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Agent-based models as behavioral laboratories for evolutionary anthropological research

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Abstract: Agent-based models can provide paleoanthropologists with a view of behavioral dynamics and site formation processes as they unfold in digital caricatures of past societies and paleoenvironments. This paper argues that the agent-based methodology has the most to offer when used to conduct controlled, repeatable experiments within the context of behavioral laboratories. To illustrate the potential of this decidedly heuristic approach, I provide a case study of a simple agent-based model currently being used to investigate the evolution of Plio-Pleistocene hominin food sharing in East Africa. The results of this null model demonstrate that certain levels of ecological patchiness can facilitate the evolution of even simple food sharing strategies among equally simple hominin foragers. More generally, they demonstrate the potential that agent-based models possess for helping historical scientists act as their own informants as to what *could* have happened in the past.

Key words: agent-based models, altruism, artificial societies, hominin food sharing, paleoanthropology

> [I]n making their experiments scientists will take some group—bacteria, mice, people—and subject that group to certain conditions. They compare the results with a second group which has not been disturbed...It is the control group which enables the scientist to gauge the effect of his experiment. To judge the significance of what has occurred. In history there are no control groups. There is no one to tell us what might have been. [McCarthy 1992:239]

Two components of McCarthy's passage should resonate deeply with paleoanthropologists. First, no living human population—hunter-gatherer or otherwise—can serve as a control group by which to gauge the effect of selection on the frequency of a particular trait or to assess the evolutionary success of a particular hominin species. Second, the only direct informants we have of the biological and cultural processes

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that have already unfolded (including the evolution of bipedalism, division of labor, and food sharing, to name just a few) are the fossil and cultural material remains and their contexts. But even these important data cannot directly inform us of what *might have been,* given different environmental conditions and historical events. This paper discusses how a relatively young computational technique, called agent-based modeling, can be used to study the evolutionary consequences of alternative histories in digital caricatures of past societies and their paleoenvironments. By allowing paleoanthropologists to conduct controlled, repeatable experiments within the context of "behavioral laboratories," agent-based models can act as unique informants about what could have occurred in the past.

It is important to note at the outset that, although archaeologists often use terms like "computer simulation" and "simulation model," few would argue that such models actually *simulate* (as in emulate, imitate, or mimic) every detail of the past. Models merely make it possible to systematically explore ideas about the past independently of the empirical data against which we must continuously test theory (van der Leeuw 2004). Equally importantly, models also allow us to see when conventional assumptions lead to implausible outcomes or when they are unnecessary to explain observed phenomena of interest. Put simply, models are interactive tools that provide opportunities to follow the implications of one's ideas to find where they are inconsistent and, from this, to build better-informed explanations of empirical data.

It follows that agent-based models are of the highest utility to paleoanthropologists when they are used to explore alternative cultural histories rather than to emulate conventional interpretations. To illustrate the benefits of this heuristic approach I will discuss some results collected from an agent-based model that I use to explore ideas about the evolution of food sharing among Plio-Pleistocene hominins. I preface this with an introduction to some of the important qualities that distinguish agent-based models from their top-down counterparts.

HOW ARE AGENT-BASED MODELS UNIQUE?

As the name implies, agent-based (or individual-based) models make use of software objects called agents. Agents are autonomous entities, equipped with limited means to perceive and react to their environment. They sense and manipulate their surroundings on an individual and usually goal-directed basis. Each agent "decides" how to act by continually comparing the current values of its state variables to desired, optimal, or ideal values. Agents may also communicate with each other via messages, commands sent from one to another during the course of a simulation. A message might prompt the receiver to enact a particular method (action) or it might be ignored, depending on the situation.

In some agent-based models, a single agent interacts with an environment through simulated time (Brantingham 2003, 2006). In others, hundreds, or even thousands, of agents interact with an environment and with each other through simulated time, thereby forming artificial societies (Dean et al. 2000; Epstein and Axtell 1996; Kohler et al. 2000, 2005; Lansing 2002; Premo 2005, 2006). Whereas the conditional rules each agent follows may be quite simple, the aggregate outcome of an artificial society of agents may be difficult to predict, even given perfect *a priori* knowledge of all possible individual actions. Thus, artificial societies often exhibit *emergent* collective properties that can be strikingly similar to those displayed by real societies. The ability to study emergent, nonlinear dynamics from the bottom-up is one of the key differences between agent-based models and top-down, deterministic models (Epstein and Axtell 1996), but there are at least three others.

First, agent-based models allow for heterogeneity among agents. Whereas equation-based models usually presume homogeneous populations, which are composed of agents that each behave similarly and often tend toward some approximation of equilibrium with their environment, agent-based models can represent each agent as an autonomous individual, complete with its own unique state variable values, behaviors, and individualistic goals. By allowing agent populations to display variation in internal states and behaviors, agent-based models provide an avenue for the study of agency in social change that is not available to traditional deterministic equation-based models.

Second, many agent-based modeling platforms (e.g., Swarm, Repast, NetLogo, Ascape) include a suite of objects dedicated to representing various types of space. In fact, agent-based models are the only type of formal model capable of including a spatial typology as an entirely distinct entity. Including space in models is no minor detail. A number of researchers have stressed that the spatial distributions of agents and of resources play crucial roles in influencing which behavioral strategies succeed in small groups of players that are privy to only localized environmental information (Lindgren and Nordahl 1994; Nowak and May 1992; Pepper and Smuts 2000, 2002; Premo 2005 and 2006).

Third, by including both heterogeneous agents and space in digital models, agent-based models allow historical contingency to play an important role. This is not the case in many other types of mathematical models, where interactions between agents are arbitrarily scheduled from the top-down. The likelihood that two agents will interact in space during the "natural" progression of agent-based model execution, however, depends on the locales of their birth and the histories of their previous movement decisions rather than on an arbitrary structure imposed upon them by the modeler. As a result, agent-based models serve as invaluable methodological tools for exploring the dynamics of models that embrace historical contingency.

The most important features of the methodology can be summarized in one brief sentence: *Agent-based models make possible the study of nonlinear cultural dynamics that emerge from the historically contingent actions of heterogeneous agents interacting in space.* As Tim Kohler (2000:2) states, the social scientific research that is currently making use of agent-based models "emphasizes dynamics rather than equilibria, distributed processes rather than systems-level phenomena, and patterns of relationships among agents rather than relationships among variables." It is because of their ability to model heterogeneous populations, space, and historical contingency that agent-based models can be used to study the very kinds of biosocial evolutionary dynamics that are usually impossible to study with top-down models.

AGENT-BASED MODELS AS BEHAVIORAL LABORATORIES

In discussing the importance of historical contingency in understanding evolutionary history, the late Stephen J. Gould (1989) introduced an interesting thought experiment. Imagine being able to pick any point in the past from which history could be restarted and certain subjects observed, as if the Earth's history had been recorded on videotape. One would expect this film to project the same story with the same characters delivering the same dialogue each time it is replayed. However, Gould explains that the tape player in his thought experiment can display very different plots depending on the contingencies of history. In other words, his cosmic tape player is capable of showing different evolutionary outcomes depending on the unique historical events (changes in climate, meteorites, epidemics, etc.) that might occur during each replay. As he puts it, "the divine tape player holds a million scenarios, each perfectly sensible...the slightest early nudge contacts a different groove, and history veers into another plausible channel, diverging continually from its original pathway" (Gould 1989:320-321). Gould's thought experiment was meant to illustrate the significance of historical contingency to evolutionary processes operating in an open system, but it also introduces a novel methodological approach for historical scientists. This approach is worthy of further exploration.

Paleontologists are interested in reconstructing the evolutionary trajectories of extinct and living species. Similarly, paleoanthropologists are interested in reconstructing the biological and cultural trajectories of hominin species, in hopes that a better understanding of evolutionary history will ultimately contribute to a more nuanced appreciation of our own species' place in the natural world. Researchers in both disciplines can access two types of empirical data sets. The first is an exceedingly incomplete and biased subset of all of that was deposited during the one and only "showing" of the tape of history. Of course, one can study many different aspects of this data set (fossils, DNA, pollen, stone tools, etc.) in an effort to obtain multiple lines of evidence, but ultimately each line of evidence is born of the same history. The second data set is composed of all that we can observe in the current (unique) scene of the evolutionary tape of history—the details of life that exists today. Keeping Gould's cosmic tape player in mind for the moment, one can see how studying these data sets in hopes of understanding the selective forces involved might prompt an intriguing question: How likely is the current scene—life as we witness it today—given all reasonable historical possibilities?

For example, while we may not know when or how food sharing evolved in hominin populations, we know from contemporary observations that it *did*. However, asking what is the likelihood that food sharing *could have* evolved in our lineage given slightly different (but plausible) historical scenarios is a different kind of question than paleoanthropologists commonly address. There is a good reason why paleoanthropologists have not asked questions like this previously: partial access to a single run of the tape of history makes it impossible to address alternative histories with empirical data only. However, agent-based models present us with tools for exploring alternative histories, and we have much theoretical ground to gain by doing so. One of the assertions of this paper is that an understanding of the tendency for observed "outcomes" (bipedality, food sharing, low genetic effective population size, etc.) to occur in different social and biological environmental settings will lead to a better understanding not only of the adaptations involved in hominin evolution, but also of how and where to look for evidence of these adaptations in the field.

Although it is obviously impossible to replay the "real" tape of history, one can look for regularities in the behavior of an agent-based model as a surrogate (Lansing 2002). An important requirement of this type of analysis is that we not truncate the modeling process after finding just one scenario that yields artificial results that match empirical data. Even if this single scenario fits well with one's preconceptions, it might prove not to be the *only*, or even the *most likely*, potential explanation upon further exploration. In fact, by allowing for the control of initial conditions while playing out multiple alternatives—i.e., replaying Gould's tape of history hundreds or even tens of thousands of times—experiments with agent-based models might identify numerous plausible scenarios. Further, each of these plausible scenarios might provide a new hypothesis that requires an attempt at falsification with empirical data. Exploratory agent-based models permit the study of multiple "what if" scenarios, which Gumerman and Kohler (2001) call "alternative cultural histories" and Binford (1987) calls "plausible alternatives." By studying a wide variety of plausible alternatives and continuously testing what we learn against empirical data, we can narrow the large number of plausible social and environmental conditions down to a smaller subset of those that probably played an important role in the evolution of many of the aspects of human behavior that we can observe today.

EXPLORING PLIO-PLEISTOCENE HOMININ FOOD SHARING

> The goal of understanding early hominid life in terms of itself can only be accomplished if we have strongly contrastive yet plausible alternatives. In this context, the intellectual challenge is then shifted to the methods of inference justification used by archaeologists rather than

> the skill with which archaeologists are capable of accommodating facts to their beliefs. [Binford 1987:21]

Food sharing is but one of many biologically altruistic behaviors exhibited by humans. Because the majority of anthropological research on human food sharing has focused on explaining its function in extant hunter-gatherer communities rather than on retracing its evolutionary history, important questions concerning when and how it evolved in hominin populations have been left largely unaddressed by analytical investigations. In the absence of unequivocal archaeological evidence and analytical models, the first attempts to reconstruct Plio-Pleistocene hominin food sharing behaviors relied upon observations of living humans as analogs (Isaac 1978, Leakey 1971, Lovejoy 1981). But as subsequent research has made abundantly clear, extant and historically documented hunter-gatherers, bound by their own historical, economic, and political contexts, and therefore representative of but a small subset of possible hominin foraging societies, probably do not provide useful referents for early hominins.

The agent-based model introduced here was built to address a simple research question without using modern humans as referents for Plio-Pleistocene hominins: What range of ecological and social conditions facilitates the spread of altruistic food sharing alleles in artificial hominin societies? Aside from finding this question simple, some might also find it strange. To be honest, it is a rather strange question for an archaeologist to ask, as we normally concern ourselves with providing a behavioral interpretation for what happened in Place A at Time X rather than with what kinds of adaptations might be selected under a wide range of plausible characteristics of Region A during Period X.

Answers to more traditional anthropological questions concerning early food sharing among hominins have focused on the presumed opportunities afforded by open grasslands and on a selfish motivation for sharing in the form of benefits to donors' fitness (e.g., Blurton Jones 1984, 1987; O'Connell et al. 2002). My theoretical approach differs fundamentally. To more accurately characterize the socio-ecological milieu of Plio-Pleistocene hominins, I (1) focus on the selective pressures associated with fragmented patches of closed (woodland) habitat and (2) expand evolutionary ecological explanations of food sharing to include the selective benefits bestowed upon supra-individual vehicles of selection (i.e., subsistence-related trait groups). As a result, this multilevel selection perspective (Sober and Wilson 1998; Wilson and Sober 1994) is a significant departure from previous anthropological reconstructions of early hominin food sharing (but see Boehm 1996, 1999; Wilson 1998). The basis for applying multilevel selection theory to this question comes from theoretical biological research by John Pepper and Barbara Smuts (2000, 2002), who have demonstrated that ecological patchiness can facilitate the evolution of altruistic traits, even among socially inept actors.

INTRODUCING SHARE: SIMULATED HOMININ ALTRUISM RESEARCH ENVIRONMENT

To explore the selective consequences of the concepts introduced above in a tractable manner, I implemented SHARE (Simulated Hominin Altruism Research Environment) as a purposefully simple agent-based model. SHARE makes use of the Objective-C Swarm libraries (Minar et al. 1996). SHARE's spatial world is a lattice of empty grid cells that has been wrapped into a torus to avoid edge effects. In the simplest version of the model discussed here, two different classes of objects—Plant and Forager—can occupy each regularly shaped, regularly spaced grid cell. A brief description of these objects will here suffice, for I describe the model more completely elsewhere (Premo 2006).

Plant agents represent closed habitat (i.e., woodlands) food resources. A more general way to put this is that Plant agents represent spatially and temporally reliable resources. Plant agents are clustered into patches, and areas absent of Plant agents represent open grasslands. Plant energy grows logistically up to a relatively low fixed maximum. Plant agents are systematically distributed at the start of each simulation run according to two experimental variables, Patch Size and Gap Size. As Patch Size decreases closed habitat shrinks, and as Gap Size increases open grasslands expand. Patch Size and Gap Size are held constant during the course of any single simulation run.

Forager agents are purposefully abstracted versions of Plio-Pleistocene hominins. Foragers follow a number of simple rules that govern reproduction and death. Forager reproduction is asexual and entails a significant energetic cost to the parent. To guarantee that each offspring inherits its parent's genotype, genetic transmission occurs through a single haploid locus with two immutable alleles (**S** = selfish and **A** = altruistic). Foragers also possess a simple set of movement rules. Foragers move to the immediately adjacent cell that possesses the highest food energy value of the eight in its Moore neighborhood. However, in the event that none of the adjacent cells contains enough energy to support a Forager for one time step, that Forager will choose one at random. These simple foraging rules effectively model hominins using individually retrieved spatial information to exploit locally available resources. The use of random walks between closed patches insures that all Foragers employ the same strategy for finding additional reliable food resources. In order to test the effect of ecological patchiness on population structure without complicating matters, Forager agents do not employ central place foraging nor do they live in socially defined groups of any kind.

Foragers can carry limited amounts of procured but unconsumed energy. Each possesses a (possibly unique) floating-point value s, $0 \leq s \leq 1$, that provides the probability that it will share a portion of its unconsumed energy when approached by another in need. The model can allow mutation to affect s, and hence for the value of this trait to evolve through time. However, for all of the runs described here, mutation is set equal to zero because my central goal in this project is to study how ecological patchiness affects the frequency of altruistic alleles in metapopulations, not how it affects the evolution of the probability of sharing. Although the evolution of the individual tendency to share food also is of great interest, especially for answering a closely related question concerning the problem of origination, exploration of that parameter space will have to wait for future research in which I plan to use mutation and the continuous version of s. For the time being, however, I employ s as a binary variable ($s = 0$ for selfish and $s = 1$ for altruistic). Foragers are considered "in need of help" when their energy level drops below a threshold of 50 units. A Forager in need may ask another in its immediate Moore neighborhood for help (i.e., a prospective recipient can ask a prospective donor to share excess food). Whether or not the prospective donor will share excess food is based on one of three distinct sharing behaviors, described below in order of increasing social sophistication.

According to the simplest sharing rule (**shareFoodWith**), a prospective donor (*D*) shares excess food with a potential recipient (*R*) when a random number between zero and one is less than or equal to

D's probability of sharing (*s*). The second food sharing method (**reciprocalShareFoodWith**) resembles the well-known tit-for-tat strategy. This strategy requires that each Forager agent remember whether others cooperated with or defected against it in their most recent social interaction. Dynamic lists of cooperators and defectors model memory. Each Forager maintains its own lists by updating them after each interaction in which it functioned as *R*. When acting as *D*, Foragers rely upon their memory to make food sharing decisions on an individual-by-individual basis according to the following rule: share excess food with those who shared with you in the most recent interaction, but refuse to share with those who refused to share with you in the most recent interaction. If *D* has no memory of a past interaction with *R* (i.e., *R* is absent from both of *D*'s lists), **shareFoodWith** is used as the default for that interaction. According to the final food sharing method (**omniscientShareFoodWith**), *D* can accurately identify whether *R* is altruistic or selfish by directly reading *R*'s phenotype. *D* uses this important information to decide whether or not to share according to the following rule: altruistic *D* shares with altruistic *R* but not with selfish *R*, and selfish *D* shares with no one. This strategy models the scenario in which Foragers use information exchanged with others (via gossip) about past social interactions to identify and respond appropriately towards prospective recipients upon their first meeting.

AN EXPERIMENTAL DESIGN FOR EXPLORATION

The goal of this experimental design is to observe the behavior of the model in a range of initial conditions, or, in other words, in a large socio-ecological parameter space. Agent-based or not, most models can be employed as either descriptive or heuristic tools. When faced with the task of creating a model to address a specific research question, one often feels tempted to incorporate all of the details one thinks one knows about the past to create a highly descriptive, seemingly "realistic" model. Unfortunately, the fact that what is used to evaluate the utility of a model is often some perceived degree of realism rather than fruitfulness provides some impetus for this practice. Although this *modus operandi* may be acceptable for creating a descriptive model, problems arise when this same tactic is used to create a model destined for use as a heuristic tool. One of the problems with including a large number of details (many of which might not be essential to the research question at hand) is that the superfluous variables usually make it impossible to explain with any degree of certainty how the results of a model are related to any of its experimental variable values. In addition, it is difficult to anticipate the combinatorial effects that additional variables might produce in any model.

A second approach, which stresses simplicity and tractability in the interest of clear comprehension, provides the best guideline for heuristic modeling. The simpler the heuristic model, the more likely one will be able to explain its results in terms of relationships between just a few initial conditions and the observed outcomes. Although it does not require that one believes "the whole" is reducible to just a few variables or processes (this is the potentially dangerous side of reductionism), the act of breaking down a complex problem into a number of smaller, more manageable parts often yields a clearer understanding of how certain variables interact than if all variables are included from the very beginning (this pragmatic side of reductionism is commonly used in science).

To effectively explore the parameter space of any exploratory model, it is important to systematically vary experimental variable values and to initiate runs with a large set of random number seeds. The practice of repeating simulation runs with the same random number seed while substituting different values for one particular experimental variable is called a parameter sweep. By sweeping each parameter independently (and then multiple parameters concurrently), one can gain an understanding of how each experimental variable influences the evolutionary dynamics of the process or trait of interest. In order to explore how different histories affect the evolution of altruistic food sharing in a variety of socio-ecological contexts, 101 simulation runs were executed for each possible combination of three experimental variables: Patch Size, Gap Size, and food sharing strategy (Table 1).

DATA COLLECTION

Agent-based models are capable of creating an extraordinary amount of quantitative data. If so inclined, one could gather longitudinal data from hundreds of different variables from tens of thousands of agents during each simulation. Axelrod (1997) notes that because contingency plays such a crucial role in most agent-based models, it is possible to use the data collected from each model run to reconstruct the particularistic

Table 1. Standard and experimental parameter settings for SHARE

Model Parameters	Value(s)
Standard Variables	
Minimum number of plants	500
Plant maximum energy (energy units)	10
Plant logistic growth rate *r*	0.2
Starting number of foragers	40 (20 of each type)
Forager starting energy (energy units)	50
Forager metabolic rate (energy units/time step)	2
Forager fertility threshold (energy units)	100
Forager birth interval (time steps)	20
Cost of reproduction (energy units/birth)	50
Forager maximum life span (time steps)	100
Forager maximum energy (energy units)	110
Forager lower threshold (energy units)	50
Probability of sharing food	0 (selfish), 1 (altruist)
Experimental Variables	
Patch size (number of cells per patch side)	2, 4, 6, 8, 10
Gap size (number of cells between patches)	2, 4, 6, 8, 10
Food sharing behaviors	shareFoodWith, reciprocalShareFoodWith, omniscientShareFoodWith

history of the artificial society it supported. Such path-dependent data, he explains, can be analyzed at three different levels.

First, one can simply describe events in chronological order. While this approach might yield a readily digestible account of the details occurring *within* each run, it does not offer much in the way of a processual explanation because it fails to address the similarities and/or differences that exist *between* runs. Second, the detailed history of each run can be reconstructed from the perspective of a single agent. While this might sound attractive, given the fact that the individualistic narrative it provides is comparable to the way in which we each experience the world, this approach does not ensure a representative description of the system in question because not every agent can partake of all there is to experience during the course of a simulation run. Third, one can describe trends in agent-based models by tracking the values of just a few important global variables through simulated time. This technique yields greater explanatory power at the expense of particularistic detail. There may be valid reasons to analyze data at any (or all) of these levels, depending upon the goals of the modeling project. My research goals are best served by the global-scale approach, which allows me not only to compare models that only differ in their "histories" (i.e., random number seeds), but also to contrast systematically the results of models that employ the same random number seed in different social and ecological environments. In this way, the effects of different histories and of controlled social and ecological experimentation can be considered independently.

The Price Equation provides an elegant tool for quantifying the relative strengths of between-group and within-group selective pressures as they fluctuate through time (Price 1970, 1972, 1995). While employing patch membership as a reliable proxy for trait group affiliation in SHARE, I can use the Price Equation to partition the overall change in allele frequency and to track selection both within and between subsistence-related trait groups. In order to confirm that altruistic alleles increased in frequency due to raised levels of between-group selection, these values and the percentage of altruistic foragers present in the metapopulation were collected during each simulation run at a rate of once per 25 time steps (Figure 1). Each run was discontinued after one allele evolved to fixation in the artificial society.

WHAT RANGE OF ECOLOGICAL AND SOCIAL CONDITIONS FACILITATES THE EVOLUTION OF FOOD SHARING IN ARTIFICIAL PLIO-PLEISTOCENE HOMININ POPULATIONS?

For each of the three food sharing strategies tested, 101 runs were executed within each of 25 possible combinations of Patch Size and Gap Size values, for a grand total of 7,575 runs. This baseline suite was used to explore how variations in ecological patchiness and in the level of social sophistication affect the success of altruistic food sharing alleles in mixed starting populations (Figure 2).

The selective influence of ecological patchiness is readily discernible in Figure 2. In the cases of shareFoodWith (2A) and reciprocalShareFoodWith (2B), the altruistic allele evolved to fixation in viable populations (populations must contain at least 10 Forager agents at the time of allele fixation to be considered viable) predominantly when low-to-intermediate Patch Sizes (2, 4, and 6) were paired with intermediate-to-large Gap Sizes (4, 6, 8, and 10). These patchiness levels are found in the so-called *transitional zone*, which divides uninhabitable patchiness levels (lower right, shaded gray) from those in which selfish alleles are usually successful (upper left, white). This pattern clearly echoes that which Pepper and Smuts (2000) found for two other altruistic traits: feeding restraint and alarm calling. The fact that altruistic alleles evolve to fixation less frequently than their selfish counterparts, even

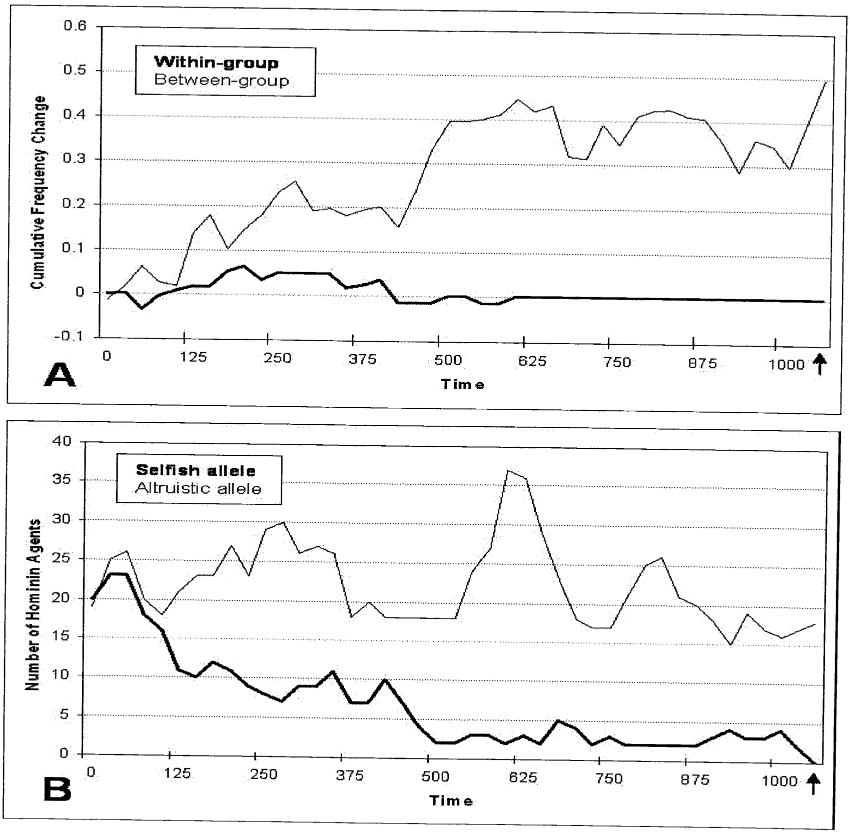
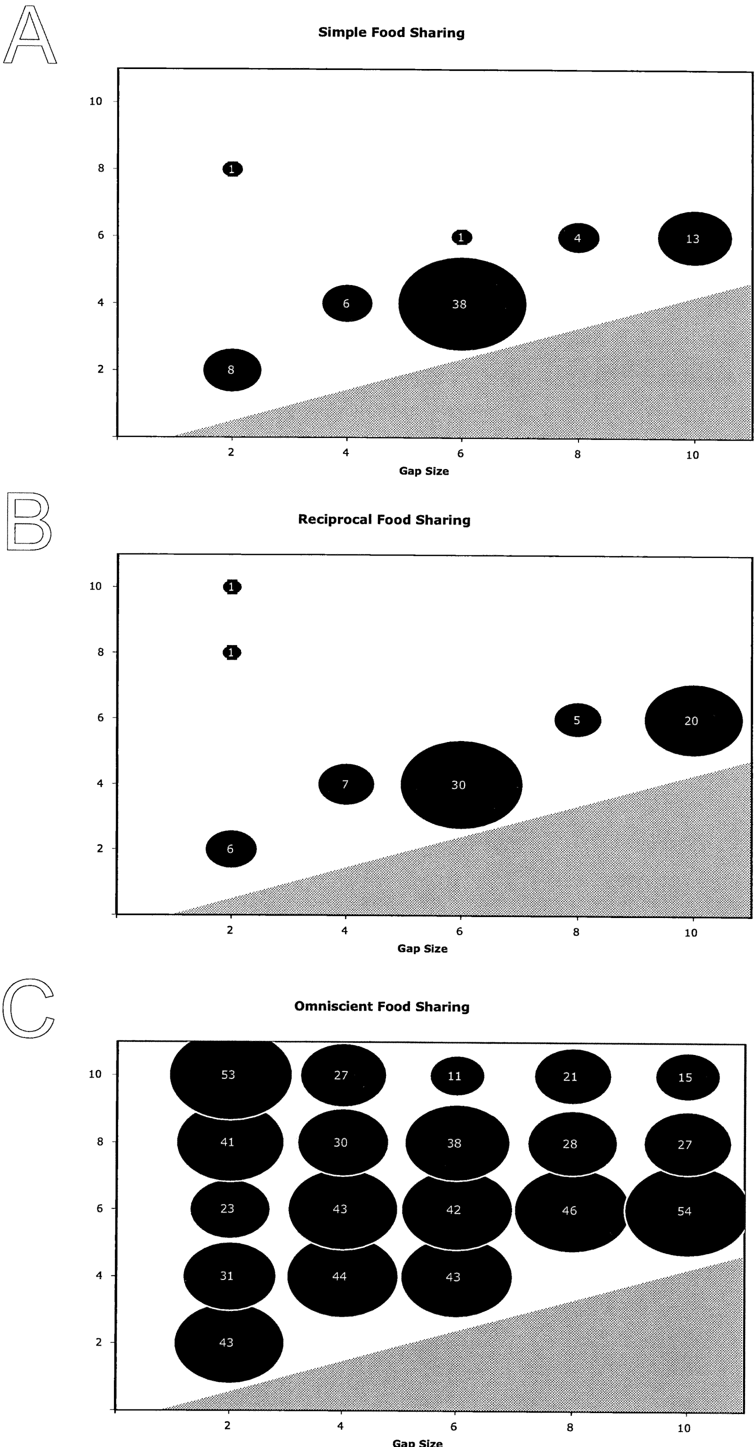


Figure 1. The Price Equation quantifies multilevel selection. A: Cumulative change in the frequency of the altruistic allele from one run of SHARE (Patch Size = 4, Gap Size = 6) due to within-group selection (bold line) and between-group selection (thin line). B: Selfish and altruistic hominin population sizes vary as a function of multilevel selective pressures. In this particular run, the altruistic allele evolved to fixation in the 1,033rd time step (black arrows) due to the relative strength of between-group selection. In A, the sum of the two lines at the time of fixation (0.5) equals the total cumulative change in the frequency of altruistic alleles.

Figure 2 (next page). Summary of population genetic results by food sharing strategy (A: probabilistic, B: reciprocal, and C: omniscient). Bubble area represents the number of runs (out of a possible 101) in which the altruistic allele evolved to fixation in a viable population for each possible patchiness scenario. The absence of a bubble in the white zone means that the selfish allele evolved to fixation in each of the runs executed in that area of the parameter space. The area of the parameter space that does not support viable populations of foragers is shaded gray.


A
Simple Food Sharing
10
8
6
4
2
1
1
4
13
6
38
8
2
4
6
8
10
Gap Size
B
Reciprocal Food Sharing
10
8
6
4
2
1
1
5
20
7
30
6
2
4
6
8
10
Gap Size
C
Omniscient Food Sharing
10
8
6
4
2
53
27
11
21
15
41
30
38
28
27
23
43
42
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54
31
44
43
43
2
4
6
8
10
Gap Size

within the transitional zone of patchiness, should not detract from the finding that ecological heterogeneity can effectively structure even socially inept foragers into evolutionarily meaningful trait groups.

It is important to remember here that the evolutionary significance of an event need not be directly related to its probability, for rare events can have major evolutionary consequences. What is most informative in this case is not any single value but the overall tendency of the altruistic allele of the two simpler sharing strategies to evolve to fixation almost exclusively in the transitional zone.

The data collected from runs with **omniscientShareFoodWith** (2C) paint a different picture. Although these results bear the same signature of the uninhabitable region (shaded gray), they also show that the altruistic allele of this strategy evolved to fixation more frequently in all remaining patchiness levels, not just in the transitional zone. Thus, there is an inverse relationship between the selective influence of ecological patchiness and the level of behavioral sophistication.

DISCUSSION

The fact that the least sophisticated form of food sharing (**shareFoodWith**) evolved to fixation at all, despite the fact that it involves neither memory of past interactions nor the ability to identify the phenotype of prospective recipients, demonstrates the powerful role that resource patchiness can play in structuring an otherwise freely mixing population of socially inept foragers. Altruistic food sharing evolves to fixation in viable populations predominantly in the so-called transitional zone of ecological patchiness in the cases of both of the simpler food sharing strategies. This transitional zone facilitates the evolution of altruism by increasing between-group selective pressures while decreasing within-group selective pressures (see Premo 2006). However, resource patchiness played only a minor role in the case of the most sophisticated sharing strategy, which spread to fixation at least once under every ecological condition capable of supporting a viable population. This means that the sophisticated cultural behavior easily supplanted ecological patchiness as the main determinant in structuring trait groups. Thus, as one might expect, the selective influence of ecological structure decreases as the cultural sophistication of sharing increases.

How do the findings from this heuristic model better inform our ideas about early hominin food sharing and Lower Paleolithic archaeology? SHARE demonstrates that under mosaic ecological conditions, representative of those documented for the Pliocene in East Africa most recently by Wynn et al. (2006), it is possible that even rudimentary food sharing behaviors could have evolved to fixation in hominin populations. This conclusion implies that if the earliest food sharing behaviors were indeed simple, a strong temporal correlation should exist between forest fragmentation and the spread of this altruistic behavior. However, SHARE also demonstrates that had early hominins been capable of more advanced food sharing strategies, which might involve gossip and/or the punishment of social cheaters, we can expect that woodland fragmentation would have played a diminished role. In this case we should not expect the archaeological record to display a strong temporal correlation between the evolution of food sharing and the fragmentation of Pliocene forests in East Africa. Of course, the same would be true if early hominins actually were capable of structuring their populations by cultural means, a possibility this version of the model does not currently address but is in the works for a future version. It may be possible to test these new hypotheses against empirical archaeological and paleoenvironmental data at some localities if we can further develop a technique to detect food sharing in archaeological distributions (Enloe and David 1992; Waguespack 2002).

Finally, the results of SHARE do not (in fact, cannot) *prove* that food sharing spread through hominin populations due to the fragmentation of closed habitats, and to think otherwise is hubris. However, the findings discussed here demonstrate that ecological patchiness can facilitate the spread of even simple food sharing behaviors in a mixed starting population. These results yield an interesting new hypothesis that deserves to be tested against empirical data: the strategy of sharing dwindling woodland resources—not stalking prey in open grasslands—laid the ethological foundation for what we recognize today as exceptionally cooperative human societies.

CONCLUSION

The lack of control groups and the unavailability of direct informants as to what might have been render the historical scientist's job more difficult than that of the physical scientist (see Wilson 1998 for a related discussion). That is, because physicists and chemists routinely make use of controlled, repeatable experiments to test hypotheses, they are able to act as their own informants about the way the world might work in a manner quite uncommon to paleoanthropologists. This paper attempts to begin a dialogue about how paleoanthropologists can best employ tractable agent-based models as exploratory tools to build better understandings of how a range of plausible, experimental scenarios might have affected the archaeology, morphology, and genomes of hominin populations. If nothing else, this approach will provide us with a more comprehensive frame of reference, which can be used to eliminate the plausible scenarios that are unlikely to have occurred, given observed characteristics of empirical data.

To believe that computer models can prove that one's ideas about the past are correct is to fall victim to the silicon siren's song. However, agent-based models provide worthy alternatives to using allegedly representative living human and nonhuman primate behaviors to interpret evolutionarily unique cultural remains, because they are capable of generating inferences about how the world *could have been* rather than about how the world *is*. This general statement holds true, however, only for agent-based models used to explore plausible alternatives rather than to emulate preconceived expectations. To borrow Gould's terminology again, by systematically exploring the parameter space of a simple model, one is able to replay the tape of history under various conditions while collecting data from artificial societies in a number of plausible channels. In the case of SHARE, this activity permits us to learn how experimental socio-ecological scenarios affect altruistic food sharing allele frequencies.

We should not treat models as if they are the immutable, final products of field research, nor should we compare two models with the sole purpose of evaluating which one is "True." We must not lose sight of the fact that our interest in modeling ultimately lies in improving our simplistic ideas about the past rather than in somehow proving the validity of an under-specified, verbal explanation. It is precisely because we as historical scientists do not have access to control groups or to direct informants of what might have been that many of our interpretations stand to benefit from the type of inference-building research that stresses exploration of many possibilities over the emulation of just a few. Thus, it is my humble conclusion that anthropologists interested in investigating evolutionary questions have much to gain by employing exploratory agent-based models as behavioral laboratories.

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