17 *Tropical and temperate seasonal influences on human evolution*

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Introduction

Climatic and subsequent habitat change has often been invoked as a driving force of evolutionary change in hominins,[1] mammals, and other taxa (Vrba 1988a, 1988b, 1992, 1995; Bromage & Schrenk 1999; Potts 1998; Bobe & Eck 2001; Janis *et al.* 2002). Global climatic change in the mid Pliocene Epoch has been suggested as a cause for hominin speciation events (Vrba 1995) and is correlated with changes in dentition and jaw morphology of two hominin lineages (Teaford & Ungar 2000). Climatic change also influences seasonality, such that drying trends, for example, likely instigate short wet seasons, while the reverse is also true. Although Foley (1987) indicated that seasonal differences were likely important in determining hominin foraging effort, and Blumenschine (1987) posited a dry-season scavenging niche for Pleistocene hominids, little attention has been given to how seasonal changes over time might contribute to differences among hominin behavioral adaptations. Seasonal changes refer to changes in the lengths of regular four-season patterns in temperate climates or wet and dry seasonal differences in the tropics over geological time.

Evolutionary changes in fossil hominins are detected through changes in morphology that represent different behavioral adaptations. Fossil hominin diets are inferred from comparisons with extant primates in features such as tooth size (Hylander 1975; Kay 1984; Ungar & Grine 1991), molar

[1] Hominins are members of the Hominidae, which, based on genetic evidence, include humans and all great apes. Bipedal taxa in this group are placed in the tribe Hominini, and the term "hominin" is thus used throughout this chapter.

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shearing crests (Kay 1984), dental microwear (Grine 1981; Teaford 1988; Ungar 1998), biomechanics (Hylander 1988; Daegling & Grine 1991), and isotopic signatures (Sponheimer & Lee-Thorp 1999; van der Merwe *et al.* 2003). These studies suggest types of food consumed, e.g. hard, grit-covered foods, fruit or leaves, or C3/C4 plant food. It is unknown, however, whether the morphology of early hominins reflects year-round diet or allows survival through lean seasons in which regular foods are scarce (Rosenberger & Kinzey 1976). In this chapter, the importance of the number of dry-season months with which hominins may have coped, and how changes to lengthier dry seasons over time may have contributed to hominin dietary adaptations and behavioral differences, is discussed. We also address foraging issues faced by hominins in environments of wet and dry seasons as well as those that lived in four-season temperate or cold environments. Hypotheses about the effect of seasonal changes through time on hominin behavior and evolution are formulated, based on information from changes of masticatory morphology compared with both habitat and seasonality evidence.

Early hominin taxa (up to the origin of *Homo*) species have been recovered from Ethiopia, Kenya, Tanzania, Chad, and South Africa. These sites (Table 17.1) are located within 33 degrees of the Equator, indicating a tropical to subtropical climate, although most localities are in the tropical range. Later *Homo* species occupied subtropical zones in Africa and Southeast Asia, and the earliest known hominin occupation of temperate climates occurred 1.7 Ma in Eurasia, at Dmanisi, Georgia (Gabunia *et al.* 2000a; Vekua *et al.* 2002). First appearance dates (FAD) and last appearance dates (LAD) for these hominin species as they are currently known (Kimbel 1995) are given in Table 17.1 so that they can be contrasted with climatic and habitat shifts through time (Table 17.2).

Climates, habitats, and seasonality

Climatic patterns

In the past ten million years, the African continent, like most of the globe, has been influenced by glacial cycles that have caused, overall, drier and more open habitats than existed previously (Crowley & North 1991). Before this time, forests and deciduous woodlands existed in eastern Africa, indicating higher rainfall (Foley 1987; Andrews & Humphrey 1999; Jacobs 2002). Water held in glaciers at both poles led to increasing aridity from ~10 Ma to ~7.0 Ma, but towards the end of the Miocene

Table 17.1 *Early Pliocene to recent hominin taxa. Species are listed with their estimated first appearance date (FAD) and last appearance date (LAD). Latitude refers to the zone that we have assigned to the regions inhabitated by each species: tropical is within 20° north and south of the Equator; subtropical is between 20 and 30° latitudes; temperate is between 30 and 60° latitudes; and cold is > 60° latitudes. Seasonal differences are those that would likely occur based on latitude*

Species	Estimated FAD	Estimated LAD	Latitude	Reconstructed habitats	Seasonal differences	Localities
Ardipithecus ramidus	5.6	4.4	Tropical	Forests/closed woodlands	Wet/dry	East Africa
Australopithecus anamensis	4.2		Tropical	Open woodlands	Wet/dry	East Africa
A. afarensis	3.6 (?4.2)	2.9	Tropical	Closed/open woodlands, bushlands, edaphic grasslands	Wet/dry (~3 months)	East Africa
A. africanus	3	2.4	Subtropical	Woodlands, bushlands, edpahic grasslands, ?secondary grasslands	Wet/dry	South Africa
A. bahrelgazalia	3		Subtropical	Open woodlands	Wet/dry	Northern central Africa
A. garhi	2.5		Tropical		Wet/dry	East Africa
A. aethiopicus	2.7	?1.9	Tropical	Woodlands, edaphic grasslands	Wet/dry	East Africa
A. boisei	2.3	1.4		Open woodlands, edaphic grasslands	Wet/dry	East Africa
A. robustus	1.9	?1.0		Open woodlands, edaphic grasslands	Wet/dry	South Africa
Kenyanthropus platyops	3.5	3.3	Tropical	Woodlands, edaphic grasslands	Wet/dry	East Africa
Homo habilis	2.33	1.6	Tropical	Woodlands	Wet/dry	East and South Africa
H. rudolfensis	2.4	1.9	Tropical	Woodlands	Wet/dry	East Africa
H. ergaster/erectus	1.8	0.4	Tropical/ temperate	Grasslands, riparian regions	Wet/dry and four season	Africa and Eurasia
H. heidelbergensis	0.8	0.15	Tropical/ temperate		Four season	Africa and Eurasia
H. neandertalensis	0.12	0.032	Temperate/cold		Four season	Eurasia
H. sapiens	0.12		Tropical/ temperate/ cold		Wet/dry and four season	Global

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Table 17.2 *Climate, habitat, and seasonal differences through time*

Geologic epoch	Approximate dates	Climate evidence	Reconstructed habitats	Possible seasonal patterns
Mid–Late Miocene	*10–5.4 Ma*	*Reduced rainfall and cooler temperatures*	*Overall trend toward habitat aridification from forests to woodlands in Africa*	*Fluctuating*
Middle Miocene	9 Ma	Reduced rainfall and cooler temperatures	Deciduous woodlands in Africa	3.3–6.9 dry-season months
Late Miocene	6.8 Ma	Beginning of warming trend, with less glaciation	Open habitats in northern Africa; more wooded habitats in east Africa	0–3.3 dry-season months
Pliocene	*5.4–1.8 Ma*	*Overall trend to arid conditions, with reduced rainfall and cooler temperatures*	*Closed woodlands/grasslands and shrublands in eastern and southern Africa*	*Fluctuating*
Early Pliocene	5.4 Ma	End of Mediterreanean crisis, and further rainfall and warming in eastern Africa	Closed/open woodlands in eastern Africa	0–3 dry-season months?
Mid Pliocene	3.2–2.2 Ma	Aolian dust levels increase and cooling evidence in SSTs; lower CO_2 levels; terrestrial temperatures and MAR lowered gradually across this time period	Woodland/shrubland in eastern and southern Africa	Increasing dry-season months
Late Pliocene	2.1–1.9 Ma	Rapid reduction of SSTs	Spread of open grasslands in Africa among woodland environments	Increasing dry-season months
Pleistocene	*1.8–10 Ka*	*Development of glacial/interglacial cycles*	*Fluctuating*	*Fluctuating*
Early Pleistocene	1.8–1.6 Ma	Aridification	Open grasslands dominate in Africa; temperate climates warmer than present day	Increasing dry-season months
Early Pleistocene	1.6 Ma	Wetter, warmer temperatures	Woodlands return to eastern and southern Africa	Decreasing dry-season months

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Mid Pleistocene	1.0–650 Ka	Extreme reduction in SSTs and intensive aridification	Grasslands and shrublands in Africa; glacial steppe in Eurasia	Increasing dry-season months in Africa; four season with extreme cold in Eurasia
Late Pleistocene	*650–10 Ka*	*100 000 glacial/interglacial cycles*	*Advance of cold habitats in Eurasia; African habitats during interglacial similar to those of today; drier during glacial intervals*	*Fluctuating numbers of wet- and dry-season months; bimodal east African pattern and unimodal South African pattern possible at times during this interval*
	150 Ka	Moderately severe climate in Europe	Polar desert and intermittent herbaceous plant cover in Europe	Four season
	130–117 Ka	Milder climate in Europe	Boreal forests Europe	Four season
	116–74 Ka	Fluctuating cold/warmer temperatures in Europe	Alternating steppe and forest	Four season
	74–59 Ka	Advancing ice sheet; colder and more arid in Europe	Gradual change from forests to tundra	Four season

MAR, mean annual rainfall; SST, sea surface temperature.
Note: Italics indicates the overall climate and habitats of entire epoch or long time span.

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Epoch this trend was reversed and only the Antarctic remained glaciated. The early Pliocene Epoch was consequently characterized by a wetter, warmer climate in Africa than in the previous five million years. Warmer temperatures and higher rainfall lasted from 5.4 Ma until ~3.0 Ma (Marlow *et al*. 2000).

Another glacial-driven cooling trend, represented by lower sea surface temperatures (SSTs), began at 3.2 Ma and continued through ~2.2 Ma. Accordingly, terrestrial temperatures and mean annual rainfall (MAR) were lowered gradually during the same time period. By 2.8 Ma, this trend caused aolian dust levels to rise, hence indicating xerification (deMenocal & Bloemendal 1995). From 2.1 to 1.9 Ma, SSTs indicate rapid cooling of sea and land temperatures (Marlow *et al*. 2000). Climates remained extremely arid until ~1.6 Ma, (deMenocal & Bloemendal 1995), when temperatures, rainfall, and aolian dust levels returned to pre-1.8-Ma values. Another climatic transition, lasting from 1.0 Ma through 650 Ka, was a time of extremely decreased SSTs and further aridification in tropical Africa (Schefuss *et al*. 2000).

Hominin occupation of other continents began at ~1.8 Ma, those occupying latitudes beyond the subtropics experiencing markedly different climatic patterns. For fossil hominin sites, we define ancient temperate climates as those similar to climates in latitudes between ~30° and ~60° today, and cold climates as those that are similar to the climate north of 60° latitude today. There are regions in which winter cold is mild within the temperate band due to ocean currents and local factors, but many temperate climates experience traditional four-season shifts, with freezing winter temperatures. We assume temperate to cold climates and four seasons for much of Pleistocene Eurasia, which, after 630 Ka, experienced 100 Ka cycles of glacial and interglacial climate changes (Marlow *et al*. 2000). These changes influenced MAR and temperatures, such that as cycles progressed, the climate became colder and precipitation decreased substantially (Gamble 1986).

Habitats

Hominin species from early to mid-Pliocene African sites existed in a variety of habitats. These environments (Table 17.3) were usually mosaic and consisted of combinations of closed to open woodlands, bushlands, riverine forests, and seasonal flood plains that produced edaphic grasslands and wetlands (Andrews 1989; Bonnefille 1995; Spencer 1997; Reed 1997, 1998, 2002; Woldegabriel *et al*. 1994; Bobe & Eck 2001; Wynn 2000; Leakey *et al*. 2001).

Table 17.3 *Categories of habitats and mammalian adaptations. Brief descriptions of each habitat are provided. These are based on broadly based characteristics, as many localities defined as forests, for example, include other microhabitats (Lind & Morrison 1974; Pratt & Gwynne 1977; White 1983; Cole 1986). Mammalian substrate and trophic adaptations are also explained. Note that the terms "browser," "mixed feeder," and "grazer" refer to terrestrial animals. Strictly speaking, monkeys could be described as browsers as they often eat leaves, but these terms usually are reserved for ungulates*

Habitat/mammial adaptation	Definition	Classification
Habitat		
Tropical forests	Tall trees with interlaced, multi-level canopies; epiphyte ground cover	
Tropical closed woodland	Approximately 60–80% tree density (shorter trees); no interlacing or multiple canopy levels; grass ground cover	
Tropical forest/grassland (mixed)	Combination of forest and grassland	
Tropical bushlands	Bushes < 3 m in height; patches of thicket, sparse grass cover	
Tropical open woodlands	Approximately 20–30% tree density; grass ground cover	
Tropical shrublands	Shrubs < 1 m in height; arid adapted plants; sparse grass cover	
Tropical grasslands	< 2% trees; continuous grass ground cover	
Mammal adaptations		
Trophic		
Carnivore	Meat (flesh)	Meat
	Meat and bone	Meat/bone
	Small mammals and invertebrates	Fauna/insects
Insectivore	Ants, termites, etc.	Insects
Herbivores	Dicotyledon leaves	Browser
	Dicotyledon and monocotyledon leaves	Mixed feeder
	Monocotyledon leaves	Grazer
	Monocotyledon leaves from wetlands	Fresh grass grazer

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Table 17.3 (*cont.*)

Habitat/mammial adaptation	Definition	Classification
	Roots and bulbs	Roots and bulbs
Frugivores	Fruit	Fruit
	Fruit and leaves/ leaves and fruit	Fruit
	Fruit and insects	Fruit
Omnivore	No preference	Omnivore
Substrate		
Aquatic	Uses for foraging or necessary for survival	
Arboreal	Forages and rarely descends to terra firma	
Fossorial	Forages by digging or burrows necessary for survival	
Terrestrial	Forages and rarely ascends to trees or swims	
Terrestrial/arboreal	Forages and travels both terrestrially and arboreally, or travels terrestrially and forages arboreally	

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There are also a few early localities in which hominins are suggested to have existed in fairly dry shrubland environments (Reed 1997; Wynn 2000). Different hominin species consequently lived in slightly different environments from one another, and, in the Hadar Formation, *Australopithecus afarensis* habitats fluctuate from closed woodland to arid open shrublands from >3.4 to ~ 2.94 Ma (Reed 1997) (Fig. 17.1).

In general, hominin species from 2.8 to 2.0 Ma lived in African habitats reconstructed as open woodlands, bushlands, and shrublands with wetlands (Reed 1997; Spencer 1997; Bobe & Eck 2001). Based on the proportions of grazing mammals, there was also more grassland area within mosaic environments than found in the early Pliocene Epoch (Reed 1997). The spread of open grasslands is indicated by carbon isotopes in soils and the increased numbers of grazing mammals at ~1.8 Ma (Cerling 1992; Reed 1997; Spencer 1997; Marlow *et al*. 2000). Hominins recovered from African sites dated to 2.0–1.0 Ma lived in habitats that were more open; grasslands dominated at ~1.7 and 1.2 Ma (Cerling 1992).

Although the overall trend in Africa was toward more open arid habitats from 3 to 1.0 Ma, the transition occurred at different rates and with different timing depending on location. For example, Bobe and Eck (2001) observe a species turnover and habitat change in the Omo at 2.8 Ma, while a habitat shift occurred slightly earlier at the Hadar locality, ~3.18–2.95 Ma (Reed). Behrensmeyer *et al*. (1997) report gradual species turnover reflecting habitat change across this entire time period at West Turkana. Hominins outside of the subtropics at ~1.7 Ma experienced temperate deciduous woodlands and grasslands or tundra (Van Andel & Tzedakis 1996). Gamble (1986) notes that deciduous forests with various trees providing fruits and nuts would have been available in some interglacial cycles. Hominins living around the Mediterranean Sea during the Pleistocene Epoch experienced milder temperatures at times than those further north, but habitats still fluctuated from evergreen and deciduous woodland to arid cold steppe (Van Andel & Tzedakis 1996).

Seasonality

Climate, as influenced by latitude, partially dictates seasonality, which in turn affects habitat type. Low-latitude forest habitats experience long wet seasons and short dry seasons, while open woodlands at the same latitudes have shorter wet seasons and longer dry seasons. Local and regional factors, as well as monsoonal patterns, also contribute to differences in the lengths of wet and dry months and to severity of winter in four-season latititudes.

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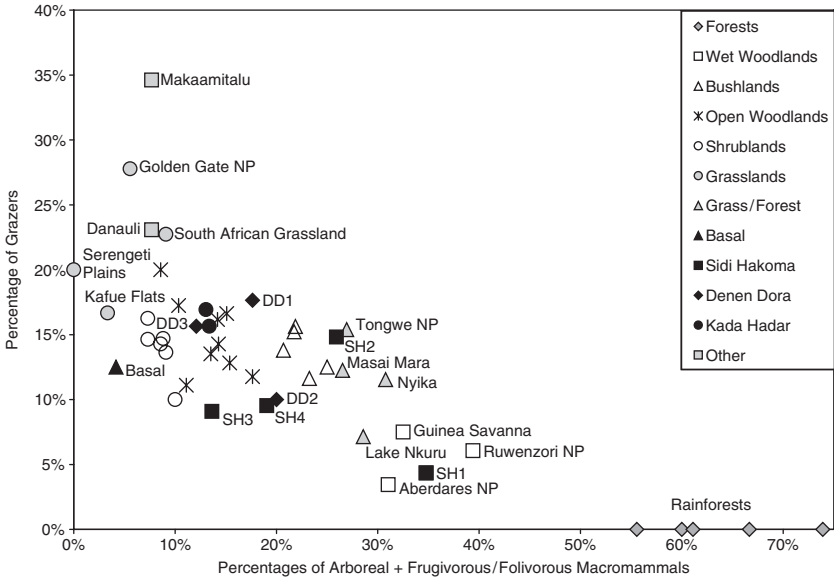

Figure 17.1 Bivariate plot of percentages of arboreal substrate use plus frugivory versus grazing animals. In general, extant sites group together, depending on the habitat from which they were derived. Fossil localities, represented by those from the Hadar Formation, group with extant habitats and, thus, their habitat is estimated from the percentages of these adaptations in the fossil fauna recovered at the site. Reconstructions for other fossil sites can be found in Reed (1997, 2002). Basal = Basal Member $\geq$ 3.4 Ma; Sidi Hakoma (SH) = 3.4 – 3.22 Ma, divided by sand units into four submembers, with SH1 being the oldest; Denen Dora (DD) = 3.22–3.18 Ma, divided by sand units into three submembers; Kada Hadar = (lower KH Member) 3.18–2.92 Ma, divided by volcanic tephras into two submembers; Upper = Kada Hadar (upper) < 2.33 Ma and representing two sites, Makaamitalu and Danauli. Extant species lists compiled by Reed (1997) from reports on African national parks, game reserves, and South African and Nigerian biomes. Classifications of habitats from forest through grassland are dependent on tree cover and overall plant type and derived from White (1983), Pratt & Gwynne (1977), Lind & Morrison (1974), and Cole (1986). All habitats except forests are considered part of the African savanna ecosystem. Mixed refers to grassland habitats with extensive amounts of riverine forests.

Seasons in the mid Miocene Epoch correspond to what is expected for forested habitats. Jacobs (1999a) has estimated dry-season months for Tugen Hills, Kenya, a Miocene fossil site using fossil plant leaves. At 12.8 Ma, dry-season months are estimated at 0–3.8 months per year (MPY). This is followed by evidence for 3.3–6.9 dry-season MPY at 9.0 Ma and corresponds to the trend of aridification (Jacobs 1999a, 1999b, 2002, Marlow *et al.* 2000). In the late Miocene Epoch, Jacobs

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detects a reduction in dry season months to 0–3.7 MPY, which is correlated with the beginning of the wet warming trend.

Early Pliocene hominin habitats indicate that dry-season months should range from four to six months per annum, with the more open habitats having the lengthier dry seasons. However, Hailemichael (1999) has identified seasonal growth changes in mollusks acquired from the Sidi Hakoma Member of the Hadar Formation, from which *A. afarensis* has also been recovered. They indicate that from 3.4 to 3.2 Ma, at least, there were yearly seasonal changes with dry seasons of approximately three months. Extant closed woodland and bushland habitats have longer dry seasons, raising the question of why there is a difference between extant and ancient habitats. We will address this by examining mammalian community structure.

Mammalian community structure is represented by the trophic and substrate adaptations of resident mammal species in extant localities of particular habitats or recovered from fossil sites (Andrews 1989; Reed 1997, 1998). There are differences between extant and Pliocene mammalian community structures that may relate to shorter dry seasons per year and greater primary productivity. Proportions of arboreal, frugivorous, and grazing adaptations within communities are dependent on habitat (Fig. 17.2 & 17.3) and these percentages have been used to reconstruct ancient habitats (Reed 1997, 1998). The complete array of community trophic and substrate adaptations also groups similar extant habitats together in a principal components analysis (PCA), but major differences are identified between early Pliocene and extant African mammal communities (Fig. 17.4). These discrepancies are related to significant differences in percentages of browsers and mixed feeders and indicate that the mammalian community structure of the African Pliocene Epoch was fundamentally different from extant mammalian communities.

Higher proportions of browsing species are unlikely to reflect taphonomic biases as there are significantly higher proportions of these mammals in early Pliocene deposits (Table 17.4) with different modes of accumulation: fluvial, lacustrine, volcanic, and animal (Reed 2002). One would not expect either mode of accumulation or time-averaging to consistently raise the frequency of the same two adaptations, or decrease all the others. We suggest that greater proportions of browsing species as well as mixed feeders possibly reflect greater primary productivity and, thus, seasonal differences between extant and, Pliocene habitats.

Pliocene habitats could support greater proportions of browsers through increased productivity in one of two ways: either plants were more abundant or plants produced more leaves over the course of the year. Browsers eat C_3 plants, which include trees, bushes, shrubs, and

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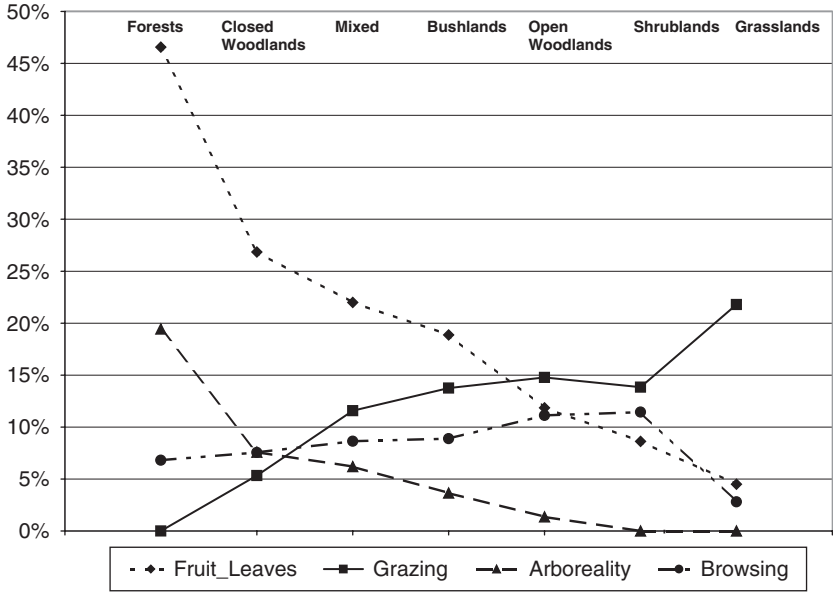

Figure 17.2 Mean percentages of arboreal substrate use, frugivory, grazing, and browsing in African habitats. The mean percentages of frugivory and aboreality decline from forests through grasslands. This corresponds to a gradient of declining annual rainfall. Conversely, the mean percentages of grazing mammals increase across the same gradient. Thus, mean annual rainfall correlates with tree cover, such that as annual rainfall declines, tree species become sparse or bush-like, finally giving way to shrubs and open grasslands. Browsing species have no particular pattern and are not significantly different among extant habitats.

herbs. It is unlikely that these plants were more abundant, as greater numbers of trees or bushes would be reflected in higher percentages of arboreal mammals and, thus, would change the reconstructed habitat, e.g. from closed woodland to forest.

An extended growing season caused by longer wet seasons rather than increased annual rainfall would account for increased primary productivity. In fact, some plants actually increase leafing productivity at the expense of fruits in a situation of prolonged wet seasons (Foley 1987). Greater production can result in increased species diversity (Connell & Orians 1964; Ritchie & Olff 1999). As the major spread of C_4 grasslands did not occur until around 1.8 Ma (Cerling 1992), greater species diversity in the early Pliocene Epoch would affect browsing and mixed feeding species that focused on C_3 plants. Frugivore diversity would not increase

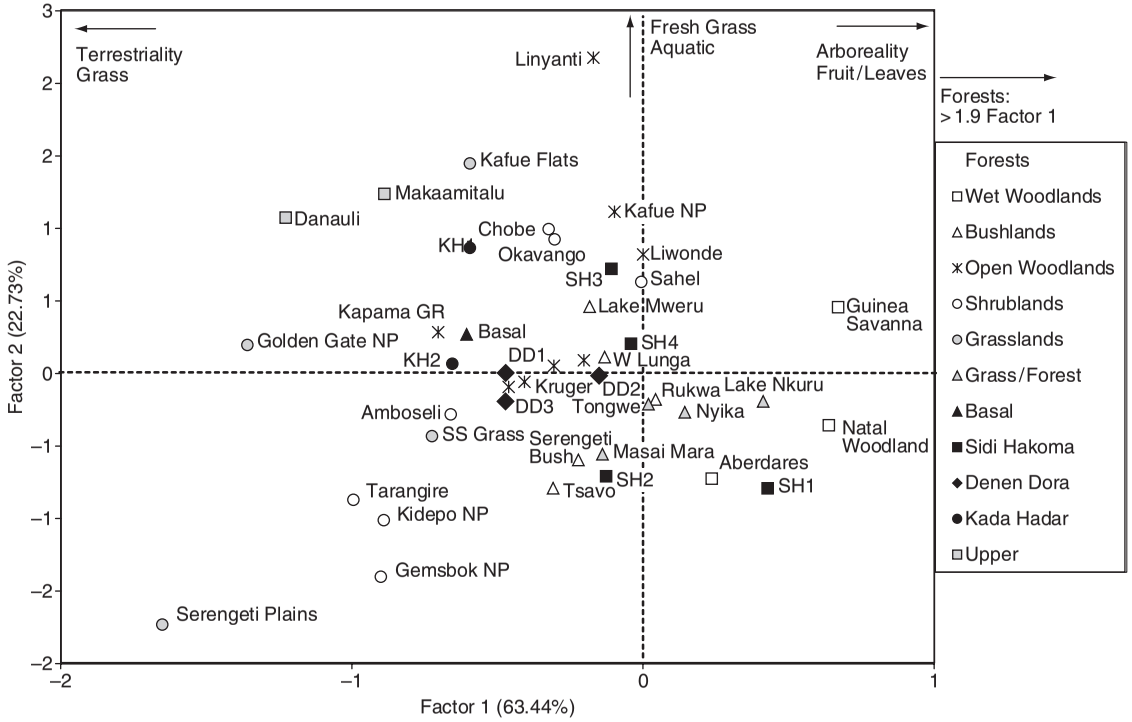

Figure 17.3 Principal components analysis using six substrate and trophic adaptations from mammals in extant and fossil communities. Adaptations found to be significantly different from one another among habitats were used to further explore relationships among fossil localities and extant habitats. These six adaptations account for 86.1% of the variation among extant communities. Fossil submembers from Hadar are again estimated to represent closed woodlands through grassland habitats. (Extant forests are eliminated from the diagram.) Those localities high on the *y*-axis have significant proportions of aquatic substrate use and fresh grass grazing from edaphic grassland. Edaphic grasslands are those that are flooded for a portion of the year. Selected extant localities labeled for reference. See Figure 17.1 for definitions.

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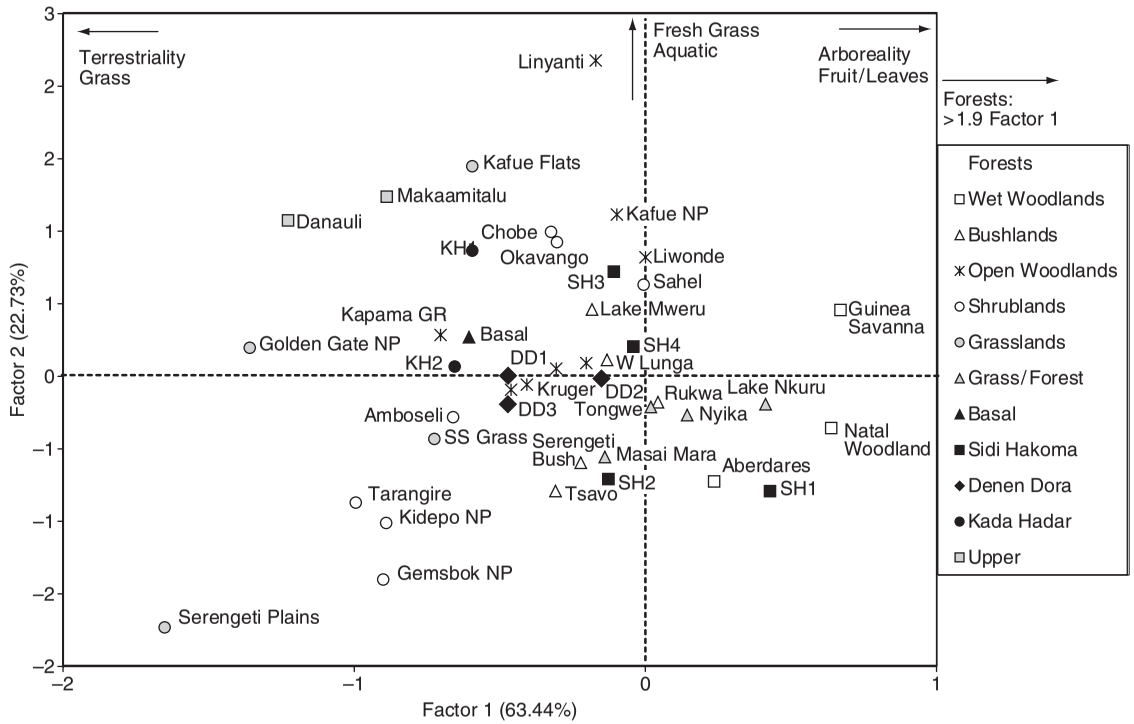

Figure 17.4 Principal components analysis (PCA) using 17 substrate and trophic adaptations from mammals in extant and fossil communities. In this PCA, only 60.8% of the variation is accounted for among extant localities, indicating that community structure differs more than specific adaptations that indicate habitats. Fossil sites plotted within this analysis show that they are still within closed woodland through grassland habitats (*x*-axis), but they have greater proportions of mixed feeding and browsing adaptations than extant localities (*y*-axis). Selected extant localities labeled for reference. See Figure 17.1 for definitions.

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Table 17.4 *Analysis of variance (ANOVA) and Tukey's studentized range test (HSD) for unequal sample sizes between extant and fossil proportions of browsing and mixed feeding adaptations. The ANOVA reveals significantly different proportions between the Hadar fossil localities and all extant habitats in both browsing and mixed feeding adaptations. The Tukey HSD further shows that the Hadar fossil localities (x = 15.73%) are also significantly different from extant forest localities (x = 6.81%) in browsing adaptations. Hadar fossil localities are not significantly different in mixed feeding adaptations from extant forest localities, as extant forests include mixed feeding species that graze on grasses in riverine and swampy areas.*

	SS effect	df effect	MS effect	SS error	df error	MS error	*F*	*P*
Browsing	0.04768189	2	0.0238409	0.101214	47	0.002153	11.07081	**0.0001**
Mixed Feeding	0.02436361	2	0.0121818	0.050254	47	0.001069	11.39297	**0.0001**

Tukey HSD for uneven sample sizes

	Extant Localities, No Forests	**Fossil Localities**	**Extant Forest Localities**
Mixed feeding	**Mean =** 5.38%	**Mean =** 10.49%	**Mean =** 8.51%
Extant Localities		**0.0002**	
Extant Forests	0.0903	0.4542	
Browsing	**Mean =** 9.04%	**Mean =** 15.73%	**Mean =** 6.81%
Extant localities		**0.0004**	
Extant forests	0.5324	**0.0012**	Significant P values in bold

df, degrees of freedom; MS, mean squares; SS, sum of squares.

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if greater leafing occured at the expense of fruit production. Increased production in C_3 plants would account for the presence of four species of browsing giraffids, a browsing perissodactyl, and higher percentages of browsing bovids in Pliocene sites than extant ecosystems.

Seasonal changes in the subtropics fluctuated from 1.8 Ma to the present as further aridification and subsequent glacial cycles created periods of longer and shorter wet seasons over time. This was likely coupled, as it is today, with monsoonal differences causing both unimodal and bimodal patterns of wet and dry seasonal change (O'Brien 1998). At the same time, glaciers in the Northern Hemisphere caused habitats to shift north and south. Other local conditions determined by immediacy to seas, mountain ranges, etc. may have caused various pockets of milder climates, and thus milder winter conditions, in areas of Eurasia (van Andel & Tzedakis 1996).

Hominin diets

Teaford and Ungar (2000) summarize differences between early hominin species and Miocene hominoids in the masticatory system. Large, low-relief molars, increased enamel thickness, increased mandibular robusticity, and broader incisors typify early hominins. Teaford & Unger (2000) review research that shows vegetation in *Australopithecus* diets probably included soft fruits, hard smaller fruits that did not require incisors to peel or extensively prepare, and possibly underground storage organs (USOs), such as roots and rhizomes (see also Hatley & Kappelman [1980]). Early *Australopithecus* species probably were not able to eat tough foods such as meat, mature or fibrous leaves, or pithy fruits (Teaford & Ungar 2000). Other evidence of early hominin diet is provided from microwear striations and pitting on incisors, suggested by Ryan and Johanson (1989) to indicate savanna vegetation, and striations on molars, suggested by Grine (1981) to indicate abrasive vegetation. Janis (1988) suggests that the height above the ground from which the food comes, rather than the properties of the foods themselves, often causes tooth abrasion, i.e. grazing close to the ground would cause ingestion of more grit compared with browsing from tall trees. The findings of Ryan and Johanson (1989) and Grine (1981) thus indicate that early hominins were eating some grit- or dust-covered foods and, therefore, possibly foraging from bushes or shrubs closer to the ground.

Carbon isotope data provide additional information about the foods of early hominins. For example, *Australopithecus africanus* is suggested to have eaten food with some C_4 isotopes (Sponheimer & Lee-Thorp 1999).

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Grasses and sedges, including their roots, seeds, and leaves, result in C_4 isotope traces in enamel, as does eating animals that eat those plant foods. While Sponheimer and Lee-Thorp (1999) favor *A. africanus* eating meat from grazing animals, others suggest that this hominin may have focused on grasses (seeds or rhizomes), sedges, or meat sources (van der Merwe *et al.* 2003). Although C_4 grasslands expanded throughout Africa at 1.8 Ma, these plants have existed since the Miocene Epoch. We think that meat-eating is unlikely for the following reasons: first, even if *A. africanus* ate meat occasionally, there is no particular reason for any early hominin to focus on ungulates that ate grasses in areas with abundant browsing animals. Second, early hominins would not have been able to process meat or marrow by relying on their dentition. They would have needed stone tools to expose marrow cavities and to remove meat from bones, but there are no stone tools associated with this species. Third, hominin masticatory morphology indicates adaptations to harder, not tougher (such as meat), food items (Teaford & Ungar 2000), and microwear studies show a certain amount of grit in the diet (Grine 1981). These data suggest that *A. africanus* and other early hominins ate plant products that were hard and gritty fairly often. USOs (both C_3 and C_4 bulbs and rhizomes) would fit these data, but species exhibiting higher C_4 isotope values may have selected USOs from grasses. Teaford and Ungar (2000) note that early hominins did not specialize on hard resources but were able to eat these foods as a critical fallback. While it is possible that these early species also scavenged in a limited way, either USOs or termites are more likely resources causing the C4 values.

Paranthropus species' craniodental morphology includes very large cheek teeth, extremely thick enamel, small incisors, and inflated malar regions (Fleagle 1999). It has been hypothesized that *Paranthropus* species were eating grittier food items than were earlier hominins, as evinced by dental microwear that shows heavy pitting on the cheek teeth (Grine 1981). Based on skull morphology, it has also been suggested that these species were eating harder foods than were previous hominins (see review by Teaford & Ungar [2000]), or they were eating hard foods more consistently (Foley 1987). In addition, tools must now be considered as part of the food acquisition process. P. *robustus*, at least, is associated with polished bone tools that are indicative of digging (Brain & Shipman 1993; d'Errico *et al.* 2001), while stone tools are allocated to *Homo* species. The masticatory morphology associated with *Paranthropus* species is likely the result of further, intensive focus on USOs (Hatley & Kappelman 1980; Teaford & Ungar 2000).

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Early *Homo* species such as *H. rudolfensis* and *H. habilis* have different morphology from *Paranthropus* and earlier hominin species, such that their cheek teeth are smaller, their incisors are larger, and their faces are reduced (Fleagle 1999). They are also usually associated with Oldowan stone tools, which although appearing around 2.6 Ma (Semaw *et al.* 1997), become ubiquitous in Africa after 2.3 Ma. These features suggest that early *Homo* species were eating foods that were not as gritty or hard as those consumed consistently by the *Paranthropus* lineage, and they were also processing food with stone tools. *Homo* species probably focused on softer fruits and vegetable products as well as incorporating meat into their diets Later *Homo* species added more meat into their diets and likely began processing vegetable products beyond simple collection (Wrangham *et al.* 1999; Aiello & Wheeler 1995). We discuss the evolutionary significance of changes in seasonality to hominin diets and behavior in the next section.

Seasonal changes and hominin evolution

Early hominins

Ecological evidence from early hominin sites shows that they were able to exist in various habitats and through changes in climate. Extended rainy seasons probably supplied preferred food items for long periods of each year. There were dry seasons, however, in which production of fruits, flowers, and flush leaves were diminished.

Due to global climate changes that began at 3.2 Ma (Marlow *et al.* 2000), primary productivity likely declined and resources were difficult to find in the dry season. As a result, there was a progressive reduction in the amount of above-ground plant material available for hominin exploitation. Plants are affected by longer periods of drought, such that, if deciduous, they store energy in USOs instead of producing leaves, shoots, or fruits (Archibold 1995). Bulbs and rhizomes therefore would be available throughout much of the dry season and provide needed nutrition to hominins.

This has implications for *A. afarensis* and other early hominins, such that a change to longer dry seasons instigated by increased aridification (Vrba, 1995; Behrensmeyer *et al.* 1997; Bobe and Eck 2001) could have pushed the species to extinction. Some populations of early *Australopithecus* species may have switched their foraging effort to USOs during long dry seasons, and over time *Paranthropus* species evolved. Other early hominin populations switched to critical resources in response to lengthening dry seasons by incorporating meat or marrow into their

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diets, obtained through the use of stone tools. There may be other species, such as *A. garhi*, that focused on other, yet unknown, resources. In any event, we conclude that longer dry seasons initiated by climatic changes around 3.0–2.8 Ma contributed to hominin extinction and speciation events.

Robust Australopithecine (Paranthropus) lineage

Aridification caused a change in resource availability of above -ground plant material after ~2.8 Ma. USOs would have been a reliable food source, possibly requiring increased foraging effort as dry seasons lengthened. *Paranthropus* existed into the Pleistocene Epoch and is almost always associated with edaphic grasslands in both eastern and southern Africa (Reed 1997). Edaphic grasslands and wetlands are often present in dry seasons because of floodwaters caused by rain in areas far away from the immediate climate (e.g. Okavango Delta). For this reason, it is possible that food resources used by *Paranthropus* species survived the aridification at the beginning of the Pleistocene Epoch (1.8 Ma) but disappeared with more extreme climate change at ~1.0 Ma. The sudden drop in SSTs and subsequent glaciation of both poles would have caused serious droughts across Equatorial areas during this time period. *Paranthropus* disappears from the fossil record at some stage in this period of increased aridity.

Early Homo

Although *Homo* species no doubt were predominantly vegetarians, this lineage most likely began consuming animal resources sometime after ~2.7 Ma, as indicated by the presence of stone tools (Semaw *et al.* 1997). Seasonal stresses, i.e. reduced availability of edible above-ground plant material in dry-season months, probably contributed to the change in diet. *Homo* species were able to scavenge carcasses for bone marrow and any remaining meat during these lean periods (Blumenschine 1987). The masticatory morphology of *Homo* suggests that they utilized different food resources from *Paranthropus*, and stone tools would have allowed the initial processing of marrow or meat. Scavenging opportunities probably occurred in riparian woodlands, and many early *Homo* sites have been located in these habitats (Blumenschine 1987; Marean 1989). In addition, scavenging was probably dangerous for *Homo*, even if they carried stone tools, so the behavior was likely opportunistic rather than consistent or

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confrontational. Opportunistic scavenging could have been an option for *Australopithecus* species as well, but it probably became critical for early *Homo*. Within the changing climate and longer dry seasons, meat would have been available relatively consistently, in contrast with usual vegetation sources utilized by *Homo*, which may have failed seasonally. Animals were likely a critical resource by the time the Oldowan industry appears. Animal resources allowed this lineage of Pliocene hominins to survive seasonal fluctuations in plant resources, whereas *Paranthropus* species survived seasonal fluctuations by turning to underground vegetable resources.

Homo erectus

The Dmanisi locality demonstrates that hominins had colonized temperate climates by the Early Pleistocene Epoch. The fauna associated with the Dmanisi hominins includes both palearctic and paleotropical species, indicating a relatively mild temperate climate (Gabunia *et al*. 2000b). Gabunia et al. (2000b) also report a high ratio of felids to hyaenids at Dmanisi, and they suggest that hominins would have had minimal competition from other scavengers and that these earliest immigrants were most likely opportunistic scavengers. Given the limited evidence for hominins in temperate climates at this early date, long-term survival via opportunistic scavenging may have been limited, particularly as the climate cooled after 1.6 Ma (de Menocal & Bloemendal 1995).

At the same time in Africa, Early Pleistocene deposits yield evidence for the first appearance of *Homo erectus sensu lato* at Koobi Fora 1.8 Ma. It has recently been argued that *H. erectus*' anatomy, social structure, and life history traits are best explained by a subsistence strategy heavily dependent upon foraging for tubers (O'Connell *et al*. 1999). We consider this scenario unlikely for *H. erectus*, especially in Africa. Given that *H. erectus* and *Paranthropus* were synchronic and sympatric in Africa, it is unlikely that they shared a dietary specialization. Further evidence may show that *H. erectus* focused on tubers as well, but we argue that *H. erectus* moved from opportunistic to confrontational scavenging, relying on animals to buffer seasonal stress for the following reasons. *H. erectus* displays an increase in stature and is the first hominin species with modern human limb proportions (McHenry 1992). Additionally, the thoracic cavity of *H. erectus* is barrel-shaped, as in modern humans and in contrast to australopithecines, suggesting both a reduction in gut size and a more efficient cardiovascular system (Aiello & Wheeler 1995). These anatomical

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features represent an adaptation to open arid habitats with high levels of activity and an extended foraging range (Cachel & Harris 1998).

In Africa, *H. erectus* is associated consistently with stone tools and large animal remains. In particular, the Acheulean industry first appears 1.5 Ma with *Homo erectus* and includes heavy-duty butchering tools such as hand axes and cleavers (Klein 1999). Recent analyses at Olduvai indicate that *H. erectus* had early access to vertebrate carcasses and focused on long bones of larger mammals for meat rather than marrow (Monahan 1996). Together, these data are consistent with the hypothesis that *H. erectus* practiced confrontational scavenging. Despite the long-term success that this strategy provided *H. erectus*, colonization of cold environments was not achieved by this species (Roebroeks *et al.* 1992; Roebroeks 2001). Survival in cold environments required primary access to animals, which can be achieved only through hunting.

Later Homo species and the evolution of hunting

The first hominin species to occupy cold climates was *Homo heidelbergensis*, which first appeared in Africa ~800 Ka, and then in Europe ~500 Ka (Rightmire 1996). Although the archaeological record for *H. heidelbergensis* is sparse, there is reason to argue that this species was a capable hunter (Thieme 1997). The relative brain size of *H. heidelbergensis* is significantly greater than in *H. erectus* (Ruff *et al.* 1997), suggesting an increase in diet quality (Aiello & Wheeler 1995; Fish & Lockwood 2003). Additionally, the continuous record of occupation in the northern latitudes of Europe after 500 Ka indicates an ability to consistently acquire high-quality animal resources to survive the long winters (Roebroeks 2001).

The importance of hunting for survival in cold climates is best illustrated by *Homo neanderthalensis*, the European descendant of *H. heidelbergensis*. Neandertals date from ~150–28 Ka and appear in Europe during the height of glacial activity (Isotope Stage 6). Neandertals have also been found in the temperate localities of Spain, Italy, and the Levant, indicating that they were not restricted to cold habitats.

The Neandertal postcranial skeleton is exceptionally robust (Pearson 2000) and has a high incidence of trauma (Trinkaus & Zimmerman 1982), which has been interpreted as resulting from intensive hunting of large animals. Neandertal faunal accumulations from sites such as Salzgitter Levenstedt, Germany (Gaudzinski & Roebroeks 2000), Marillac, France (Fizet *et al.* 1995), Mauran, France (Gaudzinski 1996), Zafarraya, Spain (Geraads 1997), Mezmaiskaya, Caucasus (Golovanova *et al.* 1999), and

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the Levantine sites of Kebara (Speth & Tchernov 1998), Amud (Suzuki & Takai 1970), and Kobeh (Marean & Kim 1998) are regularly dominated by a single ungulate species with cut marks, element representation, and age profiles indicative of specialized hunting. Additional evidence for a diet high in animal protein comes from analyses of buccal microwear patterns on the teeth of Neandertals (Lalueza Fox & Perez-Perez 1993; Lalueza *et al.* 1996) and the isotopic composition of their bones (Bocherens *et al.* 1999; Richards *et al.* 2000).

This specialized strategy is in sharp contrast with the hunting pattern associated with contemporary anatomically modern *Homo sapiens* (AMHS). The earliest AMHS appear 160 Ka in Ethiopia (White *et al.* 2003). AMHS localities of Klasies River Mouth and Die Kelders, South Africa (125–110 Ka), contain numerous species and include marine and avian fauna (Klein 1976; Grine *et al.* 1991). The abundant resources in the habitats surrounding these sites allowed AMHS to hunt a variety of mammals and gather other animal resources with no single species favored.

The different hunting strategies of Neandertals and AMHS are demonstrated most clearly by contrasting cave sites in Israel where fossil remains from both species have been identified. Both Neandertal fossils from Amud and Kebara and AMHS remains at Qafzeh and Skhul were found associated with similar Levaillois-Mousterian stone tool technology (Bar-Yosef & Meignen 1992), and many of the same ungulate species are present. However, Neandertal accumulations are significantly less rich and diverse than those of AMHS. Gazelles represent 58 and 66% of the ungulates out of six and seven total species at Amud and Kebara, respectively (Suzuki & Takai 1970; Speth & Tchernov 1998). In contrast, among the ten species found at Qafzeh, the most prevalent accounts for only 35% of the accumulation (Rabinovich & Tchernov 1995). It is also probable that Neandertals occupied caves in the Levant multiseasonally, while AMHS occupied the region in the winter and spring seasons (Leiberman 1993; Shea 2003). Despite occupying broadly similar habitats within the same geographic region, Neandertals utilized a narrower range of animal resources and hunted more (Shea 2003) compared with the generalized strategy employed by AMHS. That is, Neandertals focused on hunting irrespective of the season in the Levant (Leiberman & Shea 1994).

The specialized nature of Neandertal subsistence was certainly related to seasonal limitations on resources. Marean (1997) has suggested that the most optimal strategy for cold grassland inhabitants is tactical hunting, because it is the best way to create an abundance to survive through the long winter. Given the evidence, it is reasonable to propose that

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Neandertals had adapted to millennia of living in cold environments by developing a specialized hunting strategy. The importance of this strategy for Neandertal survival in cold climates can be measured in the fact that it seems to have become part of their lifestyle and was practiced in warmer habitats such as the Levant. In contrast AMHS evolved in a tropical climate with only wet and dry seasonal changes to face during foraging. Further improvements and innovations related to animal resource utilization first appear in subtropical Africa, and this suggests that resource excess was required for these developments. AMHS developed behaviors and adaptations that allowed more flexibility in foraging behavior over the long term.

Conclusions

Climatic changes caused by glacial cycles have influenced human evolution by changing habitats and ultimately altering resource availability. Climate change also influenced long-term seasonal differences by shifting wet and dry yearly seasonal patterns. Alterations in the number of dry season months in particular caused greater levels of foraging stress for early hominins.

Increases in dry season months between ~3.0 and 2.5 Ma probably forced important modifications in resource use. Some populations of early *Australopithecus* or other hominins turned to reliance on USOs, while other populations focused on animal resources. This assumes that the earliest hominins previously had incorporated limited quantities of both underground tuber and animal resources into their diets. Overall, increased seasonality prompted by global aridification influenced hominin diversification into two separate lineages: *Paranthropus* and *Homo*.

Paranthropus species most likely focused on USOs, at least for possibly lengthy dry seasons, while the critical resource in dry seasons for early *Homo* was marrow and/or meat scavenged from available carcasses (Blumenschine 1987). *Homo* later moved to more confrontational scavenging, possibly due to grassland expansion and longer dry seasons potentially providing more carcasses. The habitat and ecological tolerance of tropical hominins improved with the ability to acquire animals as they became more independent of plant resources. However, the lack of numerous hominin sites in temperate climates until the advent of *Homo heidelbergensis* implies that hunting in these climates was not a major foraging technique of earlier hominins.

As hominins began to occupy cold habitats with greater seasonal stress, meat became more important to the diet and Neandertals focused on

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acquiring meat. Extreme seasonal stress, even though tolerated well by Neandertals, was apparently not conducive to innovation beyond tactical hunting patterns because of possible lack of overall resources during extreme cold. AMHS, originating in subtropical Africa, had different foraging and hunting practices that better suited a variety of habitats. Abundances of resources led them to various seasonal practices that did not rely on any one resource or acquisition method. These subsistence strategies likely enabled the species to expand worldwide.

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