A Paleoeconomic Theory of Encephalization

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Introduction

The origin of human intelligence is at the heart of the quest for understanding human origins. Researchers measure a species' intelligence is by the *encephalization quotient* (EQ): the ratio of actual brain size to the predicted brain size based on body mass (Williams 2002). Human EQ is far greater than the EQ of any other known animal. For instance, Williams calculates the EQ for humans to be 62.9, almost three and one half times the largest EQ among all other extant primates –18.5 for *Gorilla Gorilla*.

Scientists generally accept that human intelligence is the result of runaway selection. Debate remains, however, on the processes involved. One theory suggests adding meat to the diet provided high-value nutrition that spurred brain development, though it is now understood that meat was only a fall-back resource for early hominins (O'Connell et al. 2002). Another theory suggests tools allowed *Homo* to become ecological generalists, which increased the benefits of brain development (Wood and Straight 2004). Others suggest the impetus was conspecific social interactions, in which the brain evolved as a social tool designed to solve interpersonal problems. These theories, however, do not address why hominin social environments developed differently and spurred unique outcomes as compared to our closest primate relatives (see Flinn et al. 2005).

Flinn et al. (2005) argue the Ecological Dominance-Social Competition (EDSC) model, as proposed by Alexander (1989; 1990), provides the answer. Alexander (1990, p. 4) argued humans had "become so ecologically dominant that they in effect became their own principal hostile force of nature." That is, the encephalization process came about from within-group and cross-group social competition and coordination. Competition and coordination enabled us to achieve such dominance over our ecosystem we were no longer subject to ecological pressures.

Flinn et al. (2005, p.15) write, “In this evolutionary scenario, the primary selective pressures acting on hominins – particularly in regard to the brain – came from their dealings with other hominins rather than with climate, predators, and food directly.” Only social pressures mattered and these spurred runaway selection for intelligence.

Still, questions arise: how did the process begin, particularly since a great deal of encephalization occurred before humans were dominant? The EQ of the first instance of *Homo*, *Homo habilis*, had already doubled relative to our nearest relatives today, chimpanzees (*Pan troglodytes*) (Williams 2002). These hominins were still largely foragers, scavengers (not yet organized hunters), and prey for more powerful predators (O’Connell et al. 2002). In addition, if complex social interactions did spur encephalization, why has encephalization apparently ceased, or declined (Ruff et al. 1997) today when humans have developed the most complicated and ecologically dominant society the world has ever known?

Similar questions arise with respect to the limited economic theory on encephalization. Prior economic work focuses on Red Queen games arising out of interpersonal interactions (Robson 2005; Ofek 2001) and on investments in somatic capital (Robson and Kaplan 2003) or in child quality (Galor and Moav 2002). For instance, Robson (2005) describes a *social intelligence hypothesis* in which runaway selection results when individuals gain from having improved rationality or intelligence relative to others. This is in line with the EDSC theory because the focus is on interpersonal interactions. Robson and Kaplan (2003) postulate an *ecological intelligence theory*, whereby investments in somatic capital co-evolve with investments in reduced mortality – so as to reap the future gains of somatic investments. The underlying argument is these investments would have paid off for early human hunters, as hunting is highly skill-intensive. Galor and Moav (2002) focused on humans’ somewhat unique ability (relative to most predators) to fashion tools and technology as a driving force, as there are positive feedbacks between innovation and human capital. As explanations of the encephalization process, these theories have difficulties explaining the significant amount of encephalization that occurred long before hominins were hunters.

We expand on this prior work by analyzing feedbacks between the ecosystem and hominin behaviors when hominins first moved into the savanna, long before they were hunters. Specifically, we explore how behaviors, both individually and at the group level (i.e., division of labor, initially combined with food sharing and later with exchange), and technology could have co-evolved with the hominin resource base to drive encephalization, as changes in encephalization should be expected to accompany changes in foraging behavior (Foley and Lee 1991). We also illustrate how slight differences among sub-populations could have led to different evolutionary paths for encephalization, physiological traits, and technology. One trajectory produced *Homo*, who relied on tools, while the other trajectory produced *Paranthropus*, who relied on physiological capital.

Our analysis is rooted in the notions of joint-determination and endogenous risk in economic and ecological systems, advocated by Crocker and Tschirhart (1992) and Shogren and Crocker (1999). We focus on hominin investments made in response to food abundance, which in turn is influenced by these investments. Initially ecological competition existed between groups, with groups which adopted more efficient behavioral or technological strategies winning the ecological battle. Over time, better social organization and improved technology reduced ecological pressures, moving society towards greater ecological dominance. As brainpower and society developed and ecological pressures diminished, the ecological rewards from enhanced encephalization would be small, and eventually encephalization ceases.

Our model is rooted in economic theories of human capital and specialization. We combine Becker and Murphy's (1992) analysis of labor specialization and knowledge with ecological theories of coalition building (Kurland and Beckerman 1985) and other interactions. Becker and Murphy find investments in specialization and human capital are reinforcing when specialization is limited by coordination costs, contrasting with Smith's (1965) theory that specialization will reduce intelligence because an individual only requires knowledge about his or her specialized skill. But, unlike Galor and Moav (2002), Becker and Murphy do not model technological advancements. They also do not model ecological interactions. Agee and Crocker (1998) show how incorporating environmental relations in a model of human capital development can lead to ambiguous results. In an ecological context, our finding that specialization initially fosters intelligence but later reduces the incentives for it is consistent with Agee and Crocker, and illustrates conditions under which Becker and Murphy's and Smith's results each hold at the evolutionary level.

Finally, our findings are a behavioral manifestation of Liem's Paradox in ecology. Liem's Paradox is the observation that some species develop specialized traits to help obtain non-preferred resources, though they do not specialize in these resources but rather remain ecological generalists and frequently reject the resources they have become specially adapted to use (Liem 1980). For hominins, nature's propensity for physiological investments gave way to behavioral investments. This in turn spurred investments by nature in encephalization, which created a runaway co-evolutionary process of selection and behavioral and technological innovations that ultimately led to the greatest generalist on the planet – humans.

A General Model

Figure 1 provides a simplified version of the hominin phylogenetic tree to illustrate the evolution of species and encephalization over time.[1] We begin with *Australopithecus*, which then branched into *Homo* and *Paranthropus*. Encephalization did not increase much in *Paranthropus* relative to *Australopithecus*, whereas encephalization ultimately more than doubled in *Homo*. In addition to encephalization, we focus on the jaw and dental structures of these genera, as they differed in important ways. Relative to *Australopithecus*, *Homo habilis* had a smaller jaw and proportionately more room devoted to incisors and canines. In contrast, *Paranthropus* had a massive jaw with very large, flat molars and very little room devoted to incisors and canines (Sponheimer et al. 2006; Ungar et al. 2008).

Any analysis of this progression of species will span millions of years and involve multiple species or genera interacting in potentially different environments. We begin by presenting a somewhat general framework that we use to model the various evolutionary branches of the phylogenetic tree in more detail. The basic model involves a single hominin population that relies on foraging, which was the way of life for all the species involved. In addition to foraging behaviors, we describe the accompanying ecosystem and evolutionary dynamics for the generalized system.

Population Dynamics

We develop a predator-prey model of population dynamics, focusing on a single hominin population (additional hominin populations are later incorporated). Early hominins, with a population of *N*, are predators who prey on various resources. Kaplan et al. (2000) define

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[1] Smithsonian (2008) provides a more complete tree. Our tree is a simplification because it does not list every intermediate species or every possible branch, and because the transitions between species are more uncertain than our figure indicates. What is important is that the basic progression of genera from *Australopithecus* to *Paranthropus* and *Homo* is generally accepted.

several classes of foods to be foraged: collected foods (e.g., fruits and easily accessible plant parts), extracted foods (e.g., seeds, roots, and nuts), and hunted foods (e.g., vertebrate meat).[2] Denote the stock of collected foods to be X^c. We assume hominins do not require specialized adaptations for processing collected foods. In contrast, the stock of extracted foods, X^e, and the stock of hunted foods (larger herbivores), X^h, are significantly more difficult to obtain and process. Extracted foods may be buried (i.e., a root) and can have a tough outer barrier. Hunted foods must be caught or scavenged, and the meat must be torn away. All stocks are denominated by their nutritional or energetic value, which amounts to scaling animal biomass by a nutritional parameter having units such as Kcal/kg.

We model collected and extracted foods as renewable resources, each evolving according to the equation of motion:

$$(1) \qquad \dot{X}^j = r^j X^j (1 - X^j / K^j) - N f^j, \quad j{=}c{,}e$$

where r^j is the intrinsic growth rate of the resource, K^j is the resource's carrying capacity, and f^j is the per capita consumption of the resource by early hominins. Logistic growth is not necessary for our results; the key element is that hominin harvests influence resource stocks, particularly in equilibrium.

We take a different approach for herbivores. Early hominins, prior to *Homo erectus*, were thought to be scavengers (O'Connell et al. 2002), and that is how we model them here.[3] The

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[2] It is difficult to force all food resources neatly into these three traditional categories, as accessibility and processing times may vary considerably within each class. But it would be unwieldy to model a large number of highly-differentiated resources. We usethese three categories, noting the set of collected foods may extend slightly beyond traditional definitions. For instance, we assume Australopithecus only foraged for collected foods. This hominin, however, likely foraged for the most easily accessible extracted and hunted foods (e.g., tiny animals), and so we implicitly include those in X^c.

[3] Questions arise whether pre-*Homo erectus* hominins hunted larger prey, and the available evidence suggests they did not (O'Connell et al. 2002). It would not affect our qualitative results to instead assume they were hunters. We do not model other interactions between early hominins and other predators, as this complicates the model without changing the basic insight derived from the analysis. The existence of predators would likely have impacted on the

supply of X^h is determined by other predators and natural mortality. Assuming early hominins constituted only a small part of the diet of other predators, it is reasonable to presume herbivores and their predators would have been in an equilibrium. Then X^h, which we define as the carcasses from natural mortality and predation that would be available for scavenging, is constant. In a later section we model a *Homo* group that has advanced to become hunters, and then we begin to model meat as a renewable resource whose growth is influenced by *Homo*'s harvests.

Hominin population growth—or fertility—depends on the available food supply, which holds with force for people living close to subsistence (see Frisch 1978; Hansson and Stuart 1990; Nerlove 1991, 1993; Dasgupta 1995). Following conventional models of predator populations (e.g., McGehee and Armstrong 1977), let the dynamics of the hominin population be described by

$$(2) \qquad \dot{N} / N = G = \rho(F / S - 1),$$

where G is per capita fertility, ρ is a growth parameter, S is a subsistence level, and F is total per capita food consumption across the set of resources foraged by the hominin.[4] The hominin may not include each resource if the time cost associated with processing one or more particular resources is too great.

The population shrinks (grows) whenever per capita consumption is below (exceeds) the subsistence level. Let S be an increasing, convex function of each of two physiological factors,

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behavioral and physiological development of hominins (though not on predators if hominins were a small part of their diet), which could explain some early encephalization and group behavior. Our focus, however, is on changes in these traits as a result of changes in diet availability. Here predators would only play a secondary role. To keep the model tractable, we do not address these secondary effects; we do mention some potential impacts in a series of footnotes.

[4] The term foraging is taken to include scavenging activities.

jaw strength (or bite force), σ, and encephalization, ε.[5] The muscular structure for a larger and stronger palate is expensive in terms of energy requirements; but greater encephalization is relatively more expensive. A third physiological trait, dental structure, γ, has a neutral effect on subsistence ($\partial S / \partial \gamma = 0$); we describe the dental structure in more detail below. We define σ and γ as net investments in physiology relative to pre-savanna hominins, so σ=γ=0 represents no *new* investments in these traits. Encephalization, ε, is defined as a cumulative investment.

Hominin Foraging as a Production Process

Individuals have *T* amount of time available to obtain food, which must be allocated between searching for food, T^s, processing food, T^p, and making tools, T^v. The per capita amount of food a hominin group encounters and consumes is given by the standard Schaefer production function (Clark 1990),

$$(3) \qquad F = \sum_{j \in J} [T^s [1 - c(n,\varepsilon)] g(n,\alpha) q^j(\varepsilon,\alpha)] X^j$$

In (3), *J* represents the endogenously-chosen set of resources over which the hominin forages. The coefficient q^j is an individual's encounter rate for species *j*, which is an increasing function of encephalization, ε, $q^j_\varepsilon > 0$.[6] Assume q^j also depends on a habitat area parameter, α, with $q^j_\alpha < 0$: search effort is less effective when X^j is spread over a larger area. We also assume, for simplicity, $q^c_{\alpha\varepsilon} = 0$.

The encounter rate is modified by the function *g*, which is increasing and concave in the

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[5] The subsistence parameter reflects a number of biological processes. For instance, the subsistence rate should vary directly with the mortality rate, and mortality should increase, given a fixed pelvis size, when encephalization increases (i.e., higher mortality during birth). Encephalization also requires energy that can alternatively be used to reduce natural mortality (Kaplan et al. 2000).

size of the search party, $n \leq N$, and decreasing in land area, $g_\alpha < 0$, with $g_{\alpha n} > 0$. This is in line with Kurland and Beckerman (1985), who discuss how search parties that fan out and communicate can increase per capita encounters relative to searches by individuals. We view this collaboration as a *division of labor* over the hunting area, with each individual specializing in searching along a particular trajectory. In this sense, production described by equation (3) is consistent with the approach of Becker and Murphy (1992), except that specialization herein does not require a significantly differentiated skill set among individuals.

Following Becker and Murphy (1992), collaboration is costly. Collaboration costs (e.g., communication costs) reduce the effective search effort level, defined as $T^s[1-c(n,\varepsilon)]$, with $c \in [0,1]$ and $c(1,\varepsilon)=0$. For $c < 1$, per unit marginal costs of collaboration increase at an increasing rate, $c_n, c_{nn} > 0$. Total and marginal per unit costs of collaboration are decreasing in ε, i.e., $c_\varepsilon, c_{n\varepsilon} < 0$; encephalization improves communication and planning, both vital to coordination. How we model coordination costs differs slightly from Becker and Murphy (1992)—we assume these costs are a function of encephalization, ε, and operate as a reduction in effective search time rather than an output cost.[7] In sum, hominin harvests follow the basic Schaefer production function when n=1. Coordination increases output at a diminishing rate when n>1.

In addition to locating food, hominins also spend effort on food processing. Processing time can influence the set of foods over which a species will forage (Robinson and Wilson 1998); Wood and Straight (2002) argue primitive hominins such as Australopithecine may have

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[6] Subscripts refer to partial derivatives.

[7] Other specifications for the time cost, such as a lump sum reduction in the total time for work, T, yield analogous results, but add significantly greater analytical complexity.

been unable to access the energy embedded in extractive and hunted foods. Let processing time per unit of food-type *j* be given as $b^j(\phi^j, \tau^j)$, where ϕ^j represents physiological capital and τ^j represents the effective level of produced tools, or hominin-made capital, in use. We describe both forms of capital in greater detail below. Collected foods do not require any special physiological capital or tools to process: $b^c_\phi = b^c_\tau = 0$, so that b^c is fixed. We assume $b^h(0,0) > b^e(0,0) > b^c$, as non-specialized hominins lacking tools find hunted resources are more difficult to access than extracted foods, which in turn are more difficult to access than collected foods (Kaplan et al. 2000). Processing time for extracted and hunted foods is decreasing in both forms of capital, i.e., $b^h_\phi < b^e_\phi < 0$ and $b^h_\tau < b^e_\tau < 0$, *ceteris paribus*. Capital investments generate a larger marginal reduction in processing time for hunted resources. The two forms of capital are substitutes in processing, i.e., $b^j_{\phi\tau} > 0$: one cracks open nuts with a tool or teeth, or one tears into meat with a knife or teeth.

The physiological capital used to process resource *j* is a function, $\phi^j(\sigma, \gamma)$, that depends on jaw strength or bite force, denoted σ, and an index representing dental structure, denoted γ. A larger value of σ indicates greater bite force, which is useful for accessing both hard foods (e.g., seeds) and tough foods (meat), i.e., $\phi^j_\sigma > 0$ (*j*=*e*,*h*). A larger value of γ indicates the hominin has larger, flatter molars (and smaller incisors), which implies he or she is more specialized for accessing small, hard foods such as seeds and nuts, i.e., $\phi^e_\gamma > 0$. Bite force and large molars are complements in procuring extracted foods, i.e., $\phi^e_{\gamma\sigma} > 0$. A smaller value of γ indicates the hominin is more specialized for accessing meat via more prominent incisors and a smaller surface area for crushing foods, i.e., $\phi^h_\gamma < 0$. Bite force and incisors are complements in accessing hunted foods, i.e., $\phi^h_{\gamma\sigma} < 0$.

We assume dental structure has only a minimal influence on the ability to access collected foods, i.e., ϕ^c is a constant for all σ and γ. Tradeoffs among dental structures only exist between extracted and hunted foods.

The hominin-made capital used to process resource *j* is a function, $\tau^j(\theta, z)$, that depends on the current level of technology, θ, and in *hominin capital* (akin to human capital), *z*. Hominin-made capital is increasing in both of these arguments: $\tau^j_z, \tau^j_\theta > 0$. Moreover, $\tau^j_{\theta z} > 0$: technology and human capital are complements in tool productivity. Hominin capital, or effective tool use, is a function, $z(T^v, \varepsilon)$, of the amount of time spent producing tools, T^v, and the current level of encephalization, ε. Hominin capital is increasing in both arguments, $z_{T^v}, z_\varepsilon > 0$, with each input being necessary for production. For simplicity, neither the function *z*, tool production effort T^v, nor encephalization ε is resource-specific. Rather, the overall level of technology, production effort, and encephalization allow one to produce tools for multiple purposes. Tool production effort could in principle be made specific to a particular production activity, but we assume effort produces tools for multiple uses. Also note that tools are non-durable, as they were initially produced using primitive materials and techniques and would have worn out or broken frequently.

We assume tool production and use is only possible whenever *n* exceeds some critical value $\hat{n}(\varepsilon)$, with $\hat{n}'(\varepsilon) < 0$. That is, the critical value $\hat{n}(\varepsilon)$ is simply a threshold beyond which tools become possible; larger group sizes do not imply more tool use. Van Schaik et al. (1999) indicate that the intellectual capacity for tool use likely existed prior to 2.5 million years ago, but not the social capacity. In particular, sufficient cooperating group sizes are needed to sustain the horizontal transmission of technology. Such threshold effects are common to technological or cultural diffusion processes in humans (e.g., Cavalli-Sforza and Cavalli-Sforza 1996), and there is evidence that they are also important in primate populations (van Schaik et al. 1999). We assume the threshold diminishes when encephalization is increased, as greater intelligence facilitates the capacity for teaching and learning, and hence diffusion. Threshold effects are important in our model because endogenous changes in group size, and evolutionary changes in encephalization, will play a role in determining when tools become a feasible option.

Hominin Foraging Behavior

Individuals take group size, *n*, the foraging set *J*, and all biological and technological parameters as fixed, though later we show the optimal group size and foraging set are chosen at the group level to be endogenous functions of the resource base. Foraging effort and tool manufacturing effort are chosen by individuals to maximize the net energetic value of food procurement, given their time constraint, because this maximizes fitness *G*:

$$(4) \qquad \underset{T^s,T^v}{Max} \quad F = \sum_{j\in J} T^s[1-c(n,\varepsilon)]g(n,\alpha)q^j(\varepsilon,\alpha)X^j$$

subject to

$$(5) \qquad T = T^j[1+\sum_{j\in J} b^j(\phi^j,\tau(\theta,z(\varepsilon,T^v)))[1-c(n,\varepsilon)]g(n,\alpha)q^j(\varepsilon,\alpha)X^j] + T^v$$

The Lagrangean associated with population *i*’s problem is:

$$(6) \qquad \begin{aligned} L = &\sum_{j\in J}[T^s[1-c(n,\varepsilon)]g(n,\alpha)q^j(\varepsilon,\alpha)]X^j \\ &+\lambda[T - T^s[1+\sum_{j\in J} b^j(\phi^j,\tau(\theta,z(\varepsilon,T^v)))[1-c(n,\varepsilon)]g(n,\alpha)q^j(\varepsilon,\alpha)X^j] - T^v] \end{aligned}$$

For a particular set *J*, the Kuhn-Tucker conditions are given by

$$\frac{\partial L}{\partial T^s} = \sum_{j\in J}[1-c(n,\varepsilon)]g(n,\alpha)q^j(\varepsilon,\alpha)X^j - \lambda(1+\sum_{j\in J} b^j(\phi^j,\tau(\theta,z(\varepsilon,T^v)))[1-c(n,\varepsilon)]g(n,\alpha)q^j(\varepsilon,\alpha)X^j) = 0 \tag{7}$$

$$\frac{\partial L}{\partial T^v} = -\lambda[T^s\sum_{j\in J} b^j_\tau(\phi^j,\tau(\theta,z(\varepsilon,T^v)))\tau^j_z z_{T^v}[1-c(n,\varepsilon)]g(n,\alpha)q^j(\varepsilon,\alpha)X^j+1] \le 0\,; \tag{8}$$

$$\frac{\partial L}{\partial T^v}T^v = 0$$

and the time constraint (5). Condition (7) is written as an equality since search effort is a necessary input into food production. Condition (8) is written in Kuhn-Tucker form. No investment in tools will occur, and

$$T^s = \frac{T}{[1+\sum_{j\in J} b^j[1-c]gq^jX^j]}, \tag{9}$$

when the marginal impact of tool production labor in reducing handling time is always less than the marginal cost of this labor in terms of foregone foraging effort, i.e.,

$$-\frac{T\sum_{j\in J} b^j_\tau(\phi^j,\tau(\theta,z(\varepsilon,T^v)))\tau^j_z z_{T^j}[1-c]gq^jX^j}{[1+\sum_{j\in J} b^j[1-c]gq^jX^j]} < 1 \tag{10}$$

This condition is satisfied when the hominin has sufficient physiological capital relative to hominin-capital (as influenced by encephalization and technology levels), resulting in b^j_τ being small in absolute value. Here investment in tools is unwarranted because the productivity gain is small relative to the foregone food production that comes from allocating some time away from foraging.

When investment in tools is warranted, the optimal allocation is the solution to conditions (7), (8) (evaluated as an equality), and (5). Otherwise, the optimal allocation is given by (9). In either case, the allocation depends on *n* and the values of the resource stocks in the exploited resource set *J*. These are group-level choices that require cooperation among individuals. It is not necessary to assume a group leader. Rather, natural selection results in values of *n* and *J* that maximize fitness *G* (Kurland and Beckerman 1985). We delay detailed discussion of these choices until we discuss specific hominins, as that is when the choices become particularly relevant.

Evolution of Physiological Traits and Technology

Hominin foraging choices, both at the individual and group levels, influence the evolution of physiological traits and also drives technological advancements. This can be shown using adaptive dynamics (Brown and Vincent 1987; Rice 2004) to model evolutionary changes in the biological traits σ ,γ , and ε, and in technology, θ. We call these "slow variables" since they evolve on a much slower time scale than *N* and X^j, which we call the "fast variables". Changes in the slow variables occur after the fast variables have equilibrated at their steady state values (Rice 2004).

First consider the evolution of encephalization, ε. Following Diekmann and Law (1996), Lande (1979), and Krakauer and Jansen (2002), this trait evolves according to

$$(11)\qquad \frac{\dot{\varepsilon}}{\varepsilon} = \mu_\varepsilon \frac{\partial G^*}{\partial \varepsilon} = \mu_\varepsilon \rho \left[\frac{S(\partial F^* / \partial \varepsilon) - F^*(\partial S / \partial \varepsilon)}{S^{*2}} \right] = \mu_\varepsilon \rho \left[\frac{(\partial F^* / \partial \varepsilon) - (\partial S / \partial \varepsilon)}{S^*} \right]$$

where μ_ε is a mutation rate and the superscript * denotes food consumption is evaluated at the *conditional* steady state values of *N* and X^j, conditional on the current values of σ ,γ , ε, and θ. The final equality in (13) arises because $F^* = S$ in a conditional steady state involving the "fast" variables *N* and X^j. Since F^* endogenously depends on hominin foraging behavior, so does the evolution of ε. Expression (11) indicates the encephalization trait ε increases (decreases) when its marginal benefit from increased food production exceeds (is less than) its marginal cost from increased subsistence. An equilibrium emerges when the marginal values are equal. The adaptive dynamics for σ and γ are analogous to equation (11), as are the interpretations (except investments in γ have no subsistence costs):

$$\frac{\dot{\sigma}}{\sigma} = \mu_\sigma \frac{\partial G^*}{\partial \sigma} = \mu_\sigma \rho \left[\frac{(\partial F^* / \partial \sigma) - (\partial S / \partial \sigma)}{S^*} \right] \tag{12}$$

$$\frac{\dot{\gamma}}{\gamma} = \mu_\gamma \frac{\partial G^*}{\partial \gamma} = \mu_\gamma \rho \left[\frac{(\partial F^* / \partial \gamma)}{S^*} \right] \tag{13}$$

Finally, technology evolves according to

$$\frac{\dot{\theta}}{\theta} = \mu_\theta \frac{\partial G^*}{\partial \theta} = \mu_\theta (\theta, z(T^{v*}, \varepsilon), n^*) \rho \left[\frac{\partial F^* / \partial \theta}{S^*} \right] \tag{14}$$

Technology advances when the marginal benefit of technology on per capita consumption is positive, along with the mutation parameter. Technological advances would not occur if there is no marginal benefit to this. In the spirit of Galor and Moav (2002), the mutation parameter is endogenous and is increasing in the current level of technology, hominin capital, and group size. Assume $\mu_\theta(\theta, 0, n^*) = 0$, i.e., technology does not evolve early on when individuals do not make investments in tool use. We assume, once the innovation process begins, technology evolves much slower than changes in populations but somewhat faster than changes in biological parameters – at least for moderate levels of technology and effort in tool production. An equilibrium level of θ is unlikely to emerge once the innovation process has begun, provided $\tau_\theta \neq 0$ for any positive value of θ once individuals have incentives to invest in tool use.

The Evolution of the Australopithecine

We now turn our attention to specific hominin populations. The earliest bi-pedal hominins moved into the patchy savannas of Africa after these habitats originated following a period of climate change around 6 million years ago (Cerling et al. 1997; Foley and Lee 1989). We refer to these first hominins in the savanna as *Australopithecus*, though technically *Australopithecus* emerged as a result of the ensuing evolutionary forces. We model this evolutionary process, focusing in particular on how behavioral choices influence encephalization.

Australopithecus are believed to have had foraging patterns similar to chimpanzees, which forage primarily for collected foods as we have defined them ($J = \{ X^c \}$) (Kaplan et al. 2000; Foley and Lee 1991; O'Connell et al. 2002). It is also believed that tools were not used to any significant degree during this period (hence $T^v = 0$) (Foley and Lee 1989; Wood and Strait 2004). Without tools and with $J = \{ X^c \}$, the optimal level of search effort comes from (9), which we write as:

$$T^s = \frac{T}{(1 + b^c[1 - c(n,\varepsilon)]g(n,\alpha)q^c(\varepsilon,\alpha)X^c)} \tag{15}$$

Assume processing time for collected foods is not too substantial, such that $b^c[1 - c(\varepsilon,\alpha)]g(n,\alpha)q^c(\varepsilon,\alpha)X^c < 1$; which implies search time accounts for more than 50 percent of the total available foraging time.

Relation (15) yields their per capita food consumption level:

$$F = \frac{T[1 - c(n,\varepsilon)]g(n,\alpha)q^c(\varepsilon,\alpha)X^c}{(1 + b^c[1 - c(n,\varepsilon)]g(n,\alpha)q^c(\varepsilon,\alpha)X^c)}. \tag{16}$$

The optimal group size solves

$$\frac{\partial F}{\partial n} = \frac{Tq^c(\varepsilon,\alpha)X^c}{(1 + b^c[1 - c(n,\varepsilon)]g(n,\alpha)q^c(\varepsilon,\alpha)X^c)^2}\big[[1 - c(n,\varepsilon)]g_n(n,\alpha) - c_n(n,\varepsilon)g(n,\alpha)\big] = 0, \tag{17}$$

which implies the term in brackets must vanish. The implicit solution to (17) is $n(\varepsilon, \alpha)$, with

$$(18)\qquad \frac{\partial n}{\partial \alpha} = \frac{c_n g_\alpha - [1-c] g_{n\alpha}}{[1-c] g_{nn} - c_{nn} g - 2c_n g_n} > 0$$

$$(19)\qquad \frac{\partial n}{\partial \varepsilon} = \frac{c_{n\varepsilon} g + c_\varepsilon g_n}{[1-c] g_{nn} - c_{nn} g - 2c_n g_n} > 0$$

Expression (18) indicates coordination increases when resources are distributed over a larger area (i.e., resource density falls), which is consistent with extant primate behavior in such environments (Foley and Lee 1989).[8] Coordination increases because the returns to coordination increase—they spend more time searching (as opposed to processing) when the resource density falls, which increases T^s and the returns to coordination. This expression implies group sizes would have likely increased when hominins first moved into the savanna, which was characterized by a lower density of nutritional resources than the forest habitats which the hominins previously occupied (Kurland and Beckerman 1985).[9]

Expression (19) indicates greater encephalization increases the returns to coordination by increasing search productivity and decreasing coordination costs. Encephalization is complementary to coordination. If coordination is also complementary to the encephalization process, so that coordination and encephalization are joint complements, then co-evolution will drive increases in both encephalization and coordination. We show this to be the case in the next section on evolution.

Now that we have derived the optimal short-run hominin choices, we turn to the long-run impacts of these choices on the conditional steady state value of *F*, as F^* influences evolutionary changes. Equation (16) indicates *F* is influenced by only two variables: *n* and X^c. The optimal

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[8] Coordination could also increase to confront an increase in predation risks in the open savanna (Foley and Lee 1989).

[9] Kurland and Beckerman (1985) use a less formal model to develop the same result.

group size is constant for a given level of encephalization and land area, and is at the same level in both the short run and in the conditional steady state. Now consider X^c. The conditional steady state value of X^c is implicitly defined by the condition $F^* = S$, which we write as $X^{c*}(\varepsilon, b^c, \alpha)$, with

$$(20) \qquad \frac{\partial X^{c*}}{\partial \alpha} = \frac{-X^{c*}(g_\alpha q^c + g q^c_\alpha)}{g q^c} > 0$$

$$(21) \qquad \frac{\partial X^{c*}}{\partial \varepsilon} = \frac{-\eta^{c*}_\varepsilon}{\eta^{c*}_{X^c}} + \frac{S_\varepsilon (1 + b^c \eta^{c*}_\varepsilon)}{\eta^{c*}_{X^c}(T - Sb^c)} \gtrless 0$$

where $\eta^{c*} = (1-c) g q^c X^{c*}$ and $T - Sb^c = T/(1 + b^c \eta^{c*}) > 0$. The conditional steady state resource stock increases when the resource becomes less dense because harvesting productivity declines.

The impact of greater encephalization is ambiguous. On the plus side, greater encephalization increases productivity for any given level of resource stock, and so less of the stock is required to maintain subsistence requirements. In contrast, subsistence requirements increase with greater encephalization, creating a need for a larger resource stock, *ceteris paribus*. The net result will depend on how much encephalization has already taken place, with the increased subsistence requirements effect dominating when ε is sufficiently large. We show below that ε and X^{c*} will be joint complements when the sign of (21) is positive, so that co-evolution will drive increases in both these variables. If the sign of (21) is negative, then increases in ε will reduce X^{c*}, which puts on the brakes for encephalization. Taken together with our earlier result on the complementarity of *n* and ε, this result suggests that ecological pressures may initially work against behavioral investments in coordination as a driving force of encephalization. But once some threshold value of ε is achieved, both effects spur encephalization.

Finally, note X^{c*} is independent of the carrying capacity of the resource stock, k^c, since the equilibrium stock size is determined by the per capita harvest function F, which does not depend on carrying capacity. Accordingly, evolutionary outcomes, which depend on per capita food consumption and hominin subsistence levels, do not depend on k_c.

Evolutionary changes upon entering the savanna

Suppose prior to entering the savanna, hominins were in an evolutionary equilibrium, i.e., $\dot{\varepsilon} = \dot{\sigma} = \dot{\gamma} = 0$. Also, $\dot{\theta} = 0$, as these hominins did not invest in hominin capital. Since it is believed that hominins focused their foraging efforts on collected foods both prior to and after their move to the savanna, the variables σ and γ were unlikely to be impacted by the move – at least not for dietary purposes.[10] We therefore focus on the impact of the move on encephalization.

When hominins entered the savanna, they likely found resources in the new ecosystem to be less dense (Foley and Lee 1989; Kurland and Beckerman 1985), as modeled by a larger value of α.[11] Starting from an initial equilibrium that would have satisfied $\partial F^* / \partial \varepsilon = \partial S / \partial \varepsilon$, we want to know how this relation would have been affected by an increase in α. The increase in α will not affect S, and so the evolutionary impact depends on how an increase in α affects $\partial F^* / \partial \varepsilon$. If $\partial(\partial F^* / \partial \varepsilon) / \partial \alpha > 0$, the marginal benefits of encephalization increase and ε increases; if $\partial(\partial F^* / \partial \varepsilon) / \partial \alpha < 0$, the reverse happens.

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[10] If hominins became subject to greater predation risks in the savannah, there could have been greater evolutionary incentives to invest in stronger jaws and sharper teeth, increasing both σ and γ.

Define $\Lambda(\varepsilon, \alpha, n^*(\varepsilon, \alpha), X^{c*}(\varepsilon, \alpha)) = \partial F^* / \partial \varepsilon$. The marginal affect of α on $\partial F^* / \partial \varepsilon$ is

$$(22) \qquad \frac{d\left(\partial F^* / \partial \varepsilon\right)}{d\alpha} = \Lambda_\alpha + \Lambda_{n^*} n_\alpha^* + \Lambda_{X^{c*}} X_\alpha^{c*}$$

Equation (22) indicates three key effects are at work: (i) Λ_α, a direct foraging productivity effect; (ii) $\Lambda_{n^*} n_\alpha^*$, an economic feedback effect as group sizes adjust in response to the lower density; and (iii) $\Lambda_{X^{c*}} X_\alpha^{c*}$, an ecological feedback effect as the resource stock adjusts in response to the change in harvest pressure. The partial derivatives of Λ are:

$$(23) \qquad \begin{aligned} \Lambda_\alpha = \frac{TX_c^*}{(1 + b_c[1-c]gq_c X_c^*)^3} \Big[& -c_\varepsilon (g_\alpha q_c + gq_{c\alpha})(1 - b_c[1-c]gq_c X_c^*) \\ & + q_\varepsilon^c [1-c]\left(g_\alpha (1 - b_c[1-c]gq_c X_c^*) - 2b_c[1-c]g^2 X_c^* q_\alpha\right)\Big] \end{aligned}$$

$$(24) \qquad \Lambda_{n^*} = \frac{TX^{c*} q^c (-c_\varepsilon g_n - c_{n\varepsilon} g)}{(1 + b^c[1-c]gq^c X^{c*})^2} > 0$$

$$(25) \qquad \Lambda_{X^{c*}} = \frac{T(1 - b^c[1-c]gq^c X^{c*})([1-c]gq_\varepsilon^c - c_\varepsilon gq^c)}{(1 + b^c[1-c]gq^c X^{c*})^3} > 0$$

The sign of Λ_α is ambiguous because an increase in α reduces search productivity, resulting in less time processing and more time spent searching. The sign will be negative if the reduction in search productivity dominates, which we believe is the most likely case, as labor reallocations are often secondary to productivity effects. In that case, the net effect is a reduction in foraging productivity. Here reduction in resource density should reduce the incentives for encephalization. The signs of both Λ_{n^*} and $\Lambda_{X^{c*}}$ are positive, as a larger equilibrium group size and a larger equilibrium resource stock both yield larger productivity when there is greater

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[11] They also might have found resources to be supported by a different carrying capacity, though as we argued earlier this feature would not affect evolutionary outcomes.

encephalization. Given expressions (18) and (20), this means the economic and ecological feedbacks both work to increase the incentives for encephalization. This is not yet the joint complementarity result mentioned earlier, in which increases in group size and equilibrium resource stock levels are both increased by encephalization and drive further encephalization. Rather, these feedbacks arise because the reduction in α stimulates increases in group size and equilibrium resource stock levels. If the net effect of (i)-(iii) is increased encephalization, however, then the joint complementarities will come into play, as we describe below.

When expressions (20) and (23)-(25) are plugged back into expression (22), it can be verified all the negative terms in Λ_α are cancelled out by several of the terms in $\Lambda_{X^{c*}} X_\alpha^{c*}$, so $d(\partial F^* / \partial \varepsilon) / d\alpha > 0$ and there is an increased demand for encephalization. The ecological feedbacks more than compensate for the effects of reduced productivity. The economic feedbacks further increase the incentives for encephalization. This result is reminiscent of Agee and Crocker's (1998) results, though in reverse. Agee and Crocker consider parent's choices for investing in own consumption and in the development of their children's hominin capital. They show how an exogenous increase in genetic-based intelligence causes economic and ecological outcomes to become "behaviorally and reciprocally linked" (p. 267), and that accounting for these feedback processes can lead to contrary results than when these processes are not considered. Here, we show just the opposite: an exogenous ecological shock (i.e., a reduction in resource density; though movement into the savanna was likely a rational choice driven by climate change) generates ecological and economic feedback processes that impact upon *nature's* demand for encephalization. This expands the scope of endogenous risk (Shogren and Crocker 1991; Crocker and Tschirhart 1992) to the evolutionary level—only truly exogenous shocks (e.g., climate change; though today not even that is exogenous) are unaffected by economic and ecological interactions. Moreover, this expands the scope of ecosystem externalities (see Crocker and Tschirhart 1992) to include evolutionary impacts, as the hominins' impacts on the resource stock affect evolutionary changes.[12]

Once the increase in α causes the process of encephalization to begin anew, economic and ecological feedbacks continue affecting how much ε increases. To see this, note the marginal benefits of encephalization, $\partial F^* / \partial \varepsilon = \Lambda(\varepsilon, \alpha, n^*(\varepsilon, \alpha), X^{c*}(\varepsilon, \alpha))$, depend on economic and ecological feedbacks. As ε increases, we know from conditions (19) and (21) that n^* increases whereas X^{c*} may increase or decrease. The increase in n^*, along with any increase in X^{c*}, further enhances the incentives for encephalization, by condition (24). Encephalization and group size are joint complements, with investments in each reinforcing investments in the other via joint economic and ecological feedback effects. The same could be said for encephalization and stock size if $X_\varepsilon^{c*} > 0$ (though these would be purely ecological feedback effects).

Without some mitigating force, the result could be runaway selection for encephalization. But this process is tempered by the subsistence costs of encephalization ($S_\varepsilon > 0$). The process would also be tempered by a decrease in X^{c*} if $X_\varepsilon^{c*} < 0$. The ecological feedback of a reduced resource stock reduces the incentives for encephalization.

The encephalization process described here echoes the results of Becker and Murphy (1992), who find knowledge and specialization (coordination in our case) to be jointly determined when specialization is limited by coordination costs and many specialists provide mainly the same skills (as in our model). But Becker and Murphy's finding that specialization,

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[12] Ecosystem externalities arise when individuals' choices affect, via ecosystem interactions, ecological state variables unrelated to the initial decision that impact on future economic welfare (Crocker and Tschirhart 1992).

and in turn knowledge, is limited by coordination costs is incomplete in the present context—physiological costs via impacts on subsistence requirements and ecological feedbacks also work to temper the encephalization process.

Encephalization among *Australopithecus* is not an example of the Ecological Dominance-Social Competition (EDSC) theory that says encephalization was the result of hominin dominance over the ecosystem. Though hominin choices (movement into the savanna and increased coordination) led to increased marginal gains from encephalization, these choices were driven by ecological processes (climate change). Further, the encephalization process was either reinforced or mediated by ecological interactions – clearly not the result of human dominance over the ecosystem.

Climate Change and the Emergence of New Hominins

The relatively stable savanna climate supported the *Australopithecine*, who subsisted on a fairly stable diet, for over a million years. A period of climatic change then occurred around 2.8 million years ago that increased seasonality and would have adversely affected resource densities within each period (e.g., de Menocal 1995; see also Wood and Strait 2004, Sponheimer 2006, and O'Connell et al. 2002). An expansion of the diet accompanied this period of climate change (O'Connell et al. 2002; Foley and Lee 1991; Sponheimer et al. 2006; Wood and Strait 2004). In this section we model how this hominin diet expansion led to physiological and non-physiological adaptations, and the accompanying effects on encephalization.

For simplicity, we model the effects of this climate change as an additional increase in α.[13] Although we just examined the short and long run effects of an increase in α, this was only

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[13] Increased seasonality would have altered both the abundance of resources, via changes in their carrying capacities, and also the distribution of resources, via changes in α. We do not address changes in the carrying capacity because,

for a given foraging set *J*. An increase in α reduces foraging productivity. If this productivity is sufficiently reduced for collected resources relative to the other resource options, hominins may have incentives to expand their diets to include other resources such as extracted foods or meat, either of which would have required additional processing time. Adopting these food resources would not have made either a preferred food option, as collected foods would still be preferable. Rather, these other food resources could be viewed as fall-back resources – at least initially prior to evolutionary or technological investments.

Until now we have assumed uniformity among the hominin population. This presumption is reasonable when the differences across individuals are not large enough to cause different sub-groups to choose different diets. We now introduce heterogeneity among reproductively isolated (non-interbreeding) sub-populations and consider what happens when the increase in α is sufficient to induce some sub-populations to expand their diets in different ways. Specifically, we examine how perturbations in a particular trait and in α affect behaviors across the sub-populations, and also the potential for the new sub-populations to invade the system and co-exist with the existing sub-population. Once we determine the multi-hominin equilibrium, we then examine evolutionary processes. This approach of introducing a distinct sub-population, characterized by a slight difference in a trait, is a standard method to investigating issues of co-existence and speciation (Rice 2004).

Suppose the *Australopithecus* population splinters into three reproductively-isolated groups, indexed by $i = A,P,H$. Group $i=A$ is *Australopithecus*, group $i=P$ is *Paranthropus* (*aethiopicus*, *bosei*, or *robustus*), and group $i=H$ is *Homo habilis*, or simply *Homo* due to our

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by the equilibrium condition $F = S$, a change in carrying capacity would not impact upon equilibrium values of X_c. Accordingly, changes in the carrying capacity would not influence long-run human behaviors and hence evolutionary outcomes. We focus on α, as this parameter does have long-run effects in our model.

focus on genera. Initially, the groups that we refer to as *Paranthropus* and *Homo* would not have constituted different species – they would have simply been splinter groups of the *Australopithecus* genus. If these groups did not inter-breed, either because they were spatially distinct or developed cultural differences, then different foraging strategies could have led to different evolutionary pressures on these groups relative to the *Australopithecine*. Over time, the result would have been a radial speciation.

We introduce heterogeneity by assuming some variation in skills across the three groups.[14] We assume the Australopithecine have greater ease in processing collected foods, i.e., $b^{Ac} < b^{Pc} = b^{Hc}$, and they harvest from only collected foods in spite of the increased scarcity. *Paranthropus* are assumed to have greater ease in processing extracted foods, i.e., $b^{Pe} < b^{Ae} = b^{He}$, which they add to their diet. Finally, *Homo* has greater ease in processing meat, i.e., $b^{Hh} < b^{Ah} = b^{Ph}$, which they optimally add to their diet. Initial processing ability differences between *Paranthropus* and *Homo* can most easily be explained by slight differences in dental structure, with $\gamma_H > \gamma_P$. Dental structure was ultimately a key difference between the genera (Sponheimer et al. 2006; Ungar et al. 2008), and it is reasonable to assume there would have initially been slight variations in this trait across sub-populations of *Australopithecus*.

Since we have already explored the impact of an increase in α on Australopithecine's behavioral choices, we now focus our attention on *Paranthropus* and *Homo*, starting with *Paranthropus*.

Paranthropus

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[14] It does not matter which group had which skills, as all groups were originally *Australopithecus*. But given the initial processing abilities that we assign, the evolutionary outcome associated with more efficient processing of extracted (hunted) foods is consistent with *Paranthropus* (*Homo*).

The climate change-induced reduction in foraging productivity could have been largely or fully offset by *Paranthropus* expanding their diet to include extracted resources, and by increasing group sizes. We can verified, even with the diet expansion and regardless of whether tool use is adopted, the optimal group size, n^{P*}, solves $\partial F^P / \partial n^P = 0$ which requires that $\left[[1 - c(n^P, \varepsilon^P)]g_n(n^P, \alpha) - c_n(n^P, \varepsilon_H)g(n^P, \alpha)\right] = 0$, as in condition (17). Optimal group size is therefore of the form $n^{P*}(\varepsilon^P, \alpha)$, which is independent of resource stock sizes and which yields the same partial derivatives as in (18)-(19).

Given the increase in group sizes, a key question is whether *Paranthropus* would invest in tools to aid in processing the extracted foods. Due to prior encephalization and the additional increase in α, group sizes may have increased enough to make tools an option. But even so, investment in tools does not occur if equation (10) holds, which depends, at least in part, on the magnitude of $| b_\tau^{Pe} |$. This value is small if hominins are sufficiently adapted to processing the foods without tools (since tools and physiology are substitutes), or if the marginal productivity of tools is small, given the current technology. By assumption, small marginal tool productivity holds in comparison to meat processing (recall $| b_\tau^{Pe} | > | b_\tau^{Ph} |$). Marginal tool productivity for extracted foods will be small in an absolute sense if some of the initial extracted foods were not too difficult to access without tools. The fact that *Paranthropus* most likely did not use tools, $T_v^{Pe} = 0$, suggests this was the case.[15] This means the optimal allocation of search labor is given by equation (9) for the foraging set $J^P = \{X^c, X^e\}$. The choices of foraging set, group size, and search effort define the optimal value of *F* in (3), the long run value of which drives

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[15] There is almost no evidence of tool use among *Paranthropus*. Some very primitive tools have been found at one site, but it is unclear whether those tools belonged to *Paranthropus* or *Homo* (Wood and Strait 2004).

Paranthropus evolution. However, as F^{P*} depends on X^c, which is also exploited by *Australopithecus* and *Homo*, we must first evaluate *Homo*'s foraging behavior and the ensuing multi-hominin equilibrium (if one exists) before we can turn to evolutionary outcomes.

Homo

Now consider the group *Homo*. The reduced resource densities initiated by climate change could have been offset by *Homo* expanding their diet to include meat (most likely as scavengers). Still, net resource densities are likely to have decreased, as animal densities were much lower than plant densities and the mobility of animals means the location of carcasses would have varied considerably. The decrease in resource densities would have led to increased group sizes (see condition (18)), which had already grown over time due to encephalization. This outcome could have made tool use a possibility. Wood and Strait (2004) indicate that early *Homo* would have required tools to access meat and marrow from carcasses, suggesting that $b_{Hh\tau}$ would have been large in absolute value. As *Homo habilis*, the first *Homo* species, did use tools for meat processing (Foley and Lee 1991; Wood and Strait 2004), $T^{Hv} > 0$, this suggests that $|b_{Hh\tau}|$ was sufficiently large. The marginal value was large because *Homo* had not evolved as a predator and only had a slightly better dental structure than *Australopithecus* for accessing meat. Moreover, *Homo*'s significant intelligence compared to other predators (as well as his hands) would have enabled him to take advantage of tool productivity.

With $T^{Hv} > 0$, the derivative $\partial L / \partial T^{Hv}$ in condition (8) vanishes and total meat consumption for *Homo* is written as

(26) $$F^H = \left[T^H - T^{Hv}(n^H, \varepsilon^H, \phi^H, \alpha, \theta^H, X^c, X^h)\right] \frac{\sum_{j \in J^H} \eta^{Hj}}{1 + \sum_{j \in J^H} b^{Hj} \eta^{Hj}}$$

where $\eta^{Hj} = (1-c) g q^{Hj} X^{Hj}$, $T^{Hv}(\cdot) = T^H - T^{Hs*}[1 + \sum_{j \in J^H} b^{Hj} \eta^{Hj}]$ and T^{Hs*} solves $\partial L_H / \partial T_{Hv}$=0 in condition (8). The optimal group size, n^{H*}, solves $\partial F^H / \partial n^H = 0$ which requires that $\left[[1 - c(n^H, \varepsilon^H)] g_n(n^H, \alpha) - c_n(n^H, \varepsilon^H) g(n^H, \alpha)\right] = 0$, as in condition (17). Optimal group size is of the form $n^{H*}(\varepsilon^H, \alpha)$, which is independent of resource stock sizes and which yields the same partial derivatives as in (18)-(19).[16] The choices of foraging set, group size, search effort, and effort in tool production define the optimal value of *F* in (26), the long run value of which drives *Homo* evolution. However, F^{H*} depends on X^c, which is also exploited by *Australopithecus* and *Paranthropus.* We therefore must analyze the multi-hominin equilibrium (if one exists) before we can turn to evolutionary outcomes.

Multi-Hominin Equilibrium and Competitive Exclusion

The evolutionary effects of the expanded diets of *Paranthropus* and *Homo* depend on whether a multi-hominin equilibrium exists and which hominins are part of that equilibrium. We examine the conditions under which competitive exclusion of one or more groups might arise. Competitive exclusion is the principle that if two similar groups occupy the same niche, only the more efficient survives and the other slowly goes extinct as they compete for resources (McGehee and Armstrong 1977). *Australopithecus*, *Paranthropus,* and *Homo habilis* occupied

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[16] Finally, for both *Homo* and *Paranthropus,* we can show food consumption for each group is increasing in each resource stock contained within the group's foraging set. It would not be optimal to include any resource stock to the foraging set if food consumption was decreasing in that stock. This result is used later to derive some of the signs of the partial derivatives in the evolution analysis, though we do not show those derivations here.

overlapping niches, and would have faced inter-group competition. While three groups can sometimes survive on three resources, it is also possible that inter-group competition could have led to the exclusion of one or more groups (McGehee and Armstrong 1977).

The equilibrium value X^c in the multi-hominin model is still determined by the Australopithecine's equilibrium condition $F^A = S^A$, provided the Australopithecine are not competitively excluded from existence. The climate change event does not affect S^A (at least prior to evolution), but it will reduce *Australopithecus* foraging productivity. To offset this so as to satisfy $F^A = S^A$, the equilibrium value of X^c must increase to $X^{c*} = X^{cA} > X^{c0}$, where we define X^{c0} as the equilibrium value of X^c prior to this second climate change (i.e., the equilibrium value of X^c defined just prior to equation (20)). Without loss of generality, assume this adjustment occurs quickly before competition with *Paranthropus* or *Homo* begins.

Entry by new hominins has a negative effect on *Australopithecus* population levels. Once *Paranthropus* and *Homo* enter the scene, their additional harvest pressure on collected resources would result in a temporary reduction in X^c, reducing N^A. As N^A falls to a lower equilibrium level, the extracted stock would increase back to X^{cA}, provided the new equilibrium value of N^A is positive. The exclusion of *Australopithecus* would occur if the result of additional hominin entry is to permanently force X^c to a new, lower equilibrium value such that *Australopithecus* can no longer sustain itself and $N^{A*} = 0$ (McGehee and Armstrong 1977).

Initially, *Paranthropus* and *Homo* would have had the same subsistence level as *Australopithecus*, i.e., $S^P = S^H = S^A$. The new hominin groups could invade the system and propagate if their initial per capita consumption rates, $F^P(X^{cA}, k^e)$ and $F^H(X^{cA}, X^h)$, exceeded the subsistence level (recall: X^h is assumed fixed, and k^e is the carrying capacity of X^e in the absence of hominin exploitation). Both new hominin groups are assumed to be slightly less productive than *Australopithecus* at processing collected foods, which means they would have relied on their fall-back resources (i.e., extracted or hunted foods) to make up the productivity difference, particularly if X^c fell in the short term.

First consider the case of *Paranthropus*. Assuming they invaded the system, their impact would have been to reduce the extracted resource stock. An equilibrium involving both *Paranthropus* and *Australopithecus* (and possibly *Homo*, provided they can subsist on X^{cA} and the hunted resource) would emerge if there exists a value of $X^e < k^e$, denoted X^{eP}, that solves the equilibrium condition $F^P(X^{cA}, X^{eP}) = S^P$. Though *Paranthropus* was better adapted than *Australopithecus* in processing extracted foods, *Paranthropus* would still have preferred collected foods if $b^c < b^e$. Below, we show that evolution will further develop the specialization of traits that aid in processing extracted resources.

Now consider the case of *Homo*. The condition $F^P(X^{cA}, X^h) > S^H$ must hold for *Homo* to invade the system. If *Homo* were initially scavengers, they would have had no influence on the value of the hunted resource stock, X^h. Holding X^{cA} constant, this means the *Homo* population would grow without bound. But as the population grew the pressure they exerted on collected foods would have increased and X^{cA} would fall. Indeed, an equilibrium with *Homo* could only have developed if X^c permanently fell. Though X^c is a preferred resource, *Homo*'s reliance on it diminishes somewhat as hunted resources become an option. Due to this diminished reliance, X^c can fall some without causing subsistence problems for *Homo*. But the reduction in X^{c} below X^{cA} reduces per capita consumption by *Australopithecus* below their subsistence level. The eventual results would have been a conditional equilibrium of $X^{c*} = X^{cH} < X^{cA}$ and the exclusion of *Australopithecus*, though this may have taken a considerable amount of time.[17]

The reduction in X^{c} also puts increased pressure on *Paranthropus*, who continue to rely heavily on this resource. *Paranthropus* have a better chance than *Australopithecine* of surviving the exclusion pressures, due to the greater diversification of their diet. At first, the outcome will be greater reliance on extracted foods and a smaller population. If they are unable to survive on extracted foods alone, however, which might be expected for a fall-back resource, then continued reductions in X^{c} will eventually result in *Paranthropus* going extinct.

The Evolution of *Paranthropus* and *Homo*

Assuming both *Paranthropus* and *Homo* were in an evolutionary equilibrium with $\dot{\varepsilon}_i = \dot{\sigma}_i = \dot{\gamma}_i = 0$ for i=*P*,*H* (and $\dot{\theta}_i = 0$, as these hominins did not invest in hominin capital), prior to climate change, we now investigate the evolutionary impacts of climate change and the expanded diet. Our analysis of *Paranthropus* is slightly less formal than that of *Homo*, as the changes that occurred in *Paranthropus* are simpler and more intuitive.

Paranthropus evolution

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[17] Similar results could have occurred if *Homo* were not scavengers, though the process would have taken longer because in that case X^{h} could adjust downward to bring about a conditional equilibrium. Technological change would have improved productivity, increasing the downward pressure on X^{h}. Evolution would have then increased S^{H}, requiring an offsetting increase in consumption to re-establish an equilibrium. Eventually, the equilibrium effect is to increase the pressure on both resources. Once pressure on collected resources results in a permanent downward shift in that resource stock, the Australopithecine are placed on an exclusion trajectory.

We begin our discussion of *Paranthropus* evolution by considering how the variables σ^P and γ^P change due to an increase in α. There are three discrete effects: (i) the change in foraging productivity for collected resources, (ii) the increase in the foraging set, and (iii) the reduction in the equilibrium level of X^c due to *Homo*.[18] Prior to the expanded foraging set, effect (i) would have no impact on σ^P or γ^P. After the expansion of the foraging set, effects (i) and (iii) would only serve to increase the reliance on extracted resources relative to collected resources, and so the effect is the same as in (ii). The expansion of the foraging set to include extracted foods increases the marginal incentives for physiological investments that reduce processing times for extracted foods, which means we could expect an increase in σ^P and a decrease in γ^P.[19] These adaptations would not have affected *Paranthropus*'*s* abilities to process collected resources; rather they would have reduced the incentive to ever incorporate hunted resources into their diets.

Now consider the effects of the increase in α and the change in the foraging set on encephalization, ε. We showed earlier the increase in α, given the original foraging set $J = \{X^c\}$, increases the incentives for encephalization. Also, holding X^{c*} constant, the addition of extracted foods to the diet increases overall resource abundance and hence productivity. As a heuristic, recall we previously showed that an increase in resource abundance increases the incentives for encephalization (i.e., $\Lambda^P_{X^{c*}} > 0$). The reduction in X^{c*} due to competition from *Homo*, however, reduces resource abundance and hence productivity. The overall net effect of

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[18] We do not examine the marginal impact of α on foraging productivity for extracted resources since extracted resources were not in use prior to the climate change event. Rather, the impact of α with regards to extracted resources is to simply add them to the foraging set.

[19] Incentives for these physiological traits could have existed even if *Paranthropus* initially did use tools to some limited degree. If so, then over time as investments in these traits occurred, the incentives for tool use would have declined – possibly to the point that tools were no longer worth the investment.

these three impacts (the increase in α, the decrease in X^{c*}, and the expanded foraging set) on encephalization is ambiguous. As encephalization increased slightly for *Paranthropus*, this suggests the impact of climate change and a larger foraging set dominated slightly. If so, the increased incentives for encephalization would have been largest immediately after the climate change and diet expansion. Over time, as processing times fell due to physiological adaptations, these incentives would have decreased again (since it can be shown that $\Lambda_b^P < 0$: intelligence and physical adaptations are substitutes for *Paranthropus*) – though not likely to their pre-climate change levels.

Now consider the cost of evolutionary investments, noting evolutionary changes would have occurred together. If $S_{\varepsilon\sigma}^P > 0$, as is believed (Stedman et al. 2004), reductions in ε would have reduced the marginal costs of investments in σ^P while investments in σ^P would have increased the marginal costs of investments in ε.[20] This further supports the notion that significant increases in σ^P would not likely have occurred with significant additional investments in encephalization.

These physiological changes happened: *Paranthropus* is characterized by large jaws with flat molars, and encephalization is not significantly different than that of *Australopithecus* (Foley and Lee 1989; Williams 2002). Dental microwear studies indicate that, though *Paranthropus* specialized in processing extracted foods, collected foods likely remained their primary diet (Sponheimer et al. 2006; Ungar et al. 2008). The specialized adaptations did not result in a reduction in diet, but rather an expansion (Sponheimer et al. 2006). Ungar et al. (2008) suggest

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[20] Stedman et al. (2004) indicate strong jaw muscles would have interfered with brain growth, making brain development more costly.

this radial speciation may be an example of Liem's Paradox. Robinson and Wilson (1998) show that Liem's Paradox can be explained by competitive forces that reward phenotypic specialization directed towards the non-preferred resource, provided the investments do not infringe on the species' ability to procure the preferred resource. Our results are consistent with this observation, as collected foods would still have been preferred if their processing times remained lower.

Homo evolution

First consider how the incentives for nature to invest in ε^H change due to the increase in α. In contrast to *Paranthropus*, there are now four discrete effects, owing to the fact that *Homo* has adopted tools: (i) the change in foraging productivity for collected resources, (ii) the increase in the foraging set, (iii) the reduction in the equilibrium level of X^c, and (iv) the adoption of tools. The first effect is analogous to the positive effect described above for *Australopithecus* and *Paranthropus*. The second and third effects are also experienced by *Paranthropus*, though to a different degree. The fourth effect is unique to *Homo*.

To explore effects (ii)-(iv), define the marginal benefit of encephalization on food consumption by

$$\Lambda^H(\varepsilon^H, \alpha, n^{H*}(\varepsilon^H, \alpha), X^{c*}(\varepsilon^H, \alpha, X^h, \theta^H), T^{Hv*}(\varepsilon^H, \alpha, X^{c*}, X^h, \theta^H), X^h, \theta^H) = \partial F^{H*} / \partial \varepsilon^H .$$

While the effort allocated to tool production is written as a function of other parameters, for now we do not consider how changes in the underlying parameters influence its value. This is because no effort was applied to tool use prior to the climate change event, and so we only consider a positive increase in tool use relative to the pre-climate change period.

The change in the incentives for encephalization due to the expanded foraging set (effect (ii)) is given by $\Lambda^H_{X^h}$, which is positive provided q^{Hh}_{ε} is sufficiently large relative to q^{Hc}_{ε}. Effect (iii), caused by a reduction in the equilibrium level of collected resources, is really an indirect effect of the expanded foraging set. This effect is given by $\Lambda^H_{X^c}(\partial X^{c*}/\partial X^h)$, which is negative since $\Lambda^H_{X^c} > 0$ and $\partial X^{c*}/\partial X^h < 0$. The net impact of the direct and indirect effects of the expanded foraging set on the incentives for encephalization is ambiguous. Finally, the change in the incentives for encephalization due to the adoption of tools (effect (iv)) is given by $\Lambda^H_{T^{Hv}} > 0$. The incentives are increased because tool use reduces processing times when the adoption of tools is optimal, and greater encephalization will further reduce processing times. Again, this last term does not arise for *Paranthropus*, so tool use results in greater incentives for encephalization for *Homo* than for *Paranthropus*.

If ε^H does increase, this initiates a runaway evolution effect in which ε^H, n^H, and θ^H grow. As described above for *Australopithecus*, a larger n^H increases the incentives for encephalization (i.e., $\Lambda^H_n > 0$), while greater encephalization increases the incentives for a larger group size (equation (19)). Moreover, increases in ε^H cause T^{Hv*} to increase ($\partial T^{Hv*}/\partial \varepsilon^H > 0$), leading to further increases in Λ^H ($\Lambda^H_{T^{Hv}} > 0$). These joint economic-ecological feedback effects are all exacerbated by increases in θ^H, which is also increased as a result of larger group sizes and a larger ε^H. These complementarity effects arising between tools, technology, and encephalization for *Homo* were not experienced by *Australopithecus* or *Paranthropus*.

Additional complementarities could arise between ε^H and X^{c*}, provided $X^{c*}_{\varepsilon} > 0$. This derivative is defined as

$$\frac{\partial X^{c*}}{\partial \varepsilon^{H}} = \frac{-\eta_{\varepsilon}^{Hc*}}{\eta_{X^c}^{Hc*}} + \frac{S_{\varepsilon}^{H}(1+b^{Hc}\eta_{\varepsilon}^{Hc*})}{\eta_{X^c}^{Hc*}(\hat{T}^{H}-S^{H}b^{Hc})} + \frac{-\eta_{\varepsilon}^{Hc*}(1+S^{H}b^{Hh})+S^{H}b_{\varepsilon}^{Hh}\eta^{Hh*}}{\eta_{X^c}^{Hc*}(\hat{T}^{H}-S^{H}b^{Hc})} + \frac{S_{\varepsilon}^{H}b^{Hh}\eta^{Hh*}}{\eta_{X^c}^{Hc*}(\hat{T}^{H}-S^{H}b^{Hc})} \gtrless 0 \tag{27}$$

The first two terms on the RHS are the same as in equation (21) (though their values may differ), and their sum is ambiguous. The third term is negative and reflects the reduced reliance on stock X^{c} due to the availability of the fall-back resource X^{h}. The final RHS term is positive, reflecting the greater need to increase X^{c} to offset the larger subsistence requirements resulting from greater encephalization. This need to increase X^{c} is greater than in the *Australopithecus*-only case, since average processing costs have increased due to the expansion of the diet. If the third RHS term dominates the fourth, then the complementarities between ε^{H} and X^{c*} are likely greater for *Homo* than for *Australopithecus* (though the magnitude of $\Lambda_{X^c}^{H}$ also matters, and this could be smaller for *Homo* since their reliance on X^{c*} is smaller than that of *Australopithecus*). Otherwise, the complementarities are likely reduced, tempering the encephalization process along with the subsistence costs of encephalization ($S_{\varepsilon}^{H} > 0$). But note: if X^{c*} falls due to encephalization, *Homo* relies even more on hunted resources, further increasing the marginal benefits of technology and fueling encephalization via an alternative route.

These results suggest the incentives for encephalization may have been larger for *Homo* than for either *Australopithecus* or *Paranthropus*. Technology is a new and important driver of encephalization. Technological advances provide incentives for individuals to invest in tools, which boosts foraging productivity and hence the marginal returns to encephalization. In turn, encephalization leads to greater tool use, which in turn generates technological advances. Galor and Moav (2002) describe how a similar pattern of reinforcing feedbacks fuels investments in technology and child quality (hominin capital), which increases the evolutionary benefits from intelligence. We expand on their results by considering how these investments endogenously affect subsistence requirements, as well as the ecological impacts of these investments, which stimulate joint economic-ecological feedbacks that influence the encephalization incentives.

The insights of Becker and Murphy (1992) and Agee and Crocker (1998) apply here as well. The diet expansion results in more tasks (i.e., tool-making) that are not significantly differentiated across individuals. The expanded number of tasks generates increased economic-ecological feedbacks and positively influences nature’s demand for encephalization. The joint feedback processes are therefore even more important in the case of *Homo*. The evolutionary incentives created by the joint feedback effects are in stark contrast to the EDSC theory, in which hominins are assumed to be above ecological constraints. Rather, the joint feedbacks arise *because* hominins are a fundamental part of the ecological system.

Now consider the variables σ^H and γ^H. Using the methods outlined above, we can show that the addition of meat to the diet increases the marginal benefits of physiological investments, namely increases in σ^H and γ^H, that reduce processing times for hunted foods. The incentives may be small for those who adopt tools, however, since tools and physiology are substitutes. This holds as technologies improve (somewhat faster than evolutionary changes) and hominin capital increases in response. At the same time, the marginal costs of investments in jaw strength would increase if encephalization increases, since $S^H_{\sigma\varepsilon} > 0$. If the marginal costs of jaw strength increase by more than the marginal benefits, the result would be a reduction in jaw strength.

These physiological and technological changes also happened: *Homo* is characterized by a smaller jaw, and encephalization is significantly increased relative to *Australopithecus*

(Stedmad 2004; Wilson 2002). Stedman (2004) posits that a reduction in strong jaw muscles, due to a new myosin gene that stopped jaw muscle growth, made increased brain growth possible in *Homo*. Our results suggest this mutation was able to spread within the *Homo* population because tools provided a substitute for these muscles, so that the energy previously required for them could be released to brain development. Also note that, though *Homo* specialized in processing meat, there is evidence that that early *Homo* remained scavengers who had infrequent success at obtaining meat in all but the most resource rich environments (O'Connell et al. 2002). Accordingly, collected foods would still have been preferred initially. This is consistent with Leim's Paradox, though specialization in this case involved the use of tools instead of physiology. Eventually, technology would have improved to the point where *Homo* had projectile weapons and became highly skilled hunters. At some point along this development path, meat would have switched from a fall-back resource to a highly-desired one. But it did not have to occur initially. Indeed, the evidence is that this did not occur until *H. ergaster* (O'Connell et al. 2002). Therefore, consuming large amounts of meat was not required for encephalization to occur.

More *Homo* advancements and evolution

Technological advancements eventually resulted in the development of projectile weaponry (spears, etc.), which would have aided in both animal hunting and processing activities and would have allowed *Homo* to move from scavenger to hunter. This discrete advancement would have again spurred investments in encephalization. Similarly, tool use would lead to further expansion of the diet set, as various types of extracted resources would become available through improved processing technologies. This diet expansion would also lead to increased encephalization. Diet expansion would also eventually lead to exclusion of *Paranthropus,* either because tool use made *Homo* more efficient exploiters of extracted resources or because their ever-increasing numbers could have overexploited this resource since *Homo* did not rely on it as the sole food source.

Trade and evolution

One of the most important hominin advances was that of trade.[21] Debate remains about when trade began, but evidence exists suggesting trading networks among early modern humans existed by at least 130,000 B.P. (Holden 1998), and trading had really taken off by about 40,000 years ago (Horan et al. 2005). Interestingly, encephalization has ceased or even declined during this same time frame (Ruff et al. 1997). Here we show these two events may be linked.

Early markets would have initially been extremely thin, with few products being exchanged. Becker and Murphy (1992) argue investments in human capital lead to a thickening of markets, as human capital allows for increased specialization and less reliance on self-provisioning. Agee and Crocker (1998) suggest research is needed on the interplay of environmental externalities in this process. We apply their ideas at the evolutionary level. The development of hominin capital has led to a reduced reliance on physiological provisioning, which paves the way for reduced self-provisioning. At some point, the number of tools and activities that *Homo* engaged in would have been too large for any individual to manage. Specialization and exchange by individuals engaged in highly differentiated tasks would have been the inevitable result.

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[21] In addition, Isaac (1983) and Ofek (2001) claim exchange began from the home base. People brought food back and exchanged, and they also specialized in tool production. Also see Horan et al. (2008), who point out how trade could have co-evolved with speech.

How do specialization and exchange influence encephalization? We address this question by now departing somewhat from our previous model, which was already complex and would become more so if we attempted to incorporate exchange. We focus on a simpler construction to illustrate the main points, which intuitively should carry over to more complex specifications. We no longer focus on coordination costs, though coordination is to some extent required when trading.[22] Rather, we focus on specialization in two distinct tasks, which contrasts with our earlier model in which specialization involved similar activities spread across the landscape.

The model we adopt comes from Horan et al. (2005). We focus on *Homo* and drop the superscript $i=H$ to simplify notation. Trade arises to exploit differences in skill, and so we introduce heterogeneity among *Homo*. Assume individuals are in one of two subgroups: (i) *skilled hunters* (indexed by $j=s$) and (ii) *unskilled hunters* (indexed by $j=u$). Members of each group derive utility from consuming meat and a possibly broad set of other goods (e.g., clothes and shelter). These other goods were not previously modeled, but they would have become increasingly important as *Homo* substituted man-made adaptations for physiological ones. Utility is a Cobb-Douglas function of meat (m) and other goods (a)

$$(28) \qquad U^{j} = m_j^{\beta} a_j^{1-\beta}, \quad j=s,u$$

where β is a parameter that is not assumed to vary by skill-class. The indices are represented as subscripts for meat and other goods to distinguish the indices from the exponents; elsewhere they are represented as superscripts.

Individuals maximize (1) subject to a time constraint

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[22] Horan et al. (2008) describe how speech could have co-evolved with trade to reduce the coordination costs associated with trade.

(29) $T^{j} = T^{jm} + T^{ja}$,

where T^{jm} is hunting effort and T^{ja} is effort directed at producing other goods. Let $a = T^{ja}$ for simplicity. We ignore processing and instead define harvesting of meat by the standard Schaefer production function (Clark 1990)

(30) $m_{j} = q^{j} T^{jm} X$,

where X represents the extant population (biomass) of wildlife (the superscript h has been dropped). Catchability is an increasing function of encephalization, $q^{j}(\varepsilon)$, with $q^{s} > q^{u}$ and $q^{s}_{\varepsilon} > q^{u}_{\varepsilon}$ for a given ε. Though individuals share the same level of encephalization, skilled hunters are able to make better use of this trait. This does not mean skilled hunters are more intelligent. Rather, the increased efficiency among skilled hunters could reflect some other traits used in conjunction with intelligence (e.g., eyesight, sense of smell) to influence hunting productivity. Encephalization does not affect production of other goods (e.g., ε has crossed a threshold such that the marginal impact of ε on the production of *a* is now zero). We could have just as easily assumed encephalization was more important for producing other goods than for hunting. The key element is simply that some activities require more intelligence than others, though everyone has the same level of ε due to interbreeding.

Finally, we modify *Homo* population growth relative to (2) to account for the heterogeneous, interacting sub-populations. The offspring of skilled hunters can be either skilled or unskilled; unskilled hunters can have either skilled or unskilled offspring. Denote the proportion of skilled hunters' offspring who are also skilled by μ^{s}; and the proportion of unskilled hunters' offspring who are unskilled by μ^{u}. Heredity is likely to bias the distribution of offspring's skills along the lines of parentage, such that $\mu^{s} > 0.5, \ \mu^{u} > 0.5$. Sub-population *j* grows according to

$$(31)\qquad \dot{N}^j = \rho\left(\frac{\mu^j m_j^*}{S} - 1\right)N^j + \rho\left(\frac{(1-\mu^i)m_i^*}{S}\right)N^i \text{ for } j{\neq}i.$$

Note that population growth is a function of meat and not other goods. Though individuals require other goods in their consumption bundle, food remains the limiting resource for *Homo* population growth. Finally, the proportion of skilled individuals is given by $\varsigma = N^s / N$, which changes endogenously over time due to natural selection.

Horan et al. (2005) derive the equilibrium consumption levels and equilibrium proportion of skilled hunters arising under self-sufficiency and under exchange, where exchange involves skilled hunters specializing in hunting and unskilled hunters specializing in producing other goods.[23] Given their results and setting $T^s = T^u = T$, average per capita consumption under self-sufficiency is

$$(32)\qquad F^{ss} = \varsigma^{ss}\beta q^s TX + (1-\varsigma^{ss})\beta q^u TX = [\varsigma^{ss}(q^s - q^u) + q^u]\beta TX\ .$$

Average per capita consumption under exchange is

$$(33)\qquad F^e = \varsigma^e \beta T q^s X + \varsigma^e (1-\beta) T q^s X = \varsigma^e T q^s X\ .$$

Horan et al.'s (2005) results imply that ς^{ss} depends on ε, while ς^e is independent of ε. This means the proportion of skilled hunters influences the marginal incentives for investment under self-sufficiency but not under trade. Horan et al. also show that $\varsigma^{ss} > \varsigma^e$: more skilled hunters arise under self-sufficiency due to the greater ecological pressures faced by unskilled hunters relative to skilled hunters in this scenario. In contrast, trade allows unskilled individuals to

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[23] Other possibilities could emerge in this Ricardian trade model, depending on the proportion of skilled hunters. If the proportion is low, unskilled hunters will engage in both activities while skilled hunters will specialize. If the proportion is high, then skilled hunters will engage in both activities while unskilled hunters will specialize. The conditions required for complete specialization are $\beta > \varsigma^e$ and $q^s/q^u > ((1-\varsigma^e)/\varsigma^e)\beta/(1-\beta)$, which we assume holds.

consume as a function of skilled hunters' productivity, and so they face fewer ecological pressures relative to skilled hunters.

Given these results, the marginal incentives for encephalization under self-sufficiency and exchange, evaluated at their respective steady states, are

$$\text{(34)} \qquad \frac{\partial F^{ss*}}{\partial \varepsilon} = \left[\frac{\partial \varsigma^{ss}}{\partial \varepsilon}(q^s - q^u) + \varsigma^{ss} q_\varepsilon^s + (1 - \varsigma^{ss}) q_\varepsilon^u \right] \beta T X^{ss*}$$

$$\text{(35)} \qquad \frac{\partial F^{e*}}{\partial \varepsilon} = \varsigma^e q_\varepsilon^s T X^{e*}$$

where the equilibrium condition $F^{i*}=S$ ($i=e,ss$) can be used to derive the steady state values of the resource stocks

$$\text{(36)} \qquad X^{ss*} = \frac{S}{[\varsigma^{ss}(q^s - q^u) + q^u]\beta T}$$

$$\text{(37)} \qquad X^{e*} = \frac{S}{\varsigma^e T q^s}$$

For a given value of ε, the marginal incentives for encephalization are larger under trade if $\partial(\Delta F)/\partial\varepsilon > 0$, and the incentives are smaller under trade if $\partial(\Delta F)/\partial\varepsilon < 0$. We investigate this by using (34)-(36) to obtain

$$\text{(38)} \qquad \frac{\partial \Delta F}{\partial \varepsilon} = \frac{q_u(1 - \varsigma^{ss})\left[\omega^s - \omega^u\right] - \dfrac{\partial \varsigma^{ss}}{\partial \varepsilon}(q^s - q^u)}{[\varsigma^{ss}(q^s - q^u) + q^u]} S$$

where $\omega^j = q_\varepsilon'^{\,j} \varepsilon / q^j$. The denominator of the RHS of (38) is positive, so the sign of (38) depends on the numerator. The first term in the numerator accounts for the marginal effect of increased encephalization on the gains from trade. The last term in the numerator reflects how increased encephalization alters the relative levels of natural selection under the two scenarios.

The sign of the first numerator term in (38) will be positive if $\omega^s > \omega^u$. With trade, skilled hunters produce meat for everyone, and so everyone benefits from the more skilled hunters having more intelligence. If increased intelligence generates a sufficiently larger proportional increase in q^s than in q^u, the gains are further enhanced and nature has even greater incentives to invest in encephalization in the trade scenario. In contrast, if $\omega^u > \omega^s$, the increase in encephalization is less under trade, as trade insulates unskilled hunters from ecological pressures associated with their own encephalization.

The sign of the second numerator term in (38) depends on the sign of

$$(39) \qquad \frac{\partial \varsigma^{ss}}{\partial \varepsilon} = \frac{\frac{q^s}{\varepsilon}\left[\omega^s - \omega^u\right]\left[\frac{\mu^s - \varsigma^{ss}}{1-\varsigma^{ss}}\right]}{(1-\mu^s)q^s \frac{1}{(1-\varsigma^{ss})^2} + (1-\mu^u)q^u \frac{1}{(\varsigma^{ss})^2}},$$

which is derived from condition (A.3) in Horan et al. (2005). The sign of this expression is ambiguous. If $\varsigma^{ss} + \mu^s > 1$, which might be expected since skilled hunters consume more meat than unskilled hunters and $\mu^s > 0.5$, then it can be shown that $\mu^s > \varsigma^{ss}$.[24] This means the sign of (39) is positive when $\omega^s > \omega^u$, negative when $\omega^u > \omega^s$, and zero when $\omega^u = \omega^s$. Greater natural selection of skilled hunters in the self-sufficiency scenario places more weight on meat consumption by skilled hunters, whereas the proportion of unskilled hunters is comparatively larger under trading. If increased intelligence generates a larger proportional increase in q^s than in q^u, average consumption increases in the self-sufficiency case, increasing the incentives for encephalization under self-sufficiency. In contrast, the comparatively larger proportion of unskilled hunters under trade are insulated from ecological pressures due to trade, and therefore experience smaller incentives for encephalization. When $\omega^u > \omega^s$, the level of natural selection of skilled hunters falls under self-sufficiency relative to trade, and the marginal incentives for encephalization become comparatively larger under the trade scenario.

These results suggest a tradeoff between the effects of encephalization on the gains from trade and on natural selection, with the dominant effect being ambiguous without greater specification of the model and its parameters. This result expands and enriches the conjectures made by Agee and Crocker (1998): increased human capital leads to a thickening of markets, which reduces externalities and in turn should increase human capital. Here, we find that a thicker market may strengthen or diminish evolutionary externalities. Moreover, the relative magnitudes of the marginal incentives for encephalization under the two programs could change over time.

If specialization and trade work to diminish the incentives for encephalization, this would add support at the evolutionary level to Smith's (1965) notion that specialization reduces intelligence. But the reasoning would be different. Smith's notion was that specialists have fewer incentives to invest in general knowledge. Here, encephalization would diminish because trade diversifies against ecological risks, thereby helping to insulate individuals from ecological pressures.

Conclusion

Ecologically-based (including behavioral ecology) models of encephalization tend to ignore feedbacks from human choices, while economic-based models tend to ignore feedbacks from ecological interactions. Here we find that both feedbacks matter a great deal. Encephalization occurred *because* hominins were fundamentally a part of the ecosystem, and so economic and ecological feedbacks jointly influenced the evolutionary incentives for encephalization. Some of these feedbacks were reinforcing and spurred increased encephalization. Other feedbacks would

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[24] This condition holds true in each of Horan et al.'s (2005) simulations.

have created opposing evolutionary incentives, putting the brakes on encephalization. Accordingly, we find there was no one event that caused runaway encephalization. Rather it was a process likely spurred by a series of different climate changes and behavioral adaptations that initially involved cooperation and specialization, spread to encompass technological innovations and expanded resource sets, and finally institutions that supported even greater specialization and resource expansion. At first the behavioral adaptations increased the marginal benefits of encephalization, though these were eventually mitigated by ecological responses. Later, the behavioral adaptations diversified ecological risks so as to diminish the marginal benefits of encephalization. The result is that simple, early behavioral adaptations led to significant increases in encephalization. But later, much more complex adaptations were required to achieve smaller increases. Thus, encephalization is a process characterized by diminishing returns to behavioral advances.

Liem's Paradox is often used in ecology to explain the process of radial speciation. Typically, the process involves physiological adaptations that allow a species to evolve to become more of a generalist. Our results suggest a behavioral explanation may be needed for the *Homo* genus, whereby hominin-made capital substituted for physiological capital and thereby increased the marginal returns to and decreased the marginal costs of encephalization.

Finally, there is a long-running debate in economics over whether specialization increases or decreases intelligence. Here we examine this issue from an evolutionary perspective and find that the answer depends on institutions and how these influence ecological interactions.

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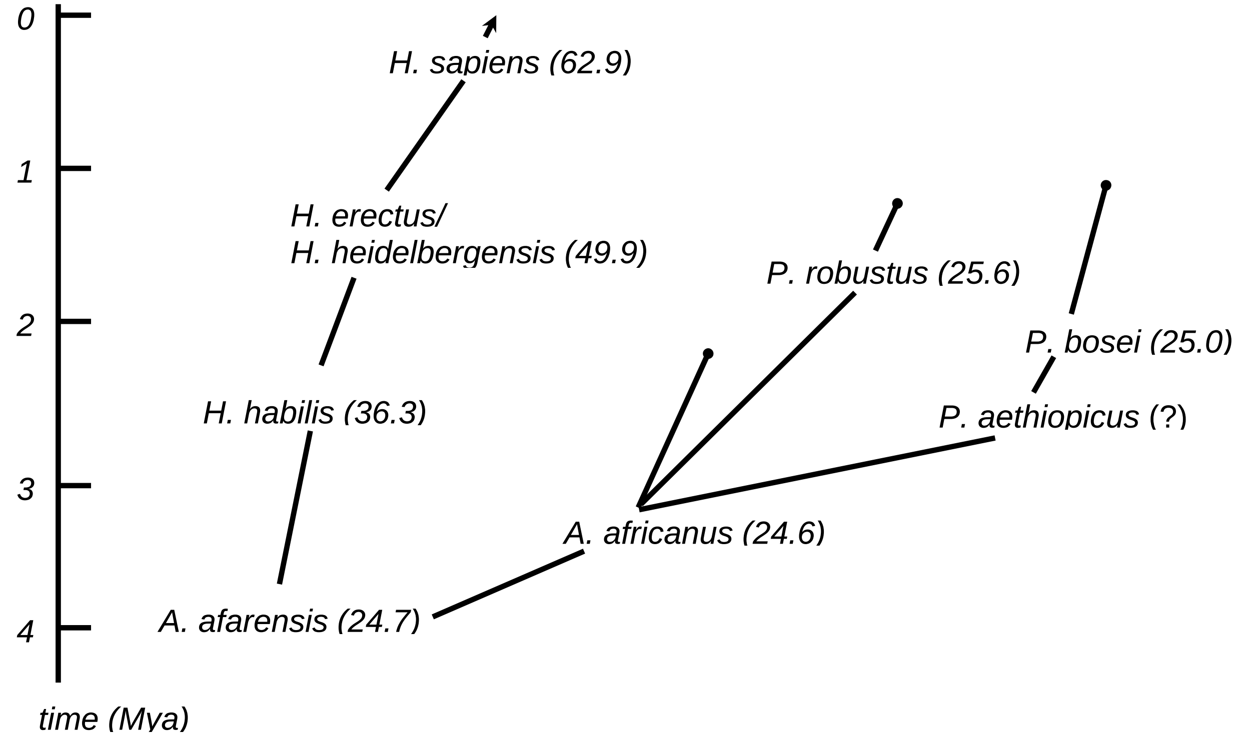

Figure 1. A Simplified Hominin Phylogenetic Tree with Encephalization Quotients (EQ).

Sources: Smithsonian (2008); Williams (2002)