspectives from northern Australia on tuber and seed exploitation. In: Harris DR, and Hillman GC, editors. Foraging and Farming: The Evolution of Plant Exploitation. London: Unwin Hyman. p 120-135.

Kazmer M. 1990. Birth, life and death of the Pannonian Lake. Palaeogeogr Palaeoclimatol Palaeoecol 79:171–188.

Keyser AW. 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. S Afr J Sci 96:189-193.

Keyser AW, Menter CG, Moggi-Cecchi J, Pickering TR, and Berger LR. 2000. Drimolen: a new hominid-bearing site in Gauteng, South Africa. S African J Sci 96:193-197.

Kimbel WH, Johanson DC, and Rak Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. Nature 368:449–451.

Kimbel WH, Walter RC, Johanson DC, Reed KE, Aronson JL, Assefa Z, Marean CW, Eck GG, Robe R, Hovers E and others. 1996. Late Pliocene Homo and Oldowan tools from the Hadar Formation (Kada Hadar member), Ethiopia. J Hum Evol 31(6):549-561.

Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating food availability. International Journal of Primatology 19:1061–1079.

Kortlandt A. 1995. A survey of the geographical range, habitats and conservation of the pygmy chimpanzees (*Pan paniscus*): an ecological perspective. Primate Conservation 16:21-36.

Kullmer O, Sandrock O, Abel R, Schrenk F, Bromage TG, and Juwayeyi YM. 1999. The first *Paranthropus* from the Malawi Rift. J Hum Evol 37:121–127.

Kuman K, and Clarke RJ. 2000. Stratigraphy artefacts industries and hominid associations for Sterkfontein, Member 5. J Hum Evol 38:827-848.

Kuykendall KL, Toich CA, and McKee JK. 1995. Preliminary analysis of the Fauna from Buffalo Cave, Northern Transvaal, South Africa. Paleont Afr 32:27-32.

Lacruz RS, Brink JS, Hancox J, Skinner, AS, Herries A, Schmidt P, Berger LR. 2002. Palaeontology and geological context of a middle Pleistocene faunal assemblage from the Gladysvale Cave, South Africa. Palaeontologia Africana 38, 99-114.

Laden G, and Wrangham RW. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. Journal of Human Evolution 49:482-498.

Lanjouw A. 2002. Behavioural adaptations to water scarcity in Tongo chimpanzees. In: Boesch C, Hohmann G, and Marchant LF, editors. Behavioural Diversity in Chimpanzees and Bonobos. Cambridge, UK: Cambridge University Press. p 52– 60.

Leakey LSB. 1965. Olduvai Gorge: 1951-1961. Volume 1. Cambridge: Cambridge University Press.

Leakey LSB, Tobias PV, and Napier JR. 1964. A new species of the genus *Homo* from Olduvai Gorge. Nature 202:7-14.

Leakey MD. 1971. Olduvai Gorge Volume 3: Excavations in Beds I and II,1960 –1963. Cambridge: Cambridge University Press.

Leakey REF. 1973. Evidence for an advanced Plio-pleistocene hominid from East Rudolf, Kenya. Nature 242:447-450.

Lewis M. 1961. The Lewis and Clark Expedition. Philadelphia: Lippincott.

Lind EM, and Morrison MES. 1974. East African Vegetation. London: Longman.

Marshall AJ, and Wrangham RW. 2007. Evolutionary consequences of fallback foods. International Journal of Primatology 28:1219–1235.

Martyn J. 1967. Pleistocene deposits and new fossil localities in Kenya. Nature 215:476-479.

Menter CG, Kuykendall KL, Keyser AW, and Conroy GC. 2000. First record of hominid teeth from the Plio-pleistocene site of Gondolin, South Africa. J Hum Evol 37:299-307.

Mitchell TL. 1839. Three expeditions into the interior of eastern Australia; with descriptions of the recently explored region of Australia Felix, and of the present colony of New South Wales. London: T. & W. Boone.

Moore J. 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew WC, Marchant LF, and Nishida T, editors. Great Ape Societies. Cambridge: Cambridge University Press. p 275-292.

Mora R, Domínguez-Rodrigo M, de la Torre I, Luque L, and Alcalá L. 2003. The archaeology of the Peninj "ST Complex" (Lake Natron, Tanzania). In: Moreno JM, Torcal RM, and Sainz IT, editors. Oldowan: Rather More Than Smashing Stones. First Hominid Technology Workshop Barcelona: Univeristat Autonoma de Barcelona. p 77-116.

Niemitz C. 2002. A theory on the evolution of the habitual orthograde human bipedalism - the “Amphibische Generalisten theorie”. Anthrop Anz 60:3-66.

Norton-Griffiths M, Herlocker D, and Pennycuick L. 1975. The patterns of rainfall in the Serengeti ecosystem, Tanzania. East African Wildlife Journal 13:347–374.

O'Connell JF, Hawkes K, and Blurton-Jones NG. 1999. Grandmothering and the evolution of *Homo erectus*. Human Evolution 36:461-485.

Pate FD. 2006. Hunter-gatherer social complexity at Roonka, South Australia. In: David B, McNiven IJ, and Barker B, editors. Social Archaeology of Indigenous Societies. Canberra: Aboriginal Studies Press. p 226-241.

Peters CR. 1987. Nut-like oil seeds: food for monkeys, chimpanzees, humans, and probably ape-men. American Journal of Physical Anthropology 73:333–363.

Peters CR, and O’Brien EM. 1994. Potential hominid plant foods from woody species in semiarid versus sub-humid subtropical Africa. In: Chivers DJ, and Langer P, editors. The Digestive System in Mammals: Food, Form and Function. Cambridge: Cambridge University Press. p 166-190.

Peters CR, O'Brien EM, and Box EO. 1984. Plant types and seasonality of wild-plant foods, Tanzania to southwestern Africa: resources for models of the natural environment. . Journal of Human Evolution 13:397-414.

Peters CR, and Vogel JC. 2005. Africa's wild C4 plant foods and possible early hominid diets. Journal of Human Evolution 48:219-236.

Pickford M, and Senut B. 2001. The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. Comptes Rendus de l'Académie des Sciences de Paris (2a) 332:145–152.

Plummer T. 2004. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. Yearbook of Physical Anthropology 47:118-164.

Prat S, Brugal J-P, Tiercelin J-J, Barrat J-A, Bohn M, Delagnes A, Harmand S, Kimeu K, Kibunjia M, Texier P-J and others. 2005. First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3-2.4 Myr. J Hum Evol 49:230-240.

Prost J. 1965. A definitional system for the classification of primate locomotion. Amer Anthrop 67:1198-11214.

Pruetz JD. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann G, Robbins MM, and Boesch C, editors. Feeding Ecology in Apes and Other Primates: Ecological, Physical and Social Aspects. New York: Cambridge University Press. p 161–182.

Pruetz JD. 2007. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at

Fongoli, Senegal: implications for thermoregulatory behavior. Primates 48(4):316-319.

Pruetz JD, and Bertolani P. 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Current Biology 17(5):412-417.

Rayner RJ, Moon BP, and Masters JC. 1993. The Makapansgat australopithecine environment. J Hum Evol 24:219-231.

Reed KE. 1996. The paleoecology of Makapansgat and other African Plio-Pleistocene hominid localities. Ph.D. Dissertation: State University of New York, Stony Brook.

Remis MJ. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores; use of variable resources. American Journal of Primatology 43:87-109.

Richardson J. 1981. Wild Edible Plants of New England: A Field Guide. Yarmouth, ME: DeLorme.

Roodt V. 1998. Common wild flowers of the Okavango delta: medicinal uses and nutritional value. Gaborone, Botswana: Shell Oil Botswana (Pty) Ltd.

Rose MD. 1974. Postural adaptations in New and Old world monkeys. In: Jenkins FA, editor. Primate Locomotion. New York: Academic Press. p 201-222.

Rose MD. 1976. Bipedal behaviors of olive baboons (*Papio anubis*) and its relevance to an understanding of the evolution of human bipedalism. Am J Phys Anthropol 44:247-262.

Rose MD. 1984. A hominine hip bone, KNM-ER 3228, from East Lake Turkana. American Journal of Physical Anthropology 63:371-378.

Ross R. 1955. The algae of the East African great lakes. Proceedings of the International Association of Theoretical and Applied Limnology 12:320-326.

Sarich VM, and Wilson AC. 1968. Immunological time-scale for hominid evolution. Science 158:1200-1203.

Sarmiento EE. 1995. Cautious climbing and folivory: a model of hominoid differentiation. Human Evolution 10(4):289-321.

Sarmiento EE. 1998. Generalized quadrupeds, committed bipeds and the shift to open habitats: an evolutionary model of hominid divergence. American Mus Natural History Novitates 3250.

Sarmiento EE. 2003. Distribution, taxonomy, genetics, ecology and causal links of gorilla survival: the need to develop practical knowledge for gorilla conservation. In: Taylor A, and Goldsmith M, editors. Gorilla Biology. Cambridge: Cambridge University Press. p 432-471.

Schoeninger MJ, Bunn HT, Murray S, and Marlett JA. 2001. Composition of tubers used by Hadza foragers of Tanzania. J Food Composition Anal 14:15–25.

Speth JD. 1989. Early hominid hunting and scavenging: the role of meat as an energy source. Journal of Human Evolution 18:329-343.

Sponheimer M, Lee-Thorp J, de Ruiter D, Codron D, Codron J, Baugh AT, and Thackeray F. 2005. Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. Journal of Human Evolution 48:301-312.

Sponheimer M, and Lee-Thorp JA. 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. Science 283:368-370.

Sponheimer M, and Lee-Thorp JA. 2003. Differential resource utilization by extant great apes and australopithecines: towards solving the C4 conundrum. Comparative Biochemistry and Physiology Part A 136:27-34.

Suwa G, Asfaw B, Beyene Y, White TD, Katoh S, Nagaoka S, Nakaya H, Uzawa K, Renne P, and WoldeGabriel G. 1997. The first skull of *Australopithecus boisei*. Nature 389:489–

492.

Suwa G, Nakaya H, Asfaw B, Saegusa H, Amzaye A, Kono RT, Beyene Y, and Katoh S. 2003. Plio-pleistocene terrestrial mammal assemblage from Konso, Southern Ethiopia. Journal of Vertebrate Paleontology 23(4):901–916.

Thackeray JF, Kirschvink JL, and Raub TD. 2002. Palaeomagnetic analysis of calcified deposits from the Plio-Pleistocene hominid site of Kromdraai, South Africa. S Afr J Sci 98:537-540.

Tindale NB. 1974. Aboriginal tribes of Australia: their terrain, environmental controls, distribution, limits, and proper names. With an Appendix on Tasmanian Tribes by Rhys Jones. Berkeley, CA.: University of California Press.

Tobias PVT. 1967. Hominid specimen found by John Martyn. Nature 215:479-480.

Tull D. 1999. Edible and Useful Plants of Texas and the Southwest: A Practical Guide. University of Texas Press: Austin, TX.

Tutin CEG, Ham RM, White LJT, and Harrison MJS. 1997. The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity and effects on biomass. American Journal of Primatology 42:1-24.

Ungar PS, Grine FE, and Teaford MF. 2006. Diet in early *Homo*: a review of the evidence and a new model of dietary versatility. Annual Review of Anthropology 35:209-228.

van der Merwe NJ. 2005. CO_2, grasses, and human evolution. In: Ehleringer JR, Cerling TE, and Dearing MD, editors. A history of atmospheric CO_2 and its effects on plants, animals and ecosystems. New York: Springer. p 293-328.

van der Merwe NJ, Masao FT, and Bamford MK. 2008. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. South African

Journal of Science 104:153-155.

Verhaegen M, Puech P-F, and Munro S. 2002. Aquarboreal ancestors? Trends in Ecology and Evolution 17:212-217.

Vignaud P, Duringer P, Mackaye HTs, Likius A, Blondel Cc, Boisserie J-R, De Bonis L, Eisenmann Vr, Etienne M-E, Geraadsk D and others. 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. Nature 418:152-155.

Vrba ES. 1976. The fossil Bovidae of Sterkfontein, Swartkrans, and Kromdraii. Transvaal Museum Memoir 21.

Walker A, Leakey RE, Harris JM, and Brown FH. 1986. 2.5 Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. Nature 322:517-522.

Walker AC, and Leakey RE. 1993. The Nariokotome *Homo erectus* Skeleton. Cambridge, MA: Harvard University Press.

Watson V. 1993a. Comparison of the Swartkrans bone accumulations in terms of skeletal parts and animals represented. In: Brain CK, editor. A Cave's Chronicle of Early Man Monograph 8. Pretoria: Transvaal Museum. p 35-73.

Watson V. 1993b. Glimpses from Gondolin: A faunal analysis of a fossil site near Broederstroom, Transvaal, South Africa. Paleont Afr 30:35-42.

Westlake DF. 1982. The primary productivity of water plants. In: Symoens JJ, Hooper SS, and Compere P, editors. Studies on Aquatic Vascular Plants. Brussels: Royal Botanical Society of Belgium. p 165-180.

Wetzel RG. 1988. Water as an environment for plant life. In: Symoens JJ, editor. Vegetation of Inland Waters. Dordrecht: Kluwer. p 1-30.

WoldeGabriel G, Halle-Selassie Y, Renne P, Hart WK, Ambrose SH, Asfaw B, Heiken G, and

White TD. 2001. Geology and palaeontology of the Late Miocene Middle Awash Valley, Afar Rift, Ethiopia. Nature 412:175-178

Wrangham RW. 1980. Bipedal locomotion as a feeding adaptation in gelada baboons and its implication for hominid evolution. J Hum Evol 9:329-331.

Wrangham RW. 2005. The delta hypothesis: hominoid ecology and hominin origins. In: Lieberman DE, Smith, R. J. & Kelley, J., editor. Interpreting the Past: Essays on Human, Primate and Mammal Evolution in Honor of David Pilbeam. Boston, MA: Brill Academic. p 231-242.

Wrangham RW, Jones JH, Laden G, Pilbeam D, and Conklin-Brittain NL. 1999. The raw and the stolen: cooking and the ecology of human origins. Current Anthropology 40:567-594.

Wynn JG. 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. J Hum Evol 39:411-432.

Yeakel JD, Bennett NC, Koch PL, and Dominy NJ. 2007. The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet. Proceedings of the Royal Society of London B 274:1723-1730.

Footnotes.

[1] Following Laden and Wrangham (2005), we use ‘savanna’ to mean all habitats other than rainforest. Savanna thus includes not only closed canopy woodlands, bush, grassland etc. but also shallow-water habitats such as lake shores, deltas and the outside bends of slow-moving rivers. [LOCATION OF FOOTNOTE: p. 3, line 6: “In savanna”]

[2] Even during glacial periods areas within 30 degrees latitude of the Equator have never been shown to undergo drastically lower temperatures. [LOCATION OF FOOTNOTE: p. 11, line 21: “than it is today”]

[3] Theoretically sites close to the equator should show two rainy seasons with one of the two seasons (winter rains) getting progressively shorter so as to virtually disappear at 6^o-10^o latitudinal distance north or south of the equator. However, the aridity of the East African climate is such that many East African sites even those very close to the equator (i.e. Peninj, Olduvai, Chesowanja and Chemeron) fail to consistently show two rainy seasons (Norton-Griffiths et al., 1975, Bonnefille and Riollet,1987, and Table 3). [LOCATION OF FOOTNOTE: p. 13, line 17: “a much wetter climate”]

[4] *Protopterus* the lungfish may also inhabit reedbeds and dig into muddy lake shores, but is highly sensitive to alkalinity and is not usually found in alkaline lakes. [LOCATION OF FOOTNOTE: p. 18, line 16: “in the lake’s reedbeds.”]

[5] Gladysvale for instance occurs on a game farm in which such glades attract baboons, antelopes and leopards. [LOCATION OF FOOTNOTE: p. 20, line 19: “game-farms with similar terrain”]

Figure legends.

Figure 1.

Monthly feeding records of underground storage organs (USOs) and fruits consumed by Okavango baboons, June 2006 to June 2007. Pearson correlation coefficient r = 0.78, n = 13 months, P = 0.002.

Figure 2.

Aerial view of Swartkrans caves. Photo from Google Earth showing distance between Swartkrans (circled in white) and the plain of the Rietspruit (outlined in white). Glades show as light patches of green on either side of the stream. The white roofs, seen on the lower right of photo, mark the approximate locality of the Sterkfontein site.

Aerial view of Swartkrans caves (circled in white) and nearby glades associated with the Reitspruit stream (outlined in white). The white roofs seen on the lower right are part of the Sterkfontein building complex. Sterkfontein caves are approximately 150m to the east outside of the picture. Photograph taken from Google Earth.

Figure 3.

Bonobo wading bipedally at Lola ya Bonobo, Democratic Republic of the Congo (© Vanessa Woods). In this sanctuary for bonobos orphaned by the bushmeat trade, bonobos wade up to their shoulders to obtain stems of Nymphaeaceae as food.

Fig. 1

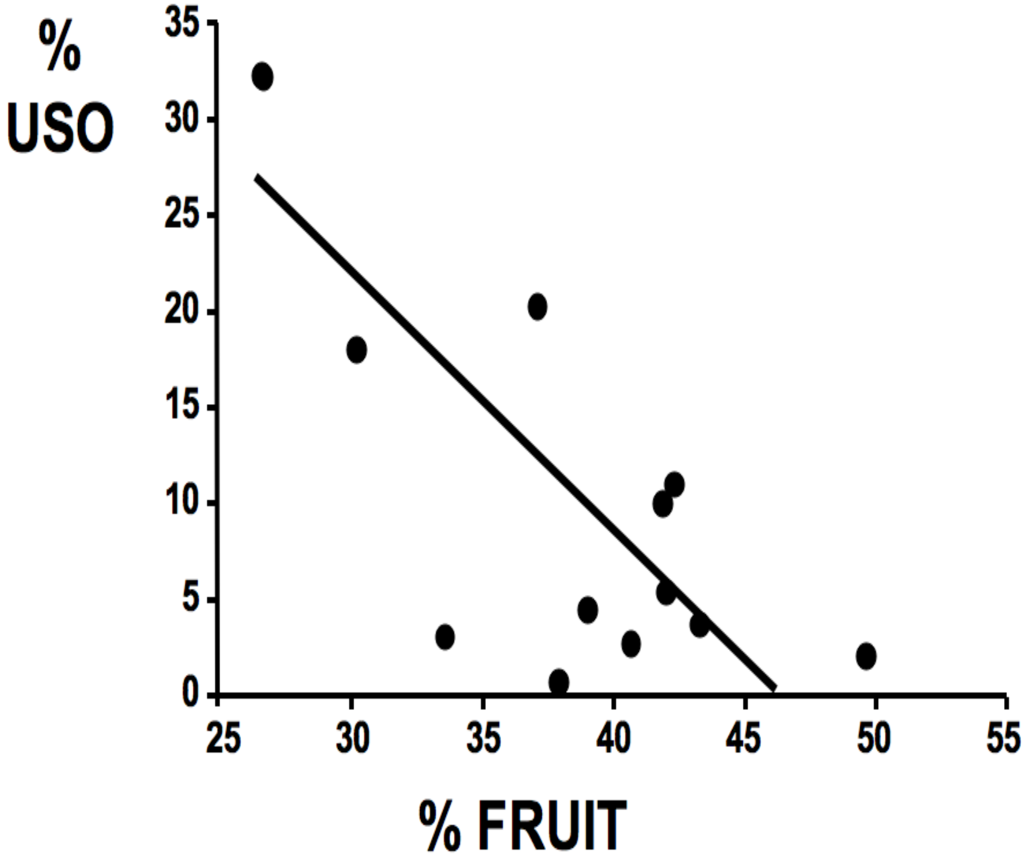

Fig. 2

Fig. 3