

S. C. Antón

Center for Human
Evolutionary Studies,
Department of Anthropology,
Rutgers University,
New Brunswick, NJ 08901,
U.S.A. E-mail:
scanton@rci.rutgers.edu

W. R. Leonard &
M. L. Robertson

Department of Anthropology,
Northwestern University,
Evanston, IL 60208,
U.S.A. E-mail:
w-leonard1@northwestern.edu


Received 8 March 2002;
revised 24 June 2002;
accepted 15 August 2002

An ecomorphological model of the initial hominid dispersal from Africa

We use new data on the timing and extent of the early Pleistocene dispersal of *Homo erectus* to estimate diffusion coefficients of early *Homo* from Africa. These diffusion coefficients indicate more rapid and efficient dispersals than those calculated for fossil *Macaca* sp., *Theropithecus darti*, and *Mesopithecus pentelicus*. Increases in home range size associated with changes in ecology, hominid body size, and possibly foraging strategy may underlay these differences in dispersal efficiency. Ecological data for extant primates and human foragers indicate a close relationship between body size, home range size, and diet quality. These data predict that evolutionary changes in body size and foraging behavior would have produced a 10-fold increase in the home range size of *H. erectus* compared with that of the australopithecines. These two independent datasets provide a means of quantifying aspects of the dispersal of early *Homo* and suggest that rapid rates of dispersal appear to have been promoted by changes in foraging strategy and body size in *H. erectus* facilitated by changes in ecosystem structure during the Plio-Pleistocene.

© 2002 Elsevier Science Ltd. All rights reserved.

Journal of Human Evolution (2002) 43, 773–785
doi:10.1053/jhev.2002.0602

Available online at <http://www.idealibrary.com> on 

Introduction

Despite similar life history parameters, including reproductive life span and parental investment, the global distribution of *Homo sapiens* contrasts with the restricted ranges of our closest living primate relatives, *Pan*, *Gorilla*, and *Pongo* (Fleagle, 1998). Human hunter-gatherers have home range (HR) sizes that are 15 to 100 times greater than those of chimpanzees (23 hectares in *Pan*, 330–2600 hectares in humans; Leonard & Robertson, 2000). Recent paleontological and geochronological work suggests that the beginning of this geographic dispersal of *Homo* from Africa was in the earliest Pleistocene, coeval with the appearance of the larger bodied/brained hominids in Africa (*H. erectus*, *sensu lato*, 1.7–1.8 Ma; Swisher *et al.*, 1994; Gabunia & Vekua, 1995; Huang *et al.*, 1995 but see Schwartz & Tattersall, 1996; Gabunia *et al.*, 2000, 2001; Larick *et al.*,

2001; Vekua *et al.*, 2002). Yet the origin and cause of this dispersal(s) is not well understood.

Neither secondary r-selection nor technological innovation appear to be primarily responsible for the initial wide dispersal of our genus. In industrialized societies humans have become ‘secondarily r-selected’ by substantially decreasing inter-birth intervals (Wood, 1994). However, reproductive patterns in human hunter-gatherers (Howell, 1979; Blurton-Jones *et al.*, 1992) suggest that this strategy for promoting population growth and dispersal is a relatively recent phenomenon that significantly postdates the initial dispersal of *Homo* from Africa. Likewise, the first hominid dispersal is unlikely to result from a *solely* technological impetus since it now appears to postdate the earliest stone tool technologies by more than half a million years (Semaw *et al.*, 1997; de Heinzelin *et al.*, 1999; Roche *et al.*, 1999) and to predate

the earliest occurrence of the Acheulean tradition (Asfaw *et al.*, 1992) by several hundred thousand years. Thus, at least the gross technological innovations currently visible in the fossil record do not correlate temporally with this dispersal. Other factors that favored the initial dispersal of our genus from Africa must also underlay the current biogeographic differences in our superfamily.

Here we use recent data from Georgia and Indonesia to estimate the rate of dispersal of early *Homo* from Africa and explore the ecological correlates of this dispersal. We first use demographic and reproductive variables to calculate diffusion coefficients (D) for the dispersal of early *Homo* from Africa, comparing these estimates to dispersal rates for other mammalian species (both modern and prehistoric). Next we examine the influence of body size and dietary patterns on home range (HR) size among extant primates to predict changes in HR size during this period of hominid evolution. Both of these independent lines of evidence suggest rapid dispersal rates for early *Homo* and highlight ecological parameters that likely promoted the dispersal. From these analyses we propose a web of factors involved in this original hominid dispersal.

Estimating the diffusion coefficient (D)

Designed to assess the advance of extant (often pest) species into new regions the diffusion coefficient (D) measures the efficiency of invasion based on three variables related as in equation 1 (Drake *et al.*, 1989; Williamson, 1996).

$$D^{1/2} = z \div (t)(2r^{1/2}). \quad \text{Equation (1)}$$

Where z is the square root of area invaded in kilometers, t is the time over which invasion occurred in years, and r is the intrinsic rate of increase of the species. It should be noted

that none of these estimates is based directly on the size or morphology of fossil remains. Although r values of extant mammals do correlate with body size, the r values used here to estimate Ds for fossil taxa are not derived from fossil body sizes but from r values of closely related living primates. Except for the use of first appearance datums (FADs) to estimate t , calculations of D are independent of the fossil record and, in particular, are independent of fossil morphology or size. Thus, the results of this line of evidence of dispersal should also be independent of our second line of evidence which uses postcranial size to estimate home range size.

Values of D for the best-documented dispersals of small, extant mammals are based on observation of the actual events and areas of invasion. These values include those for the California sea otter (*Enhydra lutris*) as it repopulated the coastline subsequent to overhunting, the muskrat (*Ondatra zibethicus*) as it invaded central Europe, and the gray squirrel (*Sciurus carolinensis*) as it invaded and largely outcompeted the red squirrel (*S. vulgaris*) in England. These values, which vary between 0.4 km² and 230 km² per annum, exhibit great geographical variation within species (Williamson, 1996; Table 1), in part due to the goodness of the ecological fit with the new territory and whether the new territory was already occupied by competitive species.

Estimating diffusion coefficients for paleotaxa requires estimates of the area and time of first occupation (z and t) and the intrinsic rate of increase (r). In all examples r values are assumed to be similar to closely related extant taxa. Time of first occupation (t) is based on first appearance datums (FADs) of fossil localities. It should be noted that, because they rely on FADs to estimate time intervals, D values calculated for paleotaxa are inherently minimum values. It is always possible that the

Table 1 D values for extant mammals and calculated D values for fossil taxa

Species	Intrinsic rate of natural increase (<i>r</i>)	Time to occupy (<i>t</i>)	Area occupied ¹ (<i>z</i>)	Diffusion coefficient (D)
Recent dispersals²				
<i>Enhydra lutris</i>	0.06	Various	Various	13.5–54.7
<i>Ondatra zibethicus</i>	0.2–1.4	Various	Various	9.2–231
<i>Sciurus carolinensis</i> —observed	0.82	Various	Various	0.4–18.5 ³
<i>Sciurus carolinensis</i> —calculated	0.82	Various	Various	1.25 ³
Ancient dispersals				
<i>Macaca</i> sp. (Europe to Asia)	0.05	1.5 Ma–10 ka	(a) NA	—
			(b) 2220	0.00001–0.2
			(c) 3135	0.00002–0.5
			(d) 4525	0.000045–1.0
<i>Theropithecus darti</i> (to South Africa)	0.05	0.7 Ma–10 ka	(a) NA	—
			(b) 1555	0.00002–0.1
			(c) 2200	0.00004–0.2
			(d) 3175	0.0001–0.5
<i>Mesopithecus pentelicus</i> (Germany to Greece and Ukraine)	0.02–0.09	2.0 Ma	(a) 1370	0.000001–0.000006
			(b) 905	0.0000006–0.000003
			(c) 1280	0.0000011–0.000005
			(d) 1850	0.0000024–0.000011
<i>Mesopithecus pentelicus</i> (Greece to Iran)	0.02–0.09	800–200 ka	(a) 1740	0.00001–0.0009
			(b) 1020	0.0000045–0.0003
			(c) 1445	0.000009–0.0006
			(d) 2085	0.00002–0.0003
<i>Mesopithecus pentelicus</i> (Greece to Ukraine)	0.02–0.09	100–10 ka	(a) 1115	0.0003–0.15
			(b) 820	0.0001–0.08
			(c) 1160	0.0003–0.16
			(d) 1670	0.0008–0.3
<i>Homo erectus s.l.</i> (to Indonesia)	0.01–0.015	200–10 ka	(a) NA	—
			(b) 3100	0.006–2.4
			(c) 4380	0.01–4.8
			(d) 6324	0.02–9.9
<i>Homo erectus s.l.</i> (to Georgia)	0.01–0.015	100–10 ka	(a) NA	—
			(b) 1885	0.01–0.9
			(c) 2665	0.02–1.8
			(d) NA	—

¹Z values are calculated as the square root of the linear distance between localities, (a) squared, (b) multiplied by a transect 600 km wide, (c) by a transect 1200 km wide, or (d) by a transect 2500 km wide. NA=not applicable, areas not calculated because transect size would include unreasonably large areas (e.g., dispersal into oceans or the Arctic). The most conservative comparisons consider the largest area for dispersal of the nonhuman primates against the smallest area of dispersal for the hominids.

²Data from Williamson (1996).

³Predicted values and observed historical spread are significantly lower than other dispersing mammals, presumably because of ecological interaction between red and grey squirrels.

earliest known fossils do not represent the earliest occupation of that taxon or that the uncertainties inherent in age estimates of paleontological sites either over or underestimate the actual speed of the dispersal. Estimates of the area invaded (*z*) are based on a range of possible areas calculated from

the linear distance between these fossil localities and transects of variable width (600, 1200 and 2500 km, respectively) and by the square of the linear distance between localities, if such a transect does not indicate unreasonable dispersal (e.g., well into the ocean or the Arctic).

Because each of the variables will be imperfectly known, we provide ranges of values for D based on the best available ranges of estimates of z , t and r . Broad differences between these “envelopes” of D values in different taxa should indicate true differences in efficiency of dispersal, although finer scale comparisons, in which groups do not differ greatly, may be swamped by the nature of the time resolution of the fossil record. In each analysis we indicate the effect that changes in each variable would have and the magnitude of the change that would be required to produce D values similar to the other groups. Although D values for paleotaxa are expected to be somewhat smaller than those for similar extant mammals, due to the grosser time resolution possible in the fossil record, D values of paleotaxa should be more comparable to one another. We have attempted to ensure comparability by carefully constructing ranges of t values that encompass the likely temporal variation at each of the sites. Likewise, in comparing D values across taxa it is useful to compare those values that derive from similar t estimates. Because our aim is to test whether D values of *H. erectus* are similar to those of other primates, we make every effort to be conservative in our estimates and comparisons—erring on the side of estimates that will bring the D values closer together rather than those that would distinguish them. That is, within the best available ranges we choose estimates of t , z , and r that minimize D values in *H. erectus* and maximize D values in the other primates (i.e., we made conservative estimates for *H. erectus*).

Paleontological evidence suggests a wave of dispersal of *Macaca* from Europe to Asia (Andrews *et al.*, 1996) with estimated D values between 0.000045 km² per year based on a long chronology and 0.00041 to 1.0 km² per year based on a shorter chronology and r values of modern macaques (Table 1; Sade *et al.*, 1977; Antón *et al.*,

2001). The long chronology is based on dispersal from Spain to India using FADs of 5.3–5.5 Ma for *Macaca* sp. in eastern Spain Mammalian Neogene (MN) 13 of Almenara-M (formerly Casablanca-M; Andrews *et al.*, 1996; Köhler *et al.*, 2000) and 3.5–2.5 Ma for *M. paleindica* in India (Szalay & Delson, 1979). The short chronology is based on two probable macaque molars from the Yushe Basin, China (Delson, 1996) that are of inexact provenience but are probably from the upper Mahui Formation, which would suggest a FAD of 5.5 to 5.0 Ma (Tedford *et al.*, 1991). To allow for the largest possible Ds, we calculated the range of D values using as the longest dispersal time a low estimate from the long chronology of 1.5 Ma (i.e., 3.5 to 5.0 Ma) and as the shortest estimate a geologically invisible 10 ka supported by the potentially negligible age difference between the Chinese and Spanish fossils. Again to allow for the largest possible D values, we estimated a large area ($z=4525$) into which the macaques dispersed based on the area of a rectangle whose side-lengths are defined as the distance between Spain and the other fossil localities and a 2500 km transect. Lower D values are achieved when transect size is limited to 1200 and 600 km. D values for both the short and long chronologies are probably overestimates because dispersal area was calculated on the basis of FADs for the genus rather than restricted to those of a particular species.

To address diffusion values in nonhuman primates at the species level and to consider differences amongst primate groups we calculated D for both a fossil cercopithecine and colobine. We used two relatively widely dispersed primate species: the cercopithecine *Theropithecus darti* and the colobine *Mesopithecus pentelicus*. For the *Theropithecus darti* dispersal between Ethiopia and South Africa in the Pliocene we used an r based on extant macaques (Table 1; Sade *et al.*, 1977) and we calculated t and z based on the

difference between FADs of 3.4 Ma in the Sidi Hakoma member, Hadar, Ethiopia (Eck, 1993) and of about 3.0 Ma in Makapansgat Member 3, South Africa (Delson *et al.*, 1993). Younger South African FADs of 2.7 Ma established by Vrba (1995) for Makapansgat Member 3 suggest a longer t of 0.7 Ma. Alternatively, an older age for Makapansgat Member 3 might suggest near contemporaneity, so we also include a geologically invisible but unlikely t of 10 ka. Based on these values, D is estimated at between 0.00002 and 0.5 km² per year (between 0.00002 and 0.006 km² per year based on the 2.7 and 3.0 Ma ages for Makapansgat, respectively).

For the dispersal of *Mesopithecus pentelicus* between Europe and Western Asia in the Miocene we calculated r based on birth and death data for the colobine *Semnopithecus entellus* (Table 1; Hrdy, 1980) and we used two alternative chronologies, because of differences of opinion regarding the earliest European *M. pentelicus*. The first (long) chronology is based on FADs of a probable *M. pentelicus* from Wissberg, Germany (Delson, 1994; Andrews *et al.*, 1996) in MN 9 (10.6–11.6 Ma; Swisher, 1996) and later FADs of MN11/12 for Pikermi, Greece and Grebeniki-1, Ukraine (ca 8.2–8.3 Ma; Andrews *et al.*, 1996). D is estimated at between 0.0000006–0.000011 km² per annum if the earliest *M. pentelicus* occurs in MN 9. The second estimate is based on a shorter dispersal chronology between Pikermi, Greece (8.2 Ma; Bernor *et al.*, 1996) and the slightly later Grebeniki-1, Ukraine (Andrews *et al.*, 1996). D is estimated between 0.0001 and 0.3 km² per annum depending upon the t used. D values are even smaller (0.0000045–0.0009 km²/year) if calculated using the somewhat longer but later dispersal of *M. pentelicus* into Iran (Table 1).

D values for *H. erectus* are at the low end of the range for dispersing extant mammals and are larger than those of other primates

(Table 1). For the reasons mentioned above, we erred toward estimates of r , t and z that would minimize D values. We used human hunter-gatherer r values (0.01–0.015; Blurton-Jones *et al.*, 1992) that are at the high end of those we calculated for the Gombe chimpanzees ($r=0.006$ to 0.015; calculated from data on birth–death rates reported in Goodall (1986) for Gombe 1968 to 1983 and 1968 to 1978, respectively). The use of these r values is conservative as lower r values would raise D values. Using the Indonesian dispersal, we made conservative estimates of the area invaded based on a band beginning in East Africa, including only coastal India/East Asia (south of the Tibetan plateau), and ending in Java. We varied band width from 600 to 2500 km, as above; however, we consider the 2500 km band width likely to be too large. Finally, we used a range of dispersal times estimated between a geologically unresolvable 10 ka based on the lack of difference between the earliest Javan and East African FADs of approximately 1.8 Ma (Feibel *et al.*, 1989; Swisher *et al.*, 1994; Gabunia *et al.*, 2000) and 200 ka based on the difference between the oldest East African and Sangiran, Java dates (e.g., 1.89 to 1.66 Ma; Swisher *et al.*, 1994). All estimates are based on fossil localities that have yielded taxonomically identifiable hominid remains. No archaeological sites are used in these analyses. D is 0.01 and 4.80 km² per annum for *H. erectus* using the Indonesian occupation times and range and a 1200 km band width. Longer time intervals would lower D values, however, a t of 2 Ma is needed for *H. erectus* D s ($D=0.00008$) to approach most of the nonhuman primate values calculated here. This interval is much longer than even the latest proposed chronology for dispersal in which *H. erectus* arrives in Indonesia slightly after 1.0 Ma (Klein, 1999; Langbroek & Roebroeks, 2000).

Recent discoveries at Dmanisi, Georgia (Gabunia *et al.*, 2000; 2001; Vekua *et al.*,

2002) provide an opportunity to test these D values using data that proponents of a short chronology would find more acceptable (e.g., Roebroeks, 2001). Using these data we calculate alternative estimates of D using only the Georgian hominids as the endpoint of the first dispersal and estimates of the area occupied from East Africa to the Republic of Georgia (Table 1). To be conservative we use only the 600 km and 1200 km transect widths in this analysis. As above, we used a range of dispersal times estimated between a geologically unresolvable 10 ka and 100 ka based on the difference between East African *H. erectus* of approximately 1.8 Ma and Georgian dates of >1.7 Ma (Gabunia *et al.*, 2000). D values are 0.01 to 0.9 km² per annum based on a band width of 600 km and dispersal times of 100 ka and 10 ka, respectively. Larger transects yield larger D values.

H. erectus D values suggest a relatively rapid spread from Africa. The differences between *H. erectus* and extant mammal Ds are likely exaggerated by comparing tropically adapted *H. erectus* with more northerly adapted recent mammals, since the relatively lower secondary productivity at high latitudes results in larger mammalian home ranges than those in the tropics. This difference in HR size should increase the observed dispersal speed of high latitude mammals. Additionally, the much grosser time scale allowed in the examination of paleodispersals is likely to depress estimates of D values relative to modern values.

Potential correlates of this rapid spread in *H. erectus*, based on our knowledge of widely dispersed extant mammals and fossil dispersals, include larger HR sizes (Ehrlich, 1989), a shift in foraging behavior (Ehrlich, 1989; Leonard & Robertson, 2000), and a somewhat slower pattern of dispersal than is seen in (presumably) gregarious fossil carnivores (Antón *et al.*, 2001). Despite the similarity in the pattern of diffusion coefficients to those of fossil carnivores, the data are

insufficient to draw conclusions regarding specific foraging niche for *H. erectus* based on its D values alone. However, several other lines of evidence, including the spatial patterning of sites (Jablonski *et al.*, 2000), community analyses (Turner, 1992), and taphonomy (Blumenshine *et al.*, 1994), also suggest that hominids and carnivores shared similar niches by at least middle and later Pleistocene times.

Estimating home range size

Our second dataset explores potential changes in HR size among early hominid species from an independent perspective. Comparative data on diverse mammalian species show that body size, dietary patterns, and ecosystem structure are important predictors of variation in HR size (McNab, 1963; Milton & May, 1976; Harestad & Bunnell, 1979; Shipman & Walker, 1989). Larger body sizes and higher quality, more carnivorous diets are associated with larger HR sizes (Harestad & Bunnell, 1979; Milton & May, 1976). Additionally, more open habitats with lower levels of primary productivity are also associated with larger HR sizes, even among animals of the same weight and trophic class (Harestad & Bunnell, 1979).

We examined HR size (hectares per individual), body weight (in kg), and diet quality in 47 living nonhuman primate species and 6 tropical human foraging (hunter-gatherer) populations (Table 2). Data on HR size and body weight for the nonhuman primates species were derived from Wrangham *et al.* (1993), Sailer *et al.* (1985) and Milton & May (1976). Data on human hunter-gatherer HR sizes were taken from Lee (1979) for the !Kung, Hill & Hawkes (1983) for the Ache, Blurton-Jones *et al.* (1992) for the Hadza, Yost & Kelley (1983) for the Waorani, and Kelly (1995) for the Guayaki and Mbuti. Body weights for each of the human groups are mid-sex averages based

Table 2 Body weight (kg), home range size (ha) and diet quality of selected primate species

Species	Weight (kg)	HR _i (ha)	Diet quality
Strepsirrhines			
<i>Galago demidovii</i>	0.06	0.80	305.00
<i>Lemur catta</i>	2.30	0.37	166.00
<i>L. fulvus</i>	2.37	0.10	129.00
<i>L. mongoz</i>	1.80	0.28	198.00
<i>Lepilemur mustelinus</i>	0.65	0.24	149.00
<i>Propithecus verreauxi</i>	3.80	1.14	159.00
Ceboidea			
<i>Alouatta palliata</i>	6.88	1.78	146.00
<i>A. seniculus</i>	7.25	0.38	177.50
<i>Ateles belzebuth</i>	5.80	14.00	181.50
<i>Callicebus moloch</i>	0.60	0.15	175.00
<i>C. torquatus</i>	1.10	5.00	208.50
<i>Cebus albifrons</i>	2.60	4.17	295.00
<i>C. apella</i>	2.10	2.50	310.00
<i>C. capucinus</i>	3.10	6.10	215.00
<i>Saguinus geoffroyi</i>	0.55	2.40	246.00
<i>Saimiri oerstedii</i>	0.60	0.76	245.00
<i>S. sciureus</i>	0.66	0.57	323.00
Cercopithecoidea			
<i>Cercocebus albigena</i>	7.90	5.10	226.50
<i>C. galeritus</i>	5.50	1.67	190.30
<i>Cercopithecus aethiops</i>	3.80	1.40	213.50
<i>C. ascanius</i>	2.90	0.47	156.10
<i>C. cephus</i>	2.90	4.00	215.90
<i>C. mitis</i>	6.00	2.80	201.50
<i>Miopithecus talapoin</i>	1.13	4.00	222.30
<i>Colobus badius</i>	8.00	2.50	121.50
<i>C. guereza</i>	8.00	2.25	118.00
<i>C. satanas</i>	9.50	3.85	163.00
<i>Macaca fascicularis</i>	5.00	1.83	200.00
<i>M. nemestrina</i>	8.30	5.00	184.00
<i>M. simca</i>	5.13	3.00	203.00
<i>Nasalis larvatus</i>	15.10	6.50	105.00
<i>Papio anubis</i>	21.40	10.00	207.20
<i>P. hamadryas</i>	13.85	33.33	199.00
<i>P. ursinus</i>	20.60	24.00	189.50
<i>Semnopithecus entellus</i>	17.20	11.86	153.50
<i>Trachypithecus cristatus</i>	6.30	0.63	163.00
<i>Presbytis johnii</i>	8.17	18.00	122.00
<i>P. melalophos</i>	6.60	1.65	163.00
<i>P. obscura</i>	6.50	3.22	152.00
<i>P. senex</i>	5.98	3.00	140.00
<i>Theropithecus gelada</i>	13.60	2.17	159.00
Hominioidea			
<i>Gorilla gorilla</i>	145.00	150.00	114.00
<i>Pan troglodytes</i>	40.70	23.00	178.00
<i>Pongo pygmaeus</i>	36.50	65.00	183.50
<i>Hylobates agilis</i>	5.70	5.29	162.50
<i>H. lar</i>	5.54	11.00	181.00
<i>Symphalangus syndactylus</i>	10.50	10.00	167.00
Humans			
Ache	55.70	714.00	263.00
Guayaki	55.70	387.00	263.00
Hadza	50.00	333.00	260.00
!Kung	43.50	1896.00	255.50
Mbuti	40.70	588.00	252.50
Waorani	55.00	2583.00	255.00

See text for sources.

on data from Leonard & Robertson (1994) and Katzmarzyk & Leonard (1998).

We measured diet quality (DQ) using an index developed by Sailer and colleagues (1985) that is based on the relative contributions of three components to the diet: (1) structural plant parts, (2) reproductive plant parts, and (3) animal material. DQ values range from a minimum of 100 (a diet of all foliage) to a maximum of 350 (a diet entirely of animal foods). For the nonhuman primate species DQs were calculated based on data provided by Sailer *et al.* (1985). Dietary data for the human foraging groups were derived from Lee (1968, 1979) for the !Kung, Hill *et al.* (1984) for the Ache, Hill (1982) for the Mbuti, Blurton-Jones *et al.* (1992) for the Hadza, Yost & Kelley (1983) for the Waorani, and Kelly (1995) for the Guayaki.

Home range size is strongly correlated with body mass, and scales isometrically (Figure 1). Yet despite this strong relationship, there are notable deviations from the regression. Human foragers, for example, have substantially larger HRs than expected from their size alone, whereas colobus (*Colobus* spp.) and howler monkeys (*Alouatta* spp.) have relatively smaller HRs (Leonard & Robertson, 2000). Analysis of the residuals, however, indicates that much of the variation in HR size that is not explained by body weight can be explained by differences in diet (Table 3). Together, weight and DQ explain 75–80% of the variance in HR size. Therefore, this relationship is useful for exploring our evolutionary past since it effectively applies to both human foragers, whose HRs are similar to those predicted for other primates of similar size and dietary habits, and to nonhuman primates.

Assuming that DQ was the same for early *Homo* and *Australopithecus*, differences in body weight alone (based on the mid-sex body weight estimates of McHenry (1994)) suggest that HR sizes of early African *H.*

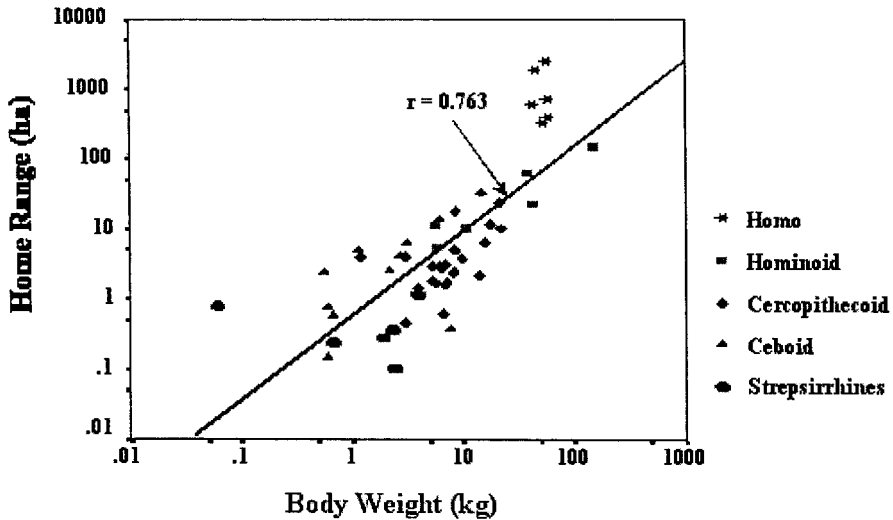


Figure 1. Log-log plot of Home Range Size (ha) vs. Body Weight (kg) in a sample of 47 nonhuman primate species and 6 tropical human foraging groups. Home range size scales isometrically with body weight [$HR=0.61(Wt^{1.21})$]. Human foragers have relatively large HRs for their body size.

Table 3 Multiple regression analysis of the predictors of variation in Log-HR size among extant primates

Independent variable	Regression coefficient (b ± SE)	Beta weight	P-value
Log-weight	1.36 ± 0.11	0.854	<0.001
Diet quality	0.009 ± 0.001	0.446	<0.001
Constant	-2.01 ± 0.29	—	<0.001

$R=0.88$; $R^2=0.77$; $P<0.0001$.

erectus would have been about double those of the australopithecines (Table 4). If there was also a modest shift in DQ between the australopithecines and *H. erectus*, as changes in craniofacial anatomy (Wood, 1995), habitat and resource preferences (Potts, 1988; Harris & Capaldo, 1993), and brain size (Leonard & Robertson, 1992, 1994; Aiello & Wheeler, 1995) imply, then using an average modern ape DQ value (164) for *Australopithecus* and a conservative (minimum) human tropical forager DQ value (252) for *H. erectus* predicts a 10-fold increase in the HR size of *H. erectus*

(~450 ha/indiv) compared with that of australopithecines (~40–50 ha; Table 4). Thus changes in both body size and dietary patterns at the origin of *H. erectus* would have dramatically influenced HR size and dispersal capability. Moreover, other factors not considered in this model, such as changes in habitat productivity associated with the increase in aridity and the spread of grasslands in East Africa, would also have contributed to expanded HR size with early *Homo* (see Leonard & Robertson, 2000).

Discussion

In contrast to the pattern in the rest of the Primate order in which the relatively r-selected monkeys radiate widely in Pliocene to recent times while the more K-selected apes undergo range retraction to occupy even smaller portions of their previous ranges (Fleagle, 1998; Jablonski et al., 2000), the K-selected hominids are able to disperse widely after 1.8 Ma with even greater efficiency than is seen in monkeys. It is not simply their dispersal

Table 4 Estimated body weight and home range size for fossil hominid species

Species	Male wt ¹ (kg)	Female wt ¹ (kg)	Avg wt ¹ (kg)	HR _r -Ape ² (ha)	HR _r -Human ³ (ha)
<i>A. afarensis</i>	44.6	29.1	37.0	40	247
<i>A. africanus</i>	40.8	30.2	35.5	38	234
<i>A. robustus</i>	40.2	31.9	36.1	39	239
<i>A. boisei</i>	48.6	34.0	44.3	51	316
<i>H. habilis</i>	51.6	31.5	41.6	47	290
<i>H. erectus</i>	63.0	52.3	57.7	73	452
<i>H. sapiens</i>	65.0	54.0	59.5	76	471

¹After McHenry (1992, 1994).

²Home range estimates assuming a diet quality equal to the average for modern apes.

³Home range estimates assuming a diet quality at the low end of the range of modern tropical human foragers.

from Africa that is unique, other paleo-primates did so over long time periods, but rather the relative rapidity of that dispersal which contrasts with usual primate patterns. It would certainly be possible over a long period of time for virtually any primate to disperse widely. Thus, discovery of earlier hominids outside of Africa would not necessarily negate the significance of this difference providing that *H. erectus* is still considered to disperse from Africa in the early Pleistocene, as would be predicted to be the case given the close morphological affinities between the Dmanisi and Koobi Fora hominids.

The two separate lines of evidence discussed here provide a means of quantifying and comparing the differences in dispersal of *H. erectus* and other primates. Both suggest that HR expansion and increasing DQ are likely to be critical factors in allowing the rapid, wide dispersal of these K-selected hominids outside their normal life history parameters. The distribution of archaeological sites within Africa also supports the idea that hominid HR was increasing at this time as the complexity of the archeological record, distance from lithic raw material sources, and the distribution of sites in non-primary areas increases at this time (Cachel & Harris, 1995).

Changes in HR and DQ are likely to have arisen from a web of documented ecological changes relating to increasing area of grasslands (Vrba, 1995; Owen-Smith, 1999) and the associated increase in herbivore biomass (Behrensmeier *et al.*, 1997; see below). Other evidence suggests that geographic barriers that exist today, such as the Sahara desert, were absent from Africa in the late Pliocene and early Pleistocene (Prism Project, 1995). Yet animals do not always disperse even given the capabilities to do so (Woodburne & Swisher, 1994) suggesting that an additional catalyst may have been necessary. Although the microprocesses involved in the initial hominid dispersal(s) may never be knowable due to the nature of the fossil record, elements of the African fauna appear in vertebrate assemblages outside Africa at about the same time as hominids (Tchernov, 1992), suggesting that one catalyst for *H. erectus* dispersal may have been the significant faunal interchange occurring at this time between Africa, Europe, and Asia (Kurten, 1968; Tchernov, 1987, 1992; Opdyke, 1995; Vrba, 1995).

Figure 2 presents a flow diagram showing the forces that appear to have promoted greater territorial needs and the potential for dispersal in *H. erectus*. The increasing aridity

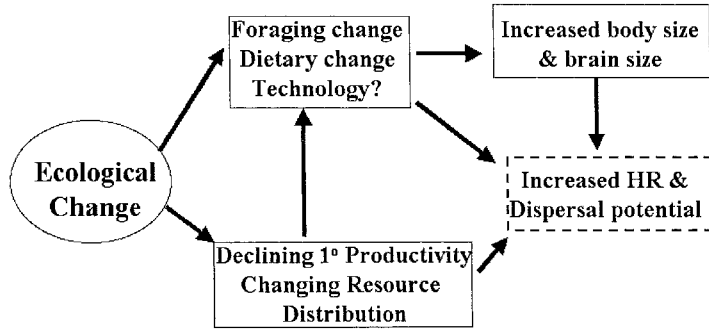


Figure 2. Flow diagram depicting the factors responsible for promoting greater territorial needs (HR sizes) and potential for dispersal in *H. erectus*. The key ultimate driving force is the expansion of grasslands and wooded grasslands in Africa (“Ecological Change”) which appears to have promoted at least three changes that would have directly contributed to larger HR needs in *H. erectus*. These changes include: (1) lower primary productivity, (2) changes in diet and foraging behavior (and possibly technology), and (3) increased body and brain size.

and expansion of African grasslands would have directly or indirectly influenced at least three factors that contribute to greater HR needs: (1) lower primary productivity, (2) changes in diet and foraging behavior (and technology?), and (3) increased body and brain size. We suggest that expansion in body and brain size in early African *H. erectus* may have resulted from even greater nutritional dependence on animal fat and protein than has been suggested to differentiate early *Homo* from *Australopithecus* (Heinzelin *et al.*, 1999; Roche *et al.*, 1999). The relative and absolute elongation of the femur in early African *H. erectus* compared with earlier hominids (Smith, 1993; Ruff & Walker, 1993; Tardieu, 1998), as part of an overall increase in body size in this species, is likely a reflection of this shift in DQ in early African *H. erectus* and possibly of changes in growth patterns (Clegg & Aiello, 1999; Antón, 2002). Additionally if, as previous ecological models of early *Homo* have discussed (e.g., Foley & Lee, 1989; Shipman & Walker, 1989; Cachel & Harris, 1995; Bar-Yosef & Belfer-Cohen, 2000), early African *H. erectus* relied heavily on migrating animals for food in addition to raising DQ this foraging shift would have mitigated other common barriers to dispers-

ing animals such as the difficulty of finding food and water. Such barriers appear to place significant constraints on dispersal among modern primate species, the great apes in particular, who are reliant on patchy, seasonal, and ephemeral resources (Milton, 1980; Jolly, 1985).

Thus expanded HR sizes may have been part of an ecological web of factors that fueled the rapid expansion of *H. erectus* from Africa into other parts of the Old World. Ecological changes provide increasing numbers of niches in grasslands and wooded grasslands for terrestrial herbivores which results in a marked increase in secondary productivity (approximately 2.5–1.8 Ma; Behrensmeyer *et al.*, 1997). Hominids of slightly larger body and brain size take advantage of this new resource, either by hunting or scavenging, and in so doing differentially increase their own reproductive success (Leonard & Robertson, 1997). Finally, changes in foraging strategy, body size, and ecosystem structure lead to increases in HR size thus enhancing dispersal capability of early African *H. erectus* over that of earlier hominids. Likewise, the dispersing herbivores provide both a dietary resource and a dispersing impetus.

Acknowledgements

Portions of this work were funded by the Ford Foundation and University of Florida Foundation. The final version benefited from discussions with S. Boinski, E. Delson, J. W. K. Harris, N. Jablonski, and C. C. Swisher III, as well as from the comments of three anonymous reviewers and those of the editor, T. Harrison.

References

- Aiello, L. & Wheeler, P. (1995). The expensive tissue hypothesis: the brain and digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199–221.
- Andrews, P., Harrison, T., Delson, E., Bernor, R. L. & Martin, L. (1996). Distribution and biochronology of European and Southwest Asian Miocene catarrhines. In (R. L. Bernor, V. Fahlbusch & H.-W. Mittman, Eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*, pp. 168–207. New York: Columbia University Press.
- Antón, S. C. (2002). Cranial growth in *Homo erectus*. In (N. Minugh-Purvis & K. McNamara, Eds) *Human Evolution Through Developmental Change*, pp. 349–380. Baltimore: Johns Hopkins University Press.
- Antón, S. C., Aziz, F. & Zaim, Y. (2001). Dispersal and migration in Plio-Pleistocene *Homo*. In (P. V. Tobias, M. A. Raath, J. Moggi-Cecchi & G. A. Doyle, Eds) *Humanity from African Naissance to Coming Millennia—Colloquia in Human Biology and Palaeoanthropology*, pp. 97–108. Florence: Florence University Press.
- Asfaw, B., Beyene, Y., Suwa, G., Walter, R., White, T., WoldeGabriel, G. & Yemane, T. (1992). The earliest Acheulean from Konso-Gardula. *Nature* **360**, 732–735.
- Bar-Yosef, O. & Belfer-Cohen, A. (2000). Early human dispersals: the unexplored constraint of African diseases. In (D. Lordkipanidze, O. Bar-Yosef & M. Otte, Eds) *Early Humans at the Gates of Europe*, pp. 79–86. Liège, Belgium: Etudes et Recherches Archéologiques de l'Université de Liège 92.
- Behrensmeyer, K., Todd, N. E., Potts, R. & McBrinn, G. E. (1997). Late Pliocene faunal turnover in the Turkana basin, Kenya and Ethiopia. *Science* **278**, 1589–1594.
- Bernor, R. L., Solounias, N., Swisher, C. C. III & Van Couvering, J. A. (1996). The correlation of three classical “Pikermian” Mammal faunas—Maragheh, Samos, and Pikermi—with the European MN Unit system. In (R. L. Bernor, V. Fahlbusch & H.-W. Mittman, Eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*, pp. 137–154. New York: Columbia University Press.
- Blurton-Jones, N. G., Smith, L. C., O’Connell, J. F., Hawkes, K. & Kamuzora, C. L. (1992). Demography of the Hadza, an increasing and high density population of savanna foragers. *Am. J. phys. Anthrop.* **89**, 159–181.
- Blumenschine, R. J., Cavallo, J. A. & Capaldo, S. D. (1994). Competition for carcasses and early hominid behavioral ecology: A case study and conceptual framework. *J. hum. Evol.* **27**, 197–213.
- Cachel, S. & Harris, J. W. K. (1995). Ranging patterns, land-use and subsistence in *Homo erectus* from the perspective of Evolutionary Ecology. In (J. R. F. Bower & S. Sartono, Eds), *Evolution and Ecology of Homo erectus*, pp. 51–66. Leiden: Pithecanthropus Centennial Foundation.
- Clegg, M. & Aiello, L. (1999). A comparison of the Nariokotome *Homo erectus* with juveniles from a modern human population. *Am. J. phys. Anthrop.* **110**, 81–94.
- Delson, E. (1994). Evolutionary history of the colobine monkeys in palaeoenvironmental perspective. In (G. Davies & J. F. Oates, Eds) *Colobine Monkeys: Their Ecology, Behaviour and Evolution*, pp. 11–43. Cambridge: Cambridge University Press.
- Delson, E. (1996). The oldest monkeys in Asia. In (O. Takenaka, Ed.) *Abstracts, International Symposium: Evolution of Asian Primates*, p. 40. Inuyama, Japan: Primate Research Institute.
- Delson, E., Eck, G. G., Leakey, M. G. & Jablonski, N. G. (1993). Appendix I. A Partial catalogue of fossil remains of *Theropithecus*. In (N. G. Jablonski, Ed) *Theropithecus: The Rise and Fall of a Primate Genus*, pp. 499–531. Cambridge: Cambridge University Press.
- Drake, J. A., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M. & Williamson, M. Eds. (1989). *Biological Invasions: A Global Perspective*. New York: John Wiley.
- Eck, G. G. (1993). *Theropithecus darti* from the Hadar Formation, Ethiopia. In (N. G. Jablonski, Ed.) *Theropithecus: The Rise and Fall of a Primate Genus*, pp. 15–84. Cambridge: Cambridge University Press.
- Ehrlich, P. R. (1989). Attributes of invaders and the invading process: vertebrates. In (J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson, Eds) *Biological Invasions: A Global Perspective*, pp. 315–328. New York: John Wiley.
- Feibel, C. S., Brown, F. H. & 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.
- Fleagle, J. G. (1998). *Primate Adaptation and Evolution*, 2nd Edn. San Diego: Academic Press.
- Foley, R. & Lee, P. (1989). Finite social space, evolutionary pathways, and reconstructing hominid behavior. *Science* **243**, 901–906.
- Gabunia, L. & Vekua, A. (1995). A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. *Nature* **373**, 509–512.
- Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C. C., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Antón, S.C., Bosinski, G.,

- Joris, O., de Lumley, M.-A., Majsuradze, G. & Mouskhelishvili, A. (2000). Earliest Pleistocene cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. *Science* **288**, 1019–1025.
- Gabunia, L., Antón, S. C., Lordkipanidze, D., Vekua, A., Swisher, C. C. III & Justus, A. (2001). Dmanisi and dispersal. *Evol. Anthropol.* **10**, 158–170.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: Harvard University Press.
- Harestad, A. S. & Bunnell, F. L. (1979). Home range and body weight: a re-evaluation. *Ecology* **60**, 389–402.
- Harris, J. W. K. & Capaldo S. (1993). The earliest stone tools: their implications for an understanding of the activities and behavior of late Pliocene hominids. In (A. Berthelet & J. Chavaillon, Eds) *The Use of Tools by Human and Nonhuman Primates*, pp. 196–220. Oxford: Oxford Science Publications.
- de Heinzelin, J., Clark, J. D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y. & Vrba, E. (1999). Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* **284**, 625–629.
- Hill, K. (1982). Hunting and human evolution. *J. hum. Evol.* **11**, 521–544.
- Hill, K. & Hawkes, K. (1983). Neotropical hunting among the Ache of Paraguay. In (R. B. Hames & W. T. Vickers, Eds) *Adaptive Responses of Native Amazonians*, pp. 139–188. New York: Academic Press.
- Hill, K., Hawkes, K., Hurtado, M. & Kaplan, H. (1984). Seasonal variance in the diet of Ache hunter-gatherers in Eastern Paraguay. *Hum. Ecol.* **12**, 101–135.
- Howell, N. (1979). *Demography of the Dobe !Kung*. New York: Academic Press.
- Hrdy, S. B. (1980). *The Langurs of Abu: Female and Male Strategies of Reproduction*. Cambridge, MA: Harvard University Press.
- Huang, W., Ciochon, R., Yumin, G., Larick, R., Qiren, F., Schwarcz, H., Yonge, C., de Vos, J. & Rink, W. (1995). Early *Homo* and associated artefacts from Asia. *Nature* **378**, 275–278.
- Jablonski, N. G., Whitfort, M. J., Roberts-Smith, N. & Qinqi, X. (2000). The influence of life history and diet on the distribution of catarrhine primates during the Pleistocene in eastern Asia. *J. hum. Evol.* **39**, 131–158.
- Jolly, A. (1985). *The Evolution of Primate Behavior* 2nd Edn. New York: MacMillan.
- Katzmarzyk, P. T. & Leonard, W. R. (1998). Climatic influences on body size and proportions: ecological adaptations and secular trends. *Am. J. phys. Anthropol.* **106**, 483–503.
- Kelly, R. L. (1995). *The Foraging Spectrum*. Washington: Smithsonian.
- Klein, R. (1999). *The Human Career: Human Biological and Cultural Origins*, 2nd Edn. Chicago: University of Chicago Press.
- Köhler, M., Moyà-Solà, S. & Alba, D. M. (2000). *Macaca* (Primates, Cercopithecidae) from the Late Miocene of Spain. *J. hum. Evol.* **38**, 447–452.
- Kurten, B. (1968). *Pleistocene Mammals of Europe*. Chicago: Aldine.
- Langbroek, M. & Roebroeks, W. (2000). Extra-terrestrial evidence on the age of the hominids from Java. *J. hum. Evol.* **38**, 595–600.
- Larick, R., Ciochon, R. L., Zaim, Y., Sudijono, Suminto, Rizal, Y., Aziz, F., Reagan, M. & Heizler, M. (2001). Early Pleistocene $^{40}\text{Ar}/^{39}\text{Ar}$ ages for Bapang Formation hominins, Central Java, Indonesia. *Proc. natl. Acad. Sci.* **98**, 4866–4871.
- Lee, R. B. (1968). What hunters do for a living, or how to make out on scarce resources. In (R. B. Lee & I. Devore, Eds) *Man the Hunter*, pp. 30–48. Chicago: Aldine.
- Lee, R. B. (1979). *The !Kung San: Men, Women and Work in a Foraging Society*. Cambridge: Cambridge University Press.
- Leonard, W. R. & Robertson, M. L. (1992). Nutritional requirements and human evolution: a bioenergetics model. *Am. J. hum. Biol.* **4**, 179–195.
- Leonard, W. R. & Robertson, M. L. (1994). Evolutionary perspectives on human nutrition: the influence of brain and body size on diet and metabolism. *Am. J. hum. Biol.* **6**, 77–88.
- Leonard, W. R. & Robertson, M. L. (1997). Comparative primate energetics and hominid evolution. *Am. J. phys. Anthropol.* **102**, 265–281.
- Leonard, W. R. & Robertson, M. L. (2000). Ecological correlates of home range variation in primates: Implications for hominid evolution. In (S. Boinski & P. Garber, Eds) *On the Move: How and Why Animals Travel in Groups*, pp. 628–648. Chicago: The University of Chicago Press.
- McHenry, H. M. (1992). Body size and proportions in early hominids. *Am. J. phys. Anthropol.* **87**, 407–431.
- McHenry, H. M. (1994). Behavioral ecological implications of early hominid body size. *J. hum. Evol.* **27**, 77–87.
- McNab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.* **97**, 133–140.
- Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*. New York: Columbia University Press.
- Milton, K. & May, M. L. (1976). Body weight, diet and home range in primates. *Nature* **259**, 459–462.
- Owen-Smith, N. (1999). Ecological links between African savanna environments, climate change and early hominid evolution. In (T. G. Bromage & F. Schrenk, Eds) *African Biogeography, Climate Change, and Human Evolution*, pp. 138–149. New York: Oxford University Press.
- Opdyke, N. D. (1995). Mammalian migration and climate over the last seven million years. In (E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burkle, Eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 109–114. New Haven: Yale University Press.
- Potts, R. (1988). *Early Hominid Activities at Olduvai*. New York: Aldine de Gruyter.
- PRISM Project Members (1995). Middle Pliocene paleoenvironments of the Northern hemisphere. In (E. S. Vrba, G. H. Denton, T. C. Partridge & L. H.

- Burkle, Eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 197–212. New Haven: Yale University Press.
- Roche, H., Delagnes, A., Brugal, J. P., Feibel, C., Kibunjia, M., Mourre, V. & Texier, J.-P. (1999). Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. *Nature* **399**, 57–60.
- Roebroeks, W. (2001). Hominid behavior and the earliest occupation of Europe: An exploration. *J. hum. Evol.* **41**, 437–461.
- Ruff, C. & Walker, A. (1993). Body size and body shape. In (A. Walker & R. Leakey, Eds) *The Nariokotome Homo erectus skeleton*. Cambridge, MA: Harvard University Press.
- Sade, D. S., Schneider, J. M., Figueroa, A., Kaplan, J. R., Chepko-Sade, B. F., Cushing, K., Cushing, P., Dunaif, J., Morse, T., Rhodes, D. & Stewart, M. (1977). Population dynamics in relation to social structure on Cayo Santiago. *Yearb. phys. Anthropol.* **20**, 253–262.
- Sailer, L. D., Gaulin, S. J. C., Boster, J. S. & Kurland, J. A. (1985). Measuring the relationship between dietary quality and body size in primates. *Primates* **26**, 14–27.
- Schwartz, J. H. & Tattersall, I. (1996). Whose teeth? *Nature* **381**, 201–202.
- Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N. & Mowbray, K. (1997). 2.5 million year old stone tools from Gona, Ethiopia. *Nature* **385**, 333–336.
- Shipman, P. & Walker, A. (1989). The costs of becoming a predator. *J. hum. Evol.* **18**, 373–392.
- Smith, B. H. (1993). Physiological age. In (A. Walker & R. Leakey, Eds) *The Nariokotome Homo erectus skeleton*. Cambridge, MA: Harvard University Press.
- Swisher, C. C. III. (1996). New $^{40}\text{Ar}/^{39}\text{Ar}$ dates and their contribution toward a revised chronology for the late Miocene non marine of Europe and West Asia. In (R. L. Bernor, V. Fahlbusch & H.-W. Mittman, Eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*, pp. 64–77. New York: Columbia University Press.
- Swisher, C. C. III, Curtis, G. H., Jacob, T., Getty, A. G., Suprijo, A. & Widiasmoro. (1994). Age of the earliest known hominids in Java, Indonesia. *Science* **263**, 1118–1121.
- Szalay, F. & Delson, E. (1979). *Evolutionary History of the Primates*. New York: Academic Press.
- Tardieu, C. (1998). Short adolescence in early hominids: infantile and adolescent growth of the human femur. *Am. J. phys. Anthropol.* **107**, 163–178.
- Tchernov, E. (1987). The age of the 'Ubeidiya Formation, an early Pleistocene hominid site in the Jordan Valley, Israel. *Israel J. Earth Sci.* **36**, 3–30.
- Tchernov, E. (1992). Biochronology, paleoecology, and dispersal events of hominids in the southern Levant. In (T. Akazawa, K. Aoki & T. Kimura, Eds) *The Evolution and Dispersal of Modern Humans in Asia*, pp. 149–188. Tokyo: Hokusan-Shen.
- Tedford, R. H., Flynn, L., Zhanxiang, Q., Opdyke, N. D. & Downs, W. R. (1991). Yushe Basin, China; paleomagnetically calibrated mammalian biostratigraphic standard for the late Neogene of eastern Asia. *J. Vert. Paleontol.* **11**, 519–526.
- Turner, A. (1992). Large carnivores and earliest European hominids: changing determinants of resource availability during the lower and middle Pleistocene. *J. hum. Evol.* **22**, 109–126.
- Vekua, A., Lordkipanidze, D., Rightmire, G. P., Agusti, J., Ferring, R., Majsuradze, G., Mouskhelishvili, A., Nioradze, M., Ponce de Leon, M., Tappen, M., Tvalchrelidze, M. & Zollikofer, C. (2002). A new skull of early *Homo* from Dmanisi Georgia. *Science* **297**, 85–89.
- Vrba, E. S. (1995). The fossil record of African antelopes relative to human evolution. In (E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burkle, Eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 385–424. New Haven: Yale University Press.
- Williamson, M. (1996). *Biological Invasions*. New York: Chapman Hall.
- Wood, B. A. (1995). Evolution of early hominin masticatory system: mechanisms, events and triggers. In (E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burkle, Eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 438–444. New Haven: Yale University Press.
- Wood, J. W. (1994). *Dynamics of Human Reproduction: Biology, Biometry and Reproduction*. New York: Aldine de Gruyter.
- Woodburne, M. O. & Swisher, C. C. III. (1994). Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate and vicariance. In (W. A. Berggren, D. V. Kent, M.-P. Aubry & J. Hardenbol, Eds) *Geochronology, Time Scales and Global Stratigraphic Correlations*, pp. 335–364. Society of Economic Paleontologists and Mineralogists, Special Publication, 54.
- Wrangham, R. W.; Giltsman, J. & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: Population density and day range as assays of exploitation competition. *Behav. Ecol. Sociobiol.* **32**, 199–210.
- Yost, J. A. & Kelley, P. M. (1983). Shotguns, blowguns and spears: The analysis of technological efficiency. In (R. B. Hames & W. T. Vickers, Eds) *Adaptive Responses of Native Amazonians*, pp. 189–224. New York: Academic Press.