Hominid Brain Evolution

Testing Climatic, Ecological, and Social Competition Models

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Abstract Hypotheses regarding the selective pressures driving the threefold increase in the size of the hominid brain since *Homo habilis* include climatic conditions, ecological demands, and social competition. We provide a multivariate analysis that enables the simultaneous assessment of variables representing each of these potential selective forces. Data were collated for latitude, prevalence of harmful parasites, mean annual temperature, and variation in annual temperature for the location of 175 hominid crania dating from 1.9 million to 10 thousand years ago. We also included a proxy for population density and two indexes of paleoclimatic variability for the time at which each cranium was discovered. Results revealed independent contributions of population density, variation in paleoclimate, and temperature variation to the prediction of change in hominid cranial capacity (CC). Although the effects of paleoclimatic variability and temperature variation provide support for climatic hypotheses, the proxy for population density predicted more unique variance in CC than all other variables. The pattern suggests multiple pressures drove hominid brain evolution and that the core selective force was social competition.

The human brain is three times larger than that of our australopithecine ancestors, in terms of absolute size (Holloway et al. 2004) and in terms of brain size scaled to body size (EQ, Jerison 1973; McHenry 1994). The australopithecines (e.g., *Australopithecus afarensis*, *A. africanus*) had modestly larger brain volumes and

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EQ values than living chimpanzees (*Pan troglodytes*) and presumably larger volumes and EQ values than the ancestor common to australopithecines, chimpanzees, and humans (McHenry 1994; Tobias 1987). Further expansion and change in brain organization are evident with the emergence of *Homo habilis* (Falk 1983; Holloway et al. 2004; Holloway and de la Coste-Lareymondie 1982; Tobias 1987), including modest expansion of the frontal and parietal lobes and an increase in number of gyri and thus more neocortical surface area. Further increases in brain volume and organization are evident with the emergence of *H. erectus* and continuing to modern humans (McHenry 1994; Ruff et al. 1997; Wood and Collard 1999). The pattern for absolute brain volume and EQ is clear, but the selection pressures that drove these dramatic changes are debated.

Each of the three classes of competing hypotheses—climatic, ecological, and social—highlights the adaptive advantages of the ability to anticipate and mentally generate strategies to cope with variation and change (for review, see Geary 2005). Climatic variation can result from long-term trends that affect populations that do not migrate (Potts 1998; Vrba 1974), and from seasonal variation for hominid populations that migrated away from central Africa. Ash and Gallup (2007) analyzed the relation between paleoclimate—based on sea-surface temperature and oxygen isotope records—and change in brain volume and EQ since the emergence of *H. habilis*. Brain volume and EQ were strongly correlated with a measure of seasonal temperature variation. Temperatures are cooler and more variable as latitude moves north or south of the equator, and brain volume and EQ were significantly correlated with distance from the equator. Kanazawa (2008) found a similar relation using mean twentieth-century annual temperature, latitude, and longitude as single-variable predictors of general intelligence (IQ), finding small to moderate relationships between these variables and IQ.

The foci of ecological models are on the selective advantages of hunting and other adaptations (e.g., tool use) that enable efficient extraction of biological resources (Kaplan et al. 2000). The basic idea is supported by findings that species with complex foraging or predatory demands have larger brain volumes and higher EQ values than related species with less complex foraging or predatory demands (e.g., Barton 1996). Changes in tooth morphology and tool sophistication with the emergence of australopithecines and in later hominids are also consistent with coevolutionary change in hunting efficiency, diet, and brain volume and EQ (Aiello and Wheeler 1995; Foley and Lahr 1997; Jolly 1970).

Alexander (1989) and Holloway (1967, 1975) argued that our ancestors reached a point at which social competition became the primary selective pressure driving hominid brain evolution, now known as the social brain hypothesis (e.g., Brothers 1990; Dunbar 2003; Humphrey 1976). Alexander's key idea was that hominids evolved adaptations that enabled increasingly efficient use (e.g., hunting, cooking) of biological resources and increasing control of physical ecologies (e.g., building shelters). The result was a shift from primarily ecological selective pressures to primarily social ones. The shift follows from reductions in mortality following increasingly efficient use of ecological resources and a corresponding increase in population size (Hill et al. 2001). Expanding populations can result in rapidly decreasing ecological resources per capita, as originally argued by Malthus (1798), which in turn create the potential for runaway within-species competition

(Alexander 1989; Flinn et al. 2005; Geary 2005; Holloway 1975)—specifically, advantages to social, cognitive, and brain adaptations that enable individuals to function in large cooperative groups that in turn compete against other groups for ecological control and control of social dynamics.

Alexander's (1989) hypothesis integrates ecological models with broad support for social competition and cooperation as core selective forces contributing to hominid brain and cognitive evolution (e.g., Brothers 1990; Dunbar 1998, 2003; Holloway 1967; Humphrey 1976). Heightened social competition and diminishing ecological resources are also predicted to result in increased migration from central Africa, as happened with *H. erectus*. Migration would result in ecological novelty (e.g., new prey species) and habitation of regions with colder and more variable climates (Kanazawa 2008). In cold climates, where ecological resources are scarcer and their availability is less predictable, there is added potential for within-species competition over ecological control. There are also fewer parasites in colder environments (Low 1990), which could result in fewer demands on the metabolically expensive immune system (Matarese and La Cava 2004). As with dietary change and the gut evolution that released energy for operation of the metabolically expensive brain (Aiello and Wheeler 1995), reduction in the metabolic demands of the immune system may have released a significant constraint on brain evolution. We provide the first, to our knowledge, test of this novel hypothesis.

The climatic, ecological, and social models of hominid brain evolution are clearly not mutually exclusive, but none of the associated studies has simultaneously assessed variables from each class of selective pressure as potential predictors of evolutionary change in hominid cranial capacity (CC). For 175 hominid crania, data were collated on CC, fossil age, a proxy for population density, and latitude, as well as parasite prevalence, temperature, and temperature variability of the location where each cranium was discovered; the latter variables were included because they were central to Kanazawa's (2008) findings and conclusion. We also included Ash and Gallup's (2007) global measures of paleoclimatic variation during the time range represented by these hominids. Temperature and temperature variability are common indicators of climatic pressures (Ash and Gallup 2007; Kanazawa 2008), and parasites represent one key ecological pressure (Low 1990). We evaluated social competition pressures using a proxy for population density—specifically, the number of hominids discovered outside a 30° radius from Al Mashriq, Ethiopia, the site where the first hominid cranium in the Holloway et al. (2004) sample was discovered. If climatic and ecological pressures were the primary source of hominid brain evolution, then latitude or the paleoclimate, temperature, and parasite variables should be the strongest predictor of variation in CC. If run-away within-species social competition was the primary source, then CC should increase most reliably with population density.

Methods

Cranial Capacity, Age, and Paleoclimatic Variables

Data on CC (cm^3) and age were provided for 109 and 44 hominid fossils, respectively, by Gallup (from Ash and Gallup 2007) and Ruff (from Ruff et al. 1997). Data for 22

additional fossils were obtained from Holloway et al. (2004). The fossils range in age from 10,000 to 1.9 million years ago (mya). The data are available online at http://dx. doi.org/10.1007/s12100-008-9054-0.

Gallup also provided data on the oxygen isotope record—the ratio of heavy (^{18}O) to light (^{16}O) oxygen isotopes, δ^{18}O—and sea-surface temperature (SST). The δ^{18}O measure is obtained based on oxygen isotopes contained in calcium carbonate formed from the shells of microorganisms such as plankton and can be extracted from ocean-floor sediment (Shackleton et al. 1990). The ratio provides a proxy of paleoclimate; ^{18}O/^{16}O varies with temperature because these heavier and lighter isotopes, respectively, condense and evaporate at different rates contingent on local temperatures. Global cooling results in the trapping of higher concentrations of ^{18}O at lower latitudes and therefore the ratio can be used, with caution (Noone and Simmonds 2002), to estimate relative global temperature. The SST variable is also derived from marine sediments and tracks trends in global cooling during the time frame we are assessing (see Marlow et al. 2000). To be consistent with previous studies, we followed Ash and Gallup's methodology for measuring variation in paleoclimate. The standard deviations of the δ^{18}O and SST measures for the 200,000 years before the time for which each cranium was dated was used to represent the potential selective effects of variation in paleoclimate.

Latitude

The latitude for the locations of the 109 Ash and Gallup (2007) fossils were provided by Gallup and latitude estimates for the Ruff et al. (1997) and Holloway et al. (2004) fossils were acquired from an electronic map (Satellite Signals 2007).

Parasites

For the ten regions in which fossil crania were discovered, data on the presence or absence of parasites that are potentially harmful to humans were obtained from Beaver, Jung, and Cupp (1984) and following Low (1990): leishmaniasis, trypanosomes, malaria, schistosoma, filariae, and spirochetes. Data for leprosy were obtained from Colorado State University, Leprosy Research Support (2005). The regions were south Africa (six crania), central Africa (32), northern Africa (5), Egypt (1), southern Europe (37), northern Europe (23), the Middle East (15), central Asia (1), India (1), China (16), Japan (3), and Indonesia (13). Parasite prevalence was the total number of these parasites present in the region.

Annual Temperature and Variability

Kanazawa (2008) provided mean annual temperature data over the twentieth century for locations near where each fossil cranium was found. For each location, mean monthly high and low temperature estimates were obtained from BBC Weather (http://www.bbc.co.uk/weather/world/). Temperature variability was the difference between the highest mean monthly high and the lowest mean monthly low. Although these values do not of course provide a direct measure of temperatures at the time our hominids were living, they do capture the important relation between latitude

and temperature and temperature variation (see Results). Use of these variables is also necessary to place previous findings in this area into the context of our multivariate assessment.

Population Density

We assume a close relationship between population density and migration patterns— this is apparent in the fossil record (see Results)—and thus created a population density proxy using the number of individuals living in surrounding areas during the hominid's ancestral history. The population density score for cranium j is represented as the number of crania dated from the same date or before j, outside a radius of 30° (in any direction) of Al Mashriq, Ethiopia.

The equation for population density for cranium j, dated from time T, where $C_q =$ all crania discovered outside the 30° radius at or before time q, is

$$j = \sum_{q=T}^{q=1.9} Cq$$

Hominids with higher scores likely spent more of their ancestral histories around larger hominid populations than did hominids with lower scores.

Data Analysis

Analyses were performed and graphics were created using R (Ihaka and Gentleman 1996). A Bonferroni correction was used ($\alpha=0.05$/number of predictors) for the multivariate regressions, to adjust for the number of statistical tests.

Results

Correlations among Cranial Capacity and Predictor Variables

Table 1 shows that each of the predictors correlates significantly with CC (p values<0.001); the magnitude of the correlation between latitude and CC in our larger sample ($r=0.61$) is similar to that found by Ash and Gallup (2007, $r=0.73$). Because each predictor correlates significantly with all other predictors, the correlations in and of themselves provide neither evidence for the unique contribution of any single predictor to the evolution of hominid CC nor evidence for the size of the relative contribution of predictors if multiple pressures were involved.

Homogeneity of Variance

Latitude and age are significantly correlated ($r=-0.55$, Table 1). However, a regression predicting the latitudes inhabited by hominids from fossil ages generates a heteroskedastic distribution of error; the absolute deviation from predicted values increases with increases in the predictor variable, producing a fan-shaped distribution, as evident in the first panel of Fig. 1. A Brown-Forsythe test, which

Table 1 Correlations among cranial capacity and predictors[a]

	CC	Age	Population Density	Latitude	Mean Temperature	Temperature Variation	Parasite	δ^{18}O
CC								
Age	−0.85							
Pop Density	0.79	−0.80						
Latitude	0.61	−0.55	0.60					
Mean Temp	−0.41	0.41	−0.51	−0.86				
Temp Variation	0.30	−0.31	0.34	0.61	−0.77			
Parasite	−0.47	0.44	−0.52	−0.85	0.69	−0.35		
δ^{18}O	0.71	−0.92	0.61	0.44	−0.32	0.26	−0.34	
SST[b]	0.55	−0.76	0.66	0.32	−0.32	0.38	−0.17	0.72

[a] All correlations are significant at $\alpha=0.001$, except for the correlation between SST and parasite.
[b] Correlations in this row are based on the 97 observations with SST values

CC = cranial capacity; Age = age of fossil; Population density estimated at time cranium was discovered; Latitude at which the fossil was discovered; Mean annual temperature for the location at which the fossil was discovered; Temperature variation = the difference between the highest mean monthly high and the lowest mean monthly low at this location; Parasite = the number of parasites (see text) at this location; δ^{18}O = SD of the oxygen isotope record for the 200,000 years before the fossil was dated; SST = SD of the sea surface temperature record for the 200,000 years before the fossil was dated

compares the error variance between the observations that fall in the first half of the predictor's range with those that fall in the second half, confirms this ($t_{168}=5.41$, $p<0.001$, one-tailed). The data indicate that some hominid individuals remained close to the equator, while others migrated north and south over time.

If climatic and ecological demands associated with living at higher latitudes were the primary selection pressures for larger hominid brain size, then a similar residual distribution should be found when CC is predicted from age. Based on this hypothesis, populations that stayed near the equator should not have evolved larger brains. However, the data do not support this hypothesis; there is no convincing
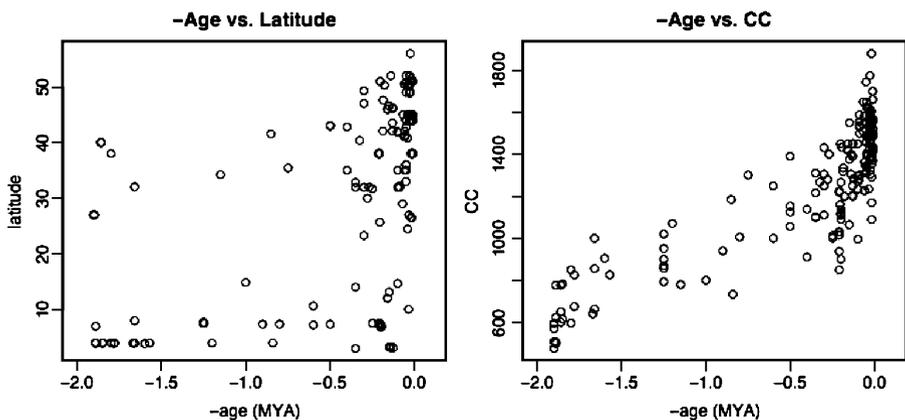

Fig. 1 Scatter plots of age (x-axis) by latitude (y-axis, deviation from equator) and age by cranial capacity (CC, y-axis)

evidence for heteroskedastic distribution of error in this model (Brown-Forsythe test: $t_{168} = 1.17$, $p > 0.05$, one-tailed); see second panel in Fig. 1.

Multivariate Prediction of Change in Cranial Capacity

The predictor variables were centered ($M = 0$) and standardized (SD=1) to allow for estimates of interactions and quadratic components orthogonal to the original variables. Therefore, the unstandardized regression (b) weights represent increase in cm^3 in CC per standard deviation increase in the predictor. Linear and quadratic components were assessed for each predictor. Our goal was to settle on a multivariate, yet parsimonious model of evolution of cranial capacity.

Because age and population density are so closely related, including both in our final model would be statistically redundant. A four-predictor regression model with age, population density, and their quadratic components was specified to determine the most useful of these variables in predicting CC. The results revealed that population density and its quadratic component contribute unique information about CC above and beyond age (t_{169} [linear]=3.92, $p < 0.001$; t_{169} [quadratic]=-2.72, $p < 0.01$; Bonferroni adjusted alpha for four predictors=0.0125), and that age does not contribute unique information above and beyond population density ($t < 1$ in both cases). The full model including the age and population density variables does not contribute unique information above and beyond a reduced model including only the population density variables ($F_{2,170} = 2.32$, $p > 0.10$). The linear and quadratic components of population density were thus retained for later analyses.

Because latitude, parasite load, temperature variation, and mean temperature are so closely related, not all can be included in our final model. Of these variables, latitude is the theoretically least specified—that is, it cannot be a selective pressure in and of itself but rather is a proxy for climatic and ecological variables that change with latitude. Parasite load, temperature variation, and mean temperature are better specified in that they can be selective pressures in and of themselves and they covary with latitude. A regression confirmed that each of these variables is associated with unique variance in CC, and together are associated with 87% of the variance in latitude. These variables do not cause latitude but change significantly with changes in latitude and are thus potential mechanisms underlying the relation between latitude and CC. In a four-predictor regression model (with the predictors being parasite load, temperature variation and its quadratic component, and mean temperature), parasite load ($t_{168} = -3.98$, $p < 0.001$) and the quadratic component of temperature variation ($t_{168} = -4.67$, $p < 0.001$) are associated with significant unique variance in CC. A full model including all four variables does not contribute unique information above and beyond a reduced model including only parasite load and temperature variation ($F_{1,170} < 1$, $p > 0.05$).

The final model, with predictors δ^{18}O variation, population density, temperature variation, and parasite load, is shown in Table 2. Population density predicts substantially more unique variance in CC (41% of the total variance in CC was unique to the population density variables) than parasite load (1%), temperature variation (7%), and δ^{18}O variation (9%) and yields much larger unstandardized regression weights than the other variables. A 1 SD change in population density is associated with several times more variance in CC than a 1 SD change in parasite prevalence or paleoclimatic variation. The quadratic components of δ^{18}O variation

Table 2 Change in cranial capacity as a function of population density, parasite load, temperature variability, and $\delta^{18}O$ variation

	VIF	Estimate	Std. Error	*t*-value	Pr(>|*t*|)
(Intercept)		1,409.452	23.787	59.254	2.00E−16
Pop Density	4.34	191.942	22.893	8.384	2.04E−14
Pop Density^2	2.74	−84.105	18.303	−4.595	8.49E−06
$\delta^{18}O$	5.52	−37.77	25.821	−1.463	0.145412
$[\delta^{18}O]^2$	5.25	−55.869	14.814	−3.771	0.000225
Temp Variation	1.4	18.578	12.986	1.431	0.154391
Temp Variation^2	1.21	−28.111	8.575	−3.278	0.001272
Parasites	1.47	−12.794	13.344	−0.959	0.339076

VIF = Variance Inflation Factor (Fox and Monette 1992). These values indicate that the predictors are not so highly correlated that substantially different unstandardized regression weights would emerge upon replication with a different sample of crania. $\delta^{18}O$ = SD of the oxygen isotope record for the 200,000 years before the fossil was dated.

and temperature variation predict significant unique variance in CC (Bonferroni adjusted alpha=0.007), but the linear components do not, indicating inverted U-shaped relationships between $\delta^{18}O$ variation changes (independently of population density, temperature variation, or parasite load changes) and CC changes, and between temperature variation changes (independently of population density, $\delta^{18}O$, or parasite load changes) and CC changes. Latitude does not predict unique variance in CC when added to this model ($t_{166}=1.52$, $p>0.10$).

Figure 2 illustrates the predicted unique contributions of population density, $\delta^{18}O$ variation, and temperature variation to the variance in CC (from the final model), across the range of each predictor in the model. The first panel shows that CC increases continuously from the lowest population density in our sample to about 1 SD above the mean of population density and then declines slightly. The amplitude of this function is about 600 cm^3. The second panel shows that cranial capacity increases with increases in $\delta^{18}O$ variation but a maximum is reached where further increases in $\delta^{18}O$ variation are associated with decreases in CC. The lowest $\delta^{18}O$ variation (i.e., a stable
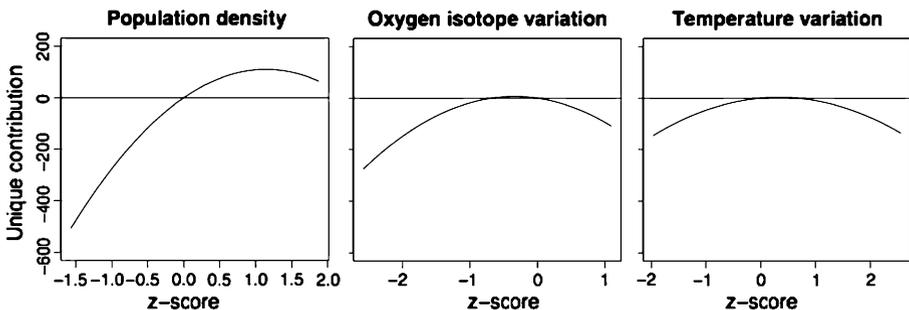

Fig. 2 Predicted relative unique contributions of population density, $\delta^{18}O$ variation, and temperature variation to variance in CC, across each variable's range of z-scores: As population density increases independently of the other variables, CC increases, then decreases slightly; as $\delta^{18}O$ variation increases independently of the other variables, CC increases and then decreases (and only in a small range of values does $\delta^{18}O$ variation contribute positive variance to CC); as temperature variation increases, CC increases and then decreases (and only in a small range of values does temperature variation contribute positive variance to CC)

paleoclimate) is associated with CC ~250 cm^3 below the mean CC. As δ^{18}O variation increases to the mean of this variable, CC increases, but CC decreases with further increases in δ^{18}O variation. The amplitude of this function is about 250 cm^3. The third panel shows a similar relationship between temperature variation and CC; as temperature variation increases to the mean of this variable, CC increases. However, at approximately 0.5 SD from the mean or higher, increases in temperature variation are associated with decreases in CC. The amplitude of this function is less than 200 cm^3.

Because the SST record used by Ash and Gallup (2007) stops at 0.093 mya, before many of the crania in our sample were discovered, we did not include this variable in the full model. However, when we include the variable with the 97 crania discovered before this time, SST variation does not predict unique variance in hominid brain size ($t_{87}=-1.93$, $p>0.05$, Bonferroni-adjusted alpha=0.006), above and beyond the influence of the variables in the final model.

Discussion

The climatic, ecological, or social pressures that drove the rapid increase in hominid brain size and organization during the past 1.9 million years are debated. Our data do not allow us to address the question of evolutionary change in brain organization (Holloway 1975; Holloway et al. 2004), but our findings for CC support and expand on previous results. Consistent with previous findings, our bivariate correlations indicate that cranial capacity increased linearly with degree of latitudinal deviation from the equator. Multivariate regressions indicate that 87% of the variation in latitudinal variation is predicted by differences in mean annual temperature, high to low variation in annual temperature, and number of potentially harmful parasites found in the region. These findings are consistent with the corresponding hypothesis that ecological novelty and harsher and more variable climates in latitudes north and south of the equator resulted in pressures that contributed to the increase hominid brain size (Ash and Gallup 2007; Kanazawa 2008; Potts 1998; Vrba 1974).

In keeping with Ash and Gallup (2007), variation in paleoclimate—as indicated by the standard deviation in δ^{18}O levels in the 200,000 years prior to the date of the hominid fossil—did predict unique variance in cranial capacity in multivariate analyses that controlled for our population density (discussed below) and other variables. The similar curvilinear relationship between twentieth-century temperature variation and CC is highly consistent with this finding. However, the unique effect of population density remained significant and was several times larger than that of the δ^{18}O variable. This is not to say that climatic variation was not a potentially important selective factor during hominid evolution, but rather it does not appear to have been the primary selective pressure for hominid brain evolution, at least not in the past 1.9 million years. Independent of population density, δ^{18}O variation predicts a parabolic effect in CC. Moving from highly stable paleoclimates (2.5 SD below the δ^{18}O mean) to more variable climates is associated with increasing CC, but this trend reverses with climates less stable than the average paleoclimate.

The function maxima for δ^{18}O and temperature variation around 0.5 SD below the mean and around 0.5 SD above the mean (panels 2 and 3, Fig. 2) and the portions of the δ^{18}O and temperature variation curves above the CC mean suggest a

"Goldilocks zone," that is, a zone in which climatic variation does not substantially affect CC (i.e., the derivative of the $\delta^{18}O$ and temperature functions is near 0)—a range from 1.0 SD below the mean to the mean for paleoclimate variation and from the mean to 1.0 SD above the mean for twentieth-century temperature variation. This effect necessarily reduces the relative contribution of climate to selective pressures on CC and results in increased potential for other pressures to affect CC. In contrast, climates more unstable than the mean are associated with decreases in CC, inconsistent with current versions of the climate hypothesis. In any case, the Goldilocks zone indicates a substantial range of paleoclimates during the past 1.9 million years during which changes in CC were not associated with changes in climatic variation as measured by these variables.

We also tested the hypothesis that one particular ecological pressure, parasite load, may have influenced hominid brain evolution. Specifically, we hypothesized that the reduction in parasite load associated with migration away from the equator may have released calories needed to maintain the immune system. In this view, reduced parasite load would not in and of itself cause an increase in hominid CC, but rather would release resources that could be used to build and maintain the metabolically expensive brain, if other pressures were operating directly on the corresponding cognitive competencies. Despite the high correlation between parasite prevalence and CC and the utility of parasite prevalence as a predictor of CC independent of mean temperature and temperature variation, parasite prevalence did not predict unique variance in CC in the final model (Table 2). This could be explained by a variety of reasons. Our operationalization of parasite prevalence was very simple and thus may not have represented the full variation in actual parasite loads across latitudes. Latitude, in contrast, was measured without error, and the variable itself contained a wider range of variation than the parasite variable; the latter results in a "statistical advantage" in multivariate analyses, independent of other factors. Of course, our hypothesis could simply be incorrect, but we suggest that the concept merits further consideration.

In any case, the latitude, temperature, parasite, and paleoclimatic variables leave much of the variation in cranial capacity unexplained, once our measure of population density is controlled. The measure is conceptually and statistically simple. We assume that migration of hominids from central Africa was due to expanding populations and a corresponding reduction in the carrying capacity of the surrounding ecology. To capture expansion, our measure counts the number of fossils outside of the central area in which the oldest specimen in our sample was found. For each fossil, the count includes all other fossils found before or at the time of the existence of this individual. It might be argued that climatic or ecological changes and not an increase in population triggered migration. However, if this were the case, then we would not expect fossils to be found in this central region throughout the time span of our study, but Fig. 1 (panel 1) shows that many of our ancestors remained in this region while others migrated. It is possible that hominids migrated from this central region and then returned after experiencing an increase in CC. However, genetic analyses of extant human populations suggest that the pattern in the data we analyzed is not likely due to large-scale return of populations that migrated from the equator (Li et al. 2008), but rather hominids in all areas of the world showed increases in CC.

In any event, the predictive power of our population density variable is clear: As shown in the first panel of Fig. 2, cranial capacity increases systematically with population density. To the extent the variable captures changes in population density during the evolution of hominids, the results provide strong empirical evidence for the social competition model of Alexander (1989), Holloway (1967), and others (Brothers 1990; Dunbar 1998, 2003; Flinn et al. 2005; Geary 2005; Humphrey 1976). The exponential increase in CC across time is particularly important for Alexander's (1989) ecological dominance and social-competition hypothesis. As hominids reduced mortality risks through improvements in hunting ability, cooking, and skill at manipulating the ecology (e.g., shelters), the relative balance of selective pressures shifted from climatic and ecological to social. In addition to increased migration, the corresponding population increases are predicted to create the potential for a within-species arms race. To the extent success at competing with conspecifics was dependent on increasingly sophisticated cognitive functions, the predicted result is an exponential increase in cranial capacity and cognitive ability (Flinn et al. 2005; Gavrilets and Vose 2006; Geary 2005). A within-species arms race would also result in increases in CC throughout the world, as we found and contra strictly climatic and ecological models. Finally, the increases in the population density variable (Fig. 2) are associated with slight decreases in CC at high levels. This decrease suggests a relaxation in selection pressures on CC with high population densities, possibility coincident with the emergence of agriculture, and larger, socially and economically organized villages and city-states (Brace 1995).

The overall results illustrate both the usefulness of and the difficulty in predicting increases in hominid brain size using proximate variables. Because predictor variables are so closely related, each variable's contribution to the evolution of hominid brain size can be inferred only after controlling for other variables. By controlling for the relation between cranial capacity and population density, the predictive values of latitude, temperature, and paleoclimatic variation on cranial capacity were substantially reduced. These results suggest the primary selection pressure for the evolution of hominid brain size was neither paleoclimatic variation nor any of the proximate climatic or ecological variables used in the present study; rather, our results provide empirical support for Alexander's (1989) and Holloway's (1967) early models and for the current social brain hypothesis (e.g., Dunbar 2003; Flinn et al. 2005; Geary 2005).

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