Orbital controls on seasonality

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Introduction

Given the significant influence of seasonality patterns on many aspects of modern human and non-human primate tropical ecology (Foley 1993; Jablonski et al. 2000), it is reasonable to assume that factors associated with seasonality provided key selective forces in the evolution of the human lineage in Equatorial Africa. Reconstructing the climatic and ecological context of early hominin innovations ultimately is critical for interpreting their adaptive significance, and much research has focused on establishing links between hominin evolutionary events and global, regional, and local environmental perturbations (Brain 1981; Grine 1986; Vrba et al. 1989, 1995; Bromage & Schrenk 1999). Attempts to correlate hominin evolution with climatic trends have typically invoked models of progressively more arid and seasonal terrestrial conditions in Africa, ultimately resulting in the expansion of grassland ecosystems. Alternative interpretations of the Pliocene fossil record of east Africa suggest pulses (Vrba 1985) or multiple episodes (Bobe & Eck 2001; Bobe et al. 2002; Bobe & Behrensmeyer 2004) of high faunal turnover correlated with major global climatic change, set within a gradual shift from forest dominance to more open habitats.

While long-term trends or abrupt turnover events may have influenced human evolution, it has become evident that climatic control of mammalian evolution, including hominins, in Equatorial Africa is much more complex than supposed previously and that this region is characterized by almost continuous flux and oscillation of climatic patterns driven primarily by orbital forcing (e.g. Rossignol-Strick et al. 1982; Pokras & Mix 1987; deMenocal 1995; Kutzbach et al. 1996; Thompson et al. 2002; Hughen et al. 2004). These short-term changes in the Earth’s orbit occur at varying cycles (Milankovitch cycles) ranging in duration from 20 to 400 Ka and affect climate by altering the amount of solar radiation by season and latitude. While establishing links between orbital shifts and
climate focused initially on the extent of ice sheets in high latitudes, changes in solar radiation also have had significant, independent effects on climatic systems in middle to lower latitudes. Regional Equatorial African climatic patterns have been shown to be highly responsive to orbitally forced shifts in radiation, which has dramatic effects on seasonal variation in precipitation and temperature. The scale of changes in African seasonality patterns associated with short-term orbital forcing matches those previously hypothesized for much longer intervals spanning millions of years. Successfully correlating and developing causal links between specific hominin evolutionary events and variations in climate, such as seasonality, therefore, ultimately requires the development of high-resolution records of the nature and timing of climatic, ecological, and phenotypic changes in the fossil record within the temporal and dynamic framework of Milankovitch cycling.

Principal controls on the distribution of vegetation, and, by extension, dietary resources and community ecology of animal consumers, in tropical and subtropical regions of Africa are total annual rainfall and the timing, duration, and intensity of the dry season(s). The complexity and difficulty in unraveling and isolating subtle and interrelated effects of these seasonality parameters in modern African ecosystems is amplified when attempting to untangle these dynamic patterns and associations in the past. While the integrity and quantity of data on general aspects of plant physiognomy and community structure in early hominin paleohabitats are sufficient at this point to initiate interpretations of hominin evolutionary innovations in a very broad ecological context, the lack of sufficiently developed empirical proxies for paleoseasonality makes it difficult to assess human evolution rigorously within the context of specific aspects of seasonality. Seasonality has proven to be a highly elusive feature to tease from the fossil record, due primarily to a lack of necessary temporal resolution in seasonal proxies, limited relevant data sets, and significant taphonomic biases inherent in the terrestrial fossil archive.

Given these caveats and concerns, the goal of this chapter is to explore a global and regional climatic framework based on orbital forcing (Milankovitch cycling) that highlights major factors controlling paleoseasonality in Equatorial Africa. Examining modern African climatic systems controlling seasonality provides a starting point for interpreting the evolution of regional climatic systems. These patterns are projected into the past to evaluate regional environmental oscillations linked to orbital forcing of climate and seasonality in Africa during the Pliocene and Pleistocene epochs. A key component involved in scaffolding hominin evolution within astronomically driven environmental change is establishing
“ground truth,” documenting specific aspects of paleoseasonality in the terrestrial fossil record that can be correlated with Milankovitch cycling. The limited number of approaches for developing these high-resolution proxies for paleoseasonality in tropical Africa is reviewed and, finally, the implications of environmental change for the evolution of African ecosystems are discussed.

Astronomical control of solar radiation

Evaluating human ecology and evolution within the framework of orbital forced seasonality shifts in Equatorial Africa ultimately requires establishing which and how specific seasonality parameters vary at the intersection of insolation oscillations with climatic systems at local, regional, and global levels. This requires a rudimentary understanding of Milankovitch cycles as well as climatic systems that have prevailed over tropical and subtropical Africa during the course of human evolution. Following is an overview of features of the Earth’s orbit that alter cyclically in response to gravitational forces in the Solar System and an explanation of how these orbital shifts effect climate.

Seasonality in tropical and subtropical Africa (and globally in general) results ultimately from variation in solar radiational heating on the Earth, which primarily is a function of the geometry of the Earth’s solar orbit. Two fundamental motions describe this orbit – the Earth’s rotation around an axis that passes through its poles and the Earth’s once-a-year revolution around the Sun (Bradley 1999; Ruddiman 2001). The tilt, or obliquity, of the Earth’s axis of rotation (currently 23.5°) relative to the plane of it’s orbit around the Sun causes seasonal changes in solar radiation received in each hemisphere as the Earth revolves about the Sun (Fig. 18.1a). During each annual revolution around the Sun, the Earth maintains a constant tilt and a constant direction of tilt in space, such that the northern and southern hemispheres alternatively receive more direct radiation in their respective summers. In addition, the Earth’s orbit is slightly eccentric or elliptical, and the distance to the Sun changes with Earth’s position in its orbit, which directly affects the amount of solar radiation that the Earth receives. At present, Earth is in the perihelion position (closest to the Sun) on January 3 and in aphelion (furthest from the Sun) on July 4 (Fig. 18.1a). These dates correspond roughly to the winter solstice (shortest day) and summer solstice (longest day), respectively, in the northern hemisphere, resulting in higher winter and lower summer radiation in the northern hemisphere (the opposite is true for the southern hemisphere) than would occur in a perfectly
Obliquity—Changes in the tilt of the Earth’s axis, which occur on a cycle of 41,000 years.

Eccentricity—Changes in the shape of the Earth’s solar orbit, which occur on two major cycles of 100,000 and 413,000 years.

Precession of the ellipse—Elliptical shape of Earth’s orbit precesses in time.

Axial Precession—Wobbling of the tilt axis.

Precession of the equinoxes—the combined effect of these two precessional motions causes the solstices and equinoxes to move around the Earth’s orbit, completing one full 360° orbit around the Sun every 23,000 years (see Fig. 18.2).

Figure 18.1(a) Schematic diagram of the Earth’s eccentric orbital geometry, depicting the current timing of the solstices (shortest and longest days) and equinoxes (equal days and nights) and the tilt of the Earth’s rotational spin axis relative to the plane of the Earth’s orbit (23.5°). Earth is closest to the Sun at perihelion on January 3, just after the December 21 solstice, and most distant at aphelion on July 4, shortly after the June 21 solstice. (b) Cyclical variations in the Earth’s orbit (obliquity, eccentricity of orbit, relative position of the solstices and equinoxes around the elliptical orbit) due to the mass gravitational attractions among Earth, its moon, the Sun, and other planets and their moons.
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A circular orbit. Relative to tilt, the effect of the Earth’s elliptical orbit on seasonality is small, enhancing or reducing the intensity of radiation received by only about 3–4%.

The position and orientation of the Earth relative to the Sun, however, is not fixed over long intervals of time. Due to gravitational effects on the Earth of the Sun, the Moon, and other planets, variations occur in the degree of orbital eccentricity around the Sun, the obliquity of the Earth, and the seasonal timing of perihelion and aphelion (precession of the equinoxes) (Figs. 18.1b and 18.2). These longer-term variations in Earth’s orbit result in cycles ranging from about 20 Ka to 400 Ka and cause cyclic variations in the amount of insolation (solar radiation received at the top of the atmosphere) by latitude and season (Fig. 18.3). Changes in solar heating driven by variations in Earth’s orbit are the major cause of cyclic climatic change over the ten thousand- to 100 thousand-years
timescale, and explicit theoretical links between orbital parameters and climate have been recognized and developed over the past 150 years (Croll 1875; Milankovitch 1941; Berger 1978; Imbrie & Imbrie 1979). These variations in insolation underpin the overall basis for seasonality and provide a framework in which to assess changes in seasonality in Equatorial Africa relevant to early hominin evolution.

Following are brief descriptions of the basics of the three key orbital variables that mediate climate change at different frequencies (see also Figs. 18.1–18.3).

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**Figure 18.3 Variations of eccentricity, obliquity, and precession (precession index) between one and two million years ago (generated using AnalySeries v.1.2 [Paillard et al. 1996]).** Superimposing these orbital variations creates complex patterns of insolation through geologic time. (a) The precessional index changes mainly at a cycle of 23,000 years, with the amplitude of the cycle modulated at eccentricity periods of 100,000 and 413,000 years. (b) Changes in axial tilt are periodic, with a mean period of 41,000 years. (c) The eccentricity (ε) of the Earth’s orbit varies at periods of 100,000 and 413,000 years. Eccentricity of an ellipse is related to the lengths of its longer axis (a) and shorter axis (b), such that $\varepsilon = (a^2 - b^2)^{1/2}/a$. Eccentricity has varied between values of 0.005 and nearly 0.0607, and the current value of 0.0167 lies toward the almost circular end of the range.
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1. **Obliquity (tilt)**. Over time, the axial tilt of the Earth varies periodically in a narrow range, cycling back and forth between 22.2 and 24.5°, with a mean period of 41 Ka. Changes in tilt cause long-term variations in seasonal solar insolation received on Earth, and the main effect is to amplify or suppress the seasons. Variation in obliquity has relatively little effect on radiation receipts at low latitudes, but the effect increases towards the poles. Increased tilt amplifies seasonal differences, whereas decreases in tilt diminish the amplitude of the seasonal differences. As the tilt is the same in both hemispheres, changes in obliquity affect radiation receipts in the southern and northern hemispheres equally and cycles are fairly regular, both in period and amplitude (Figs. 18.1b and 18.3b).

2. **Eccentricity**. Variations in orbital eccentricity are quasi-periodic, with two main periods, both of which are far more irregular than the 41 000-year obliquity cycle (Figs. 18.1b and 18.3c). One eccentricity cycle consists of four cycles of nearly equal strength and with periods ranging between 95 and 131 Ka, which blend to form a single cycle near 100 000 years. This cycle controls insolation variability associated with glacial/interglacial cycles. The second major eccentricity cycle has a wavelength of 413 000 years. The orbit has varied from almost circular – essentially no difference between perihelion and aphelion – to maximum eccentricity, when insolation varied by about 30% between perihelion and aphelion. Eccentricity variations affect the relative intensities of the seasons, with an opposite effect in each hemisphere.

3. **Precession**. Changes in the seasonal timing of perihelion and aphelion result from a slight wobble in the Earth’s axis of rotation as it moves around the Sun. The Earth’s wobbling motion (axial precession) is caused by the gravitational pull of the Sun and the Moon on the slight bulge in Earth’s diameter at the Equator and effectively results in the slow turning of Earth’s axis of rotation through a circular path, with one full turn every 25 700 years (Figs 18.1b and 18.2). Axial precession, when combined with the slow rotation of the elliptical shape of Earth’s orbit in space in time (precession of the ellipse), causes the solstices and equinoxes to move around the Earth’s orbit, completing one full 360-degree orbit around the sun every 23 000 years. This combined movement, known as the precession of the equinoxes, describes the absolute motion of the equinoxes and solstices in the larger reference frame of the universe and consists of a strong cycle near 23 000 years and a weaker one near 19 000 years, which together average one cycle every 21 700 years. Thus, roughly 11 500 years in the future, perihelion will occur when the northern hemisphere is tilted towards the Sun (mid June) rather than in the northern hemisphere’s midwinter, as is the current configuration...
(Fig. 18.2). Ultimately, the effects of precession of the equinoxes on insolation are modulated by changes in the eccentricity of Earth’s orbit (discussed above). When the orbit is near-circular, the seasonal timing of perihelion is inconsequential, whereas at maximum eccentricity, when differences in solar radiation are up to 30%, seasonal timing is crucial. The combined effects of the precession of equinoxes and changing eccentricity are termed the precessional index or eccentricity-modulated precession. Long-term variations in the precessional index occur in cycles with periods near 23,000 years and exhibit large variations in amplitude due to the modulation effect caused by eccentricity (Fig. 18.3a).

The variability of these orbital parameters and the resulting amount of insolation arriving on Earth at any latitude and season can be calculated for any point or range of time in the past (Fig. 18.4a). In general, monthly seasonal insolation changes are dominated by precession at low and middle latitudes whereas high latitudes, are affected mostly by variations in obliquity. Eccentricity is not significant as a direct cycle of seasonal insolation and is important primarily in modulating the amplitude of the precession cycle. Considered together, the superimposition of variations in eccentricity, obliquity, and precession produces a complex, ever-varying pattern of insolation through evolutionary time. The cumulative effects of these cycles through time are complicated further by the fact that the relative strength of the various cycles can shift at any given location, there can be varying modulation of amplitudes, and there are a number of additional astronomical and Earth-intrinsic climatic feedback mechanisms that mediate external forcing. Despite this complexity, the periodicities associated with orbital variations have been identified in many paleoclimatic records and it is clear that orbital forcing is an important factor in climatic fluctuations on the timescale of 10 Ka to 1 Ma and perhaps much longer throughout most of the Earth’s history. The precise mechanism of how orbital forcing is translated into a climate response remains unclear, and much research currently is focusing on exploring links between cyclic variations in insolation and climate change, including changes in seasonality through time.

**Modern climate and seasonality in Equatorial Africa**

Climatic and atmospheric circulation patterns of Africa today provide an appropriate construct for interpreting climatic parameters in the Pliocene and Pleistocene, given that regional paleogeography (Guiraud & Bosworth 1999) and general climatic variables have remained relatively
Figure 18.4 Effects of orbital variations on insolation and climatic proxies for African environments between one and two million years ago. (a) Insolation for July at a latitude of 30° N plotted using Analyses (Paillard et al. 1996). Increases in the amount of summer (e.g. July) insolation at approximately this latitude have been linked to stronger monsoonal circulation (Kutzbach 1981), resulting in increased seasonal precipitation in tropical and subtropical Africa. The amplitude of the monsoon response should be related to the amount of increase in summer insolation forcing and follow the tempo of the dominant cycle, in this case orbital precession. (b) Increasing terrigenous dust flux into marine sediments has been utilized to assess source-area aridity. Variability in the aeolian dust contribution to Ocean Drilling Program (ODP) core sites 721/722 in the Arabian Sea correlates with periodicities associated with orbital forcing. Aeolian variability before 2.8 Ma occurs at the 23–19-Ka precession cycle but then shifts to increased 41-Ka variance, with further increases in 100-Ka variance after 0.9 Ma, suggesting that the African climate, including seasonality, became more arid and dependent on high-latitude climatic forcing (deMenocal 1995). (c) The oxygen isotope record ($\delta^{18}O$) of foraminifera shells provides a proxy for past global climate states. These data record combined effects of changing ice sheet size, changing sea-water temperature, and changing salinity. Shown here is a compilation of isotopic values from sites ODP 677 and ODP 846 in the eastern Pacific (Shackleton et al. 1995) and indicate variable global temperatures associated with orbital forcing. Global cooling, as reflected by this record, typically is associated with increasing aridity and seasonality in low latitudes, which generally is supported by comparison of the oxygen isotope and dust flux profiles depicted here. Sapropels (organic-rich mud layers) identified in eastern Mediterranean Sea sediment cores have been linked to high freshwater and organic influx from the Nile. As the Nile headwaters drain the east African highlands, this record reflects east African precipitation patterns (Rossignol-Strick et al. 1982). Plotted on the figure are sapropel occurrences between 1 and 2 Ma as vertical lines based on the timescale of Lourens et al. (1996). Sapropels occur at regular 23 000-year intervals that coincide with summer insolation maxima as well as high African lake levels. Also apparent is that sapropels correlate roughly with low aeolian dust influx, both indicative of moist conditions.
conservative during this interval. In general, the distribution of modern climates is more or less symmetric about the Equator (Fig. 18.5a). The northern and southern extremities of the continent project into temperate areas and experience Mediterranean summer-dry climates. These temperate areas are bordered on the Equator-ward side by subtropical deserts, the Sahara Desert to the north, and the Namib coastal desert to the southwest. A wide belt of tropical climates separates the two arid subtropical zones, forming the climatic region in which much of early hominin evolution likely occurred. Almost all hominin material recovered outside of South Africa is from localities associated with the eastern branch of the East African Rift System, and most interpretations of early human evolution have focused on reconstructions of east African ecosystems. However, recent hominin discoveries in Chad and a complete lack of fossils that can be linked unequivocally to *Pan*, *Gorilla*, or a last common ancestor of the African ape and human lineages open the possibility that significant events in human evolution may have occurred in other portions of tropical and subtropical Africa where fossil recovery is limited by preservational and recovery biases.

Equatorial African climate currently is controlled by the intersection of three major air streams and three convergence zones, superimposed on and influenced by regional factors associated with topography, lakes, coastal currents and upwelling, and sea-surface temperature fluctuations in the Indian and Atlantic oceans (Nicholson 1996a). As a result, climatic patterns are markedly complex and highly variable. In general, most of Africa is characterized by a strong seasonal cycle in rainfall regime and a pronounced dry season. The pattern of wet and dry seasons is produced by a shift of all general circulation features toward the summer hemisphere (Fig. 18.5b,c). In tropical Africa, precipitation patterns are controlled mainly by the strength of the African-Asian monsoonal circulation and the seasonal migration of the Intertropical Convergence Zone (ITCZ), produced when the northeast and southeast trade winds meet. The zone of maximum rainfall follows the latitudinal position of the overhead Sun, resulting in a general bimodal seasonal distribution of rainfall, with maxima occurring in the two transitional seasons (April–May and October–November) associated with the passage of the ITCZ. Seasonal distribution of rainfall varies, in general, along a west–east gradient across Equatorial Africa due to different circulation patterns, rift-related topography, and large inland lakes that may modify African monsoon flows and the influence of the Indian monsoon. In addition, aspects of seasonality change dramatically within distances on the order of tens of kilometers, and there are regions in Equatorial Africa with one, two, and
Figure 18.5 (a) Generalized climatic types in Africa (Nicholson 1996b). (b,c) Monsoonal circulation patterns over Africa, showing a moist inflow of monsoonal air toward the low-pressure center over north Africa in boreal (northern hemisphere) summer and a dry monsoonal outflow from the high-pressure center over the land in boreal winter. Precipitation follows the northward shift of the Intertropical Convergence Zone (ITCZ) in boreal summer and Equatorial regions; some areas experience two rainfall maxima during the course of the year as the ITCZ traverses the Equator as it shifts toward the summer hemisphere. Superimposed on this basic pattern are numerous localized patterns of rainfall dictated by topographic relief, shoreline and maritime effects, and local wind systems (Nicholson 1996a).
even three rainfall maxima during the seasonal cycle (Nicholson 1996a). The more semi-arid regions of Equatorial Africa are notable in their extreme year-to-year rainfall variability, and drought is a common occurrence. These localized variations in precipitation probably relate to factors such as topographic relief, shoreline and maritime effects, and local wind systems.

Evidence of orbital forcing and seasonality in Equatorial Africa

Solar radiation is significant in sustaining tropical convergence, and studies of shifts in Equatorial African paleoenvironments and paleoclimate have implicated orbitally forced changes in insolation. Although obliquity (41 Ka), eccentricity (100 Ka), and precession (23 Ka) signals have all been identified in paleoclimatic proxies, Pliocene and Pleistocene circulation in the tropics appears to have been paced primarily by precessional variations in insolation (Fig. 18.4)(Pokras & Mix 1985, 1987; Bloemendal & deMenocal 1989; Molfino & McIntyre 1990; Tiedemann et al. 1994).

Equatorial African climate is affected not simply by insolation changes at low-latitudes but also by mid- to upper-latitude insolation, which controls systems such as the Asian monsoon and Atlantic sea-surface temperatures that are central ingredients in African climate. Climatic flux in Equatorial Africa has been linked to high-latitude glacial–interglacial amplitudes, low-latitude precessationally controlled insolation changes driving monsoonal circulation intensity, and direct insolation at the Equator at half-precession cycles. Climatic proxies including eolian and biogenic dust transport (Pokras & Mix 1987; Clemens et al. 1991; deMenocal et al. 1993; deMenocal 1995; Moreno et al. 2001), upwelling patterns adjacent to the African coast (Gorgas & Wilkens 2002), biochemical and biotic bedding patterns in coastal sediments (D’Argenio et al. 1998), and rhythmic stratification patterns in subtropical African lakes (Scholz 2000; Johnson et al. 2002; Ficken et al. 2002) indicate eccentricity and obliquity amplitudes or timing that suggest that sub-Saharan moisture patterns are linked to glacial/interglacial cycling. Numerous studies have also shown that low-latitude precessationally controlled insolation changes driving monsoonal circulation intensity exert control over hydrological patterns in Equatorial Africa (Street-Perrott & Harrison 1984; Kutzbach & Street-Perrott 1985; Pokras & Mix 1985, 1987; Gasse et al. 1989; Lamb et al. 1995). Other studies (Trauth et al. 2003) suggest that precipitation patterns are, in part, also triggered by increased March or September insolation on the Equator,
which intensifies the intertropical convergence and convective rainfall in the region.

The coexistence of all main Milankovitch cycles in spectral data may provide evidence for a complex interdependence and influence of high- and low-latitude orbital parameters influencing climatic regimes in Equatorial Africa. Fluctuations in precipitation linked to the El Niño Southern Oscillations (Verschuren et al. 2000), threshold effects resulting in abrupt transitions (deMenocal et al. 2000; Thompson et al. 2002), tentative correlations with millennial-scale phenomena such as Heinrich events and Dansgaard–Oeschger cycles (Stager et al. 2002), and linear and non-linear Earth-intrinsic feedback mechanisms of the climatic system (Kutzbach et al. 1996; Gorgas & Wilkens 2002) further complicate simple interpretations of external forcing of tropical African paleoclimates.

Pliocene and Pleistocene evidence of short-term climatic change in the East African Rift has been documented at a number of early hominin sites, including Olduvai (Hay 1976; Liutkus et al. 2000; Ashley & Driese 2003), Olorgesailie (Potts et al. 1999), and Turkana (Feibel et al. 1989; Bobe & Behrensmeyer 2004), but it has been difficult to link these perturbations to astronomically mediated insolation patterns and seasonality patterns unequivocally. Studies in the Baringo Basin of the Central Kenyan Rift Valley have identified lake cycling 2.5 and 2.7 Ma at hominin localities consistent with 23-Ka Milankovitch precessional periodicity (Kingston et al. 2000). These shifts in paleohydrological patterns in the Baringo Basin represent a window on a much more pervasive pattern of environmental change that is generally obscured locally and regionally by rifting activity. Environmental variability, reconstructed from pollen data, at Hadar corresponds with global climatic events documented in the marine record and may track a precessional cycle (Bonnefille et al. 2004).

Determining the specific effects of astronomical cycling on climatic patterns is complex and remains poorly understood. Pleistocene and Holocene lake-level fluctuations in Equatorial Africa document important changes in the precipitation–evaporation balance and indicate that the timing and duration of humid and dry periods are controlled by a number of factors, including Equatorial insolation, northern hemisphere insolation, and monsoonal intensity (Fig. 18.4) (Street-Perrott & Harrison 1984; Pokras & Mix 1985, 1987; Trauth et al. 2003). Interannual variation in rainfall amounts indicated by high lake stands is suspected to result mainly from prolonged rainy seasons rather than more intense rainfall. Precession-modulated cycling of precipitation and seasonality patterns in the rift valley presumably resulted in dynamic fluctuations in the physiognomy and taxonomic representation of flora in the region, with more
arid and seasonal climatic regimes associated with more widespread open woodland and grassland habitats. The main response of vegetation to short-term climatic variability would likely have involved a reshuffling of the relative coverage of different plant communities rather than whole-scale extinction or speciation events. Studies of Quaternary paleovegetation records indicate that Equatorial African ecosystems are highly sensitive to orbitally forced climate change, associated atmospheric CO₂ shifts, and vegetation–soil feedbacks, resulting in rapid shifts in pollen assemblage (Lezine 1991; Bonnefille & Mohammed 1994; Elenga et al. 1994), charcoal fluxes (Verardo & Ruddiman 1996), and relative proportions of C₃ (trees, shrubs, cold-season grasses and sedges) and C₄ (warm-season grasses and sedges) biomarkers (Huang et al. 1999; Ficken et al. 2002; Schefuss et al. 2003).

Cumulatively, these data suggest that Milankovitch cycles are highly relevant to understanding variation in climate and seasonality in equatorial Africa and that hominin evolution in the rift valley, and tropical Africa in general, should be evaluated in the context of continuous orbitally forced environmental flux as well as long-term (> 10⁵) trends.

**Proxies for paleoseasonality**

While evidence suggests that orbital forced climate change was significant throughout hominin evolution in Equatorial Africa, it remains essential to document the specific effects of these oscillation on paleoseasonality at discrete times and locations relevant to human evolution. The fundamental constraint in characterizing seasonality in the past, especially in the terrestrial realm, is accessing climatic archives that resolve at the level of weeks or at least less than one month. Proxies for intra-annual variation in precipitation, temperature, humidity, and precipitation/evaporation ratios and resultant shifts in vegetation and the diet, ranging behavior, life history patterns, and stress indicators of animals provide means of assessing the timing, intensity, and relative lengths of wet/dry portions of seasonality. A number of approaches to documenting seasonality in the terrestrial fossil record are being developed, including: (i) isotope analyses of monthly growth increments in invertebrate shells that correlate with rainfall patterns (Rye & Sommer 1980; Abell et al. 1995; Tojo & Ohno 1999; Rodrigues et al. 2000); (ii) periodicity of repetitive linear enamel hypoplasia in primate teeth that have been linked to seasonal fluctuations in environmental parameters (Macho et al. 1996, 2003; Dirks et al. 2002; Skinner & Hopwood 2004); (iii) serial microsampling of vertebrate enamel

These techniques for characterizing seasonality in the past hold great potential, despite the complications and confounding variables inherent in the approaches. Currently, proxies for paleoseasonality in Equatorial Africa are poorly developed and are too scarce in space or time to construct a comprehensive profile of seasonality parameters or patterns during the Late Miocene and Pliocene epochs. What is suggested by existing data sets is varying patterns and intensity of seasonality at various localities through time.

**Climate change and evolution of Equatorial African ecosystems**

If short-term climatic fluctuations result in oscillating seasonality patterns, then what specifically are the evolutionary consequences for mammalian paleocommunities in general and hominins in particular? Mean duration of fossil mammalian species typically ranges from 1 to 3 Ma (Van Valen 1985; Sepkoski 1992), and most species have experienced many orbitally forced climatic oscillations on the order of $10^5$ to $10^7$ years. Various adaptive strategies have been proposed as options for terrestrial taxa faced with environmental instability, including habitat tracking, phenotypic plasticity, developmental plasticity, and behavioral flexibility (generalism). It has been argued that recurrent and rapid climatic oscillations favors speciation, resulting in higher taxonomic diversity and phenotypic disparity (Valentine 1984; Vrba 1992; Moritz et al. 2000). Shifting periodicities can affect the duration of phases during which species’ geographic distributions remain continuously fragmented and organisms must exist beyond vicariance thresholds (outside optimal range), increasing the incidence of speciation and extinction (Vrba 1995). Others have suggested that orbitally forced climatic shifts generally increase gene flow directly by reshuffling gene pools and that any microevolutionary change that
accumulates on a timescale of thousands of years consequently is lost as communities reorganize following climate change (Bennett 1990). Fluctuations select indirectly for vagility (dispersal ability and propensity) and generalism, both of which reduce extinction in the long run and also slow speciation rates (Dynesius & Jansson 2000; Jansson & Dynesius 2002). According to the variability selection hypothesis (Potts 1998), the complex intersection of orbitally forced changes in insolation and Earth-intrinsic feedback mechanisms results in extreme, inconsistent environmental variability selecting for behavioral and morphological mechanisms that enhance adaptive variability. Potts (1998) notes specifically that orbital-scale variations alter landscapes and resources to a far greater extent than do seasonal or annual variations, with the former resulting in overall revision of regional and local hydrology, vegetation, and animal communities rather than simply shifts in temperature and moisture. Evidence from other research suggests that specific taxa appear to respond individually to climate change and that communities are rearranged massively and repeatedly (Graham 1986; Bennett 1990). Strong selective pressures may develop in response to cumulative effects or shifts in mode of dominant oscillations, resulting in differential response of various lineages. Assessing the relative validity of these evolutionary models ultimately hinges on developing a level of temporal and spatial resolution in the faunal record to anchor speciation and extinction events in the context of short-term environment shifts that specifically include seasonality patterns.

**Summary**

Climatic and geological instability have characterized much of Equatorial Africa during the course of hominin evolution over the past 8–7 Ma. Combined with regional and local habitat heterogeneity, environmental flux has resulted in highly dynamic selective forces on early hominins and their communities. An emerging consensus is that although long-term global and regional climatic trends and specific events have influenced hominin evolution, short-term astronomically driven climatic change coupled with intrinsic feedback loops, threshold effects, and local or regional factors may represent a more significant factor in forcing evolutionary change. This climatic flux can be linked to cyclical shifts in the geometry of the Earth’s solar orbit, which alter the amount of solar radiation reaching different latitudes and hemispheres at different times of the year. These changes ultimately affect systems that control Equatorial African climate, such as the intensity and nature of African-Asian
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monsoonal circulation and the seasonal migration of the ITCZ. These regional changes are experienced by ecosystems in tropical and subtropical Africa primarily by dynamic shifts in seasonality patterns, specifically the length, intensity, and duration of wet–dry seasons. Consequently, paleoseasonality in Equatorial Africa during hominin evolution must be assessed at the temporal scale of orbital cycles or even millennial events. Given the intimate connections and significant effect of seasonality patterns on primate foraging, ranging, reproduction, and social strategies, even subtle changes in seasonality patterns could significantly alter selective pressures. Invoking notions of increasing seasonality over timescales of a million years or more, while perhaps true, does not necessarily inform attempts to provide adaptive scenarios for hominin evolutionary innovations, given the occurrence of short-term changes in seasonality of the same or even greater magnitude. Within the framework of climatic flux in Equatorial Africa, manifested to a large extent by oscillations in seasonality, the challenge remains to identify and link specific shifts in early hominin ecological paleocommunities, intraspecific diversity, and biogeographic patterns to specific varying seasonality parameters. A lack of developed paleoseasonality records from low-latitude regions such as Africa currently limits our understanding of specific effects of global climatic variability, including Milankovitch cycling, on precipitation patterns in Equatorial Africa and ultimately its effect on early hominin evolution.

References


