

## Niche Construction through Cooperation: A Nonlinear Dynamics Contribution to Modeling Facets of the Evolutionary History in the Genus *Homo*

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### CA+ Online-Only Material: Supplement A

The transition from early members of the genus *Homo* to *Homo erectus/ergaster* is marked by subtle morphological shifts but resulted in substantial changes in evolutionary trajectory. Predation pressures on the hominins may have been significant in influencing this transition. These contexts might have stimulated a shift in behavior and modes of engagement with the environment that initiated a complex suite of changes facilitating the emergence of current features of humanity. In this report we outline a potential model for these shifts based on nonlinear dynamical interactions involving niche construction and increased reliance on complex cooperation as an antipredator strategy. Modeling proposed selective predation pressures on early humans, leading to the idea that increasingly complex sociality, patterns of cooperation, and niche construction laid the foundation for the successful emergence and spread of the genus *Homo* and potentially a concomitant decline for the genus *Paranthropus*.

The transition by an early hominin group to the genus *Homo* is marked by subtle morphological shifts but resulted in substantial changes in evolutionary trajectory and range of adaptation (Conroy 2004; McHenry and Coffing 2000; Wells and Stock 2007; Wood and Collard 1999). Predation and other ecological pressures on Australopithecines and early members of the genus *Homo* may have been significant in this transition (see Hart and Sussman 2005; Lockwood et al. 2007; Treves and Palmquist 2007; Wood and Strait 2004). These contexts might have stimulated a shift in behavior and modes of engagement with the environment that initiated a complex suite of changes facilitating the emergence of some key current features of humanity. It is our contention that predation pres-

ures, cooperation, and the relationship between *Homo* and other sympatric hominins are core facets of our evolutionary histories and that nonlinear models incorporating niche construction can facilitate understanding of these histories.

Substantial change occurred in behavioral patterns during the transition from earliest forms of the genus *Homo* (late Pliocene) to early and middle *Homo erectus/ergaster* (early Pleistocene; Antón 2003; Wells and Stock 2007). These changes most likely included increased cooperative behavior, enhanced foraging capabilities, and substantially augmented manipulation and utilization of extrasomatic components of the environment (Aiello and Wells 2002; Antón 2003; Fuentes 2004; Hawkes et al. 2003; Hrdy 2005; Ungar et al. 2006; Wells and Stock 2007). These changes are also associated with a significant range expansion of *Homo* and eventually the extinction of all non-*Homo* sympatric hominins.

Between ~2.5 and 1 million years ago (mya) there were two sympatric lineages of hominin in eastern and southern Africa, the genus *Homo* and the genus *Paranthropus*. Throughout this period we see substantial climatic fluctuations occurring and the spread of the genus *Homo* throughout Africa and across Eurasia (eventually giving rise to modern humans; Potts 1999; Wells and Stock 2007). This period is also characterized by significant turnover in the species structure and overall sizes of the major carnivorous mammals in Africa and across Eurasia (Agusti and Antón 2002; Van Valkenburgh 1999; Werdlin and Lewis 2005). By approximately 1 mya, the genus *Paranthropus* was extinct (Wood and Constantino 2007). The most common assumptions/models for the evolution of the genus *Homo* include a series of innovations/changes that led to an expansion of the realized niche for the genus *Homo* and a substantial expansion in geographic range. These models include a focus on increased ecological efficiency, “big” brains and increased cognition, extrasomatic manipulation (tool use), hunting and/or increase in meat consumption, and “culture” or information sharing. Behavioral responses to variable ecologies, niche construction, and expanded “colonizing capability” were recently proposed as core features in this expansion (Potts 2004; Wells and Stock 2007).

While many researchers (e.g., Potts 2004; Richerson and Boyd 2005; Tattersall 2004; Tomasello 1999; Ungar et al. 2006; Wells and Stock 2007) do focus on behavioral flexibility and extrasomatic manipulation as central to the adaptive success of the genus *Homo*, there have been fewer proposals that specifically focus on aspects of cooperation and predation and their relationship to selection pressures in scenarios for the evolution of the genus *Homo* (but see Fuentes 2004; Hart and Sussman 2005).

There is a widespread recognition that single-trait explanations for complex evolutionary pathways are incomplete at best, and it is apparent that any relationship between the success of the genus *Homo* and the extinction of the genus *Paranthropus* would involve multiple factors. However, the most often-used explanation for *Homo*'s success and *Par-*

*anthropus*'s extinction is Robinson's dietary hypothesis: members of genus *Homo* were generalist foragers (eurytopic), and the members of the genus *Paranthropus* were specialist foragers (stenotopic); thus, ecological pressures of changing environments favored *Homo* (Ungar et al. 2006; Wood and Strait 2004; and see Verhaegen and Puech 2000).

Dental and related fossil analyses indicate that *Paranthropus* was not particularly stenotopic (specialist) and that *Homo* was not more eurytopic (generalist) than *Paranthropus* (Lee-Thorp and Sponheimer 2006; Sponheimer and Lee-Thorp 2007; Sponheimer et al. 2006; Wood and Constantino 2007; Wood and Strait 2004; and see Codron et al. 2008). Wood and Strait (2004) demonstrate that Robinson's dietary hypothesis is not supported across a majority of morphological and ecological variables—both genera appear relatively eurytopic. If this is the case, then dietary strategies and flexibility in foraging behavior may not account for the differential survivorship between the two genera. Wood and Strait (2004) propose that we should consider at least seven variables to explain the success of *Homo* and the extinction of *Paranthropus*. Those variables are locomotor mode, degree/mode of tool use and/or production, predator avoidance/predation pressure, competition from other primates or mammals, competition between *Homo* and *Paranthropus*, social group structure, and the capacity for learned behavior.

In this report, we follow the lead of Hart and Sussman (2005), Treves and Palmquist (2007), and Wood and Strait (2004) and also consider the evidence for predation on *Paranthropus* and *Australopithecus* (see Berger and Clarke 1995; Lockwood et al. 2007). We propose a model wherein a focus on the role of predation and differential ability to share information and cooperatively modify functional facets of the environment provide an important component of the explanation of the success of the genus *Homo* relative to the affiliated hominin taxon *Paranthropus*.

### Niche Construction and the Success of the Genus *Homo*

Between 2.5 and 1 mya, members of the genera *Homo* and *Paranthropus* were likely sympatric and overlapped in morphological, locomotory, dietary, and some behavioral facets (Ciochon and Fleagle 2006; Conroy 2004; Wood and Strait 2004). Therefore we (and others; see Hart and Sussman 2005 for a review) suggest that both may have been under pressure from similar predators. Lockwood et al. (2007) in a review of 35 South African *Paranthropus* specimens suggest that damage to the fossils examined indicates that predation was likely a significant selection pressure for *Paranthropus*, especially males. Wells and Stock (2007), among others, emphasize the concept of a suite of adaptations associated with range expansion, including niche construction, as a major factor in *Homo erectus* success. Multiple authors have noted the substantial climatic shifts during this period, with many suggesting that this pattern of environmental instability may have

contributed to changes in hominin evolutionary trajectories, especially in regard to behavioral responses to selection pressures (e.g., Potts 1999; Wells and Stock 2007). We suggest that incorporating a niche construction perspective into standard models of population growth and the impact of predation can facilitate a better understanding of the relationship among *Homo*, *Paranthropus*, and predation and its outcomes.

Niche construction is defined as the modification by organisms of the functional relationship between themselves and their environment through an active change of one of the factors of that environment. "Through niche construction organisms not only influence the nature of their world, but also in part determine the selection pressures to which they and their descendants are exposed, and they do so in a non-random manner" (Day, Laland, and Odling-Smee 2003:80). As organisms respond to environmental selective pressures that are themselves modified by the organisms, a feedback mechanism is created, and such feedback loops can fundamentally alter the outcome of evolutionary scenarios (Kylafis and Loreau 2008; Cuddington, Wilson, and Hastings 2009).

We propose a model that includes a major role for selection pressures from predation along with competition and social cooperation (Fuentes 2004) and couches it in the context of the Pleistocene fossil record (i.e., *Homo* resilience and expansion and *Paranthropus* extinction). Approaching human evolution using a feedback model perspective in the context of niche construction theory (Odling-Smee et al. 2003) can provide a strong conceptual tool and support the notion that ameliorating predation pressures may have been a boon to *Homo* but a bane to *Paranthropus*.

A simple mathematical model examining population growth, predation, and carrying capacities suggests that as effectiveness of intragroup cooperation increases, the impact of factors such as predation and carrying capacity can shift and diminish (see also Bowles 2006). Human ancestors' social cooperation, including information transfer, and its concomitant alteration of local ecology may have been a major factor in human evolutionary success. In fact, Fuentes (2009) and Richerson and Boyd (2005), among others, provide scenarios where increased behavioral complexity, especially aspects of communication and cooperation, can result in altering evolutionary trajectories for humans. While acknowledging that such a simple system will not offer a truly accurate model of human evolution, we hold that it might produce a set of perspectives that help explain the patterns in the fossil record and simultaneously demonstrate how small changes in cooperative behavior resulting in niche construction can radically alter relationships between species in shared environments.

Major assumptions laying a baseline for our model are a set of selective pressures, a set of hypothesized responses, and hypothesized relationships emerging from these responses that result in niche construction. The selective pressures include initially roughly equivalent predation pressure on *Homo* and *Paranthropus* and increasing physiological (energetic) and child-rearing (increased dependency period) costs for the ge-

nus *Homo*. The hypothesized responses to these pressures by members of the genus *Homo* include a suite of cooperative intragroup patterns associated with changes in foraging and child-rearing behavior (associated with an increase in communicative complexity and information sharing; see Fuentes 2004; Hrdy 2005; Richerson and Boyd 2005; also see Wall-Scheffler et al. 2007), increased effectiveness at avoiding predation (including active antipredator strategy, possibly including tools, projectiles, other extrasomatic manipulation, and multi-individual coordination of antipredator behavior), and an expansion of types and patterns of habitat exploitation (niche expansion).

We suggest that these responses result in niche construction altering the patterns of selection pressures on the hominins *Homo* and *Paranthropus*. As *Homo* becomes more costly for predators (due to the above responses), the predators shift emphasis to more accessible prey items of similar size in roughly the same environments, which in this case could potentially be both baboons (*Theropithecus*) and *Paranthropus*. This has an impact of reducing the overall selective pressure of predation on the genus *Homo*. As predation pressures wane (relatively) on *Homo*, there is increased opportunity for social interactions, range exploration, and testing a variety of novel foraging opportunities and targets. With increased cooperative interactions between members of *Homo* groups (and potentially between groups in local areas), foraging efficiency, predator avoidance, and care for offspring further increase in effectiveness (positive feedback), facilitating the observed range and habitat expansion in the period 1.8–1.0 mya.

### Details of the Model

The aim of a mathematical model of population growth is twofold: to predict the population of a species at some point in time and to understand how specific factors might affect that population. While all models are approximations, effective models may predict behaviors that intuition and the fossil record alone cannot. Table 1 lists four population models in order of increasing complexity. The exponential model predicts the increase of a population with no resource limits.

The logistic model considers the depletion of resources by large populations and imposes a limit on the ultimate population size. We propose two additional models, the single-species and two-species cooperation models (see CA+ online supplement A for details of the mathematical analysis of these models). These take into account cooperation within one species and the effect such cooperation may have on a second species. These models include the positive feedback that a cooperative population may exert upon itself, illustrating the basic principles of niche construction.

The simplest population growth model is the exponential model. It stipulates that the change in the size of a population— $dH/dt$ —is given by the product of the size of that population  $H$  and some fixed intrinsic growth rate  $r$  (basic reproductive rate of the species). Since both  $H$  and  $r$  are positive, the rate of growth is likewise positive—that is, the population will grow, and there is no limit on its growth. Figure 1A illustrates how the population  $H$  may grow with time, given some initial population. The growth rate is controlled by  $r$ , but qualitatively the effect is the same for any value of  $r$ : the population explodes. Figure 1B emphasizes this result by compressing the time axis and illustrating that all starting population sizes will grow without bound.

This population explosion predicted by the exponential model amounts to an approximation of what a real population does when no resource limits are imposed. Of course, as noted by Malthus, Darwin, and countless researchers since, resources are never infinite and will ultimately curb the growth of any real population. Such factors are external to this simple model and pose a limit to its range of validity (Cuddington 2009), yet it remains useful as an indicator that large-scale changes in the population may occur.

The logistic model takes resource limits into account by reducing the growth rate as the population approaches some fixed size. After a long enough time, the population reaches this carrying capacity, regardless of whether it started larger or smaller than this size. In the logistic model, the parameter  $K$  specifies the carrying capacity (Kingsland 1995). Figure 2A illustrates how the population approaches the carrying ca-

Table 1. Model equations

Model name	No. species	Equation
Exponential	1	$\frac{dH}{dt} = rH$
Logistic	1	$\frac{dH}{dt} = r\left(1 - \frac{H}{K}\right)H$
Single-species cooperation	1	$\frac{dH}{dt} = r\left(1 - \frac{H}{K} + SH^2\right)H$
Two-species cooperation	2	$\frac{dH}{dt} = r_H\left(1 - \frac{H}{K_H} - S_P P^2 + S_H H^2\right)H$ $\frac{dP}{dt} = r_P\left(1 - \frac{P}{K_P} - S_H H^2 + S_P P^2\right)P$

Note.  $r$  = intrinsic growth rate,  $K$  = nominal carrying capacity,  $S$  = cooperation,  $\beta = SK^2$  = cooperation parameter (combined),  $H$  = *Homo* population size, and  $P$  = *Paranthropus* population size.

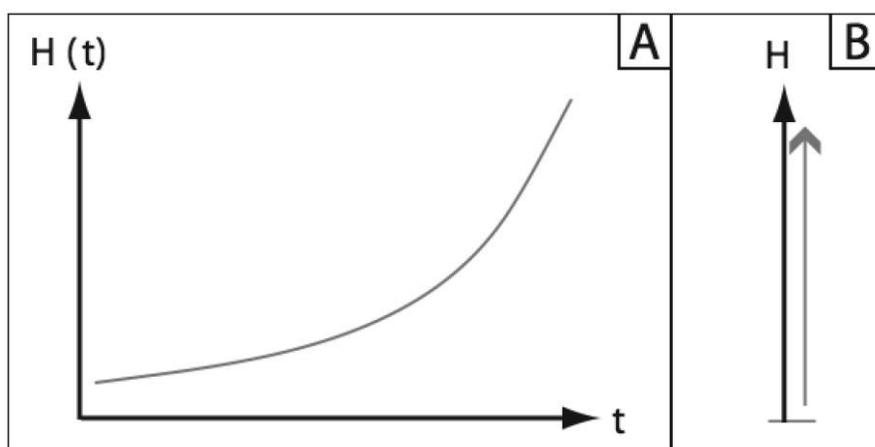


Figure 1. Exponential model. *A*, How a population will grow in time under the exponential model. *B*, With time implicit, a population of any (nonzero) size will grow without bound.

capacity, whether by increasing from a smaller population or decreasing from an excessively large population size. Figure 2*B* makes time implicit and emphasizes the stability of the equilibrium population size, or the carrying capacity.

While the logistic model successfully predicts the effects of resource depletion on population growth, it cannot account for the effects of niche construction (Krakauer et al. 2009; Odling-Smee et al. 2003). Resource usage in the logistic model is proportional to population size. The effect of niche construction, on the other hand, is a *nonlinear* function of population size. For instance, the resources, per individual, devoted to predator avoidance in a small group may be much greater than those in a large group, resulting in fitness that increases more quickly than group size. Such economies of scale create positive feedback in populations and are central to niche construction, and they cannot be accounted for by a constant  $K$ .

The central importance of feedback in niche construction has been recognized by other authors (Cuddington et al. 2009; Gurney and Lawton 1996; Krakauer et al. 2009) who modify the logistic equation by including the niche as an external variable that is modified by, and in turn modifies, the population. Our models differ from previous work in that they consider niche construction based on behavior, with no direct changes to the physical environment per se. Related mathematical models have been shown to accurately predict the population dynamics of competitive *Drosophila* species (Gilpin and Ayala 1973).

The single-species cooperation model attempts to account for effects that are not proportional to population size. The parameter  $S$  defines the degree of cooperation in a population, and the strength of its contribution is the square of the population size. As a result, its effects are negligible for small populations and increasingly dominant for large ones.

A population with a positive  $S$  engages in niche construction; as a result, larger populations have, effectively, a higher fitness. Intuitively, we can understand that this may increase their equilibrium carrying capacity above the level given by the parameter  $K$  (see also Krakauer et al. 2009; Kylafis and Loreau 2008). In order to understand the effects of  $S$  in more detail, further analysis of the system for a broad range of  $S$  values is necessary.

It is convenient, for the sake of analysis, to define a new parameter:

$$\beta = SK^2.$$

The  $\beta$  still controls the degree of cooperation of the population model, and we will call  $\beta$  the “cooperation parameter.” Note that when  $\beta = 0$ , the cooperation model reduces to the logistic one.

Figure 3*A* shows how the population changes over time for one particular value of  $\beta$ . If the initial population is less than the critical size (given by  $H_{\text{unstable}}$ ), it will grow or shrink until it reaches the size given by  $H_{\text{stable}}$ . This is the carrying capacity in the single-species model—qualitatively, the population behaves like that in the logistic model. If, however, the starting population is larger than the critical size ( $H_{\text{unstable}}$ ), then it will grow without bound, as in the exponential model.

While figure 3*A* illustrates the behavior over time for one specific  $\beta$  value, the diagram in figure 3*B* shows how the system behaves for all values of  $\beta$ . In particular, figure 3*B* shows how  $H_{\text{stable}}$  and  $H_{\text{unstable}}$  change as  $\beta$  changes. Consider three cases: (1)  $\beta = 0$ : the population behaves like in the logistic model, growing or declining until it equals the carrying capacity given by  $K$  whatever the initial conditions; (2)  $\beta$  between 0 and 1/4: depending on its initial size, the population may reach a stable population size given by  $H_{\text{stable}}$

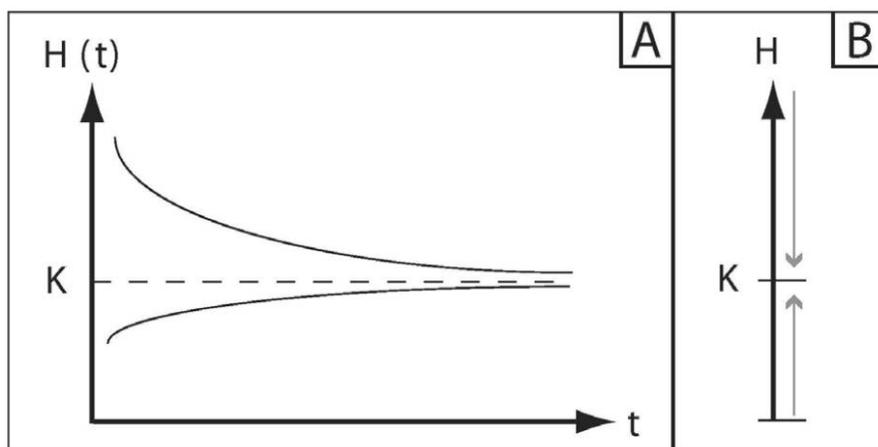


Figure 2. Logistic model. Under the logistic model, small populations increase in size and large populations decrease until the carrying capacity (given by  $K$ ) is reached.

(whose value is between  $K$  and  $2K$ ); or, the population may explode and grow without limit; and (3)  $\beta > 1/4$ : no stable population size exists, and the population will grow indefinitely regardless of the initial population size.

As illustrated in figure 3, cooperation as a niche-constructing element can have a profound effect on the growth of a population. When the cooperation is moderate, a small population grows to its carrying capacity (and this carrying capacity is somewhat larger than that in the logistic model). However, if the population starts off large (larger than  $H_{\text{unstable}}$ ), it will grow without bound. As a result, for moderate cooperation ( $\beta$  greater than 0 but less than  $1/4$ ), the ultimate size of the population depends on the initial population size. This critical population size decreases with increasing cooperation, and at  $\beta = 1/4$  the  $H_{\text{stable}}$  and  $H_{\text{unstable}}$  population sizes are equal. For the cooperation parameter larger than  $1/4$ , all populations will grow without bound, just as in the exponential model.

Finally, we consider a two-species cooperation model: the population of one species is given by  $H$  and of the other by  $P$ . Each species has its own intrinsic growth rates  $r_H$  and  $r_P$ , nominal carrying capacity  $K_H$  and  $K_P$ , and cooperation  $S_H$  and  $S_P$ , respectively. We define the cooperation parameters  $\beta_H$  and  $\beta_P$  as  $S_H \cdot K_H^2$  and  $S_P \cdot K_P^2$ , respectively.

The growth rates of the two species are like that for the single-species cooperation model, with the exception that the benefits of cooperation in one species result in an equivalent detriment in the other. Specifically, cooperation in  $H$  results in an increased rate of growth of  $H$  given by  $S_H \cdot H^2$ ; in turn, the rate of growth of  $P$  is decreased by the same amount, and vice versa. This coupling of the rate of growth of the species then models the transfer of, for example, predation pressure from the more cooperative species to the less cooperative one. Note that aside from sharing predation pressure there is no

direct competition for resources in this model (via the  $K$  parameters).

Introducing a second species complicates the analysis somewhat, in part because visualizing all possible solutions is more difficult. For the discussion that follows, we will assume that the cooperation of species  $P$  is fixed at some intermediate value, for example,  $\beta_P = 1/8$ . Figure 4 shows how populations of  $H$  and  $P$  change with  $\beta_H$  while  $\beta_P$  remains fixed. With  $\beta_H$  less than  $1/4$ , both species coexist. Small changes in  $\beta_H$  not near the critical value of  $1/4$  result in only small changes to the equilibrium populations, analogous to small changes in the carrying capacity for the logistic model. As  $\beta_H$  increases past the value of  $1/4$ , however, this system undergoes a fundamental shift: the equilibrium solution disappears. Now, the *Homo* population will explode, while *Paranthropus* will decline to extinction. Such a bifurcation causes the system to change rapidly and fundamentally with only small changes to the parameter  $\beta_H$ , a phenomenon that does not occur in linear models. As a result, models with the feedback that is inherent in niche construction can behave in ways fundamentally different, and not predictable, from simpler models where such feedback is ignored.

This is an important result in the context of *Homo/Paranthropus* evolutionary history, illustrating how increased cooperation by *Homo* and its subsequent niche construction effects may have contributed to the extinction of *Paranthropus* even in the absence of direct competition for resources. This simple model is based on a number of assumptions about the relationship between *Homo* and *Paranthropus* and their predators and does not include any detailed assessment of specific factors related to resource use or environmental manipulation. We do not suggest that this particular cooperation model accurately describes the actual population dynamics of *Homo* around 2–1 mya. However, the model does illustrate

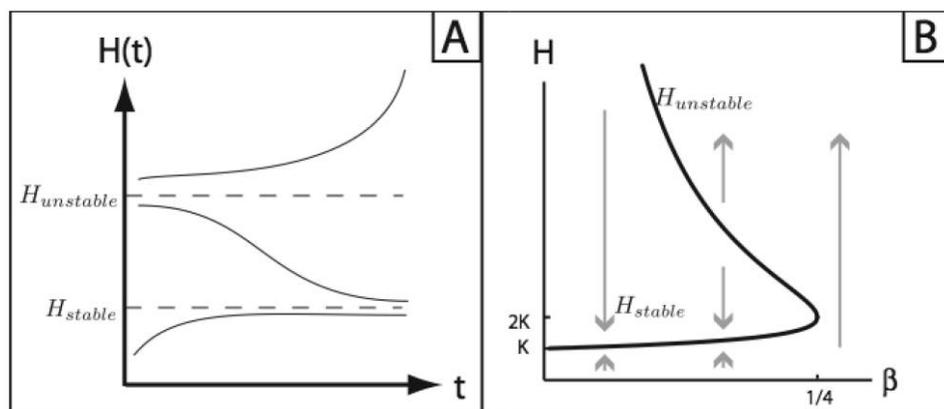


Figure 3. The single-species cooperation model. The equilibrium population size depends on the initial conditions in the single-species cooperation model. A shows how the population varies with time for some value of the cooperation parameter  $\beta$  between 0 and  $1/4$ , illustrating dependence on initial conditions. B depicts the fate of populations, given different starting sizes, for all values of  $\beta$ .

how cooperation, as it shifts predation pressure from one species to another, can engage a feedback mechanism that influences the decline, or even eventual extinction, of a species. The inclusion of cooperation and positive feedback in ecological models of human evolution—essential components of niche construction (Odling-Smee et al. 2003)—can have profound consequences on evolutionary trajectories. Feedback generally implies nonlinear terms in mathematical models and results in behavior—such as dependence on initial population size or sensitivity to small changes in parameters—which may be surprising or even counterintuitive when considered with regard to simpler linear models (DeAngelis et al. 1986).

#### Is There Any Support for the Scenario We Propose?

We contend that the underlying concepts behind this model are supported via theoretical and fossil evidence. Niche partitioning between similar species, when sympatric, is common among many living primate species (e.g., Buzzard 2006; Hill and Weingrill 2007; Mendes Pontes 1997; Porter and Garber 2007; Stanford 2006; Sushma and Singh 2006; Sussman 1974), suggesting that a similar pattern for *Homo* and *Paranthropus* would fit within a primate trend. However, niche partitioning usually appears to relate to foraging pressures, not predation; even in mixed-species populations with primates occupying nonoverlapping niches, predation can impact multiple species equally (see overview in Miller 2002; Miller and Treves 2007). Current studies indicate that open savannah/woodland primates (baboons, vervets) do experience predation and exhibit behavioral strategies to avoid it (e.g., Swedell 2006; Hill and Weingrill 2007); thus, hominins living in similar environments most likely also shared a similar experience and context

(Hart and Sussman 2005; Miller and Treves 2007; Treves and Palmquist 2007).

In our closest relations (*Pan* and *Gorilla*), we see a pattern of substantial niche overlap with important dietary divergence when both genera exist in the same geographic area (Stanford 2006, 2008; Stanford and Nkurunungi 2003). We also know that the same predators (e.g., leopards) potentially prey on gorillas and chimpanzees (Miller and Treves 2007), suggesting that even if *Homo* and *Paranthropus* did diverge in use areas, they still could have been under similar pressures from the same predators.

Evidence of predation appears to be common in Australopithecine and especially *Paranthropus* fossils (Berger and Clarke 1995; Hart and Sussman 2005; Lockwood et al. 2007). This suggests that it was also a factor for sympatric *Homo*; however, there are too few fossils to build a reliable data set to effectively test this. There is evidence that the species assemblage of potential hominin predators was undergoing radical shifts during the time period of interest. An overall decrease in the size of hyaenids and a shift from saber-toothed felids to smaller conical-toothed felids in predator communities sympatric with hominins characterized the time periods between 2.5 and 1 mya (Marean 1989; Werdlin and Lewis 2005). This shift in predator size and species composition combined with a shift in *Homo* behavior (that made them more costly targets) could have shifted the predation ecology such that *Homo* benefited from reduced predation pressures. It is also suggested that in this same time period *Homo* may have increased their exploitation of saber-tooth felid kills as scavenge sites (Marean and Ehrhardt 1995), giving them simultaneously increased energy intake and more experience dealing with the predators and possibly a better knowledge

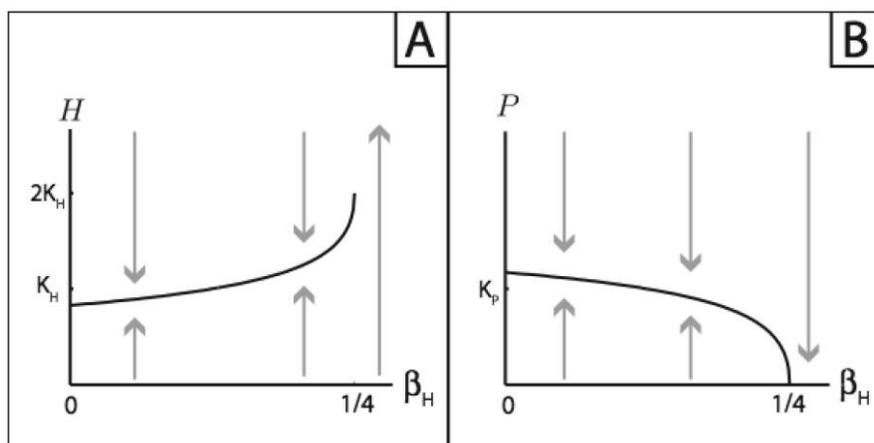


Figure 4. The two-species cooperation model. Two phase plots, one for species  $H$  (A), the other for species  $P$  (B), illustrating the equilibrium fate of populations for different values of  $\beta H$ , given that  $\beta P$  has a fixed value of  $1/8$ . As in the one-species model, the final population sizes are dependent on the initial sizes, with the parameter  $\beta H$  modulating this dependence.

of predator behavioral patterns. Regardless of the direct evidence for predation, early *Homo* shares many general morphological characteristics with sympatric *Paranthropus* and appears to have exploited similar environments, suggesting that an initial overlap in predation pressures is a relatively secure assumption and that behavioral divergence could have led to differentiation in these pressures. Fossil evidence supports the contention that *Paranthropus* becomes increasingly rare and eventually extinct by 1.0–1.4 mya (Wood and Constantino 2007).

While cooperation is important and central as a behavioral pattern and locus of energetic investment across primate species, humans differ in a number of ways from other primates. Species that are able to exploit a more complex manner of cooperation via social bonds and complex cognitive interactions may have an advantage over other species with less developed capacities (Dunbar and Schultz 2007; Hermann et al. 2007; Silk 2007). As *Homo* individuals, via increased cognitive capabilities and concomitant increased cooperation, were able to exploit resources, raise offspring (Hrdy 2005), and avoid predation more effectively, they may have become “winners” in scramble and contest competition, forcing *Paranthropus* to shift toward lower-cost foraging and possibly higher predation risk.

The transition from early *Homo* to *Homo erectus/ergaster* is marked by a substantial body-size and brain-size increase, with estimated energy costs increasing by as much as 40% (Aiello and Wells 2002). Such a radical change in the cost of running one’s body suggests a change in behavioral patterns to increase energy intake/conservation/efficiency (Aiello and Wells 2002). These patterns, if they involved substantive enhancements in cooperative abilities and within-group coord-

ination of range use/habitat exploitation, could have resulted in improved efficiency of child rearing, group movement, and overall access to resources relative to *Paranthropus*. Potts (1999) suggests that given the rapid and broad fluctuations in climate and microhabitats during the period 2.5–1 mya, the ability to adapt behavior (via shifting/plastic behavioral strategies) would have been favored over investment in targeted morphological adaptations (see also Hrdy 2005; Stock and Wells 2007). Potts (2004) argues that this is where social complexity and behavioral flexibility in the larger-brained *Homo* come to the fore as a major interface with the environment, one that was potentially unavailable to the same extent in *Paranthropus* (given our assumptions about their cognitive and behavioral constraints relative to *Homo*). Specifically, this could include greater density of information transfer and sharing, more group members involved in child rearing (Gettler 2010), and extended cooperation across age classes and sexes within groups in *Homo*. It is also possible that there might have been some selective intergroup cooperation as well (Fuentes 2004, 2009). These patterns would result in *Homo* having a wider range of behavioral possibilities and social networks than did *Paranthropus* in the same environments, especially in regard to avoiding/ameliorating the pressures of predation.

Fossil (Antón 2003), genetic (Templeton 2002), and physiological (Wells and Stock 2007) data support a very rapid and widespread range expansion by *Homo* during the terminal Pliocene and early Pleistocene (1.8 to ~1.0 mya). Initially the expansion (1.8–1.5 mya) was not accompanied by a radical shift in material culture (e.g., stone tool types/kits). So there must have been shifts in behavioral patterns as the following elements changed when *Homo* moved into novel and/or

changing environments: types of foodstuffs, types of annual seasonal cycles, types of predators, and types of other animals competing for similar resources. As the predator communities were also changing at this time, the ability to exhibit substantive flexibility in response to changing predator strategies would also have been a boon. At least some expansion between 1.5 and 1.0 mya is associated with novel tool types (Ciochon and Fleagle 2006; Conroy 2004). We see no evidence of range expansion in *Paranthropus*; rather, their presence in the fossil record diminishes to extinction during this same period of increased *Homo* success.

The largest Pleistocene sample of genus *Homo*—the 19 individuals from Atapuerca, Spain (Sima de los Huesos, *Homo heidelbergensis*, ~500,000–400,000 years ago)—stand in specific support of cooperation in the fossil record. This sample reveals a relatively equal mix of males and females and a wide age range (but fewer children than expected); there were no skeletal indications of sexual division of labor but some indications that life expectancy was short and that females began reproducing very young (Bermudez de Castro et al. 2004). With high mortality in young adults, the possibility for orphans increases and cooperative child rearing is likely (Hrdy 2005). This notion of cooperative support is enhanced by existence of at least one blind and one deaf adult in the sample, suggesting group assistance to these individuals (Arsuaga et al. 1997). While this is a population much more recent than those we focus on in our proposed model, it is assumed to have derived from a population of *H. erectus/ergaster* and thus displays potentially shared patterns of behavior (Arsuaga et al. 1997; Bermudez de Castro et al. 2004). Also, Wells and Stock (2007) summarize what they term the “biology of the colonizing ape,” referring to the types and patterns of biological adaptations that emerged with *H. erectus* and are associated with its dispersal around and out of Africa. These elements include behavioral and physiological plasticity, complex information sharing, slowed developmental patterns with long-term learning requirements, and niche construction. This suite of characteristics is predicated on substantial cooperation between individuals, more than is evident in any living primate aside from humans.

Finally, recent contributions to evolutionary theory have demonstrated the importance of niche construction in shaping evolutionary trajectories (Fuentes 2009; Kylafis and Loreau 2008; Odling-Smee et al. 2003) and established that behavioral plasticity can be a prominent result of successful adaptation (Nussey et al. 2007; West-Eberhard 2003). Developmental systems theory and its notions of extended inheritance and multimodal systems evolution (Oyama et al. 2001) also support assumptions about the role of modified environments and the inheritance of extrasomatic contexts. These basic perspectives add to fundamental assumptions of natural selection in evolutionary theory, and they all potentially provide support to the scenario laid out above.

## Conclusion

We suggest that increased behavioral flexibility and cooperative interactions allowed for a successful pattern in the genus *Homo*, one that characterizes our genus and species through today (Wells and Stock 2007). The transition to *Homo erectus/ergaster* is marked by a shift in primary selection pressures, including fluctuating environmental conditions combined with increased body size and ensuing energetic and child-rearing costs, to which *Homo* responds with behavioral changes resulting in reduced predation and increased manipulation of extrasomatic materials and the environment. These behavioral changes most likely involve enhanced cooperation and information transfer leading to increased foraging success and effectiveness in antipredation behavior. Simultaneously, predator community compositions shifted toward smaller species that *Homo* may have been more effectively able to avoid and/or deter through their cooperative action. The combination of these patterns results in substantial niche construction and the selective landscape for hominins shifts in a positive direction for members of the genus *Homo* and, potentially, a negative one for members of the genus *Paranthropus*.

The positive feedback in populations that construct their niches can be modeled only by nonlinear mathematical terms, such as those introduced in the models proposed here. The two-species cooperation model allows for a compelling description of some forces related to both an expansion and an extinction event. The two species existed at equilibrium for an evolutionarily long period of time. As *Homo* acquired enhanced cognitive abilities, enhanced extra-somatic manipulation of the environment, and increasingly sophisticated social structure, cooperation in the groups increased, an effect captured in the cooperation parameter  $\beta H$ . Small changes in such a system typically yield small changes in population size. There are critical regions, however, where small changes yield disproportionate, even catastrophic, changes to the system as a whole and populations crash or explode.

While simplistic and obviously not a full representation of the complex selective landscapes for the genera *Homo* and *Paranthropus* in the terminal Pliocene/Early Pleistocene, our model does emphasize a few important points. A predominant implication is that nonlinear effects can have dramatic impacts on population dynamics, with bifurcations potentially leading to both sudden changes in behavior and possible extinctions. This suggests that cooperation and niche construction can be significant aspects of evolutionary processes as organisms modify the environment in substantial ways and those modifications in turn alter evolutionary pressures. Such feedback effects are inherently nonlinear and probably play an important role in developing more accurate reconstructions of human evolutionary history. We suggest that this perspective and approach are an important contribution to anthropological explorations of our evolutionary past.

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