PATCHINESS AND PROSOCIALITY: MODELING THE EVOLUTION AND ARCHAEOLOGY OF PLIO-PLEISTOCENE HOMININ FOOD SHARING

by

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A Dissertation Submitted to the Faculty of the

DEPARTMENT OF ANTHROPOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

2006

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

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ACKNOWLEDGEMENTS

Over the last five years, many people have contributed (in one way or another) to my research project. My biggest thanks go to my family—Anna, Ben, Joda and Steve—whom have always been supportive. In addition to a great family, I have been lucky enough to enjoy the support of a great group of friends, the rare kind of people who are as sharp in the classroom as they are fun at the Tap Room. So, to Seth, Jon, Scott, and Boley: thanks for all the good times. I also feel fortunate to have had the opportunity to work with such a knowledgeable and encouraging committee, a group who gave me a longer leash than many others would. Steve Kuhn served as a thoughtful sounding board during the modeling process. He provided invaluable comments during the analysis and write-up, too. My frequent visits to his office were always relaxing, fun, and enlightening. In short, I don't think I could have asked for a better advisor. Mary Stiner's well-crafted and well-placed inquiries forced me to wrestle with troublesome issues that needed clarification, and her comments on drafts were always spot-on. I hope this document reflects some of what she has taught me about writing. I would not have come up with this research topic if not for Steve Lansing. Steve has a knack for introducing anthropologists to useful ideas that come from exotic places and interesting disciplines. I am glad my perspective was influenced by his holistic view of anthropology. John Olsen was always enthusiastic about this project, and not just because I was tackling issues that were near and dear to his old professor's heart. Somehow, his door was always open and he was the quickest to provide comments, even though he was probably the busiest of all. Gary Christopherson provided invaluable advice on everything GIS. He and Peter Johnson, both at the Center for Applied Spatial Analysis (CASA), were instrumental in helping me apply the local spatial autocorrelation statistics that I learned about from Brigitte Waldorf and Mike Sawada to archaeological distributions within the GIS environment.

In order to do the research I had in mind, it was necessary for me to learn to use an entirely new tool—agent-based modeling. I thank my colleagues in the student-founded and student-run Agent-based Modeling Group at UA, who helped get me started on Swarm and Objective-C. A special thanks to John Murphy, for I could not have gotten so far so quickly without his patience and considerable programming skills. I am still in his debt for customizing a handy data analysis script for me free of charge. Paul Johnson, John Pepper, Rick Riolo, and Steve Railsback also each provided helpful agent-based modeling related tips over the last few years. I wrote the code in beautiful Vancouver, B.C., a great place to program and to ski and to eat raw fish.

Last, but not least, I am happy to acknowledge that this research was supported in part by an Emil W. Haury Graduate Fellowship and a Janet Upjohn Stearns Foundation Individual Research Grant, both awarded by the Department of Anthropology at the University of Arizona.

DEDICATION

There is little doubt that my family's regular habit of gathering everyone around good food and drink is largely responsible for my interest in the evolutionary implications of food sharing. So, to my family: thanks for all the altruism, this is dedicated to you.

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ABSTRACT

This dissertation begins with a comprehensive review of the evolutionary biological debate over the evolution of altruism and a discussion of how various models of mechanism have influenced the models of circumstance that paleoanthropologists continue to use in reconstructing details about the level of cooperation displayed by early hominin societies. The remainder of the dissertation concerns itself with systematically exposing previously unquestioned assumptions to potential falsification as well as with exploring some new scenarios concerning the evolution and landscape archaeology of Plio-Pleistocene hominin food sharing, all via a null agent-based model called SHARE. This heuristic model was built to address two major questions: (1) What range of ecological and social conditions facilitates the evolution of food sharing in artificial Plio-Pleistocene hominin populations and (2) Is food sharing at central places necessary for the formation of the so-called "scatter and patches" archaeological landscapes that are characteristic of the Plio-Pleistocene record in East Africa? In answer to the first question, population-level genetic results collected from artificial societies of hominin agents demonstrate that the so-called *transitional zone* of ecological patchiness can facilitate the evolution of altruistic food sharing in mixed starting populations, even if foragers lack the ability to remember past interactions or to avoid social cheaters. In answer to the second question, ecological patchiness can affect the movements of simple foragers such that the artificial archaeological landscapes they create display the same spatial signature that characterizes observed Oldowan landscapes. That is, in ecological conditions marked by fragmented food resources, archaeological landscapes composed of

both concentrated patches and diffuse scatters can form as a result of solitary foragers using simple routes that are in no way tethered to culturally-defined and culturally-maintained central places. In the end, SHARE provides new hypotheses about how ecological patchiness could have influenced both the evolution of altruistic food sharing and the structure of Lower Paleolithic archaeological landscapes. The latter can be tested in the field by looking at the relationship between artifact density and the paleoenvironmental characteristics of locales both in which artifacts are abundant *and* from which they are conspicuously absent.

CHAPTER 1. DEFINING A NEW DIRECTION

> “The human adaptation on which all else depended was sharing, cooperation.” [Lancaster 1978:89]
>
> “When the food came in, the human beings were quiet and trusting and beautiful. They shared.” [Vonnegut 1971:70]

Though anthropologists often stress the singularity of humanness, it should not be forgotten that we comprise but one of the trillions of species that have lived on this planet, all of which were (or still are) characterized by equally unique adaptations. In this sense, humans truly are just another unique species (Foley 1987). Ironic as it may seem after making such a statement, the research I am about to introduce focuses on a phenotypic characteristic that is often lauded as one of the hallmarks of humanity—widespread altruistic behavior. However, the goal of this research is not to illustrate how the human species alone is selfless. Rather, the goal is to generate some understanding of the social and ecological conditions under which an altruistic behavior that is now ubiquitous among *Homo sapiens* could have evolved in Plio-Pleistocene (~3.5 – 1 MYA) hominin populations. This is an evolutionary ecological study of hominin food sharing.

1.1 Defining altruism

Biologists use the terms altruism, spite, selfishness, and cooperation to define a set of social behaviors that affect both the fitness of an actor and the fitness of at least one recipient (Wilson and Dugatkin 1992). It is important to be concise about my use of "altruism" at the outset, not only because researchers in various disciplines define it differently but also because it carries baggage from common use. The earliest definition of altruism can be traced back to Auguste Comte. He defined altruism rather generally as the behavioral expression of a need to "live for others" (Compte 1875: 556). Naturally, Comte illustrated altruism by juxtaposing it with egoism, a less ambiguous concept that refers to selfish behaviors that increase the well-being of an actor, sometimes at a significant cost to others.

Those familiar with the way in which social psychologists, evolutionary psychologists, and philosophers use the term in their research will recognize the following definition: "altruism is a motivational state with the ultimate goal of increasing another's welfare" (Bateson 1991:6). According to this modern definition of *psychological altruism*, a positive social behavior must be motivated solely to aid another before it can be deemed altruistic. Thus, psychological altruism requires a proximate mechanism of intentionality, whereby an altruist must knowingly intend or be otherwise motivated by its own accord to provide aid. Psychological altruism also requires that the ultimate and only goal of this motivation be to benefit another individual's "welfare." Here, welfare encompasses a large number of dimensions of well-being including, but not restricted to, the absence of pain, anxiety, stress, fear and the presence of ease, relaxation, security, and satisfaction (Bateson 1991). It is unlikely that welfare could refer directly to reproductive fitness, though individuals enjoying positive levels of well-being would probably also enjoy higher reproductive fitness. Note that this definition of psychological altruism does *not* require personal sacrifice on the part of the actor. That is, a psychological altruist can aid another at no cost to one's self. In response to other psychologists who include self-sacrifice in their definitions of altruism, Bateson argues that because the true motivation of the actor may be unknown (even to one's self), when defining psychologically altruistic actions it is more important to focus on the "benefit to the other" than to focus on the "cost to self" (1991:7). His point is illustrated by the following example: when a brave bystander jumps into an engorged arroyo, risking his own life to save that of an anonymous drowning child, does he do so because he genuinely intends to aid the child and cares nothing for external rewards, because he knows the national news report on his actions will garner widespread respect and fame, because he believes it is the "right" thing to do and jumping into the swirling waters will alleviate the intense guilt he would feel if he did nothing at all, or because of some combination of these reasons? In this scenario, only the first motivation would qualify this daring rescue as a psychologically altruistic behavior. It is obvious that the focus of psychological altruism is on the motivation of the prosocial behavior rather than on the outcome of the rescue attempt (i.e., was the child saved and the hero's fitness enhanced, or did both perish?). Such is the stuff of psychological studies of altruism.

Unlike psychologists and philosophers, evolutionary biologists study altruism only in terms of how altruistic actions affect the differential survival and reproduction of donors and recipients. Because they have no analytical purchase on internal states, motives, intentions, or other such proximate mechanisms, biologists define altruism in a way that emphasizes the fitness effects of a social behavior and ignores its (often empirically unknowable) motivation. The definition of *evolutionary* (or *biological*) *altruism* is quite simple: "a behavior is altruistic when it increases the fitness of others [recipients] and decreases the fitness of the actor" (Sober and Wilson 1998:17). Self-sacrifice is a fundamental component of evolutionary altruism: one cannot act altruistically in the evolutionary sense without incurring a cost to one's fitness. Additionally, evolutionary altruism does not require that an actor have an intention, a motive, or even a mind in order to display an altruistic (or, for that matter, selfish) behavior. Trematode parasites, genes, and humans, alike, can act altruistically as long as the behavior in question benefits the fitness of at least one recipient at an expense to the actor's fitness.

Because my research is concerned with the evolution of altruistic behaviors rather than the evolution of the proximate mechanisms that motivate them, let it be clear that I am interested in evolutionary altruism, not in psychological altruism. I consider altruistic any behavior that benefits at least one recipient's fitness at a cost to that of the actor. Whether a prosocial action is intentional or instinctive is of no concern here. Whether the ultimate and only goal of the behavior is to benefit the recipient's welfare or to initiate a reciprocal relationship is also irrelevant. Therefore, there is no need to distinguish between "hard-core" and "soft-core" altruism (Wilson 1978:155) or to split hairs with other such distinctions (Wilson 1990). My interests lay only in how the fitness effects of such actions affect their frequency in populations through time.

As any introductory textbook in anthropology is sure to state, humans display a surprisingly high level of cooperation. Some anthropologists reserve a special place in the pantheon of human adaptations for this particular characteristic (e.g., Lancaster's quote at beginning of this chapter). Because the term "cooperation" has been used in a variety of ways by researchers in various disciplines, it, too, deserves some attention here. By convention, evolutionary game theorists define a player's other-regarding strategy as "cooperate" and its self-regarding strategy as "defect" (see Axelrod 1984). In game theory, then, cooperation is said to occur when a player chooses to employ the other-regarding strategy despite the fact that the selfish strategy yields higher personal benefits. The cooperative strategy certainly is not selfish due to the fact that the alternative choice (i.e., defect) always yields higher fitness benefits, but neither is it synonymous with evolutionary altruism because those who cooperate in the social game can, and often do, increase their individual fitness as a result. Whether cooperation in this sense provides some benefit to a player depends upon the strategy employed by one's partner as well as the game's payoff matrix. Another use of the term is found in some behavioral ecological studies, where "cooperation" refers to coordinated actions that raise the fitness of those who participate in a group activity relative to those who do not partake. However, many prefer to use the more specific term of "by-product mutualism" to describe coupled behaviors benefiting both actor and recipient such as those observed in group hunting and communal defense (Mesterton-Gibbons and Dugatkin 1992, 1997).

Finally, in some cases "cooperation" is redefined and used as a synonym for evolutionary altruism (e.g., Pepper and Smuts 2000).

Due to the term's ambiguity, I do not often refer to cooperation in the chapters that follow. And in those rare instances when it appears, cooperation is used as a synonym for "prosocial behavior." In biological terms, prosocial behaviors benefit the fitness of recipients regardless of whether they tax the fitness of the actor. Therefore, prosocial behaviors include both altruism and by-product mutualism (Figure 1.1). Prosocial behaviors are the antithesis of antisocial behaviors, such as selfishness and spite, which reduce the fitness of recipients at the benefit (selfishness) or detriment (spite) to the actor's fitness.

1.2 Why all the commotion over cooperation?

In his influential and controversial book, entitled *Sociobiology: The New Synthesis*, E. O. Wilson deemed altruism the "central theoretical problem of sociobiology" (1975:3). The problem to which Wilson refers stems not from finding examples of altruism, for they abound in nature and are an obvious characteristic of ant, bee, and human societies, to name but a few. Rather, as Rosenberg (1992:19) states, the trouble is "explaining how the actual is possible" or, in other words, how the existence of altruism is consistent with the mechanism of natural selection. According to Darwin's theory, any trait that reduces one's fitness should be selected against at the level of the individual, and yet a variety of altruistic traits are displayed by a number of species, not just our own. Darwin was well aware of this fly in the ointment, and to his credit he did not shy away from acknowledging an extraordinary example of evolutionary altruism in his most famous publication:

> “No doubt many instincts of very difficult explanation could be opposed to the theory of natural selection,—cases, in which we cannot see how an instinct could possibly have originated…I will not here enter on these several cases, but will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities…from being sterile they cannot propagate their kind.” [1859:235-236]

This example seems to defy classical individual selection. If natural selection works to increase the reproductive fitness of a population by selecting against deleterious phenotypes, how could individuals incapable of reproduction (the ultimate in altruistic traits) exist within ant colonies? In studying this problem, many evolutionary biologists have encountered the same impasse that Darwin found. Assuming that altruism is not exempt from natural selection, how can both selfish and altruistic behaviors evolve according to the same set of selective forces? This tantalizing question has been addressed by some of the brightest evolutionary biologists, and many of their innovative techniques and insights are reviewed in Chapter 2.

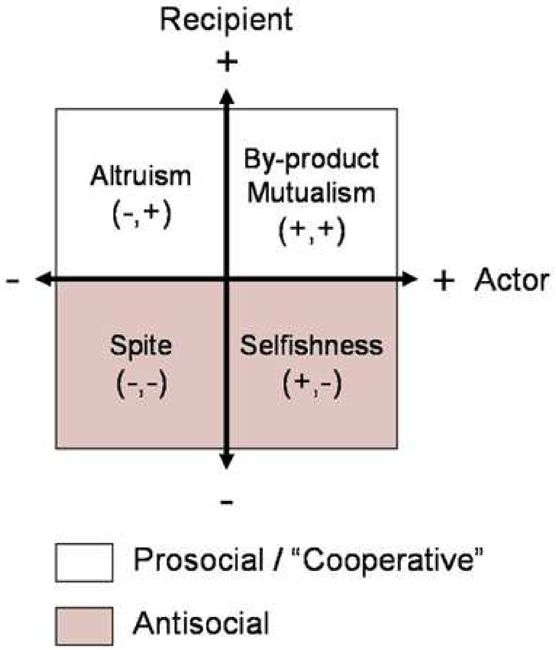

Figure 1.1. Defining social behaviors graphically. Positive and negative effects to the fitness of actors (donors) and recipients are represented by the X and Y axes, respectively.

Humans are remarkably altruistic in comparison to much of the animal world, though it would be easy for one to think otherwise considering the many antisocial acts (i.e., assault, theft, murder, warfare, etc.) that the media regularly cover. Like many other animals, humans often act altruistically towards their close relatives and those they encounter repeatedly (these instances of cooperation were addressed directly by kin selection and reciprocal altruism, respectively). However, unlike most other species, humans often cooperate with unrelated individuals—even complete strangers—as well as those who are unlikely to repay the act or those who may never again be encountered. For those of you who unfortunately cannot recall examples of this type of generosity from your personal lives, it has also been illustrated in experiments with anonymous single iteration Prisoner's Dilemmas (Marwell and Ames 1981).

Humans worldwide often voluntarily sacrifice their own resources to benefit the fitness of recipients whom they likely will never meet. Such examples of über-altruism are unique to humans and require some explanation. Why, how, and when did hominins evolve this penchant for prosociality? Because anthropologists and primatologists do not see altruism displayed *to the same extent* in other hominoid species, a safe place to start is with the assumption that humans evolved this characteristic since the split from our last common ancestor with chimpanzees at least 6-7 million years ago:

> "Our ancestors six million years ago in the Miocene presumably cooperated in small groups mainly made up of relatives, as contemporary nonhuman primates do. There was no trade, little division of labor, and coalitions were limited to a small number of individuals…Sometime between then and now, something happened that caused humans to cooperate in large, complex, symbolically marked groups. What caused this radical divergence from the behavior of other social mammals?" [Richerson and Boyd 2005:195-196]

A less likely alternative is that other great ape species lost this trait while hominins in the lineage leading to humans retained the derived feature from our last common ancestor with hominoids. Though both alternatives are logically possible, given the present state of knowledge, my research on the evolution of altruistic food sharing is based on the former, which I consider to be more parsimonious and more likely.

1.3 Food sharing and hominin evolution: A new direction

Food sharing is but one of the many intriguing altruistic behaviors exhibited by living humans. In the context of hominin societies, food sharing refers to the transfer of procured food resources between individuals, with the exception of calories or nutrients provided to helpless infants and toddlers. This activity is better defined as parental provisioning, or nurturing. By sharing food a donor sacrifices the energetic yield of resources in his possession, thereby lowering his own fitness in order to benefit the fitness of a recipient who may (or may not) lack adequate food resources. Although ethologists recognize that ours is not the only species to display this evolutionary altruistic behavior, the rich diversity of food types involved in intragroup resource transfers and the high frequency at which food sharing occurs between unrelated individuals, whom may never again meet, distinguish our version as quantitatively, if not qualitatively, unique from the sharing behaviors documented among ravens (Heinrich and Marzluff 1995), vampire bats (Wilkinson 1990), social carnivores (Kruuk 1972; Mech 1970), olive baboons (Strum and Mitchell 1987), and chimpanzees (de Waal 1989; Stanford 1996; Teleki 1981). This subtle, yet significant, distinction has not been lost on social scientists interested in studying uniquely human adaptations. In fact, over the last two decades, much anthropological research has focused on documenting and explaining food sharing behaviors in extant hunter-gatherer communities (see Kuhn and Sarther 2000; Winterhalder 1996, 1997 for reviews). The results of many of these studies will be reviewed in Chapter 2.

According to some paleoanthropological reconstructions, food sharing behaviors akin to those observed in contemporary human societies might have been displayed by Plio-Pleistocene hominins. Some interpretations of archaeological assemblages in East Africa ascribe modern human-like sharing behaviors to hominins that were alive nearly two million years ago (Isaac 1976, 1978a, 1978b; Lovejoy 1981). As a general rule, mapping modern human behaviors directly onto the material remains of Plio-Pleistocene hominins is unwarranted and almost certainly misleading. In addition, the inability to identify material signatures that are unequivocally attributable to food sharing has further hindered the widespread acceptance of these Plio-Pleistocene interpretations. Nevertheless, Isaac's provocative food sharing model cannot be discounted out of hand. Researchers have not yet systematically explored ideas about when and how food sharing could have evolved[1] in early hominin populations, and they have not yet comprehensively tested these ideas against the Lower Paleolithic archaeological record.

To move towards a better understanding of early hominin food sharing we must (1) employ conceptual models to identify social and ecological circumstances that facilitate the evolution of altruistic food sharing as well as the formation of "scatter and patches" archaeological landscapes and (2) develop quantitative methods that can be applied to material distributions to identify spatial signatures left by food sharing behaviors. The current research concerns itself mainly with the former. It does so by addressing two principal questions. First, in what range of ecological and behavioral

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[1] The general definition of "evolution" is simply a change in the allele frequency of a population through time. However, for the purposes of this project when the terms "evolution," "evolve," "evolved," and "spread" are used in the context of SHARE's results, they synonymously refer not just to a change but specifically to an *increase* in the frequency of an allele (e.g., altruistic food sharing).

conditions could food sharing have evolved in Plio-Pleistocene hominin populations? Second, are modern human central place foraging behaviors required to produce archaeological assemblages like those found in East Africa, or have previous reconstructions assumed too much of the hominin behaviors responsible for the spatial structure of Lower Paleolithic assemblages? The motivation of the second line of questioning is to develop a quantitative method that can detect and characterize the possibly multi-scale spatial signatures of food sharing in archaeological landscapes, so that archaeologists can *demonstrate*—rather than *invoke*—the presence of this altruistic behavior.

To more accurately model the socio-ecological milieu of Plio-Pleistocene hominins, I propose to (1) refocus the traditional "savanna hypothesis" away from open grasslands and toward fragmented patches of closed habitat and (2) enlarge evolutionary ecological explanations of food sharing to include the selective benefits bestowed upon hierarchical levels that exist directly above that of the individual (i.e., at the level of the trait group). With the synthesis of these perspectives this research marks a significant departure from previous anthropological studies of early hominin food sharing (but see Boehm 1996, 1999; Wilson 1998). This approach yields a new model that tests the hypothesis that the altruistic phenotypic trait of sharing food could have evolved in Plio-Pleistocene hominin populations due to the benefits it bestowed upon the fitness of subsistence-related trait groups competing with one another in an increasingly patchy ecological environment.

This novel reconstruction implies that the strategy of sharing resources obtained from fragmented closed habitats could have laid the ethological foundation for what we recognize today as an exceptionally altruistic "human nature." The observation that all contemporary human foragers share food to some degree, though they do not all live in the same kinds of patchy habitats that might have fostered the evolution of the trait, should direct additional questions to the types of cultural mechanisms—conformist social learning (Boyd and Richerson 1985; Henrich and Boyd 1998; Richerson and Boyd 2005) and social norms of moralistic (strong) reciprocity (Boyd and Richerson 1992; Gintis 2000; Richerson and Boyd 2005)—that could have helped to maintain the altruistic trait in the face of changing ecological and social conditions. If food sharing is a relatively primitive behavioral adaptation, which has influenced the trajectories of genetic *and* cultural evolution for over two million years, then it might be wise to expect the versions we observe today among living humans to be quite distinct from those that Plio-Pleistocene hominins displayed. Although it is important to learn as much as possible about sharing strategies among extant species, paleoanthropologists will fail to find a perfect analogy to early hominin food sharing behavior in studies of how contemporary hunter-gatherers, chimpanzees, or baboons divvy up their spoils (Foley 1991). In the absence of modern analogs, conceptual (rather than referential) models should be the tools of choice for those who wish to pursue the evolution of human behavior (Tooby and DeVore 1987).

My research relies upon a multilevel agent-based model called the Simulated Hominin Altruism Research Environment (SHARE). This analytical modeling tool, described in Chapter 4, explores a large parameter space of social and ecological scenarios for the basin of attraction that facilitates the evolution of food sharing. Using the language of nonlinear dynamical systems research in the context of SHARE, there exist two mutually exclusive *attractors*: (1) the altruistic allele evolves to fixation in the population of foragers and (2) the selfish allele evolves to fixation in the population of foragers. The *parameter space* is defined by the entire set of the social and ecological initial values that could possibly be represented in the model. A *basin of attraction* includes only the set of initial conditions from which the model will probabilistically "flow" into one of these *attractors* (see Lansing 2003). By identifying the basin of attraction that supports altruistic food sharing I am gaining a better understanding of the model's dynamics by distinguishing those parameter values that facilitate the evolution of altruism from those that support the evolution of self-interest. Thus, varying some of SHARE's experimental parameters allows one to investigate how issues such as ecological patchiness, predator danger, large unpredictable food packages (meat), information concerning the regional structure of resources, the ability to base a social decision on one's memory of past social interactions, and the ability to recognize social defectors without the aid of previously-obtained information affect the frequency of food sharing traits in artificial societies of hominin foragers. The population-level genetic results (i.e., allele frequencies) collected from these experiments are presented and discussed in Chapter 5. Learning more about how food sharing *could have* evolved to fixation in Plio-Pleistocene hominin populations is only one part of the equation, however. As an archaeologist, I am also interested in whether or not this altruistic behavior is reflected in their cultural material, which is known synonymously as the Oldowan, the Early Stone Age, or the Lower Paleolithic.

The Oldowan tool tradition dates to as early as ~2.6 million years ago in East Africa (Semaw 2000; Semaw et al. 1997) and is characterized by stone choppers and flake tools. Although the Oldowan is often described as a "simple" technology, interpreting spatial distributions of Oldowan artifacts has never been a simple task. Archaeological interpretation is based on inference, and inferences can be constructed through experimentation, referential models (analogy), and conceptual models. Glynn Isaac's and Owen Lovejoy's famous interpretations of Plio-Pleistocene archaeological distributions (see Chapter 3) were based on inferences gained through referential modeling, a technique which employs an empirically observable phenomenon in the place of an unobservable referent. But because null models have not traditionally been included in the referential technique, the following question has not been asked until now: Would it have been possible for Plio-Pleistocene assemblages to have formed in lieu of a sophisticated land use strategy like central place foraging? As some have done for other aspects of archaeological distributions (Brantingham 2003), I employ SHARE as a null model to test whether central place foraging is necessary to explain important spatial characteristics of East African Lower Paleolithic assemblages (see Chapter 6). This is a second application of the model that is more concerned with archaeological landscape formation and spatial statistical analysis than with population genetics. Because these two applications of the agent-based model are distinct but related, Chapter

7 synthesizes the genetic and archaeological findings before proposing some important avenues for future research.

CHAPTER 2. ALTRUISM AND HOMININ BEHAVIORAL ECOLOGY

The preceding chapter introduced food sharing as a biologically altruistic behavior. This chapter reviews the evolutionary biological research that has been most influential in advancing our understanding of the evolution of altruism. Following Winterhalder's terminology, this work is responsible for providing *models of mechanism*, which are concerned with "the processes by which natural selection is brought to bear on the evolution of behavior" (Winterhalder 1997:123). It is crucial to understand the development of these fundamental explanations because human behavioral ecologists have incorporated components of them into their *models of circumstance*, which describe socio-ecological scenarios that foster altruistic behaviors, like food sharing, in small-scale human societies (Winterhalder 1996, 1997). Connections between specific models of mechanism (e.g., individual selection, reciprocal altruism, etc.) and their associated models of circumstance (e.g., tolerated theft, risk reduction, etc.) will be made apparent below. The chapter concludes with a discussion of how the present research incorporates and builds upon previous work in evolutionary biology and anthropology.

2.1 The biological debate over the evolution of altruism

Charles Darwin (and Alfred Wallace) provided evolutionary biology with the mechanism of natural selection. The mechanism of natural selection explains how allele frequencies within a population change through time. Individual-level selection is stressed throughout Darwin’s most famous work, *On the Origin of Species*: “Natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each” (Darwin 1859:201). But Darwin also noted that a number of species—from insects to humans—display altruistic traits that are not only immediately deleterious to the individual possessing them but also beneficial to the fitness of conspecifics competing for resources and mating opportunities. According to the tenets of Darwin’s theory, altruistic phenotypes would surely be eliminated by natural selection, yet he recognized in nature many examples of biologically altruistic traits. The nagging question of how natural selection could explain the persistence of both selfish and altruistic traits has been called the puzzle of prosociality (Gintis 2003). This section reviews the evolutionary biological research that has attempted to make the existence of altruistic traits consistent with Darwin’s mechanism of natural selection.

Charles Darwin was a keen, honest observer. He recognized that altruistic adaptations in ants, bees, and humans posed serious, possibly “fatal,” threats to his entire theoretical framework. To his credit, he did not downplay or overlook the significance of altruistic behaviors. In fact, his initial thoughts concerning the possible benefits of such behaviors mark the beginning of evolutionary biological research on altruism. It turns out his educated hypotheses concerning altruistic behaviors would later influence some of the most sophisticated work on the topic.

Darwin's brief passage on the observation of sterile castes in ant colonies (provided in Chapter 1) is about sacrificing one's ability to reproduce for the advantage it affords the group. Darwin states that the presence of this extremely altruistic trait could be feasible through natural selection if "such insects had been social, and it had been profitable to the *community* that a number should have been annually born capable of work, but incapable of procreation" (1859:236, emphasis added). Similarly, in reference to bees that sacrifice their lives in defense of their hives Darwin states, "we can perhaps understand how it is that the use of the sting should so often cause the insect's own death: for if on the whole the power of stinging be useful to the *community*, it will fulfill all the requirements of natural selection" (1859:202, emphasis added). He later expressed the same community-level sentiment in explanations of the evolution of altruistic behavior in human societies: "There can be no doubt that a tribe including many members who…were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection" (Darwin 1871:166). In stating that altruistic traits could be beneficial at the level of an insect "community" or a human "tribe" though detrimental at the individual level, Darwin raised the intriguing possibility that groups of individuals who share a common fate might become vehicles of selection.

Darwin also implied that the degree to which individuals are related to one another might influence the expression of altruistic behaviors. In *The Descent of Man*, he made an obvious yet important point that "a young and timid mother urged by maternal instinct will, without a moment's hesitation, run the greatest danger for her infant, but not for a mere fellow-creature" (1871:87). He also noted that members of a group act altruistically toward those within their group more regularly than toward those outside of their group. Thus, even Darwin's initial thoughts about altruism hinted that genetic relatedness might play an important role in how they functioned within human societies. Although he did not flesh-out either idea, Darwin wove his first thoughts on altruism with two distinctive threads: group-level benefits and kin-based expression.

Darwin's musings about altruistic traits were little more than educated hypotheses requiring both analytical and empirical testing. It was not until the 1930s and 1940s that evolutionary biologists reengaged the question of altruism. The founding fathers of population genetics each briefly focused his attention on the evolution of traits that are maladaptive at the individual level but beneficial at the group level. Ronald. A. Fisher, J. B. S. Haldane, and Sewall Wright all recognized the significance of Darwin's sparing discussions of the possibility that altruism might evolve via group-level benefits. These early twentieth century biologists were equipped with new statistical tools and an understanding of Mendelian genetics which enabled them to explore Darwin's hypotheses with new analytical models. Ultimately, all three biologists reached the same conclusion about altruistic traits: they could not be explained by evolution within single populations, they required some sort of intergroup selection that was believed by most to occur rarely in nature (Fisher 1930, Haldane 1932, Wright 1945). Of the three, Sewall

Wright (1945) provided the more complete mathematical model of the evolution of altruism, and this he rather discreetly presented in the context of a book review.

In an attempt to illustrate how intergroup selection might be considered "as creative a process as that of traits which make for individual survival," Wright provided a mathematical model in which a "socially favorable" allele (A_2), defined as "a character of value to the population, but disadvantageous at any given moment to the individuals [possessing it]," might evolve to fixation in a structured population (1945:416-417). Wright's equation for the rate of change of A_2 demonstrates that the altruistic allele disappears in a single randomly breeding population due the cost it incurs on the fitness of altruists. According to his equation, the socially favorable trait is always selected against within mixed groups even when a population is subdivided into a number of smaller geographically isolated groups. Wright recognized that even in those rare cases in which the altruistic allele might evolve to fixation in a local sub-population due to the vagaries of genetic drift, it could not spread throughout the entire population in the absence of migration (see Wilson et al. 1992 for a more contemporary illustration of this point). However, he speculated that by incorporating an additional term, one which allows migration between groups, it *might* be possible for A_2 to evolve to fixation in the global population because altruistic groups (here, again, the rare results of genetic drift) would outcompete their selfish counterparts by persisting longer and colonizing new geographic locales at a faster rate, thereby increasing the frequency of their alleles in succeeding generations.

While one might question Wright's goal to prove the "creativity" of intergroup selection (of course, we now recognize that selection does not create variation but rather always works to minimize that which mutation continuously provides), the work it motivated marked the first mathematical model of the evolution of altruism. Although Wright's model is elegant and foreshadows a multilevel selection perspective, it suffers from at least one serious deficiency. The equations clearly capture the within-group disadvantages of altruistic behaviors, but they fail to describe the process by which an altruistic allele can evolve to fixation in a partially isolated group via differential fitness *among* groups. To mitigate this failing, Wright resorted to the randomizing effects of genetic drift, which he presented as the only means by which A_2 can evolve to fixation within any group. The assertion that one must rely upon a relatively weak and non-directional force of evolution to initiate the spread of altruism via intergroup selection helped convince skeptics that, though theoretically possible, the process Wright modeled was not probable.

Nevertheless, Wright's brief mathematical model of the evolution of altruism provided a promising return to an important issue that had not previously enjoyed this type of analytical attention. The statement, "it is indeed difficult to see how socially advantageous but individually disadvantageous mutations can be fixed without some form of intergroup selection," implies Wright felt the existence of altruistic traits served as empirical evidence that some form of selection was acting upon subdivided populations, despite the fact that his initial model could not fully describe that selective process (1945:417).

George C. Williams and Doris C. Williams provided a second mathematical model concerning the "effect of natural selection on genes that influence individually harmful but socially advantageous characters" (1957:32). In doing so they modified Wright's fitness equations to address a different type of population structure. Wright envisioned geographically separated groups whose memberships were initially formed by randomly selecting individuals from the global population. In his model, group membership could change through time as a function of births, deaths, and migration. In contrast, each group in Williams and Williams' model is composed of genetic siblings (sibgroups), which are geographically isolated for only a short time. Once offspring mature, sibgroups dissolve and their members rejoin the global panmictic population to find mates and produce their own clutches of offspring, which in turn constitute the sibgroups of the next generation. Many species of nesting birds display this type of population structure. Recall that Wright's model relied solely upon genetic drift to increase the frequency of altruistic alleles within sub-populations. Fortunately, it is unnecessary to rely so heavily upon genetic drift to provide for an increase in the frequency of altruists in Williams and Williams' model because the genotypic frequencies of each sibgroup are determined by their parents' genes, not by chance bottlenecks that just happen to result in positive assortment.

Because they are isolated from the rest of the population, sibgroup members' behaviors only affect the fitness of those in their group. As long as the group benefits bestowed by altruistic behaviors are sufficiently large relative to the individual costs incurred on those who provide them, each sibgroup's fitness will be directly proportional to its frequency of altruists. This holds true despite the fact that altruists always possess a lower relative fitness than their selfish brethren when both are present in a mixed sibgroup because selfish individuals never shoulder any of the costs associated with the altruistic acts from which they benefit. According to Williams and Williams' mathematical model, sibgroups with a larger proportion of altruists contribute a proportionally larger number of healthy young adults when they dissolve back into the global population. By concentrating on a well-defined population structure centered on sibgroups, Williams and Williams avoid the ambiguity that hindered Wright's original formulation of the problem. Although they successfully demonstrate the evolution of altruism by intergroup selection, the model they provide is suitable only for the narrow range of species that display the type of life cycle in which sibgroup population structure plays a significant role. It may have been because many animals (including humans) do not fit this requirement that their paper was not enthusiastically received. However, though it specifically targets sub-populations composed only of siblings, Williams and Williams' (1957) research provides the first complete mathematical model of the evolution of altruism via differential group fitness. Unfortunately, almost two decades would pass before research along this line would continue.

A Scottish biologist by the name of Vero C. Wynne-Edwards will forever be associated with what many biologists call "naïve group selection." In *Animal Dispersion in Relation to Social Behaviour*, Wynne-Edwards (1962) addressed the topic of population size regulation. He believed that certain social behaviors, such as territoriality and bird song, served to help some animals self-regulate their populations so as not to exceed the carrying capacity of their surroundings. Wynne-Edwards thought that animals possessing the ability to sense global population size via any one of a variety of social adaptations would be better equipped to regulate their reproductive rate to avoid outstripping available food resources. According to his account, those groups composed of members that could avoid extinction by effectively regulating their reproductive rates would later be rewarded with expansion into the newly-available areas vacated by groups that had been less successful in controlling their numbers. Note that while Wright's and Williams and Williams' socially advantageous character causes populations to grow *more* quickly, Wynne-Edwards' altruistic behavior (reproductive restraint) causes populations to grow *less* quickly. Thus, while the others modeled differential group productivity, Wynne-Edwards addressed differential group extinction (Wilson 1983).

Repressing one's reproductive rate is a biologically altruistic behavior; reproductive restraint is detrimental to the fitness of an individual while beneficial to the fitness of the group's members that continue to reproduce. Wynne-Edwards realized that restrained reproduction qualifies as a biologically altruistic trait and, as such, that it could not be explained by individual selection within a single population. It is easy to imagine how selfish cheaters would exploit restrained reproducers within geographically isolated mixed groups. Because selfish individuals refuse to regulate their rates of reproduction even during times of high population density, the frequency of social cheaters in each group will increase with each generation due to their proportionally larger number of offspring. The key to evolutionary success in this case is different than it was in the previous models. Because restrained reproduction decreases the number of offspring that an altruistic group can contribute to the succeeding generation, the only way that it can evolve to fixation is if the selfish groups drive themselves to extinction.

Wynne-Edwards knew that without some form of group selection, unrestrained reproducers would outcompete restrained reproducers within each group. However, despite the fact that his entire argument hung on successfully describing a mechanism by which an altruistic behavior such as restrained reproduction could evolve in a population by means of group benefits, he discussed group selection only briefly. What he did mention was borrowed from Wright's model and, unfortunately, was presented as if it was the final word on the question of the evolution of altruism when, in fact, it had marked just the beginning. It appears as though Wright's model had thoroughly convinced Wynne-Edwards that group selection was a prevalent and powerful evolutionary force:

> "Evolution at this level can be ascribed, therefore, to what is here termed group-selection—still an intraspecific process, and for everything concerning population dynamics, *much more important than selection at the individual level*…Where the two conflict, as they do when the short-term advantage of the individual undermines the safety of the race, *group-selection is bound to win*, because the race will suffer and decline, and be supplanted by another in which antisocial [selfish] advancement of the individual is more rigidly inhibited." [Wynne-Edwards 1962:20, emphasis mine]

Although Wright differed from Fisher and Haldane in believing that group selection was more than an insignificant force, he never went so far as Wynne-Edwards to state that it was "much more important" than individual selection or that it was always "bound to win" when in conflict with individual selection. These are clearly Wynne-Edwards' additions, and they are indicative of a perspective thoroughly imbued with the concept of differential group extinction. If one believes that populations which do not regulate themselves will inevitably overshoot their carrying capacity and go extinct, it makes considerable sense to argue that they will be replaced by populations that are better at regulating their numbers. This perspective, combined with a misunderstanding of group selection as a powerful force, led Wynne-Edwards to believe that populations whose individuals were better at regulating their reproductive rates would inevitably supplant those whose members failed to curb their numbers appropriately. However, in championing this group-level adaptation without providing a mechanism of differential group fitness, he glossed over the important point that Williams (1966) would raise repeatedly: within all groups reproductive restraint is selected *against* due to the lower relative fitness of altruistic individuals. Although it is not entirely correct because it does not account for Simpson's paradox (discussed further below), this statement by Williams sealed the fate of Wynne-Edwards' naïve view of group selection:

> "Selection at the individual level will cause the population to evolve a decreased level of control on its numbers…even the best controlled populations would be evolving a loss of control…Selection among populations cannot cause evolution to go in one direction, when each of the populations is evolving in the opposite direction." [Williams 1966:11]

Granted, Wynne-Edwards' grossly overstated the power of group selection, but Williams' (1966) classic response was so well-formulated and convincing, and its reception so complete among the biological community, that it redirected nearly an entire generation of researchers interested in the evolution of altruism away from group-functional arguments of any kind. Unfortunately, models that included differential group fitness (this included the only complete one, which ironically was coauthored by none other than Williams) were mistakenly included under the umbrella of this taboo topic even though they predated Wynne-Edwards' perspective. In biological circles, Wynne-Edwards' naïve version of group selection became as heretical as Lamarckism, and as a result of this drastic reorientation biologists began to doubt whether supposedly altruistic behaviors were at all detrimental to donors. Maybe "altruistic" (note: "altruism" in quotes refers to the self-interested version of genuine altruism) traits evolved through individual selection, just like selfish traits do, because they actually provide the actor with some previously unrecognized benefit. The biologists who began to search for previously unrecognized benefits that "altruists" might enjoy by behaving in this manner ushered in a new age of research on the evolution of altruism, one based on redefining altruistic behaviors as secretly selfish. In all fairness, the practice of looking for the benefits that "altruism" might bestow upon donors started a few years before Williams' scathing review of naïve group selection was published, and the man responsible for beginning that trend is also responsible for providing the first gene-level model of altruism.

In 1963, William Hamilton published a brief note in *The American Naturalist* simply entitled, "The Evolution of Altruistic Behavior." This paper outlines an innovative evolutionary mechanism by which "altruistic" behaviors can evolve when a donor preferentially bestows benefits upon closely related individuals. Hamilton took pains to develop an analytical model that did not include intergroup selection, which he believed should be "treated with reserve so long as it remains unsupported by mathematical models" (Hamilton 1963:354). As an alternative to modeling the ways in which differential fitness at the group level could aid the spread of group-level adaptations (Williams and Williams 1957; Wright 1945), Hamilton focused on differential fitness at the gene level. He argued that regardless of whether a behavior is beneficial or deleterious to the *individual*, it would spread throughout a population as long as it ultimately benefits copies of the *gene*(*s*) responsible for its display.

In a more detailed discussion of this concept, Hamilton (1964a, 1964b) formally defines inclusive fitness and distinguishes it from classical individual fitness. One's inclusive fitness includes its own individual fitness plus the individual fitness of conspecifics weighted by their degree of relatedness. Degree of relatedness is important in this case because it acts as a mathematical proxy for the likelihood that two individuals will share the same allele. In diploid species each parent has a 0.5 probability of sharing a particular gene with its offspring, because they can expect to share about ½ of their genetic material, as do siblings (unless they are identical twins). Because cousins share only about ⅛ of their genes, the probability that they will share the same allele drops to 0.125. To maximize inclusive fitness, it is beneficial to act altruistically towards individuals that have a high probability of possessing the same allele. In other words, according to this gene-level model, the fitness of alleles responsible for "altruistic" behaviors stand to benefit when the individual in whom they reside aids other individuals who carry the same alleles.

One must consider the relative sizes of the costs and benefits as well as the degree of relatedness between donors and recipients when identifying circumstances that will select for an apparently "altruistic" trait to spread among kin. According to Hamilton, any "altruistic" trait will benefit a donor's inclusive fitness when it provides the individual fitness of a recipient, whose degree of relatedness to the donor is r, with a benefit that is greater than k-times the cost to the donor's individual fitness:

$$k > 1/r, \tag{1}$$

where k is the benefit-to-recipient/cost-to-donor (b/c) ratio and r is the degree of relatedness between donor and recipient. Thus, inclusive fitness will increase (and there will be a net increase in the number of "altruistic" alleles) if the resulting benefit to the recipient is greater than twice the cost to the donor in the case of siblings, or greater than eight times the cost to the donor in the case of cousins. Note that in all cases that satisfy Hamilton's rule, the donor's individual fitness decreases but its inclusive fitness increases.

Hamilton's model was highly innovative. When faced with the self-imposed restriction of modeling the evolution of altruism without invoking any form of group selection, Hamilton simply redefined fitness so that "altruistic" traits could indirectly benefit the donor's inclusive fitness as well as directly benefit the recipient's individual fitness. But if an apparently altruistic act actually benefits a donor's inclusive fitness, is it still an example of biological altruism? The meaning of altruism becomes ambiguous in the presence of inclusive fitness.

Unlike Wynne-Edwards' book, Hamilton's papers about inclusive fitness and its implications for the evolution of altruism were received well by the evolutionary biological community. One prominent biologist was especially quick to incorporate Hamilton's ideas into the mainstream of the discipline. In 1964, John Maynard Smith wrote an article with the intent of further distinguishing Hamilton's inclusive fitness model from group selection. In this article, Maynard Smith renamed Hamilton's model "kin selection," a term that has stuck for four decades. According to Maynard Smith, kin selection did not require the same type of "improbable events" that group selection did: "In kin selection, improbable events are involved only to the extent that they are in all evolutionary change—in the origin of genetic differences by mutation" (1964:1145). By improbable events, Maynard Smith was referring to genetic drift, which in the early mathematical models was the only way in which altruists would evolve to fixation against the current of individual selection. Here, Maynard Smith had a point: with kin selection the frequency of altruists within any kin group is determined by the parents' genotypes, not by chance assortments or by random processes. But remember that this also was the case with Williams and Williams (1957) group selection model of sibgroups. In addition, Maynard Smith stated that while group selection models require that sub-populations be at least partially isolated, kin selection does not "require any discontinuities in population breeding structure," and that "partial isolation is not essential" because behaviors are structured by degree of relatedness rather than by spatial proximity (1964:1145). He proved his points with the "haystack" model, in which he assumed that the worst-case scenario for group selection was the default in nature. Although it was used at the time to support the argument that Hamilton's kin selection was more probable than group selection, a reevaluation of Maynard Smith's haystack model demonstrated that it was also supportive of group selection when the extreme assumptions were relaxed and values were provided for the costs and benefits associated with altruistic behaviors (Wilson 1987). Nevertheless, at the time of its publication Maynard Smith's stamp of approval further popularized Hamilton's highly touted individual selection alternative to the evolution of altruism by group selection.

Implicit in Hamilton's model of kin selection is the assumption that donors not only know the costs and benefits associated with their "altruistic" behaviors but also possess the ability to accurately recognize their kin out of a large population of conspecifics. One could successfully argue that for most animal species this was assuming too much. Even in those cases that siblings are fairly well known to the donor (such as in most human societies and in eusocial insect colonies), one might not be able to accurately predict the costs and benefits associated with any particular altruistic act. In addition, Hamilton's model of kin selection is not applicable to a large proportion of altruistic behaviors, including those that occur between unrelated conspecifics or between individuals of different species. This is not to deny that kin selection explains altruism among close relatives, but it clearly does not provide a model that can be applied to every altruistic interaction, especially in contemporary human populations.

In 1971 Robert Trivers published an influential essay in which he tackled the issue of altruism among non-kin by presenting a new model "designed to show how certain classes of behavior conveniently denoted as 'altruistic' (or 'reciprocally altruistic') can be selected for even when the recipient is so distantly related to the organism performing the altruistic act that kin selection can be ruled out" (1971:35). He proposed that altruism could evolve in a population of unrelated individuals when two conditions are met. First, an altruistic act's benefit to the recipient must exceed its cost to the donor. This condition is similar to Hamilton's rule, but in this case Trivers does not include the recipient's degree of relatedness in calculating the cost-to-benefit ratio. Second, any recipient of an altruistic act must habitually reciprocate the behavior to the donor at some time in the future. This second condition was unique to Trivers' model, and it emphasized the exchange of benefits between a dyad of altruists rather than benefits preferentially bestowed upon the small subset of individuals that were most likely to contain a copy of the altruistic allele in question. According to Trivers' perspective of reciprocal altruism, donors should act "altruistically" not just towards close kin, but towards all individuals from whom they could expect to receive the benefits of an equivalent behavior in the future. In his own words:

> "Reciprocal altruism can also be viewed as a symbiosis, each partner helping the other while he helps himself. This symbiosis has a time lag, however; one partner helps the other and must then wait a period of time before he is helped in turn. The return benefit may come directly, as in human food-sharing…or the return may come indirectly, as in warning calls to birds…" [Trivers 1971:39]

Trivers' model is built upon what he calls "altruistic situations," which refer to interactions between two individuals in which one's actions can provide a benefit unto the other that exceeds the cost to the donor (1971:37). The selection for reciprocal altruism will be greatest when each altruist is involved in a *large number* of *symmetrical* altruistic situations with the same *small subset* of individuals. Three components of that statement deserve further discussion. First, the average number of altruistic situations per individual lifetime is an important variable of any reciprocal altruism model. All else equal, selection for altruistic alleles increases as the number of altruistic situations per lifetime increases. Populations of individuals that rarely interact with one another will not be fertile grounds for the spread of altruistic traits by reciprocity. Second, symmetrical relationships are those in which altruists are able to provide one another with comparable benefits at comparable costs throughout their lifetimes. In short, symmetrical relationships refer to a roughly equivalent relationship in which neither of the participants receives a significantly larger (or smaller) proportion of the benefits and/or pays a significantly smaller (or larger) proportion of the costs. Third, it is crucial that the large number of symmetrical altruistic situations take the form of repeated interactions. Repeated interactions include those in which the same two individuals interact with each more than once. The likelihood that individuals will interact repeatedly increases as group size decreases; hence, the significance of small subsets of individuals.

Trivers' model of reciprocal altruism depends upon sequential exchanges of unilaterally-provided benefits, between which there are time lags. Donors will act altruistically in the present if they expect to receive benefits from the recipient in the future, when the roles are reversed. Of course, the future is uncertain and donors do not actually know if, when, and where their altruistic act will be repaid by the prospective recipient. In many animal societies, donors do not know if they will ever meet the recipient again. The time lag between repeated interactions might be so long that one of the participants dies or migrates out of the region before it has the opportunity to repay the benefits it was provided (this can occur even in very small groups). And even if a donor could see into the future and know that it would again meet the prospective recipient, it still would not be able to tell whether the once grateful recipient would faithfully reciprocate an equivalent act (as an "altruist" would), selfishly refuse to help at all (Trivers called this strategy gross cheating), or slyly reciprocate in such a way that provides less benefit than the donor provided (Trivers called this subtle cheating). Ultimately, the time lag between social interactions brings many of these uncertainties into play, and it distinguishes reciprocal altruistic behaviors apart from what would otherwise be considered by-product mutualism or trade. Nevertheless, like Hamilton's model of inclusive fitness, Trivers' model of reciprocal altruism implies that individual selection alone can favor apparently "altruistic" behaviors. However, unlike Hamilton's inclusive fitness model, Trivers' reciprocal model does not require relatedness; rather, the "altruistic" individual's fitness benefits when an altruistic deed is reciprocated in the future.

To be exact, Trivers' model of reciprocal altruism describes *direct* reciprocity. With direct reciprocity, the beneficial return for an altruistic act is expected to come directly from the individual (i.e., the dyad partner) who benefited as the recipient during the previous interaction. Thus, direct reciprocity requires repeated interactions in which partners often switch between the roles of prospective donor and prospective recipient—also known as symmetrical relationships. Richard Alexander (1979, 1987) discussed another form of reciprocity, one by which altruism could evolve without repeated interactions between the same individuals. This form of altruism was coined *indirect* reciprocity because donors could benefit from individuals other than those to whom they had directly provided aid. In order for altruism to evolve via indirect reciprocity, a donor should be more likely to act altruistically towards those that are likely to act altruistically towards others, some of whom will act altruistically towards the donor at some point in the future, thereby providing an indirect return on the donor’s social investment. Indirect reciprocity does not require repeated interactions between any particular pair of actors, but it does presuppose relatively sophisticated players that are capable of assessing (and continually reassessing) the likelihood that those whom they help will aid others. This is a crucial aspect, because indirect reciprocity breaks down when altruists confer benefits unto social cheaters who never pay the costs to confer benefits upon others.

Alexander argued that prospective donors could base their decision to cooperate or not on their perception of the prospective recipient’s reputation. Various models of reputation followed upon the heels of Alexander’s statement. Sugden (1986) introduced the concept of good standing, which was revisited by Leimar and Hammerstein (2000). According to this model of indirect reciprocity everyone starts out with a good standing—that is, everyone has a good reputation—and everyone’s reputation is observable by the entire population. Good standing can be lost only if one refuses to help a prospective recipient that has good standing. Good standing can be regained by acting altruistically towards a prospective recipient. Sugden argued that the best strategy for the evolution of altruism by indirect reciprocity in this scenario is for a prospective donor to offer help under only two circumstances: (1) when not in good standing or (2) when the prospective recipient is in good standing. Sugden’s standing strategy always takes into consideration the reputations of both the prospective recipient and the donor.

Nowak and Sigmund’s (1998) well-known study of indirect reciprocity included a similar conceptualization of reputation, called the image score. Each individual possesses an image score, which is known to each member of the population and serves as a proxy for status within a group. Individuals with high image scores have good reputations/high status. In Nowak and Sigmund's model, each individual begins with an intermediate image score, which can be raised or lowered depending on the how the individual behaves when acting as the prospective donor. The image scores of donors who decide to act altruistically increase by one unit, while the image scores of donors who decide to act selfishly decrease by one unit. Recipients' image scores are not changed. Nowak and Sigmund (1998) explain that by increasing one's image score by cooperating at the expense of a personal short-term cost, an "altruistic" donor actually increases one's chance of obtaining future benefits as a recipient. Selfish donors that punish prospective recipients with low image-scores do so at a cost to their own image score, thereby lowering their likelihood of benefiting as recipients in the future. As one might expect, Nowak and Sigmund conclude "cooperation based on indirect reciprocity depends crucially on the ability of a player to estimate the image score of the opponent" (1998:575). Furthermore, they demonstrate that in order for altruism to evolve by individual selection via indirect reciprocity the "probability of knowing the image of another player has to exceed the cost-to-benefit ratio of the altruistic act" (1998:576). While each cites a distinctive avenue through which individual fitness benefits are ultimately conferred upon the "altruistic" donor, it should be clear that models of kin selection and (direct and indirect) reciprocal altruism were "designed to take the altruism out of altruism" (Trivers 1971:35).

Trivers, Hamilton, and Alexander were not the only ones working on the evolution of altruism in novel ways in the 1970s. An interesting polymath named George

Price did not let his Ph.D. in chemistry narrow his career choices to those that involved titrations or beakers. In fact he had conducted medical research, worked on the Manhattan Project, and dabbled in computer design for IBM before dropping in for a short, but exceedingly productive, spell on the field of evolutionary biology. Hamilton's papers on inclusive fitness focused Price's interest in the evolution of altruism. In fact, he became so interested in the topic that he traveled to England at his own expense to learn more about evolutionary biology.

Price's formal training in evolutionary biology was nontraditional, and nowhere was this more apparent than in his revolutionary mathematical model for the evolution of altruism. Price's work harkens back to the models of differential group fitness presented by Wright and Williams & Williams, as if he was unaware of or—probably more accurately—indifferent to the fact that the idea of group selection had recently been razed by the most respected patriarchs of the discipline. As a result, while biologists like Hamilton and Trivers were busy devising models that allowed for the evolution of apparently "altruistic" behaviors among kin groups and among dyadic reciprocal partnerships by means of individual selection, Price was interested in explaining every type of altruism (kin, reciprocal, etc.) with one universal model. In Price's elegant mathematical model, henceforth referred to as the Price Equation (Price 1970, 1972, 1995), change in the allele frequency of a global structured population is calculated as the sum of two terms: one is the average evolutionary change within sub-populations (groups) and the other is the average evolutionary change caused by differential group fitness (Sober and Wilson 1998). The publication of the Price Equation marked the first time that individual and group selection were clearly separated in one elegant formula (see Chapter 4 for the Price Equation). Darwin's observation that altruistic traits would be selected against at the individual level but selected for at the group level finally had an intuitive mathematical expression thanks to Price. Unfortunately for the discipline, Price's interest in evolutionary biology burned brilliantly but briefly, like a roman candle. Soon after his breakthrough was released in just a couple of succinct publications, Price had moved on to less academic but no less important pursuits, some of which included providing aid to homeless alcoholics living in the slums of London.

In a simple twist of fate, Price's research on altruism had the greatest impact on the very person that had first inspired him to study the topic. It was none other than Hamilton who was quick to recognize that Price had done an excellent job of modeling the conflicting forces of individual and group selection. He also realized that Price had succeeded in provided a universal model, one that explained the evolution of altruism among kin as well as it explained the evolution of altruism among groups of repeatedly interacting non-relatives. Upon realizing the genius of Price's work, Hamilton admonished him to publish more on the group selection implications of his model. However, these suggestions fell upon deaf ears, for Price had already moved on from his stint with evolutionary theory. Thus, Hamilton was left to present the message that Price was no longer interested in delivering himself.

The paper in which Hamilton applied Price's findings to altruism in human societies is important for a number of reasons. The first half of his paper reintroduces Price's mathematical model as "a recent reformulation of natural selection…[that shows]…how two successive levels of the subdivision of a population contribute separately to the overall natural selection" (Hamilton 1975:136). In describing examples of how the Price Equation works for both asexual haploid populations and sexual diploid populations, Hamilton stresses that group selection is strengthened when altruists bestow benefits upon other altruists within groups with a higher probability then they would in the global population. Hamilton introduces a coefficient (*F*) to describe the correlation between similar types of individuals. In other words, *F* is a measure of the degree to which individuals are positively assorted in sub-populations of the global population. When *F* is large and positive, groups will display great within-group genetic homogeneity and great between-group genetic heterogeneity and altruists are more likely to bestow benefits upon other altruists than upon nonaltruists. Furthermore, Hamilton recognized that because common descent is only one method by which phenotypes would be positively assorted within groups, Price had provided a more general model for altruism than had his kin selection. In his own words:

> "Because of the way it was first explained, the approach using inclusive fitness has often been identified with 'kin selection' and presented strictly as an alternative to 'group selection' as a way of establishing altruistic social behaviour by natural selection (e.g. Maynard Smith 1964; Lewontin 1970). But the forgoing discussion shows that kinship should be considered just one way of getting positive regression of genotype in the recipient, and that it is this positive regression that is vitally necessary for altruism…in the assortative-settling model it obviously makes no difference if altruists settle with altruists because they are related (perhaps never having parted from them) or because they recognize fellow altruists as such, or settle together because of some pleiotropic effect of the gene on habitat preference." [Hamilton 1975:140-141]

Hamilton, whom previously had written that group selection models should be handled with caution until they were better supported by mathematical models (1963), apparently found in the Price Equation the support he required. He was so convinced, in fact, that he found it preferable to redefine kin selection as a sub-type of group selection:

> "If we insist that group selection is different from kin selection the term should be restricted to situations of assortation definitely not involving kin. But it seems on the whole preferable to retain a more flexible use of terms; to use group selection where groups are clearly in evidence and to *qualify* with mention of 'kin',…'relatedness' or 'low migration',…or else 'assortation', as appropriate." [Hamilton 1975:141, emphasis mine]

One might think that such a revelation coming from a prominent evolutionary biologist—nonetheless, one who had recently become famous for his alternative to group selection models of altruism—would have sent shockwaves through an evolutionary community that had busied itself looking in any direction but that of group selection for explanations of altruism. But the shockwaves never came. The utility of the Price Equation and the power of Hamilton's argument for group selection were lost on all but a few theoretical biologists (Sober and Wilson 1998). Thanks to the one-sided debate between Wynne-Edwards and Williams in the early 1960s, group selection had become so demonized among evolutionary biologists that Hamilton's (really Price's) breakthrough did not spread through the scientific network. It seemed as though years of vilifying any explanation that even remotely connoted naïve group selection had almost completely inhibited biologists' receptivity to group selection models of altruism. Incredibly, to most of the evolutionary community, it was as if Hamilton's later paper had never been published, and his name continued to be associated with the popular feat of providing an alternative to group selection, despite his own efforts to argue to the contrary.

There were a few biologists who paid attention to Price's mathematics and Hamilton's reconsideration. Evolution's "new heretics" (Lewin 1996) maintained that, despite Wynn-Edwards' naïve application, some utility remained in the original notion of group selection as Darwin had articulated it. David Sloan Wilson led a small cadre of researchers who continued to work on the concept. Although various names have been used over the years to describe this family of models, including structured demes (Wilson 1975, 1977), intrademic group selection (Wade 1978), and new group selection (Dugatkin and Reeve 1994), the paper trail of this cohort's publications documents the development of what is now known as multilevel selection theory.

Although unfairly handicapped by the intellectual baggage left by the naïve group selection of the 1960s (see discussion in Wilson 1983; Sober and Wilson 1998; Wilson and Sober 1994), multilevel selection theory (Hamilton 1975; Price 1970, 1972; Wade 1976, 1977, 1978; Wilson 1975, 1977) is an elegant conceptual framework that builds upon the mathematical models of Wright (1945) and Williams and Williams (1957) rather than upon the flawed verbal descriptions that derailed the study of differential group fitness in 1962. Multilevel selection theory is predicated on the idea that natural selection concurrently operates on two levels of the biological hierarchy, called *within-group* and *between-group* (Sober and Wilson 1998; Wilson and Sober 1994). One can explore the levels of the biological hierarchy by frame shifting through nested vehicles of selection: a population of genes is an individual, a population of individuals is a group, and a population of groups is a metapopulation.

Synonymous with the generalized meaning of individual selection, within-group selection promotes phenotypic traits that allow an individual to maximize one's individual fitness, regardless of how those actions affect the fitness of others in the group. On the other hand, between-group selection promotes phenotypes that are beneficial to the fitness of others while costly to that of the actor; between-group selection fosters the evolution of biologically altruistic traits. Within-group and between-group selective forces vary with respect to particular traits, individuals, groups, and environments. As the Price Equation demonstrates and as Hamilton (1975) argued, the relative strengths of these opposing selective forces determine which alleles become more common at the metapopulation level. For instance, when within-group selection is stronger than between-group selection, the frequency of selfish traits in a metapopulation increases. Alternatively, when between-group selection is stronger than within-group selection, the frequency of altruistic traits in a metapopulation increases. Price's equation is impressive because it measures the relative strengths of these two components of selection separately, making it possible for one to see altruistic alleles evolve in global populations when between-group selective forces outweigh their within-group counterparts.

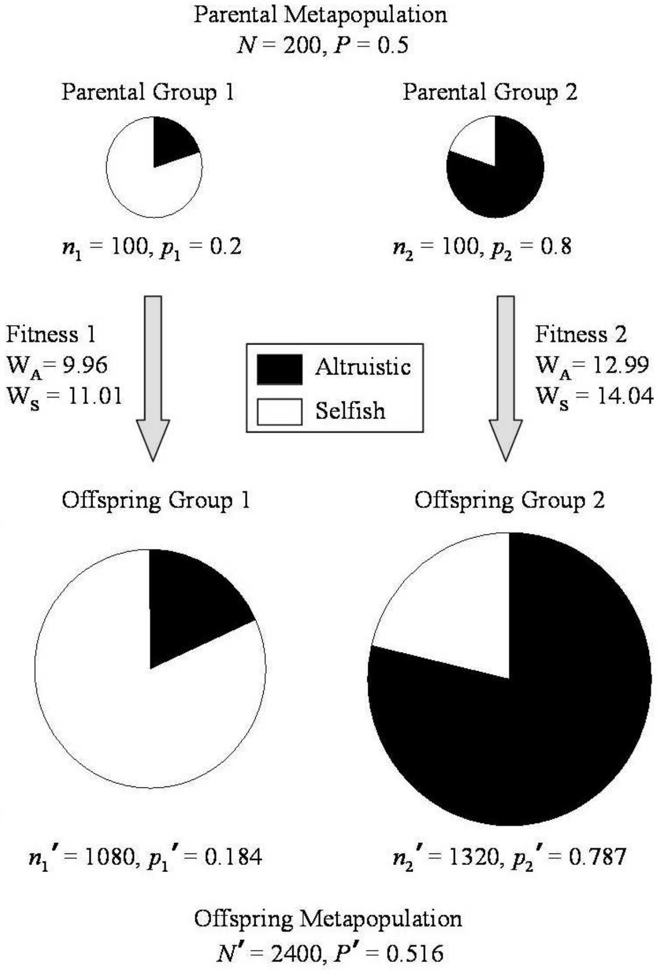
As critics of naïve group selection correctly identified, natural selection does not favor an *individual* who sacrifices for the good of the group, for that individual will always have a lower fitness relative to the other individuals in the group that benefit from the altruistic behavior without paying the associated costs (Williams 1966). There is nothing new in that statement, however, for Darwin (1871), himself, discussed scenarios in which natural selection will favor altruistic *groups* over selfish *groups*, not altruistic individuals over selfish individuals. The key to understanding this tenet, which is of fundamental importance to multilevel selection, lies in how one defines groups. In multilevel selection, one uses the concept of a *trait group* to define group membership (Wilson 1975). Trait groups are not defined spatially or by common descent (though spatially proximate individuals [Pepper and Smuts 2002; Premo 2005] and kin [Hamilton 1975] can meet the requirements of a trait group in some situations). Rather, a trait group is defined as "a set of individuals that influence each other's fitness with respect to a certain trait but not the fitness of those outside the group" (Sober and Wilson 1998:92). Williams and Williams' (1957) characterization of nestling sibgroups as important units in their group selection model foreshadowed this concept.

Sober and Wilson (1998) use the analogy of a college study group to illustrate the characteristics of a trait group. Imagine a student who belongs to a biology study group composed of eight members who meet at the university library the evening before each exam. The study group is a trait group because each member influences how well the other seven members perform on the exam but not how well other students who are in the library during the same time perform on their various assignments. While the study group sits around one large table for most of the night, membership within the trait group is not defined by proximity to that locale; friends who come by to chat are not part of the group and study group members who temporarily wander off to retrieve additional study material from the stacks do not lose their status of being a member because they are away from the group. In addition, the composition of study group has nothing to do with relatedness; one needs not be closely related to another in order to help them learn the material and score well on the exam. Also notice that this is just one of many such trait groups to which a student could belong, and others might include a Spanish study group or an intramural softball team. Thus, one can belong to a different trait group for each of a wide variety of traits.

It might be useful to extend the trait group definition to individuals we will be discussing at greater length below, hominin foragers. Consider a hypothetical subset of 25 hominins that regularly forage together for food. By influencing how much food other members of the group can consume through decisions affecting where to forage, how long to forage, whether to share excess foodstuffs, how much to consume/leave for others, etc., each member has an impact on the fitness of the other 24 members of the trait group with respect to this subsistence activity. This is true regardless of the hominins' degree of relatedness or whether some wander off farther than others while foraging in the same patch. Trait groups are not static; membership is fluid with individuals joining, leaving, and founding new groups through time. Imagine a scenario in which there are two groups (*A* and *B*) of hominin foragers. If dissatisfied with foraging returns in *A*, one might decide to leave *A* to join *B* if its members enjoy higher returns. If one chooses to forage alone, then it has founded another group, *C*. This simple example illustrates membership in multiple trait groups as a function of time. However, because individuals display numerous traits that influence the fitness of others, one concurrently functions as a member of multiple trait groups, each of which is likely to be comprised of different subsets of individuals. For example, though one's allegiance to particular trait groups might shift through time, as demonstrated above, at any one point in time each hominin is a member of multiple trait groups (i.e., foraging, territoriality, child rearing, alarm calling, etc.) just as the student was a member of multiple trait groups (i.e., biology study group, Spanish study group, intramural softball team, etc.).

It is important to restate categorically that, within a mixed trait group composed of both altruists and nonaltruists, altruists are *always selected against* due to their lower relative individual fitness. Thus, within a mixed group, the frequency of altruists always decreases through time. However, under selective conditions in which between-group selection is stronger than within-group selection, the percentage of altruists *in the metapopulation will increase* through time. How can the frequency of altruistic alleles increase at the metapopulation level while always being selected against within each trait group composed of both altruists and nonaltruists? Is this not what Williams (1966:11, see quote above) said was impossible? Simpson's paradox states that what is true for "the parts" is not necessarily true for "the whole." The multilevel process by which the proportion of total altruists in the metapopulation increases while, at the same time, the proportion of altruists in each mixed trait group decreases is an example of Simpson's paradox. Though at first counterintuitive, this process is ultimately a function of differential group (not individual) fitness.

A structured population is composed of groups that vary in their genetic composition; some will have a higher proportion of altruists than others. This genetic variation is heritable and affects the fitness (i.e., reproductivity and persistence) of the groups. When between-group selection is stronger than within-group selection, trait groups with more altruists are more fit than groups with fewer altruists. Being more fit, altruistic groups yield a larger number of offspring than selfish groups, thereby slightly increasing the proportion of altruists in the metapopulation's succeeding generation (assuming that offspring regularly, if not always, display their parents' phenotype). Thus, within each mixed trait group the proportion of altruists *decreases* because as *individuals* they are less fit than the nonaltruists within their group ($W_A < W_S$), but at the metapopulation level the frequency of altruists *increases* due to the higher reproductive rates displayed by *groups* composed of greater proportions of altruists (Figure 2.1).



Parental metapopulation (N) = 200
Frequency of altruists in parental metapopulation (P) = 0.5
Parental trait group population (n) = 100
Frequency of altruists in parental trait group (p) = 0.2, 0.8
Baseline fitness (X) = 10
Benefit to recipient (b) = 5
Cost to altruist (c) = 1

Fitness of altruist (W_A) = $X - c + [b(np - 1) / (n - 1)]$
Fitness of egoist (W_S) = $X + [bnp / (n - 1)]$
Offspring trait group population (n') = $n[pW_A + (1 - p)W_S]$
Frequency of altruists in offspring trait group (p') = $(npW_A) / n'$
Offspring metapopulation (N') = $\sum n'$
Frequency of altruists in offspring metapopulation (P') = $\sum(n'p') / N'$

Figure 2.1. The evolution of altruism by multilevel selection. Due to differential group fitness, the frequency of the altruistic allele increases in the offspring metapopulation ($P' > P$) despite that fact that it decreases within each trait group ($p_1' < p_1$ and $p_2' < p_2$). [After Sober and Wilson 1998: Figure 1.1, Box 1.1, and Box 1.2]

Multilevel selection dutifully applies to trait groups the same three components of natural selection—genetic variation, heritability, and differential reproductive success—that Darwin (1859) so insightfully applied to individuals. Williams (1966) did not recognize differential group fitness as an example of Simpson's paradox and so he was incorrect in stating that altruism could not evolve in the metapopulation if it was selected against in each group. Though it requires strong between-group selection (relative to within-group selection), multilevel selection models demonstrate how altruistic alleles can evolve in the metapopulation despite decreasing in frequency in each mixed group. While Wilson and a small group of theoretical biologists sought to develop Price's equation and Hamilton's ideas into the full-blown framework of multilevel selection theory, other evolutionary biologists continued to explore how altruism could evolve by individual selection. Before moving on to discuss human behavioral ecological models of circumstance for food sharing in small-scale human societies, it is important that we address two research programs that were founded after the publication of Price's equation as individualistic alternatives to group selection: evolutionary game theory and selfish gene theory.

Game theory is the mathematical study of conflict among intelligent, distrusting, and possibly deceitful "players," who possess perfect knowledge of the rules of the game as well as of the possible outcomes of each their strategies. Each player's only goal is to win. The French mathematician Émile Borel published the first papers about bluffing and finding optimal strategies in games, but he is not credited as the founder of game theory because he failed to provide suitable mathematical support for his ideas. Instead, the 1928 paper entitled “Theory of Parlor Games” by the Hungarian mathematician, Jon von Neumann, holds the distinction of being the seminal paper of game theory (Poundstone 1992). Von Neumann later teamed with economist Oskar Morgenstern to develop his theory of games for a wider audience. He believed that game theory would benefit scientists outside the field of applied mathematics because it applies to many types of social dilemmas and can be used to resolve many types of conflicts. Even now, after six decades have passed since its publication, *Theory of Games and Economic Behavior* (von Neumann and Morgenstern 1944) remains one of the more challenging and important works a social scientist interested in conflict should read.

Beginning in the mid 1960s evolutionary biologists began to adapt game theory to the study of altruistic behavior. Verner (1965) and Hamilton (1967) were the first to discuss genetically determined sex ratios as “strategies.” Hamilton’s treatment cites many similarities between his biological research and the “theory of games” and uses the term “unbeatable” to describe extremely successful behaviors in the same sense that it is applied to the minimax strategy of a two-person game (1967:486). Trivers’ (1971) model of reciprocal altruism also draws upon the tenets of game theory with its repeated interactions between pairs of individuals that choose altruistic or selfish strategies (i.e., to “cooperate” or to “defect” using game-theoretic terms). Though these early works draw from traditional game theory, John Maynard Smith (1982) and his colleagues (Axelrod and Hamilton 1981; Maynard Smith and Parker 1976; Maynard Smith and Price 1973) are credited with developing evolutionary game theory in the 1970s. Evolutionary game theory differs slightly from von Neumann’s game theory in two important ways. First, whereas traditional game theory models strategies as conscious decisions by rational players, in evolutionary game theory strategies simply exist as phenotypes that allow players to compete in a Darwinian fashion (Sober and Wilson 1998). The fitness of each individual is proportional to the fitness of its strategies/phenotypes, and successful strategies/phenotypes will yield a greater number of offspring. Second, evolutionary game theory models were developed with the primary goal of explaining the evolution of altruism among non-relatives by way of individual selection. Thus, evolutionary game theory—much like kin selection and reciprocal altruism—was designed as an alternative to group selection.

The simplest evolutionary game theory models involve a Mendelian population of individuals that sequentially pair off (usually randomly) to play a game. One game that is commonly used in these models is the Prisoner's Dilemma (Axelrod 1980a, 1980b, 1984). In the Prisoner's Dilemma, each player may simultaneously choose one of two strategies: cooperate or defect. The payoffs (benefits to individual fitness) associated with each strategy vary depending on that played by one's partner (Figure 2.2). When both players choose to cooperate, they both receive a Reward payoff of 3 for mutual cooperation. When both players choose to defect, they both receive a Punishment payoff of 1 for mutual defection. However, in situations where one player chooses to cooperate and the other defects, the cooperator receives the Sucker's payoff of 0 while the defector receives the Temptation to defect payoff of 5. Given this payoff matrix it is obvious that both players would earn the highest payoffs per interaction if they both decided to cooperate. However, a player becomes vulnerable to the Sucker's payoff of zero by cooperating. As it turns out, regardless of which strategy one's partner plays, choosing to defect *always* yields a higher payoff (if the partner cooperates, defection yields 5 and if the partner also defects, it yields 1) than cooperating (if the partner also cooperates, it yields 3 but if the partner defects, cooperation yields 0). Thus, even though both players know that mutual cooperation yields the highest possible payoff for both of them per interaction, rational individuals should choose to defect in a single iteration Prisoner's Dilemma because defecting secures a higher payoff than cooperating when the other player cooperates (T > R) *and* when the other player defects (P > S). Therein lies the dilemma.

	Player 2 Cooperates	Player 2 Defects
Player 1 Cooperates	R = 3, R = 3	S = 0, T = 5
Player 1 Defects	T = 5, S = 0	P = 1, P = 1

Figure 2.2. A Prisoner's Dilemma payoff matrix. A PD payoff matrix must satisfy two conditions: T > R > P > S and R > (S+T)/2. Player 1's payoffs are listed first in each cell.

Single iteration games are of little interest to evolutionary game theorists because most organisms interact repeatedly over their lifetimes. Thus, most evolutionary game theory models randomly pair and repair players from a single population during a large number of iterations and allow them to play games using more involved strategies such as Always Defect, Always Cooperate, or Tit-for-Tat (cooperate on the first interaction and then mimic one's partner's previous strategy from then on). Each time step, players have the opportunity to reproduce asexually according to the accumulated fitness afforded by their strategy. Players that secure the largest payoffs will have the highest reproductive fitness and the most descendents. Eventually the most successful players, fueled by their successful strategies/phenotypes/alleles, will increase in frequency, possibly to the point that they become fixed as the only phenotype in the population. If that fixed strategy cannot be invaded and usurped by any other strategy, then it is called an Evolutionarily Stable Strategy (ESS) (Maynard Smith and Price 1973).

John Maynard Smith argued that when an Evolutionarily Stable Strategy (even an "altruistic" one like TFT) ascends to fixation in a single population, it does so because it is selected for at the individual level: "an ESS is a consequence of selection acting at the individual level; individuals do not calculate or attempt to maximize the group [population's] payoff" (1983:446). Axelrod and Hamilton (1981) echo this sentiment at the end of an interesting paper in which they demonstrate that when there is a high probability that interactions between two players will continue, reciprocal altruism (TFT) can become an ESS of the Prisoner's Dilemma (at least after it surpasses a threshold frequency thanks to kin selection or spatial clustering resulting in positive assortation), *even* if it begins in a predominantly selfish population. Their paper's brief conclusion, quoted here in its entirety, reiterates their intended focus on individual selection via evolutionary game theory:

> "Darwin's emphasis on individual advantage has been formalized in terms of game theory. This establishes conditions under which cooperation based on reciprocity can evolve." [Axelrod and Hamilton 1981:1396]

It is rather surprising that Hamilton failed to recognize trait groups in his evolutionary game theory model, because the population structure it describes is identical to the one he used in his 1975 paper to illustrate group selection. Indeed, trait groups exist within evolutionary game models despite Maynard Smith's, Axelrod's, and Hamilton's best efforts to argue that they are dealing with single large populations in their models. Granted, the groups in evolutionary game theory models can be quite small (only two individuals in a 2-person game, but up to *n* individuals in an *n*-person game [see Dugatkin 1990]) and they can be together as a group only temporarily, but the act of pairing players means that their social interactions have an effect only on each other's fitness. This effectively creates a structured population composed of many small groups that depends not on kinship or spatial clustering, but on mutual participation in a social game. As Axelrod and Hamilton allude but never state in these terms, the altruistic strategy of TFT often evolves not because it outcompetes the selfish strategy ALLD (always defect) when it is paired in the same group (i.e., evolution by individual selection), but because pure altruistic groups (TFT/TFT) have a higher fitness than both mixed groups (TFT/ALLD) and purely selfish groups (ALLD/ALLD) *and* mixed groups have a higher fitness than purely selfish groups. The possible group combinations for a 2-person game from highest to lowest fitness are as follows: TFT/TFT > TFT/ALLD > ALLD/ALLD. Thus, as was the case in multilevel selection theory models, group fitness is directly related to the proportion of altruists in each group. The altruistic strategy of TFT evolves to fixation because it benefits the fitness of the group in which it occurs, not because it benefits the individual displaying it. In fact, just as we saw before in the case of multilevel selection, within mixed groups altruists have a lower individual fitness than that of selfish players. With evolutionary game theory, we see a technique that, although originally developed as an alternative to group selection, is just another example of a multilevel selection approach; the perspectives are slightly different, but the evolutionary processes they describe are not (Dugatkin 1990; Dugatkin and Reeve 1994; Sober and Wilson 1998; Wilson 1983; Wilson and Sober 1989).

Richard Dawkins was unconvinced by Price's (1972), Hamilton's (1975), and Wilson's (1975) arguments for the evolution of altruism via differential group fitness. His now famous response—selfish gene theory (Dawkins 1976)—revisits Hamilton's (1964a, 1964b), Williams' (1966), and Lewontin's (1970) gene's-eye view of selection. It was meant to function as a decisive argument against the multilevel approach that Price, Hamilton, and Wilson were developing, and for a while it did. Dawkins (1976, 1982) reminds us that Williams (1966) argues in his famous publication that to be considered a unit of selection an entity must be able to replicate itself faithfully. Asexual organisms and genes are the only entities that can do this; thus, they are the only true "replicators." According to Dawkins, groups cannot replicate themselves accurately and therefore cannot be considered genetic replicators or units of selection. If sexually reproducing diploid individuals are not true replicators, then how can natural selection mold adaptations at the individual level? To make the precious process of individual selection consistent with selfish gene theory, Dawkins argued that because genetic replicators have a shared fate in the fitness of the individual in which they reside, they must coalesce into one adaptive unit in order to have a chance at replication. In this way the individual becomes a "vehicle" of selection that the group of replicators uses to its own evolutionary advantage. However, if a set of genes with a shared fate can form a valid vehicle of selection at a higher level—the individual—what is to stop a set of individuals with a shared fate from forming a valid vehicle of selection at a higher level—the group? In actuality, Dawkins' insistence on evolution at the gene-level and his focus only with the lower level of the biological hierarchy (genes among an individual) cannot be used to argue against the multilevel selection perspective if one can just as easily apply the vehicle concept to higher levels, such as individuals among a group and groups among a metapopulation. As Sober and Wilson state:

> "In short, the concept of genes as replicators, widely regarded as a decisive argument against group selection, is in fact *totally irrelevant* to the subject. Selfish gene theory does not invoke any processes that are different from the ones described in multilevel selection theory, but merely looks at the same process in a different way." [1998:88]

2.2 Human behavioral ecological models of food sharing

The previous discussion reviewed the ways in which evolutionary biologists have addressed the question of *how* altruistic traits might evolve in a population. We now turn to a related field of human behavioral ecology, which during the last thirty years (Winterhalder and Smith 2000) has focused on explaining (among other things) *why* altruistic traits like food sharing are prevalent in contemporary hunter-gatherer societies. Human behavioral ecologists' interests lie in describing the social and ecological circumstances that facilitate altruism in small-scale human societies in addition to the evolutionary process(es) working on behavioral strategies. With this as their goal it makes sense that human behavioral ecologists work with *models of circumstance*. To provide a feasible model of circumstance, one must describe how a forager's surroundings allow for the propagation of altruism. This allows one to test and perhaps apply the selective framework provided by models of mechanism. Because human behavioral ecology came into being during the 1970s, a time when invoking selection at any level above the individual was considered an anathema, the vast majority of models of circumstance are based on individual selection. As we saw above, such models purposefully turn biological altruism on its head; self-sacrifice is explained away and "altruism" is presented as a means by which individuals increase their own individual and/or inclusive fitness. The following models of circumstance for food sharing will be discussed below: tolerated theft, variance reduction, showing-off, and costly-signaling. In the case of each, its connection to an evolutionary model of mechanism will be made apparent.

Nicholas Blurton Jones (1984, 1987) proposed that the earliest forms of food sharing might be better conceptualized as "tolerated theft." His model begins with the premise that many hunter-gatherer groups commonly obtain large packages of meat by hunting. In most environments, however, not every hunter in a group will be successful every day. This results in an unequal distribution of food among the members of a group. Whether the meat comes in the form of caribou, giraffe, or elephant is inconsequential; what is important is the fact that the package is so large that the successful hunter can only consume a percentage of it before becoming satiated. Thus, the fitness value of food that comes in large packages follows a diminishing returns curve (Figure 2.3).

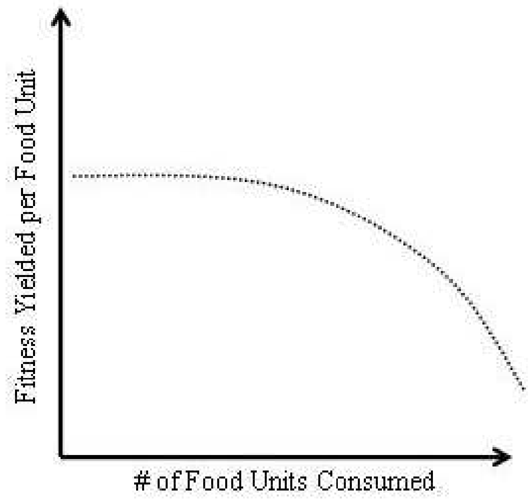


Figure 2.3. A diminishing returns curve.

For any resource that exhibits diminishing returns there exits a point in the number of units consumed beyond which each additional unit of food provides less benefit to a hunter's fitness than the previous unit. Once the nutritional needs of the successful hunter have been met, the value of the remaining food has diminished. Note, however, that while the value of the remaining food has diminished in the eyes of the hunter with the full belly, it is still quite high to the majority of band members, all of who were unsuccessful in capturing their own meal. As long as a large package of meat is not regularly obtained by everyone in a group at the same time, its presence will present a situation in which the same portion of food has different values to different parties: specifically, a low value to the party that has already consumed some and a high value to the party that has not.

As is usually the case, a donor must *offer* an altruistic act; recipients usually cannot extort and altruistic act. An attempt to rescue a drowning man provides a good illustration of this point. Because the drowning man cannot physically force anyone on the shore to dive in after him, his hero will have to offer the rescue attempt herself. But food sharing is a unique kind of altruistic behavior in this respect. In the case of food sharing, a "recipient" can instigate an interaction by taking (or threatening to take) a "donor's" food through the use of force. Of course, individuals are more likely to fight for higher potential fitness gains than for lower ones. And from the successful hunter's point of view, units of meat beyond the point of diminishing returns are not worth enough to risk possible injury at the hands of desperate conspecifics that have much to gain from obtaining what they perceive as extremely valuable portions of meat. Thus, Blurton Jones' (1987) model of circumstance proposes that apparently "altruistic" individuals tolerate the theft of food in order to selfishly avoid unnecessary physical confrontations with those for whom the same food holds much greater value.

This model has some important implications. First, rather than actively redistributing portions of a large food package to needy relatives, to sexually receptive females, or to those who will return the favor, the tolerated theft model proposes that "donors" simply relinquish a portion of their food to contestants in order to avoid unnecessary physical confrontations that could result in personal injury or death. Second, this model only applies to situations in which the fitness provided by a large package of food follows a diminishing returns curve. Third, redistribution by tolerated theft should result in providing roughly equal shares for everyone involved in the interaction, including the "donor."

Kaplan and Hill (1985) tested Blurton Jones' tolerated theft model with ethnographic data from Ache foragers, despite the fact that the model was not originally intended to be a sufficient explanation for contemporary examples of food sharing. Kaplan and Hill found that contestants did not provoke food sharing among the Ache in many cases. In fact, shares of food were reserved for individuals who were not even present at the time of distribution. In addition, they found that Ache food sharing did not result in an equal distribution of food—the hunters actually received smaller shares (Kaplan and Hill 1985). Given these results, Kaplan and Hill proposed that food sharing might be better explained as a cultural adaptation that serves to buffer resource variation rather than a rational decision to avoid an unnecessary confrontation. They argued that by sharing high variance food resources among all members of a group, each member would reduce one's risk of experiencing a dangerous prolonged shortfall in food and, thereby, increase one's individual fitness.

In an interesting reanalysis of the tolerated theft model, Wilson (1998:76) argues that, contrary to his own goal to concentrate on individual interests, the evolutionary scenario Blurton Jones' explains with the tolerated theft model is "virtually identical" to the early group selection model by Sewall Wright (1945). In both models, the altruistic behavior is selected against within groups at the same time that it benefits the fitness of everyone in the group. Blurton Jones acknowledged this characteristic of food sharing in the following passage:

> "…under these conditions foragers [altruistic donors] always do worse than scroungers [selfish recipients]. We can also see that the bigger the proportion of foragers there are in a group, the better everyone does." [Blurton Jones 1987:445]

Blurton Jones accurately depicts food sharing as an altruistic trait with his own admission that it fairs worse than the selfish alternative when both are present within a group, yet he insists on classifying it as a self-interested behavior. After recasting the tolerated theft model in a multilevel selection mold, Wilson (1998) demonstrates that, not only does a multilevel selection version replicate the results that Blurton Jones ascribed to individual selection, but also that one can gain additional insights that were impossible to address with his model of self-interest.

Although others (Cashdan 1985, 1990, 1992; Smith 1988) recognized that hunter-gatherers often lived in the high-risk ecosystems, Kaplan and Hill (1985) were the first to propose that food sharing might reduce that risk through the evolutionary mechanism of reciprocal altruism (Trivers 1971). High variance resources provide ample opportunities for people to alternate between the roles of prospective donor and prospective recipient. For instance, in high variance ecosystems most hunters will come home empty handed every day. The few successful hunters face a decision between sharing their spoils with those less fortunate (acting altruistically) and attempting to hoard their catch (acting selfishly). Successful hunters must weigh these options knowing that they might not get another animal for days, weeks, or longer.

According to the tenets of reciprocal altruism theory, a successful hunter will decide to act altruistically towards those he believes will reciprocate the act when the roles are reversed. An altruist might significantly reduce its risk of going without food by securing a large number of reciprocal relationships with other hunters. Thus, a group of altruists will minimize the individual risk each member faces by reciprocally sharing unpredictable, large packages of calories. Indeed, Kaplan and Hill (1985) found that the strongest predictors of the food types shared among the Ache were package size and the likelihood that they would be procured at the same time by numerous individuals—large packages that were procured asynchronously were the most likely to be shared. As a result, they conclude that food sharing among the Ache is a variance reduction adaptation that actually increases altruists' individual fitness and evolves by individual selection.

A central prediction of the reciprocal altruism model holds that hunters who donate food more frequently should be more likely to receive food from others than the social cheaters who rarely (if ever) share. In their recent study of Meriam food sharing (also see Bliege Bird and Bird 1997), Bliege Bird et al. (2002) found that their observational data did not uphold this central tenet of the "risk reduction reciprocity model." They found that the amount of food received by households that shared more often and more generously was not statistically greater than that received by households that donated food less often and in smaller amounts. In other words, altruistic and selfish households received shares of approximately the same size at similar frequencies. The second prediction of the risk reduction model is that one should expect reciprocal partners to share comparable amounts, thereby repaying previous acts of generosity in kind. However, there was not a significant positive correlation between the amounts transferred between "partner" Meriam households, so Bliege Bird and colleagues found that reciprocal dyads did not share equivalent amounts. In fact, many of the food transfers were entirely unidirectional. Finally, in order for a system based on reciprocal food sharing to evolve by individual selection, altruists must be able to exclude, punish, or, at the very least, discriminate against selfish cheaters. Therefore, a third tenet of the risk reduction reciprocity model is that altruists should not share with known social cheaters as much as they share with altruistic partners. The empirical data from the Meriam show that altruistic households apparently did not discriminate against stingy households; the amount of food that a household received was not positively correlated with the proportion of harvested calories it shared with others. Hence, households that shared very little of what they harvested received the same amount of shared food as households that generously donated a large proportion of what they harvested. Among the Meriam, cheaters were not discriminated against and food sharing was still prominent. These conclusions imply that something other than reciprocal altruism must be involved in some food sharing scenarios.

To address the types of intragroup food sharing that she believed tolerated theft and risk-reducing reciprocity could not explain on their own, Kristin Hawkes invoked the evolutionary mechanism of sexual selection (Campbell 1971; Darwin 1859, 1871) in the show-off hypothesis (Hawkes 1990, 1991, 1992, 1993). Sexual selection is an intraspecific force in which (1) the members of one sex compete with each other for a chance to mate with members of the opposite sex and (2) the differential choice by the members of one sex decides which members of the other sex acquire mating opportunities (Darwin 1871; Trivers 1971). In short, members of one sex actively select from the variation displayed by the other—hence, the term *sexual selection*.

Hawkes sets the stage for the show-off hypothesis by reviewing the form of sexual division of labor found in almost all hunter-gatherer societies: men hunt high-variance resources and women gather low-variance resources. Further, she notes that high-variance resources, like meat, are shared more frequently and more often with people outside of one's immediate family than are smaller, low-variance resources. This fundamental pattern indicates "a sex bias in resource choice and a difference in the spread of resources acquired by men and women" (Hawkes 1991:31). She argues that these distinct food acquisition and redistribution strategies are based on the conflicting reproductive strategies of males and females.

Trivers (1972) outlined the ways in which the reproductive strategies of males and females conflict, resulting in differing optimal levels of parental investment. Males can increase their individual fitness more by increasing the number of mates with which they may produce offspring than by expending their energy in provisioning offspring that may or may not be theirs. This is in contrast to females, who gain relatively little fitness by acquiring additional mates. Instead, choosing mates that contribute to the survival and reproductive success of their offspring can enhance their fitness best. Thus, the maximizing strategies of both sexes are at odds: males can increase their fitness when they invest in their offspring nothing more than sex cells and concentrate their efforts on obtaining as many sexual partners as possible, while females stand to gain large fitness benefits by obtaining a male who invests a significant amount of time and energy in provisioning and protecting her and her offspring.

A traditional assumption is that males hunt high-variance resources in order to provision their immediate family with large amounts of the highest quality resources. Given the nature of the reproductive strategies described above, male provisioning is in the best interest of females, whose fitness would benefit from such significant male parental investment. But this might not be the most effective reproductive strategy from the male perspective. According to Hawkes' model, the common assumption that males hunt to share their spoils with their immediate families is incorrect, and the actual reason why males hunt and share is quite different. A show-off male increases his fitness by sharing highly variable, widely distributable (which also make them indefensible) resources with a number of females in return for reproductive opportunities. On the other hand, a female enhances her fitness by exchanging chances at paternity for otherwise unattainable resources used to better provision herself and her extant offspring. Thus, food sharing is not used to avoid fights or to reduce risk, but to mediate conflicting reproductive strategies in such a way that members of both sexes are able to increase their individual fitness (Hawkes 1991).

Hawkes used data from the Ache (1991), Hadza (Hawkes et al. 1991), and !Kung (Hawkes 1993) to illustrate that male foragers preferentially procure plant and animal resources that can be distributed more widely to the exclusion of those that can be shared less widely, despite the fact that the latter are more frequently encountered and more easily obtained than the former. The Ache data illustrate that the sex of the provider accounts for the majority of the variance in sharing patterns. This pattern is presented as evidence for the show-off hypothesis, but not for any of the alternatives. Although some of their findings are logically consistent with Kaplan and Hill's (1985) risk minimizing model, Hawkes et al. (1991) believe that only the unique reproductive interests of the two sexes can propagate food sharing in human societies because free riders (social cheaters) would successfully undermine a system based on reciprocal altruism. It is obvious from this statement that Hawkes recognizes that biologically altruistic food sharing could not evolve by individual selection within a mixed group, but she still characterizes it as an individually beneficial trait.

While admittedly elegant, Hawkes' show-off hypothesis is not without its detractors (see Hill and Kaplan 1993). Dwyer and Minnegal (1993) tested some of the expectations of the show-off hypothesis with Kubo data. They did not find support for the central prediction that show-off males would display a higher reproductive fitness (as quantified by the number of surviving offspring) than provisioning males. In the same year, Hawkes (1993:349) added that show-off males who regularly share high-variance food might also gain "deference in decisions about travel" and "support in disputes" in addition to "enhanced mating opportunities." Thus, through the act of sharing high-variance food, apparently "altruistic" individuals might in fact gain social influence that extends their benefits beyond the realm of reproductive opportunities. If this broader definition were accurate, then Dwyer and Minnegal's fitness measurement would be too narrow to include all of the possible benefits bestowed upon a show-off male.

Like Hawkes' show-off hypothesis, costly-signaling involves sexual selection. But, unlike the show-off hypothesis, females who are sensitive to costly-signaling do not mate with males in direct exchange for portions of meat. Rather, females use a male's ability to obtain meat as an indirect phenotypic indicator of his genetic quality (Bird 1999; Bliege Bird et al. 2001; Boone 1998; Smith and Bliege Bird 2000; Sosis 2000). According to costly-signaling theory, signals must meet two requirements in order to benefit both the sender and the receiver (Grafen 1990; Zahavi 1975). First, a costly-signal must be honest. That is, it must serve as a reliable indicator of the genetic quality being advertised. Second, the cost imposed on the signaler must be directly related to the quality of the genetic characteristic in question, so that "faking" a high-quality signal costs a low-quality signaler more than the signal is worth.

Food sharing can be considered a costly-signal because only skilled providers can afford to consistently donate large amounts of food to others while still supporting themselves and their families (Gurven et al. 2000). Thus, food sharing can be explained by costly-signaling theory if chances at paternity and political coalitions are offered, not in direct exchange for calories, but because being a generous food provider acts as a reliable phenotypic indicator of high quality characteristics such as bravery, coordination, strength, stamina, eyesight, patience, and leadership abilities. According to the costly-signal model, an individual "generously" donates food only in the interest of accumulating social capital, which can be used to increase one's individual fitness via enhanced mating opportunities and beneficial coalitions with other group members (Bliege Bird et al. 2001; Gurven et al. 2000).

Gurven (2004) points out two important differences between the show-off hypothesis and costly-signaling, which superficially seem very similar. First, food sharing as costly-signaling does not require tolerated theft, but the show-off hypothesis does. Therefore, the costly-signal model does not assume that sharing is solely dependent upon package size and resource variance. Second, whereas in the case of the show-off hypothesis recipients are expected to repay donors for transferred food directly, this is not the case in the costly-signaling model of food sharing. In costly-signaling, someone is expected to repay the donor to offset the costs associated with signaling through food sharing, but it need not be the individual who received the food. In fact, in the case of costly-signaling, the donor should not expect recipients to reciprocate nor should recipients feel obligated to do so. This prediction of costly-signaling is opposite that associated with showing-off, where a donor expects direct reciprocation (in some form) from each recipient, and each recipient feels obligated to return the favor personally. Because the currency in costly-signaling is reputation rather than calories or nutrients, costly-signalers play by different rules than show-offs. This subtle point has larger implications.

For instance, say a hunter gains prestige only if he physically provides someone with a piece of meat, as per the show-off hypothesis. Thus, a show-off gains social influence and secures reciprocal obligations only among those that receive a portion of meat, which in many cases may be a relatively small subset of a group. On the other hand, a hunter who signals his reproductive fitness through the act of slaying and sharing a large and formidable prey item has the ability to broadcast his prowess to anyone who hears of this feat, regardless of whether they witnessed the kill or received a portion of it. In this case, the costly-signaler does not have to provide food to everyone, for his reputation as an über-provider communicates that he possesses high quality genes for desirable characteristics. Although a signaler secures a reciprocal obligation from no one, his reputation as a successful hunter and generous provider reaches a large number of people, all of whom are eligible (and would benefit themselves) to provide him with other sorts of benefits that cover the costs of this display.

Rebecca Bird (1999) suggests that she witnessed food sharing functioning as a costly-signal in male-provisioned Meriam turtle feasts and recognizes its pattern in other ethnographic cases, such as male Melanesian yam growers and male Hadza big game hunters. Costly-signaling theory has also been applied to hominins. James O'Connell et al. (2002) recently hypothesized that the principal reason why large carcasses were obtained by Plio-Pleistocene hominins was because the dangerous activity of usurping a kill from carnivores provided an irresistible arena for costly-signaling. They argue that early *Homo* males engaged in aggressive scavenging to display skill-intensive behaviors to a large, receptive audience of both males and females. Not surprisingly, the costly-signaling explanation falls neatly in line with those based on the mechanism of individual selection—males unconditionally share to increase their own reproductive fitness through successful displays, and as long as this sharing serves as a costly-signal, women benefit mutually by incorporating quality genes in their offspring.

2.3 Summary

> "A group selectionist would explain these behaviors by saying that groups that…share outcompete other groups. Those who reject group selection are challenged to find explanations based on selective forces that operate within groups." [Wilson 1998:73-74]

By definition, a biologically altruistic behavior benefits a recipient's fitness at a cost to the fitness of the actor. Because a nonaltruistic recipient (social cheater, defector) is able to enjoy the benefits of altruistic deeds without paying the associated costs, the successful cheater always possesses a higher relative fitness than the donor of whom he takes advantage. How can an altruistic trait evolve in a mixed population if individuals who display it are less fit than individuals who do not? Failure to answer this reasonable question was largely responsible for naïve group selection's complete dismissal in the 1960s. At that time, if an attempt was to be made to reconcile this well-understood individual selection principle with empirical observations of the existence of altruistic behaviors, evolutionary biologists would have to face a difficult dilemma: to widen one's perspective of natural selection to include fitness benefits bestowed upon levels above that of the individual, or to look for means by which seemingly "altruistic" traits actually benefit the individuals displaying them. Due to the spectacle made of naïve group selection, the majority of interested biologists chose to pursue the second option—explanations based on individual (within-group) selective forces.

Simply put, for food sharing to evolve via individual selection, this biologically altruistic trait must be redefined as a biologically selfish trait. As a result, human behavioral ecological models employing evolutionary mechanisms such as kin selection, reciprocal altruism, and sexual selection envision food sharing as a means by which "donors" attempt to increase their own individual and/or inclusive fitness. Each of these models implies that seemingly "altruistic" acts of food sharing are, in fact, thinly veiled egotistic attempts to increase individual fitness. While models of circumstance based on individual selection have provided some interesting insights when tested with contemporary hunter-gatherer data, their perspective does not provide the best theoretical framework with which to pursue a general understanding of the evolution of genuinely altruistic behaviors. Therefore, instead of joining the search for additional selfish interests in food sharing, I would like to discover what the other option—considering the benefits that altruistic acts bestow upon levels above the individual (specifically, the trait group)—can contribute to an understanding of the evolution of food sharing in early hominins. Unlike most previous models, which view altruism from the perspective of individual selection only, explanations that make use of multilevel selection theory allow altruistic traits to retain the self-sacrificing characteristic that defines them (Wilson 1998). Winterhalder speaks to the potential that multilevel selection holds for reworking, refocusing, and reenergizing evolutionary ecological research on biologically altruistic traits, like food sharing: "models of interdemic [multilevel] selection…promise to broaden the routes and the range of conditions under which evolution can shape cooperative, supraindividual social behavior" (1997:148). The time is right for paleoanthropologists to realize that promise.

CHAPTER 3. FOOD SHARING AND PLIO-PLEISTOCENE ARCHAEOLOGY

> "…the practice of modeling the life of early humans, although shunned by many anthropologists, is nevertheless a scientific game played with great determination; its reward is the right to propound a view of human nature." [Fedigan 1986:26]

The previous chapter reviewed the models of mechanism proposed to explain the evolution of altruistic traits as well as the models of circumstance proposed to justify the presence of food sharing in small-scale human societies. It is important to note, however, that many paleoanthropological studies of early hominin food sharing have not been influenced directly by either of these types of models (but see Zihlman and Tanner [1978] for an exception). Rather, most Plio-Pleistocene hominin food sharing reconstructions have been formulated using a combination of referential models based on observations of contemporary human hunter-gatherers and nonhuman primates and interpretations of the Plio-Pleistocene archaeological record. This chapter considers the paleoecological and behavioral assumptions of previous paleoanthropological reconstructions as well as the referential modeling technique used to create them. Where germane, I briefly discuss how the assumptions of my model compare to those of previous works.

3.1 Plio-Pleistocene paleoecology of East Africa

> "Both contemporary and ancient Africa can be understood as a pattern of ecological islands . . . I am suggesting that greater attention be paid in future to identifying and reconstructing the ecology of identifiable ecological 'islands.' This topic should be an essential dimension of evolutionary studies…" [Kingdon 2003:10,32]

Raymond Dart provided paleoanthropology with a number of intriguing concepts. He argued that *Australopithecus africanus* was a bloodthirsty killer ape that scoured open grasslands for large game. With emphatic brushstrokes he painted a picture of the Pliocene in which unlucky savanna herbivores were gruesomely dispatched by hominin hunting parties armed with "osteodontokeratic" weapons fashioned directly from parts of their prey's skeletons. Interestingly, despite the fact that neither his reconstruction of *Au. africanus* as a savanna carnivore nor his interpretation of the so-called osteodontokeratic weaponry has survived the rigors of subsequent research, Dart's notion that open grasslands served as home for early hominins was sown into the collective consciousness of paleoanthropologists. It later re-emerged as the "savanna hypothesis."

Vrba's (1974, 1975, 1980, 1985) extensive research on African Pliocene climate change crystallized the perceived bond between early hominins and grasslands by providing empirical support and what initially appeared to be significant explanatory power. Her work with bovid fossils documents the regional effects of cooler, drier Pliocene global climatic conditions on African vegetation and fauna communities. Vrba (1985) used diachronic trends in the ratio of closed woodland-preferring to open grassland-preferring bovid fossil taxa as a proxy for climate change, arguing that between 2.5 and 2 million years ago large grasslands spread throughout sub-Saharan Africa at the expense of the previously dominant Miocene forests. According to her environmental argument, the ecological shift from woodlands to grasslands provoked evolutionary changes across many taxa, including multiple speciation/extinction events in hominin evolution (Vrba 1985). For better or for worse, her widely cited reconstructions of the African Pliocene paleoenvironment provided support for the notion that early hominins and open grasslands were inseparable.

Following Vrba's conclusions about mid-Pliocene paleoenvironmental conditions, paleoanthropologists interested in the emergence of bipedalism (Day 1986; Hewes 1961, 1964; Jolly 1970; Wheeler 1991; Zihlman and Tanner 1978), the process of encephalization (Stanley 1992), and the frequency of scavenging opportunities available to early hominins (Blumenschine 1986, 1987), incorporated the idea of expanding open grasslands into their explanatory models. Even the discourse concerning early hominin food sharing could not escape the influence of the traditional savanna hypothesis (Lancaster 1978; Zihlman and Tanner 1978). Zihlman and Tanner argued that African grasslands required of hominins "a new feeding pattern in a new environment that led to the invention of tools for obtaining, transporting, and preparing a range of foods that could potentially be shared with more than one individual" (1978:163). To the contrary, I will argue that early food sharing is probably more strongly correlated with habitation in lingering fragments of Pliocene woodlands than in expanding open grasslands. Thus, *it is feasible that some sort of widespread food sharing strategy was a necessary (but not sufficient) prerequisite for the move from closed to open habitats, not vice versa.*

Although few, if any, would deny that savannas expanded at the expense of closed forests at various times during the Pliocene, not every researcher believes that open grasslands played as prominent a role in hominin evolution as the models cited above would have one believe. Because many of the models that were influenced by the traditional savanna hypothesis overlook the mosaic nature of *savannas*, equating them solely with *open grasslands*, it is necessary to reemphasize the distinction between the two terms. Savanna biomes are generally defined by the co-occurrence of grasses, shrubs, and trees. By definition savannas refer to mosaics of both open grasslands and closed woodlands/forests (Owen-Smith 1999). In addition to a high level of intra-savanna variation, Owen-Smith (1999) reminds us of the impressive variation that exists among contemporary savanna habitats worldwide. His survey implies that using only one generalized reconstruction of the African Pliocene savanna does not provide paleoanthropologists with the paleoenvironmental breadth required to study the entire range of possible hominin-ecological interactions (also see Tappen 2001).

The present research considers savanna structure at the level of closed and open habitats. Closed habitat includes moist forests, gallery forests, riverine forests, and woodlands, and open habitat refers to predominantly treeless grasslands. While some earlier works acknowledged the ecological importance of savanna heterogeneity (Behrensmeyer 1978a; Isaac 1976; Lovejoy 1981; Potts 1988), only recently has research on Miocene and Pliocene paleoenvironments actively investigated the mosaic nature of encroaching savannas (Feibel 1999; Kingdon 2003; O'Brien and Peters 1999; Owen-Smith 1999; Sikes 1999; Wesselman 1995). This recent work has served to move reconstructions of Pliocene savannas away from a grassland-dominated ideal, which Tappen (2001) refers to as the “Serengeti hypothesis,” and toward a more holistic understanding of savannas as composites of spatially and temporally heterogeneous environmental elements. The simulation presented in the next chapter follows the lead of these studies.

Vrba’s deterministic argument that hominin use of expanding Pliocene grasslands *caused* hominin evolutionary events has received criticism on more than one front. Stable carbon isotopic analyses of paleosol carbonate from a number of East African hominin localities indicate that open grassland environments, which Vrba (1985) hypothesized were directly responsible for dramatic evolutionary events including the speciation of early *Homo* and *Paranthropus* approximately 2.5 million years ago, might not have been present until as recently as 1 million years ago (Cerling 1992). To reconsider Vrba’s statements in light of Cerling’s findings prompts an obvious question: How could hominin speciation events have been caused by open grasslands that postdate them by well over one million years? Regardless of the actual timing of major ecological changes and speciation events, McKee (1999) argues that external environmental change could not possibly have caused evolutionary change among hominins. His perspective of autocatalytic evolutionary change is diametrically opposed to Vrba’s model of external environmental selection. These hypotheses embody both extremes of the environment-agency spectrum; surely a more appropriate explanation can be found somewhere between them.

Contrary to the predictions of the savanna hypothesis, paleoenvironmental and archaeological evidence indicate that Plio-Pleistocene hominin skeletal and material remains are associated with a variety of microhabitats including swamps, treeless to wooded grasslands, woodlands, and gallery forests—not just open grasslands (Kingdon 2003; Lovejoy 1981; Sikes 1994). After synthesizing the results of many archaeological investigations, some researchers have gone so far as to argue that the earliest late Pliocene hominins appear to have been frugivorous, partly arboreal, and primarily associated with closed woodland or forest ecosystems (Andrews and Humphrey 1999). Some postcranial morphological traits of *Australopithecus afarensis* such as relatively long, curved phalanges and a large humero-femoral index have long been argued as evidence that Plio-Pleistocene hominins possessed adaptations for life in and around the trees (Kimbel et al. 1994; Potts 1998; Stern and Susman 1983; Susman et al. 1984, 1985). Kingdon's (2003) recent synthesis of a wide range of morphological and archaeological findings proposes that, in addition to *Au. afarensis*, many other Plio-Pleistocene hominin species shared this reliance on closed habitats (*Homo ergaster*/*erectus* being the first to possess the ability to regularly obtain resources in open habitats). Obviously, these archaeological findings do not fit the expectations of the traditional savanna hypothesis. So, where does the contradictory archaeological and paleoenvironmental data leave the traditional savanna hypothesis, does it retain any utility for contemporary paleoanthropological research?

There is no doubt that the Pliocene spread of open habitats was an important environmental process that had far-reaching effects on the community ecology of sub-

Saharan Africa. However, contrary to the emphasis of the traditional savanna hypothesis, the evolutionary significance of this ecological shift might not have come from the expansion of open grasslands *per se*, but rather from the fragmentation of closed habitats. The savanna hypothesis overemphasizes the selective influence of spacious, open grasslands at the risk of slighting the selective power of shrinking ancestral forests. As a result, the traditional savanna hypothesis is too grassland-centric.

It is worth mentioning some of the few studies that have tried to deflect the focus of the savanna hypothesis away from open treeless plains. In a thought-provoking article that is now nearly a quarter of a century old, Lovejoy argued against what he called the "savannah selection theory" by stating that "all present evidence…indicates that [the] hominin clade evolved in the forest or mosaic conditions, or both, rather than only on grassland or savannahs" (1981:343). As an interesting aside, he went on to propose that the adaptation that proved crucial to the regular occupation of the open grasslands was "intensified social behavior," not bipedalism (1981:342). Similarly, in the conclusion of a paper that discusses the locomotor adaptations of *Au. afarensis* specimens from Hadar, Susman et al. (1985:191) also emphasize the selective significance of closed patches:

> "It may be that these [closed] areas, however small, were where small-bodied hominins lived. It may have been these areas shrinking through time in relative proportion to the overall habitat, that the hominins sought out for food and as a haven from predators…As time went on, increasing body size, tool use, and social cohesiveness would have eventually freed hominins from reliance on trees."

Most recently, ecological islands of gallery woodlands and moist coastal forests played prominent roles in Kingdon's (2003) reconstruction of the evolutionary environment in which early Pliocene hominoids adapted an upright posture.

These researchers find it hard to believe that Pliocene hominins—seemingly still very much adapted to closed habitats—would have abandoned habitable woodland patches for perceived opportunities in open grasslands. I echo Lovejoy's, Susman's and Kingdon's sentiments when proposing that the converse of the traditional scenario embodies a more plausible evolutionary framework. More specific to the purposes of this research on food sharing, I argue that those Plio-Pleistocene hominin trait groups that could successfully utilize familiar, but shrinking, closed habitat resources would have enjoyed increased relative fitness over those groups that could not. This scenario implies that despite significant environmental changes caused by a cooling and drying climate Plio-Pleistocene hominins continued to evolve behaviorally in ways that extended and enhanced their connection with closed woodland patches, not open grasslands.

Romer's Rule illustrates how this type of selective process could occur. Romer, a vertebrate paleontologist interested in the process by which a small subset of fish evolved into terrestrial organisms, studied how the adaptation (legs) that may have eventually made terrestrial life possible was originally selected to enable fish isolated in seasonal pools to migrate over dry land to find safety in more substantial bodies of water. Romer (1960) argued that morphological adaptations in the structure of fins initially aided these populations in maintaining their ancestral system of water dwelling despite facing substantial external environmental stress. Initially, legs helped fish continue to utilize the limited resource of shallow pools of water. Only later were legs used for an entirely different purpose—to colonize dry land. Although Romer's "fish out of water" reconstruction has recently come under fire from the "fish with legs" camp, which presents a number of new fossil finds in support of its perspective, Romer's recognition that incremental adaptations tend to bind populations to familiar resources rather than equip them for comparatively exotic surroundings is apt to this discussion.

Gould and Vrba (1982) define traits that function in a way other than that for which they were originally selected as *exaptations*. Romer's account of early fish legs provided an example of an exaptation before the definition was penned. The very same legs that some populations of fish evolved to remain in contact with fragmented bodies of water later allowed their descendants to move onshore, completely altering their environmental surroundings and evolutionary potential. In his brief review of Romer's research, Kottack (1999) reminds us that we should expect complex systems to adapt incrementally. Note that the process of incremental change does not imply that complex adaptive systems remain static or in homeostasis with their surroundings, which they most certainly do not. However, this incremental process does allow for earlier adaptations to be used in the future in interesting, "unintended" ways.

For the moment, consider Pliocene hominins and fragmented woodland (closed habitat) patches as roughly analogous to Romer's fish and seasonally drying pools, respectively. Just as Romer argued that some sub-populations of fish underwent incremental adaptations to better utilize spatially and temporally patchy water resources instead of more abundant dry land, so, too, could some hominin sub-populations have adapted incrementally to shrinking, yet familiar, forest patches rather than arbitrarily to a more abundant and exotic set of grassland resources. Furthermore, just as legs originally selected among fish to *maintain* contact with water eventually were used to leave it behind, biologically altruistic food sharing behaviors, originally selected to *maintain* a subsistence system dependent upon closed habitat resources, eventually could have been used to leave that environmental setting and make possible life in open grasslands and beyond. This perspective privileges the selective pressures associated with the distribution of closed habitat resources over those associated with open grasslands. It also views food sharing as a behavioral exaptation that may have been vital to life in open grasslands, but probably evolved initially through incremental adaptation to shrinking closed habitats, not by a haphazard jump into a new and dangerous ecological niche.

The present research investigates an idea that few previous paleoanthropological studies have made explicit: shrinking ecological islands of woodland resources may have created selective conditions that would have facilitated the evolution of altruistic food sharing tendencies in hominin populations. Well-defined and well-separated resource patches can restrict the foraging movements of many individuals to just a few localized areas and, as a result, foster assortative interactions between a small group of individuals. Regardless of whether they are mediated by ecology or culture, assortative interactions effectively subdivide large demes into smaller evolutionarily meaningful trait groups. Pepper and Smuts (2000, 2002) demonstrated this effect when they found that, when inhabited by a mixed population of altruists and nonaltruists, patchy resource distributions alone are sufficient to facilitate the spread of altruistic traits throughout an entire metapopulation. By selecting for altruistic traits that would aid survival in fragmented closed patches, the between-group selective pressures presented by waning forest resources ultimately “preadapted” hominins for open grassland habitation much like, by selecting for legs, the selective pressure of fragmented pools may have "preadapted" finned fish for life on dry land.

According to this hypothesis, hominin populations evolved food sharing in patches of closed habitat and later applied the behavior to new sets of selective pressures in open grasslands only after small pockets of ancestral forest could no longer offer sustainable resources. Thus, the act of sharing carcasses in open grasslands, which is normally associated with *Homo erectus* and their descendents, could be considered a behavioral exaptation. Even after closed habitats became too fragmented to house Plio-Pleistocene hominins full-time, wooded riparian zones and scattered clumps of trees continued to act as loci for many activities, such as sleeping, feeding, and/or defense, as evidenced by the archaeological record (see below). This revised version of the savanna hypothesis acknowledges the encroachment of woodlands by grasslands but refocuses our attention on the savanna's fragmented patches of closed habitat as the actual loci of much Plio-Pleistocene hominin behavioral evolution.

3.2 An archaeological perspective of Plio-Pleistocene hominin behavior

Plio-Pleistocene archaeological remains rarely yield unequivocal material evidence of hominin behavior at the resolution required to address many intriguing ethological research questions, including those that address food sharing. The prospect of relying solely upon fragmentary archaeological assemblages to reconstruct hominin evolutionary history is akin to describing the scene depicted on a jigsaw puzzle the size of a baseball field provided only with the number of pieces required to fill a cigar box. Given the difficulty of this charge one should not be surprised that for decades paleoanthropologists have relied upon observations of contemporary human foragers and living nonhuman primates to help fill the gaps between empirical clues. As a result, modern primate (including human) behaviors have been employed as referential models for a variety of hominin behaviors including: pair bonding, sexual division of labor, tool use, male provisioning, carnivory, and food sharing. Though on the surface they seem quite helpful, such models suffer from a number of disconnects, most of which stem from treating hand-picked, isolated characteristics of contemporary species as modern day analogs for those of evolutionarily unique fossil species.

In the absence of unequivocal archaeological evidence and analytic models, previous attempts to reconstruct Plio-Pleistocene hominin food sharing behaviors have relied heavily upon combinations of extensive field experience and referential modeling techniques. According to Tooby and DeVore (1987), referential models employ one observable phenomenon (e.g., a behavior observed among contemporary hunter-gatherers) as a model for the targeted referent (e.g., hominin behavior), another phenomenon that is real but extremely difficult, if not impossible, to study directly. As we shall see below, when Glynn Isaac used referential modeling to reconstruct an early hominin “adaptive complex” centered around the activity of sharing food at home bases, he used inferences drawn from observations of contemporary human foragers to interpret East African concentrations of chipped stone tools and fossilized bones as “protohuman” versions of modern hunter-gatherer base camps (Isaac 1978a:104).

Though popular among paleoanthropologists for a number of years, referential models have serious limitations for building inferences for hominin behavior. First, recall that this approach requires that a unique *known* phenomenon be used to model an equally unique, but *unknown*, referent. This inductive characteristic of referential modeling would be less distressing if one could follow an independently validated procedure for selecting appropriate known phenomena to serve as models. However, currently one must assume that contemporary referential models are chosen arbitrarily unless conceptual models are included to substantiate model suitability—a feat that is accomplished rarely (Tooby and DeVore 1987). Second, referential reasoning overemphasizes the similarities that purportedly exist between known phenomena and their referents while obscuring potentially important differences (Tooby and DeVore 1987). When perceived through the lens of referential reasoning, the unobservable referent can only seem more like its observed model. This inherent characteristic of referential models obfuscates the study of hominin traits that contemporary foragers no longer exhibit:

> "By their nature, referential models tend to ignore or obscure the most important question in human evolution: where did our most crucial and novel adaptations come from?" [Tooby and DeVore 1987:187]

Some paleoanthropologists consider Tooby and DeVore's characterization of referential and conceptual models to be unfair, or even misleading (McGrew 1992; Moore 1992; Quiatt and Huffman 1993; Stanford and Allen 1991), while others discuss methods for utilizing the best aspects of both. For example, in a thought-provoking paper about the use of social theory in paleoanthropological studies of food sharing, Steve Kuhn and Kate Sarther (2000) present an argument for the combined use of formal social theory based on "highly simplified, mechanistic" conceptual models and what they call social-science theories (i.e., referential models) that are built on assumptions about universal characteristics of modern human nature drawn from contemporary observational data. While they admit that formal theory "offers a better fit with the limitations and goals of human evolution research," they note that referential social theory still has an important (albeit secondary) role, which should not be forgotten or ignored (Kuhn and Sarther 2000:82). In their words:

> "Whereas formal theory may provide the most useful working models for application in an evolutionary time scale, ideas about how social relations are actually realized within and among human groups are the only source of verisimilitude for these simple models. Formal models can be used to analyze the general evolutionary motor behind long-term changes in human social behavior, but theories of society from the human sciences provide vital perspectives on the unique historical directions taken by the evolutionary process." [Kuhn and Sarther 2000:82]

Although the present modeling project emphasizes formal conceptual models over referential ones, it attempts to follow Kuhn and Sarther's challenge to include some aspects of both. Before addressing the research at hand, however, it is necessary to review past paleoanthropological research on Plio-Pleistocene food sharing, most of which has relied upon referential modeling techniques.

The home base (or food sharing) hypothesis

Glynn Isaac's name will forever be associated with research on Plio-Pleistocene hominin food sharing. Isaac developed his ideas about early hominin food sharing while excavating Lower Paleolithic scatters of Oldowan and Acheulean tools and fossilized animal bones at a number of locales in East Africa. In a set of papers published in 1978, he presented one possible behavioral explanation for the archaeological distributions he had documented in the field. This explanation became known as the "home base" hypothesis (or alternatively, the food sharing hypothesis) after the term he used to describe the locales at which Plio-Pleistocene hominins allegedly conducted a variety of behaviors including food transport, food sharing, sleeping, stone working, etc. It is important to note that Isaac stressed the term "hypothesis," for his goal was to draw scientific attention to a specific research question rather than to argue in favor of any one answer at such an early stage of the game. Although his 1978 papers are cited most frequently because they are the first to present the complete version of the home base hypothesis, Isaac had proposed pieces of his reconstruction separately in earlier articles which are also worthy of a look (Isaac 1971, 1972, 1976).

Isaac was neither the first nor the only researcher to speculate on the important role that food sharing might have played in hominin evolution. Many of his paleoanthropological colleagues believed that early hominins were accomplished hunters

(Washburn and Lancaster 1968), so discussions concerning how meat resources were shared among individuals seemed to them a logical next step. For instance, Hewes (1961) had already presented a model that describes how transporting food with the purpose of sharing with others could have selected for bipedalism in the earliest of all hominins. At roughly the same time that Isaac began writing about home bases, F. Le Gros Clark openly speculated as to how Plio-Pleistocene hominin food sharing might have affected the development of many social behaviors:

> "The sharing out among a whole group of the flesh of game animals represents a further qualitative advance in culture…From the beginning it must have implied a combination of two factors—extended hunting expeditions for food of animal origin, and some kind of emotional "leap forward" in social awareness…it is indubitable that the original *food-sharing* habit was the groundwork for all the subsequent divisions of social roles and social labour." [Le Gros Clark 1971:21]

Similarly, Lancaster argued that the behavior of carrying food to be shared—not tool using, encephalization, hunting, or aggression—afforded early hominins the "immediate advantage necessary to initiate these changes as well as the long-term advantage necessary to perpetuate them" (1978:89). Following Isaac (1976) and Leakey (1971), she believed that the so-called "living-floors" found in Olduvai and at Koobi Fora served as evidence of Plio-Pleistocene hominin carrying and sharing. Tanner (1981) also proposed that home bases played a pivotal role in an evolutionary scenario that emphasized a food sharing system fueled by female provisioning at central places.

The primary purpose of Isaac's home base hypothesis was to formalize and make explicit these speculations, thereby allowing archaeologists to test them against the material record. Earlier, Isaac (1967:31) had applauded paleoanthropology's "marked change of emphasis" from a preoccupation with artifact morphology and classification to an interest in addressing larger behavioral questions, and it appears that to further encourage that trend he promoted an impelling socio-ecological research program centered on questions concerning early hominin subsistence and land use strategies.

According to Isaac (1978a, 1978b), the acts by which behaviorally modern human foragers (1) postpone food consumption until rejoining others at a predefined locale (i.e., a "home base") and (2) actively share food with others clearly distinguish them from extant great apes. He argued that these two subsistence characteristics are so uniquely human that they probably played an important role in the evolutionary development of our species. But how ancient are these human characteristics: did they arise relatively recently "just prior to the appearance of fully modern man" (Binford 1985:321), or did the very first Miocene hominins display these behavioral traits in addition to bipedalism long before the time of stone tools (Tanner and Zilhman 1976:599)? Indeed, in his first attempts to answer this question, Isaac hypothesized that an archaeological assemblage documented by his work at Koobi Fora as well as the "living floors" described by Mary Leakey (1971) in Olduvai Gorge present nearly 2 million years-old evidence of delayed food consumption and food sharing at central places.

Plio-Pleistocene archaeological assemblages are notoriously difficult to interpret. Little more than ambiguous scatters and amorphous concentrations of choppers, flake tools, and modified animal bones, Oldowan assemblages leave much to the imagination. In fact, much of Isaac's (1971, 1972, 1976) earlier work explored methods that could be used to distinguish between different types of "occupation sites," including transitory camps and so-called home bases. These techniques considered the relative densities of bone and stone artifacts (see Isaac 1971:Figure 10a) as well as the frequencies and types of animal parts represented in the faunal assemblage of each "site." Later he tried to make sense of these distributions by categorizing them as one of three types: A, B, or C (Isaac 1978a, 1978b). Type A assemblages are composed of lithic tools and debitage only; they lack significant amounts of animal remains. These assemblages were often described as "workshops" or "quarries," locales where few activities other than stone working were thought to have occurred. Type B assemblages are composed of lithics in association with the remains of just one (large) animal. Such assemblages were thought to be evidence of butchering or kill "sites" where an individual carcass was processed by tools made onsite and/or transported to the locale. Finally, a Type C assemblage is composed of a scatter of lithic tools in association with skeletal remains of *multiple* animal (often times including hominin) species. Isaac deduced that Type C lithics were imported by hominins from sources up to three kilometers distant, and he assumed that the bones had been transported to the locale over a relatively short time period by hominins interested in sharing the meat that clung to them and/or the marrow contained within them. It was examples of these Type C assemblages in Olduvai Gorge and at Koobi Fora that Isaac (1976, 1978a, 1978b) proposed might serve as evidence for early hominin food sharing events.

To flesh-out this framework, Isaac (1978a:100) turned to "recorded data concerning primitive human societies," a methodological decision that would later be criticized by a number of researchers. In the attempt to formulate a testable hypothesis, Isaac mapped historic hunter-gatherer home base activities onto Type C assemblages and postulated that early hominins may have been practicing "food-sharing as the behavior central to a novel complex of adaptations that included as critical components hunting and/or scavenging, gathering and carrying" (1978a:102). He even added that a sexual division of labor, akin to that which anthropologists have witnessed in many ethnographically documented human foragers, might already have been present in the early hominin society responsible for Type C accumulations. Despite a concerted effort to call these early hominins "protohuman" and a clear acknowledgment that there are no modern counterparts for the cultural system practiced by early hominins, the implications of his bold model characterize Oldowan behaviors as extraordinarily (and, to most paleoanthropologists, uncomfortably) modern-like. Central place foraging, food sharing, sexual division of labor, and sophisticated resource transport behaviors were not characteristics commonly associated with pre-*Homo erectus* hominins in East Africa prior to Isaac's work. Despite his careful wording, many paleoanthropologists thought he was arguing that early hominins were "relatively placid, cooperative, gentle creatures who lived essentially human lives, less a few trappings of cultural elaboration" (Isaac 1981:187). Of course, this was not Isaac's intention. Nevertheless, as one set of researchers clearly recounts:

> "[The] home-base hypothesis implied that our ancestors of nearly 2 million years ago had developed a pattern of land use and sociality that was more analogous to that of contemporary hunter-gatherers than to that of extant nonhuman primates." [Rose and Marshall 1996:309]

Isaac reconsiders, proposes central places in place of home bases

Isaac's provocative statements acted like a potent catalyst in a chemistry experiment. A few researchers, including Owen Lovejoy, not only accepted but also added to Isaac's hypothesis without testing it empirically. In an article entitled "The Origin of Man," Lovejoy (1981) provided his own reconstruction of early hominin society, which incorporates many other modern human characteristics. He upped Isaac's ante by arguing that monogamous pair-bonding, nuclear families, and male provisioning also "may have their ultimate origin long before the dawn of the Pleistocene" (Lovejoy 1981:348). Alternatively, other paleoanthropologists set out to disprove some of Isaac's more speculative proposals via directed research projects. For the most part, Isaac's pot-stirring triggered research programs that proceeded along two parallel trajectories. One line of study, based in vertebrate taphonomy, focused on the role that faunal resources might have played in Plio-Pleistocene hominin diet and how animal bones came to be incorporated into Lower Paleolithic assemblages. The other investigated hominin resource transport behavior.

A myriad of zooarchaeological analyses were conducted to test Isaac's assumption that hominins habitually transported bones to home bases in order to share the calories they provided. These studies had a number of goals including: determining whether hominins were hunting or scavenging; determining whether hominins or carnivores were primarily responsible for the dense accumulations of bone; and determining what types and quantities of food resources the animal remains would have yielded to hominin procurers (Binford 1981; Bunn 1981, 1983; Bunn et al. 1980; Potts and Shipman 1981; Shipman 1983, 1984). Although considerable disagreement exists between some of these researchers, given the results of their analyses on the whole it seems unlikely that Oldowan hominins were regularly carrying large packets of meat "home" from fresh kills. Evidence of hominin- and carnivore-inflicted damage to the bones implies that, in many cases, hominins may have been able to commandeer the bones only after they had been stripped of flesh but still contained marrow and tendons (but see Bunn's argument). By utilizing faunal resources, hominins may have had direct (and possibly dangerous) contact with other carnivorous hunters and scavengers at some death sites, and carnivores (in conjunction with or independent of hominins) probably played a significant role in concentrating and/or modifying some of the bones found in so-called Type C assemblages.

Isaac's hypothesis was directly responsible for zooarchaeological research on Plio-Pleistocene assemblages, which has not abated (Binford 1985; 1988; Blumenschine 1986a, 1986b, 1987, 1988, 1989, 1991, 1995; Blumenschine and Cavallo 1992; Blumenschine and Marean 1993; Blumenschine and Selvaggio 1988; Bunn 1991, 1994; Bunn and Ezzo 1993; Bunn and Kroll 1986; Capaldo 1997, 1998; Cavallo and Blumenschine 1989; Dominguez-Rodrigo 1997; Dominguez-Rodrigo et al. 2005; Lupo and O'Connell 2002; Monahan 1996; Shipman 1986; Tappen 1995, to name just a few). Isaac used early zooarchaeological findings and additional data collected from his own field investigations, designed "to prove [his original] predictions false" (1981:187), to reevaluate the plausibility of the home base hypothesis just five years after introducing it to the paleoanthropological community. He admitted that although it seemed perfectly reasonable at the time to invoke food sharing at prearranged loci, it no longer seemed necessary to use this modern subsistence strategy in order to explain the material record. In his own words:

> “the recurrent *transport* of meat and bone to favoured locales is indicated, but does this imply active food sharing? Contrary to my earlier writings, I would now agree with various critics, Binford included, in admitting that while it may mean this, it need not necessarily do so…The transport need not have been motivated by ‘provisioning’ or ‘sharing’ intentions…” [Isaac 1983:13,15]

Isaac also addressed his prior use of contemporary hunter-gatherer behaviors as referential analogs for those of Plio-Pleistocene hominins:

> “I now recognize that the hypotheses about early hominid behavior I have advanced in previous papers (e.g. Isaac 1978[b]) made the early hominids seem too human. It is important that we be as ruthlessly analytic as we can. I now favour relabelling the ‘food sharing hypothesis’ as the ‘central-place-foraging hypothesis.’” [1983:15]

This semantic change alleviated much of the baggage associated with loaded terms like “home base,” while preserving the aspects of the hypothesis that stood a more realistic chance of being tested—repeated transport of materials to discretely defined loci. The most beneficial result of this seemingly superficial change was that researchers were able to conserve their energy and ink for studying and explaining characteristics of the archaeological record rather than venting over Isaac’s hypothesis for the behaviors responsible for it.

The stone cache model

While many researchers were conducting the taphonomic studies described above, Richard Potts was also investigating early hominin resource transport behavior. Like Isaac, Potts believed that Oldowan hominins were capable of carrying various resources including food and stones. However, Potts did not believe that clusters of stone tools and associated animal remains necessarily represented home bases (*sensu* Isaac 1978a, 1978b) or even central places (*sensu* Isaac 1983) where hominins processed carcasses, shared meat, slept, made tools, and may have conducted other social behaviors as a group. In a series of papers Potts (1982, 1984, 1987, 1988) has argued that early hominins solved two important problems by actively redistributing stone raw materials over the paleolandscape: (1) they buffered themselves against the spatial incongruity of carcasses and the stone resources required to access calories within them and (2) they avoided predation by carnivores in the vicinity of animal death sites by moving food to safer locations.

Because Plio-Pleistocene hominins lacked the dental adaptations that carnivores use to obtain meat and marrow from carcasses, paleoanthropologists have generally assumed that they could effectively process faunal resources (especially bone marrow) only with the aid of stone implements such as Oldowan choppers, hammerstones, and utilized flake tools. However, naturally occurring outcrops of the raw materials used to create stone tools rarely overlap perfectly in time or space with animal carcasses; they may be separated by many kilometers. Potts argued that upon obtaining a carcass hominins would face a serious spatial dilemma: to carry choice parts of the carcass to the nearest source of stone or to retrieve stone tools from a distant locale and risk losing the unguarded carcass to scavengers? By leaving stone materials and tools at particular locations like original death/butchery sites, under shade trees, or near other limited resources like water, hominins would eventually (and possibly inadvertently) redistribute highly patchy stone material throughout their foraging area, making its distribution more uniform, more predictable. Hominins would transport animal remains to these nascent stone caches, thereby avoiding both long periods spent at possibly dangerous death sites and the expenditure of large amounts of energy in either retrieving stone from a distant source or carrying parts of the carcass over a long distance to one of a few naturally-occurring stone sources. In this way, redistributed caches of raw stone material and previously used tools acted as “attractive magnets,” repeatedly pulling hominins finding themselves in possession of animal parts away from the sites in which the animals were found or killed and toward adjacent clusters of stone (Potts 1991).

According to Potts, Oldowan hominins need not have displayed all of the uniquely human social behaviors attributed by Isaac (1978a, 1978b). The only unique adaptation necessary to the stone cache model is an important shift in the spatial utilization of two patchy resources: stone and animal carcasses. Another note of historical significance and especially germane to the present study is that Potts’ stone cache model was the first Plio-Pleistocene reconstruction to showcase the use of a computerized conceptual model. He employed computer models to explore the amount of energy required to move stone (from one known source locale) and to move randomly scattered carcasses to predefined, regularly spaced "sites" on a two-dimensional space (Potts 1982, 1984, 1988; Potts and Walker 1981).

Routed foraging and resource transport among favored locales

In 1984 (and then again in 1987) Lewis Binford outlined an alternative to Isaac's central place model. The routed foraging model had a significant impact on later studies of resource transport and hominin land use. According to Binford, Plio-Pleistocene hominins did not have the ability to make shelters near locales that provided important limited resources, nor could they provision one site with all of the necessary goods. As a result, the foraging routes of early hominins were rigidly routed through a small number of areas that could satisfy their needs for secure shelter, water, and food given the spatial structure of crucial resources in the environment. According to Isaac's home base model, Plio-Pleistocene hominins display a complex and flexible system of provisioning themselves by transporting resources to central places. However, Binford's idea was that hominins lacked this central place foraging technique and so they continuously moved themselves to the resources. He argued that, lacking central place foraging, hominins would have become entrenched in their routes, moving robotically between the same sets of resources with little deviation in the *zones* separating these important *places*.

> "Sites, under the conditions of this model of land use, are not 'central places,' positioned so the hominid group may operate out into the environment in terms of mobility and labor concerns; they are instead focal points in the environments…" [Binford 1984:264]

This distinction between central place foraging and routed foraging has important implications for resulting archaeological assemblages. Because routed foragers have little choice but to spend most of their time in the vicinity of critical resources, their use of these valuable locations is “regular, repetitive, and frequent” (Binford 1984:264). How this type of mobility pattern could affect material assemblages is not difficult to predict:

> “If the creature using these locations is capable both physically and emotionally of carrying things, then we can expect there to be an increasing concentration of transported items at such locations as a function of the regularity with which such places are used.” [Binford 1984:264]

Like Potts, Kathy Schick (1987) was interested in studying how the habitual transport of resources such as stone and food resulted in Plio-Pleistocene accumulations. Her work was influenced by Binford’s model of routed foraging and his ideas about recurrent use of certain places. And, like Potts and Binford, Schick argued that the method of applying recent human socio-economic organization to Lower Paleolithic assemblages was unsubstantiated. However, these similarities did not stop her from describing what she thought were deficiencies of Potts’ stone cache model. Its most significant shortcoming was in explaining the wide range of variation in artifact concentrations—especially the presence of very dense concentrations of stone tools and raw material. Stone transport costs at any one “site” would follow a diminishing returns curve, which means that beyond some point in the amount of stone accumulated, importing additional stone would cost more energy then it would conserve in carcass transport costs. If the principle reason for the formation of stone caches was to minimize summed (both stone and carcass) transport costs, stockpiles of stone would eventually reach a density beyond which the transport and accumulation of additional materials to the same locale would cost more total energy than it would conserve. It seems that this would hold true even if, as Potts' (1988) argues, "extra" stone were brought in anticipation of future use. The stone cache model explicitly addresses how the number of caches affects the amount of energy spent on summed transport costs, but it does not account for the large range of assemblages encountered—from small, Type A scatters to large, Type C concentrations.

Schick argued that a model must adequately explain variations in assemblage size, density, and the relative proportions of artifact types and that the stone cache model fails to address these issues. Her model takes into account technological evidence that speaks to stone transport behaviors both *to* and *from* certain "key positions in the environment" (Schick 1987:795-796), a phrase which echoes Binford's thoughts about focal sites in the environment. In Schick's model, hominins habitually carry stone tools and raw materials in mobile toolkits as they forage for food. Over time items discarded from these toolkits accumulate into archaeologically recognizable concentrations in areas where "stone was repeatedly brought in but not removed in equal quantities" (Schick 1987:800). Thus, according to Schick's model stone would accumulate in some areas "not through a deliberate stockpiling motive, but as a by-product of the import-export imbalance" (1987:800).

Schick outlined a number of factors that would affect the formation of Plio-Pleistocene assemblages. First, as Binford mentioned in 1984, one should expect frequently used, favored locales, like reliable feeding, drinking, and/or safe resting areas, to experience higher levels of stone import given the increased presence of hominin foragers. On the other hand, rarely visited locales would experience very little stone import (or export, for that matter) simply because hominin presence is minimal. These two propositions would hold true regardless of whether central place foraging was practiced by hominins. Jeanne Sept (1992) also wrote about this idea of favored areas accumulating greater amounts of cultural debris solely due to an increased frequency of visits. She tested whether chimpanzees living along the Ishasha River in Zaire displayed the propensity to revisit previous sleeping sites, thereby leaving a greater amount of debris (resting nests) in certain parts of the habitat than in others. She chose chimpanzees not because she thought they provided a good analogy for Plio-Pleistocene hominin behavior, but because they practice routed foraging, not central place foraging, and this is quite different from the strategies used by modern human hunter-gatherers. Sept reported that the refuse of the Ishasha River chimps displayed the same three-tiered hierarchy of spatial patterning that previous researchers reported for Plio-Pleistocene assemblages (Kroll and Isaac 1984). Even though the chimps' material assemblage was quite different from that left by Plio-Pleistocene hominins—sleeping nests as opposed to stone tools and modified bones—many of the spatial characteristics of the two assemblages were comparable. Over a short period of time (two dry seasons) the chimps created both dense clusters and thinly dispersed scatters of debris through redundant use of preferred locales. By testing the significance of favored locales against an empirical record of land use Sept's (1992) preliminary study illustrates how a routed foraging strategy can yield archaeological landscapes that previously had been attributed solely to more complex strategies involving central place foraging, food sharing, and family provisioning.

Schick also proposed a number of factors that might reduce pressure to export stone from any locus to which it had already been imported. For instance, pressure to export the same amount of stone that had been imported would be reduced if it was necessary to carry other items (food, wood, etc.) away from a locale, to abandon an area suddenly, or if planned activities were going to take place at a different locale where a sufficient quantity of raw material was known to exist. Over time, both raw materials and stone tools would accumulate in areas where hominins experienced relaxed export pressures. Schick's conceptual model is easily summarized:

> "Locations used very often by hominid individuals or groups could have had substantial quantities of stone material imported over a period of time, and, if the pressures to export materials away from the site were then reduced for any of the above reasons, artifact concentrations would develop." [Schick 1987:801]

Binford's routed foraging model, Schick's emphasis upon resource transport pressures, and Sept's field study all hint at a *null model* of artifact accumulation. Instead of invoking intentional behaviors like central place foraging, food sharing, or stockpiling (but see Potts 1988 for his explanation of why stone-caching need not be an "intentional" behavior), the scale and density of Oldowan concentrations might just as easily be explained as unintended by-products of hominins experiencing fluctuations in export pressures at favored locales along an entrenched foraging route or (fasten your seatbelts) along an even simpler foraging route that involves nothing more than moving towards the area of highest perceived resource abundance. As we shall see, the agent-based model presented in the following chapter tests Binford's, Schick's, and Sept's proposition that frequently visited areas might accumulate concentrations of artifacts in the absence of central place foraging or caching behaviors, but it does not model diachronic changes in the import-export imbalance (which is assumed to be constant in SHARE). Schick's model yields a host of other predictions concerning a number of technological aspects of Lower Paleolithic stone assemblages (i.e., raw material diversity, presence of exotic material, relative abundance of conjoinable pieces, relative abundance of debitage, artifact diversity, artifact density, etc.), which I believe can be tested both empirically and experimentally, but are not tested here with SHARE.

Empirical archaeological tests of the home base, stone cache, routed foraging, and resource transport/favored locales models call for the use of a landscape archaeological approach because, as Blumenschine and Masao (1991) point out, it is difficult to evaluate the validity of a number of hypothetical socio-ecological models of land use strategies when the majority of pertinent archaeological data comes only from "mega-sites"—large Type C concentrations characterized by relatively high archaeological visibility and stratified vertical deposits. This unequal attention to so-called living floors and/or home base "sites," has provided important information about a few Plio-Pleistocene hominin locales, but very little about how the artifact densities and compositions of the assemblages found there compare to contemporaneous material remains in surrounding regions. Blumenschine and Masao were not the first to express concern over the research bias towards "patches" of Plio-Pleistocene artifacts. As early as 1975, Isaac and Harris (1975, 1980) attempted to sample artifact distributions at different loci to obtain a better idea of the spatial variability displayed by Plio-Pleistocene assemblages. They called this the "scatter-between-the-patches" approach to emphasize their belief that the material remains found between dense concentrations were equally important in answering large-scale behavioral questions. Soon, others began thinking in terms of lateral—rather than just vertical—sampling methods, and a number of them described their thoughts on how best to conduct this type of research in the field using “nonsite” (Thomas 1975), “off-site” (Foley 1981a, 1981b, 1981c), “siteless” (Dunnell and Dancey 1983), and “distributional” (Ebert 1992) archaeological approaches.

Robert Blumenschine has led the Olduvai Landscape Paleoanthropology Project’s investigations of the lowermost Bed II times in Olduvai Gorge (Blumenschine and Masao 1991; Blumenschine and Peters 1998; Peters and Blumenschine 1995, 1996). He and his group have applied so-called ecological archaeological approaches to examine the synchronic variability of artifacts across paleolandscapes. This involves survey and test excavations outside the boundaries of traditionally defined “sites.” Preliminary results of their distributional archaeological work in the scatters between the patches demonstrate that “the vast majority of archaeological remains, and hence behavioral information derivable from them, are located ‘off-site’” (Blumenschine and Masao 1991:456). While the authors agree that hominins “did at times concentrate artifacts and carcass parts for processing” (1991:459), they warn that:

> “The apparent continuous distribution of artifacts and associated bones…and their often higher densities in areas lateral to the [main] excavation, suggest that home bases, or repeatedly visited focal locations for *multiple* hominid activities, have not been shown to exist during basal Bed II times.” [Blumenschine and Masao 1991:458, emphasis in original]

As this promising paleolandscape research continues to gather distributional data in Olduvai and similar projects commence in other regions, we may gain a more comprehensive understanding of Paleolithic archaeological landscapes at a regional scale.

The resource-defense model

Lisa Rose and Fiona Marshall (1996) revisit Isaac's home base/central place hypotheses with their resource-defense model. They disagree with the assertions of Binford (1981, 1984, 1987) and Potts (1988), who envision Type C assemblages as the remains of temporarily occupied food-processing sites and not as the remains of safe refuges that functioned as hubs of Plio-Pleistocene social behavior. Furthermore, they argue that the risk posed by carnivore predation at locales containing transported bone and meat would not be great enough to discourage central place foraging among early hominins. Quite to the contrary, they present a model in which the presence of dangerous carnivores would have selected for an *increase* in cooperative social behaviors and food transport to central places, where groups of hominins could capably defend themselves and their resources from other hominin groups as well as from sympatric carnivores. To illustrate how intensive cooperative behaviors and group cohesion can aid in the defense of resources, they cite a variety of behavioral strategies (vigilance, alarm-calling, and cooperative physical defense) practiced by extant group-living nonhuman primate species when facing predation risk. Rose and Marshall are clear in their statement that carnivore competition may have been a driving—rather than debilitating—selective pressure for Plio-Pleistocene central place foraging:

> "…the presence of carnivores is not sufficient basis for discarding the home-base hypothesis and…the risk of carnivore predation and competition may instead have promoted cooperative social behaviors and the regular transport of meat resources to specific defensible sites." [1996:311]

Defensible sites would logically be located near important fixed resources. A list of such resources would include but not be restricted to: water, fruit, shade, escape trees, and safe sleeping sites. The authors recognize that many behaviors besides resource transport and group defense (e.g., carcass butchering, tool making, and food sharing) *could* have taken place at these defensible central places while they were occupied by groups of hominins. However, because their resource-defense model does not require modern human behaviors like food sharing, pair bonding, or the sexual division of labor it stops well short of merely applying a fresh coat of paint to Isaac's original version of the home base hypothesis. Recall that Isaac's home base hypothesis privileged food sharing "as the behavior central to a novel complex of adaptations" (1978a:102). Rose and Marshall replace altruistic food sharing with cooperative resource-defense as that pivotal behavior. Thus, the resource-defense model hinges on the validity of two premises: (1) as a result of increased carnivory hominins transported parts of carcasses as a coordinated strategy to mitigate competition with carnivores and (2) cooperative group defense allowed hominins to conduct multiple activities at focal sites during both day and night.

Battle of the sexes

As stated at the start of this chapter, paleoanthropological reconstructions traditionally have been based on archaeological inferences built from observations of contemporary primates. They have rarely borrowed theory from evolutionary biology or human behavioral ecology. In fact, only recently have developments in the related field of evolutionary ecology influenced paleoanthropological reconstructions of Plio-Pleistocene hominin behavior. The two examples covered in this brief section incorporate (to varying degrees) the themes of gender-specific reproductive strategies, scrounging, and costly signaling.

In 1999 Richard Wrangham and colleagues presented an ambitious new hypothesis to explain the speciation event of *Homo erectus*. It deserves mention here because central place foraging and sex-based reproductive strategies play central roles in their multivariate explanation. The technique of cooking food not only increases the number of food types that can be shared but also makes food more valuable and, therefore, more vulnerable to theft. They hypothesize that cooking at central places could have its roots in the Plio-Pleistocene. If they are correct, the presence of cooked foods in a known locale could have precipitated a producer-scrounger game between those individuals who collected and prepared the food and those who did neither (Barnard 1984). In a producer-scrounger game dominant individuals scrounge (steal) from subordinate producers who have already spent time and effort preparing a good, which in this case is cooked food. Wrangham et al. argue that, given their larger size, early hominin males would have played the part of scroungers and females the part of producers. To protect themselves against constant scrounging at central places, females may have developed protective alliances with individual males, who would act as "bodyguards" against the theft of cooked items. The model goes on to explain that extending female sexual receptivity would function to attract and retain the best bodyguards, while males might attempt to provide protection to a number of females in exchange for additional reproductive opportunities. Other changes in body size and life history accompany this explanation, but those details surpass the scope of this review. However, it is important to note that Wrangham et al.'s version of central places is quite different from Isaac's. In Isaac's original version hominins frequent central places to share food with kin and other group members, but in Wrangham et al.'s reconstruction hominins frequent central places to cook food, to steal food from others, or to defend against scrounging in return for sexual access. In the latter case, the presence of sharable foods drives the evolution of selfish strategies, not altruistic behaviors.

Another recent paper concerns itself with male strategies in the Plio-Pleistocene. The main thrust of O'Connell et al.'s (2002) argument is to further the hypothesis that large animal carcasses were obtained by (male) Plio-Pleistocene hominins as a means to advertise their value as mates and to acquire social capital through costly signaling, rather than to provision their young at home bases. After reviewing both the hunting and home base hypotheses, O'Connell and colleagues conclude that the Plio-Pleistocene archaeological evidence from Olduvai, Peninj, and Koobi Fora supports neither. Instead, scatters of large mammal bones serve as evidence of opportunistic (and often aggressive) scavenging events. As actualistic studies have noted, savanna carcasses quickly attract a crowd. Many different kinds of scavengers, from hyenas to vultures, usually find their ways to join carnivorous hunters at recent kills. O'Connell et al. suspect that early *Homo* groups also would have been early on the scene at these kill sites. However, because they were not big game hunters, early *Homo* groups were forced to displace those that possessed the carcass if they hoped to consume any of it. When hominins found themselves in close proximity to heavily contested meat resources, O'Connell et al. argue that:

> "…[the] very danger and the presence of a large audience would also have created a sometimes irresistible opportunity for males to display their qualities as desirable allies and dangerous competitors…Rock-throwing and/or stick-wielding advances would have allowed males to distinguish themselves in a very public manner." [2002:861]

In other words, by participating in a potentially deadly and easily observable activity, such as driving a pack of lions from their kill, a male (or group of males) could procure meat for himself and his group while at the same time signaling the quality of his physical abilities (strength, speed, bravery, intelligence) to potential mates as well as to potential male allies through a scavenging display.

While the authors make a good case to support the interpretation that Plio-Pleistocene assemblages are more indicative of active and passive scavenging events than of home bases, they provide little evidence to support the hypothesis that hominins used this venue to display their rock-throwing and stick-wielding abilities in the context of male status rivalries and no evidence to support the assertion that these aggressive scavenging events would satisfy the requirements of a costly signal. In the final analysis, the costly signaling explanation falls in line with those based on the mechanism of individual selection: males unconditionally share food recovered through impressive physical displays to increase their own reproductive fitness, not to benefit other individuals at their own expense.

The recent studies by Wrangham et al. and O'Connell et al. mark a departure from earlier reconstructions. Recall that Isaac, Lovejoy, and others argued that the presence of biologically altruistic behaviors like food sharing was a driving evolutionary force in Plio-Pleistocene societies. However, the more recent models turn altruistic strategies, such as dangerous acts of aggressive scavenging and self-sacrificial acts food sharing, into selfish attempts by members of both sexes to protect their own resources and/or increase their reproductive opportunities. Thus, these later studies clearly reflect a strong and pervasive predisposition to individual-level selection.

3.3 Conclusion

For decades the traditional savanna hypothesis permeated thoughts on early hominin evolution. The study of important adaptations including bipedalism, encephalization, and food sharing were discussed in terms of how they might benefit hominin species moving between and through open grasslands or utilizing resources found only in open habitats. Recently, however, researchers have begun to appreciate the mosaic nature of Plio-Pleistocene savannas. My research follows with that trend by concentrating on the fragmented pieces of ancestral habitat rather than on the growing expanses of open grasslands. As we shall see in the following chapters this new emphasis on the patchiness of closed habitat illuminates evolutionary trajectories that were not previously apparent.

Glynn Isaac pioneered the study of Plio-Pleistocene hominin behavior only 30 years ago. His provocative home base hypothesis attracted many others to investigate some of the earliest known archaeological traces with larger behavioral questions in mind. Although some researchers studied taphonomic issues and others dealt with resource transport and land use strategies, they all shared with him the larger goal of reconstructing hominin socio-economic behavior from enigmatic material assemblages. Early models drew heavily from modern hunter-gatherer behaviors as a means to supplement an understanding of the meager remains. For this reason it is not surprising that the first Plio-Pleistocene interpretations stressed central place foraging and altruistic food sharing—characteristics that many hunter-gatherer populations exhibit. Later reconstructions eschewed the notion that Plio-Pleistocene hominins could be described as ancient facsimiles of contemporary hunter-gatherers. Some of these models stressed asocial mechanisms, like total transport energy and import-export pressures, as the principle components behind early archaeological assemblages. Others reemphasized those social behaviors other than food sharing (e.g., group defense) might have had similar affects on the accumulation of stone and bone. Most recently, paleoanthropological reconstructions have adopted a distinctive individual-level perspective, marked by discussions of male and female strategies in the Plio-Pleistocene of East Africa.

The following chapter introduces the agent-based modeling technique and specifies a new conceptual model for the evolution of altruistic food sharing and the formation of Plio-Pleistocene archaeological assemblages which attempts to achieve a balance between formal evolutionary theory and social science theory (Kuhn and Sarther 2000) by borrowing equally from theoretical biology and paleoanthropology. An agent-based version of this model is used to explore a number of familiar questions concerning routed foraging, favored locales, and resource transport as well as a few that are new to the discipline.

CHAPTER 4. AGENT-BASED MODELING THE EVOLUTION AND ARCHAEOLOGY OF PLIO-PLEISTOCENE HOMININ FOOD SHARING

> "The questions of most immediate relevance to Pleistocene social theorists should be (1) what is the basis of the unique development of intensive sharing and economic cooperation among humans, (2) how might that unique condition have evolved, and (3) what are the implications of these evolutionary scenarios for changes in archaeologically monitorable phenomena such as technology, foraging ecology, or land use?" [Kuhn and Sarther 2000:86]

The previous chapter reviewed the ways in which biological altruism has been studied by evolutionary biologists and by human behavioral ecologists. It introduced and discussed a number of models, emphasizing those that have made contributions to paleoanthropological explanations of the evolution of food sharing among Plio-Pleistocene hominins in East Africa. This chapter concerns itself with yet another model; however, this one is being presented in detail for the first time. First, I provide a general introduction to the agent-based modeling methodology and a brief discussion of how it can be used to create "behavioral laboratories." An outline of a new conceptual model which refocuses our attention away from open grasslands and towards fragmented patches of closed habitat and expands traditional evolutionary ecological explanations of food sharing to include fitness benefits bestowed upon hierarchical levels above that of the individual follows the agent-based modeling primer. Finally, I specify SHARE, the evolutionary agent-based model that was built to test two central predictions of the new conceptual model: (1) that the altruistic phenotypic trait of sharing food could have evolved in Plio-Pleistocene hominin populations due to the benefits it bestowed upon the fitness of subsistence-related trait groups competing with one another in an increasingly fragmented ecological environment and (2) that dense clusters of Oldowan artifacts (i.e., so-called “home bases”) could have formed in lieu of central place foraging.

4.1 Agent-based models as behavioral laboratories

> “...in 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 insightful passage should resonate deeply with those interested in reconstructing past behaviors from the cultural materials we find in the present. First, in an historical science like paleoanthropology there exists no control group by which one can gauge the effect that natural selection has had on the frequency of a particular trait or the success of a particular species. In other words, although the environmental stresses faced by each group will inevitably vary over space and through time, no species or population is altogether immune from all selective pressures. Hence, there is no “second group” that “has not been disturbed”—no single archetypical hunter-gatherer society or nonhuman primate species can act as a behavioral control group by which one might compare one’s ideas about Plio-Pleistocene hominins. Second, while it is true that selection continues to act on human populations, many of the biological and cultural processes we are currently interested in studying—the evolution of bipedalism, modern life-history, encephalization, the division of labor, and even food sharing—have already unfolded (at least once), leaving only the “results” readily observable to us today.

Paleolithic archaeologists interested in reconstructing biological and cultural change have long recognized the fact that “there is no one to tell us what might have been”—for example, to tell us how bipedalism, food sharing, or larger brains evolved in hominin populations. In lieu of informants we must rely upon cultural material remains and their archaeological contexts.

In many ways, this lack of control groups and direct informants renders the so-called “soft” historical sciences much more difficult than the “hard” physical sciences. Physicists and chemists routinely make use of controlled, repeatable experiments to test hypotheses about the way the world works. In effect, this enables them to act as their own informants in a manner uncommon in archaeology. Or, I should say, in a manner uncommon in archaeology until recently. Agent-based modeling provides a relatively new methodology by which archaeologists can conduct controlled, repeatable experiments on their ideas about the past within the context of “behavioral laboratories.” Agent-based models enable archaeologists to act as their own informants about the way the world *might* have worked in the distant past.

An archaeological knowledge of the past must rely on inference, often from scant material remains. Outside of the subfield of ethnoarchaeology, archaeologists are denied the opportunity to directly observe their subjects. One can study the distributions of artifacts fashioned and dropped by bipedal primates two million years ago, but one can never watch Plio-Pleistocene hominins interact around a bovid carcass. However, a relatively new type of modeling methodology afforded by advances in computer technology offers a way to view the consequences of the dynamics of past behaviors and site formation processes as they unfold in digital caricatures of past societies and paleoenvironments. It is important to note here that although the terms "computer simulation" and "simulation model" are used often in the archaeological literature, no computer model *simulates* (i.e., emulates) every detail of reality. Instead, each model encodes the investigator's concepts of reality and makes it possible to *explore* ideas about the past independently of the empirical archaeological data against which we must continuously test theory (van der Leeuw 2004). Thus, a computer model is not an end-product that proves the validity of any one interpretation. Rather, it is an interactive tool that provides opportunities to follow the implications of one's ideas to find where they are inconsistent and to build new theoretical frameworks of explanation for empirical data. This section defines some key terms and introduces some of the important characteristics that distinguish agent-based modeling from other formal modeling techniques.

An introduction to the agent-based modeling technique

Although computer scientists interested in artificial life originally developed agent-based modeling, the technique has since been applied to research questions in physics, evolutionary biology, political science, economics, and archaeology. As the name implies, agent-based models (ABMs) use software "objects" called agents. Agents are specified by means of one of a few "object-oriented" languages (Java, Objective-C, MAML, etc.). Object-oriented languages possess a number of unique characteristics that make them appropriate for this type of modeling endeavor. Three that deserve mention in this introduction are encapsulation, inheritance, and polymorphism.

Encapsulation refers to the capability of each agent to “hide” its own behaviors and variables from other agents. This means that the only entity that can modify an agent’s internal variables (e.g., age, hunger, reproductive fitness, etc.) is that agent. Contrast this with procedural programs (Fortran and C), which commonly make use of look-up tables that are accessible to many (or all) of a model’s components and global variables that are shared by all of a model’s components. In short, encapsulation provides individual agents with a greater measure of autonomy and a greater potential for heterogeneity, two important characteristics to which we will return below.

The concept of *inheritance* is best illustrated with a hypothetical example. Say someone has already programmed a fruit object, which possesses only those characteristics that are common to all types of fruit. But we are interested in modeling apples and oranges in a fictional agent-based model called FruitWorld. In order to model apples and oranges accurately we need to use objects that are more derived than simply fruit. Inheritance allows us to *extend* the original object (fruit) to create two new objects (apple and orange). By means of inheritance, any subclass of objects (apples and oranges) will inherit all of the superclass object’s (fruit) state variables and methods, while still allowing for the addition of new state variables and/or methods that distinguish the extended object from its more general ancestor. In the case of FruitWorld, additions to the apple objects and orange objects might include state variables like color, sweetness, growing season length, price, pest resistance, etc.

The third feature of object-oriented programming, polymorphism is especially important to research concerning artificial societies composed of many interacting agents. *Polymorphism* refers to the ability to create many *instances* of one object class. Each instance (i.e., individual agent) shares the same basic state variables (e.g., color, sweetness, etc.) but possesses its own unique values for them. Polymorphism allows modelers to create large, heterogeneous agent populations quickly and easily. If we extend our FruitWorld example here, polymorphism would allow a modeler to create a population of 10,000 oranges in which each orange agent had its own floating point value for sweetness. Of course, it is up to the modeler to determine how each state variable should vary (i.e., normally, bimodally, uniformly, etc.) in a population.

Despite all of this technical jargon, agents are simply autonomous software entities that are equipped with limited means to both perceive and react to aspects of their virtual environment. This means that agents can both sense and manipulate their surroundings on an individual (and usually goal-directed) basis. Agents “decide” when and how to act by continually comparing the values of their internal state variables to desired, optimal, or ideal values. Because their internal state values are derived from sensing their physical and social environmental surroundings, agents’ actions are ultimately a response to their environment. Agents communicate with each other during simulations via messages. Messages are simply commands sent from one agent to another. A message might prompt the receiver to enact a particular method or it might be ignored, depending on the situation.

In some ABMs, a single agent interacts with an environment through simulated time (Brantingham 2003). In others, hundreds, or even thousands, of agents interact with each other, forming artificial societies (Dean et al. 2000; Epstein and Axtell 1996; Kohler et al. 2000, 2005; Lansing 2002; Premo 2005). Whereas the conditional rules each agent follows may be quite simple (e.g., if body temperature exceeds an acceptable threshold, then move to a cooler locale), the aggregate outcome of a population of agents may be difficult to predict (e.g., the migration of a group of agents to a cooler locale might take a direction not allowed to any individual agent). Artificial societies often exhibit *emergent* collective properties that can be strikingly similar to those displayed by real societies. The dynamics observed are generated from the bottom-up, in that emergent properties arise from the individual agents' actions just as the global properties of an actual society emerge from the actions of, and interactions between, individual persons. Thus, evolutionary agent-based models can provide a generative understanding of evolutionary processes as simulated populations evolve through time according to their own particular population dynamics.

ABMs can be used to experiment *in silico* with various combinations of behavioral rules and selective pressures not unlike how a chemist might experiment with various chemical concentrations. To make this type of research possible, the most important elements of the model are reduced to simplified essentials, and the parameter space defined by the entire suite of pertinent ecological, social, and behavioral experimental variables is open to strategic exploration. Through systematic parameter sweeps, simple models provide an opportunity to gain an understanding of some of the combinatorial effects of just a few minimal assumptions in ways that more complicated models do not. If one's goal is to learn how different variables affect the behavior of a dynamical system, elegant models are highly preferable to more "realistic" ones.

In addition, ABMs can encompass large temporal and spatial scales, while making many details available for analysis. For example, consider the utility of a data set that documents the daily movements, interactions, and resulting archaeological correlates of 100,000 people over 1,000 years. Using ABMs allows one to control the initial conditions of the model and maintain perfect knowledge of every agent's health, memory, reproductive fitness, etc. throughout the duration of the experiment. Given this ability to collect accurate data from millions of agents over extended periods of simulated time, ABMs yield richer data sets than those to which archaeologists are normally privy, and these, in turn, lead to questions that could not be addressed with any other technique.

ABMs also provide a methodology by which archaeologists can replay the "tape of history." In discussing the importance of 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—the Cambrian explosion, the last glacial maximum, etc.—from which history could be restarted and certain subjects observed. Of course, if one replays a videotaped movie, the film will project the same story with the same characters delivering the same dialogue. However, Gould explains that his divine tape player could display very different plots depending on the contingencies of history. Unlike a videotape of *The Natural*, which will faithfully depict an injured Roy Hobbs launching an improbable home run into the stadium lights and rounding the bags one final time under a cascade of sparks and cheers, Gould's divine tape player is capable of showing different evolutionary outcomes depending on the sequence and types of unique historical events (changes in climate, meteorites, epidemics, etc.) that might occur during each replay. If one were to replay *The Natural* in Gould's divine tape player, Hobbs might swing at and miss an unexpected slider in the dirt, thereby striking out and ending his crucial at-bat. In Gould's own words, "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 is meant to illustrate the importance of historical contingency, the component of cultural and biological evolution that is often downplayed by those concerned with uncovering universal Laws. Shennan reemphasizes history's importance to evolutionary reconstruction in this restatement:

> "In contrast to the processes and material studied by physics or chemistry, which are universal in time and space and therefore amenable to specification in terms of laws, biological and cultural phenomena cannot be understood without reference to their specific space/time position and the previous steps in the process by which they reached it." [2002:254]

But Gould's thought experiment also introduces a novel research methodology to everyone involved in the historical sciences. Paleontologists are interested in retracing the evolutionary trajectories of extinct and living species. Paleoanthropologists are interested in retracing the evolutionary trajectories of hominin species, in hopes that a better understanding of history will ultimately contribute to a more nuanced appreciation of our own species' place in the natural world. Researchers in both disciplines have access to two types of empirical data sets. The first is an exceedingly incomplete and biased subset of all of the physical matter (fossils, DNA, pollen, stone tools, etc.) deposited during the one and only run of the tape of history. The second is composed of that which we can observe in the current "scene" of the evolutionary tape of history. This current scene includes all of the details of life, as it exists in front of our eyes today.

One question that comes to mind when studying these remains and the selective forces that operated on the organisms responsible for them is: How likely is the current scene—life as we witness it today—given all plausible historical possibilities? For instance, given our empirical observations of the current scene, we know that humans are bipedal animals, but what is the likelihood that bipedalism would have evolved in our lineage given a slightly different historical scenario, perhaps one that involved a slightly different climate? The same can be asked of food sharing: Is the universal altruistic social pattern we see today among humans robust, or would it change if we were to rerun the tape under different conditions of a slightly altered history? Of course, archaeological landscapes are also open to the same kinds of "what if" questions: How do various behaviors affect the spatial distributions of cultural material, and are the archaeological patterns we see robust or are they sensitive to small changes in behavior?

Studying these historically contingent processes poses Bayesian-like problems that must be worked in reverse. We know that bipedalism did indeed evolve in hominin populations, but the likelihood of these developments under a wider variety of potential conditions remains a mystery because we have only partial access to a single run of the tape of history. A better understanding of the adaptations involved in these evolutionary processes lies in discovering the probability that observed outcomes would also occur in other experimental social and biological environmental settings. This is impossible to do in reality, because the “real” tape of history cannot be rerun. However, this feat can be realized by looking for regularities in the behavior of nonlinear agent-based models (Lansing 2002; McGlade 1995).

Simulation models cannot tell us exactly what happened in the past, nor can they *prove* that our ideas about the past are correct. To believe otherwise is to fall prey to the siren’s song. But by allowing one to control initial conditions while playing out multiple alternatives—to replay Gould’s tape of history hundreds, or even tens of thousands, of times—simulations provide a way to identify and refine plausible scenarios, as well as to see when one’s assumptions and expectations lead to implausible or impossible outcomes. In short, they permit the exploration of multiple “what if” scenarios, or what Gumerman and Kohler (2001) call “alternative cultural histories.” This characteristic was recognized early on as an important feature of all simulation models (Aldenderfer 1981; Cordell 1972, 1981), and it certainly applies to ABMs. ABMs have additional characteristics that make them especially amenable to the exploration of evolutionary dynamics in complex and emergent systems, including coupled human-environmental systems. These features are reviewed below.

What else can agent-based models offer archaeologists?

Agent-based models are fundamentally different from deterministic mathematical models, which traditionally include ordinary and partial differential equations. First, ABMs allow for artificial populations of heterogeneous agents. Whereas deterministic mathematical models presume homogeneous populations composed of agents that tend toward some approximation of equilibrium with their environment, ABMs provide a methodology by which each agent is represented as an autonomous entity, complete with its own unique state values, behaviors, and individual goals, which often run counter to group homeostasis. By allowing agents to display variation in internal states and behaviors, ABMs provide an avenue for the study of agency in social change in a manner that is not possible within the framework of traditional mathematical equation-based models.

Second, though not the *final* frontier, formal models did not explore spatial problems until recently. This is probably due to the fact that ordinary differential equations are unable to cope with space, and methods used to incorporate spatial parameters into partial differential equations usually render once elegant formulations awkward and opaque. In contrast, many agent-based modeling platforms (Swarm, Repast, NetLogo, and Ascape) have included from the very beginning a suite of objects dedicated to representing various types of space. Thus, ABMs are the only type of formal model capable of including a spatial dimension as an entity that is entirely distinct from other agents. Whether a 2-D lattice, a 3-D torus, a social network, or some other conceptual space is of interest, ABMs can model spatial components as separate entities on which agents live and interact. Including space in models is no minor detail, as a number of researchers have stressed that the spatial distribution of agents and resources plays a critical role in influencing which behavioral strategies succeed in small groups of players privy to only local information (Lindgren and Nordahl 1994; Nowak and May 1992; Pepper and Smuts 2000, 2002; Premo 2005).

A third difference is that, by including both heterogeneous agents and space in digital models, ABMs save an important role for historical contingency. By contrast, deterministic mathematical models do no such thing. The majority of deterministic mathematical models simply represent agent populations as pools (actually lists) of possible players. From these pools one could either randomly choose a subset of agents and prompt them to interact with each other or force each agent to interact with a randomly chosen partner (often from a different pool) during every time step. Agent interactions within such models are essentially arbitrary and determined from the top-down; hence, the use of the term *deterministic* model. This is not true of ABMs, which allow heterogeneous agents to interact only when the opportunities to do so present themselves during the "natural" progression of a model run. For instance, in an ABM that includes a 2-D lattice, it would be reasonable for only those agents that are in close spatial proximity (say, occupying adjacent cells) to be able to communicate and interact with each other. Here, historical contingency is in play because the two agents finding themselves in close spatial proximity have the locales of their birth and the histories of their previous movement decisions to thank for the opportunity to interact. Their meeting and subsequent interaction are historically contingent upon their previous life histories rather than determined by a higher-level algorithm or an arbitrary structure imposed upon them by the modeler. In general, whenever the spatial distributions of agents and resources and/or the sequence of agent actions are likely to play important roles, so, too, is historical contingency. ABMs serve as invaluable methodological tools for exploring model dynamics in these rather complex cases.

Although the task of programming an ABM requires a nuanced technical know-how—a skill that is beginning to find its way into a growing number of graduate student-led research groups and anthropology department computer labs around the country—the most important and unique features of the methodology can be summarized in one brief sentence: ABMs make possible the study of *non-linear* cultural dynamics that emerge from the *historically contingent* actions of *heterogeneous* agents interacting in *space*. As Kohler (2000:2) states, the social scientific research currently making use of ABMs "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 ABMs can be used to study the very kinds of biocultural dynamics that are impossible to solve analytically with either ordinary or partial differential equations.

To date, archaeologists have underutilized agent-based models despite these positive characteristics. The final section of this chapter describes a recent attempt to employ an evolutionary agent-based model as a behavioral laboratory. The goals of this project include learning more about how altruistic food sharing traits could have spread throughout Plio-Pleistocene hominin populations and how comparable archaeological assemblages could have been formed in the absence of modern central place foraging techniques.

4.2 A new conceptual model of hominin food sharing

Conceptual modeling provides an important alternative for paleoanthropologists interested in building inferences for hominin behavior. Unlike referential models, which employ observable phenomena as analogies for unobservable target phenomena, conceptual models are purely theoretical constructs, and as such they are constrained not by what we can observe around us, but by the innovation and imagination of those interested in exploring plausible alternatives. My conceptual model was inspired by recent research in theoretical biology that investigates how ecological patchiness and niche construction influence the evolution of altruistic traits. Brief summaries of this influential research precede the introduction of my multilevel selection model.

Ecological patchiness can aid the evolution of some altruistic behaviors

Researchers have used multilevel agent-based models to systematically explore many ecological, ethological, and demographic variables in search of those regions in the state space of initial conditions, or *basins of attraction*, that allow altruistic alleles to evolve to fixation in a large population. John Pepper and Barbara Smuts (2000, 2002) present an elegant multilevel selection simulation, called ECO, which they use to explore the state space of both ecological and social variables for basins of attraction that foster the evolution of two altruistic traits—alarm calling and feeding restraint—in populations of generalized foragers. Pepper and Smuts purposefully do not invoke kin selection or reciprocal altruism in their model. Instead, they find that when inhabited by a mixed population of altruists and nonaltruists, patchy resource distributions alone are sufficient to facilitate the spread of altruistic traits throughout the entire metapopulation.

These intriguing results are a function of fragmented food patches effectively forming trait groups of foragers who, by way of historically contingent individually-based (i.e., solitary) foraging decisions, come to inhabit the same patch. In this way, restrictive feeding patches facilitate assortative interactions that effectively subdivide large demes into evolutionarily meaningful trait groups (Wilson and Dugatkin 1997). As Pepper and Smuts demonstrate, within each of ECO's patches each trait group member indirectly influences all others' fitness by the ways in which it modifies the common food resource (feeding restraint) and directly affects the fitness of other foragers with whom it interacts in defending the group from predators (alarm calling). Among ECO's patches, trait groups compete to provide more offspring for future generations at the level of the metapopulation. Although Pepper and Smuts do not explicitly model either food sharing or hominins with ECO, their conclusion that "groups emerging through the behavior of individual agents in patchy environments are sufficient to drive the evolution of group beneficial [and individually costly] traits" (2000:70) can be applied to Plio-Pleistocene hominin evolutionary environments under the revised savanna hypothesis (see discussion in Chapter 3).

Cultural niche construction can aid the spread of altruism

At first blush Pepper and Smuts' model might seem just as environmentally deterministic as Vrba's turnover pulse hypothesis. However, it is important to recognize that resource patchiness in no way *causes* the evolution of altruism in ECO forager populations, it merely *facilitates*. Although ecological patchiness creates a selective environment that is conducive to the evolution of altruism, it is ultimately the foragers' behavior and demography that drive population-level changes in allele frequencies. Thus, while ecological patchiness and some foragers tending to behave altruistically (a tendency that, in this model, is genetically determined and inherited by offspring through vertical transmission) are both necessary ingredients for the spread of altruism in ECO. Neither is sufficient on its own. As ECO demonstrates for the specific cases of alarm calling and feeding restraint, when just a few cheaters are present, altruism cannot evolve to fixation if the resource distribution lacks the patchy structure responsible for facilitating assortative interactions among socially inept foragers. However, altruism will also fail to spread through a metapopulation of foragers living in a sufficiently patchy environment if altruists do not exist in sufficient number *and* regularly (i.e., nonrandomly) interact with other altruists in at least one of the trait groups. Because the parts played by history and demography are just as important as that played by ecological heterogeneity, these evolutionary ecological models should not be viewed as environmentally deterministic.

Indeed, the fact that both ecological inheritance and genetic inheritance are crucial to the evolution of cooperation in ECO exemplifies the concept of cultural niche construction (Laland et al. 2001, Odling-Smee et al. 2003). Building on the works of Lewontin (1983) and Odling-Smee (1988), Laland et al. (2001:23) argue that "organisms not only adapt to environments but in part also construct them" thereby modifying "the natural selection pressures to which they and their descendants are exposed" through their behaviors. Pepper and Smuts' (2000, 2002) research on the evolution of feeding restraint provides a simple illustration of cultural niche construction. In ECO, there is a clear relationship between feeding behavior and patch productivity—unrestrained feeding quickly depletes plant productivity. It is not surprising that groups of mostly unrestrained feeders can quickly eat themselves "out of house and home," especially when food resources are extremely heterogeneous and/or slow-growing. When the distance to another patch is great, many unrestrained feeders will not survive relocation to a less depleted patch. Thus, intensive foraging behaviors detrimentally modify local environments, which, in turn, affect the reproductive fitness of current inhabitants as well as the fitness of foragers who might inherit the damaged food patch in the near future. Restrained feeders also negatively impact their local environment by consuming plant resources, but they do so to a much lesser degree. In ECO, a trait group of restrained (altruistic) feeders can maintain a sustainable food patch, which they use to fuel their own reproductive fitness as well as that of their descendants. In the case of feeding restraint, cultural niche construction and multilevel selection explain how the trait groups with a greater proportion of altruists sustain their limited local environment and outcompete mostly selfish groups that fall prey to the tragedy of the commons (Hardin 1968). In the next section I argue that hominin food sharing might also be better explained from the perspectives of cultural niche construction and multilevel selection. This hypothesis is tested with the agent-based model specified below.

A new scenario for the evolution of Plio-Pleistocene hominin food sharing

Previous simulations have shown that, in times of dietary stress, a foraging strategy that involves even minimal food sharing is more effective than one that increases diet breadth (Winterhalder 1986). Though it remains to be demonstrated whether this holds true in the more specific case of ecological fragmentation, according to Winterhalder's findings one could hypothesize that when faced with dietary stresses associated with the fragmentation of closed habitats during the Plio-Pleistocene, those hominins that shared food resources displayed a more advantageous behavioral phenotype than those who broadened their diets in an attempt to include less frequently encountered and more exotic grassland foodstuffs. While the strategy of sharing food might be selected over the strategy of widening diet breadth according to this scenario, it is important to note that the strategy of highest individual fitness would be to accept shared food from others without reciprocating the act—or, in other words, to be a social cheater. Thus, although the cooperative food sharing strategy might outcompete the diet broadening strategy, as Winterhalder's study suggests, the former would be under constant pressure of being eroded away by selfish social cheaters, while the latter would not. It is possible that Plio-Pleistocene hominin trait groups that frequently shared closed habitat resources, such as tubers, nuts, fruit, small game, and possibly even scavenged meat, could have sustained a viable local food patch even as the once-abundant Miocene woodlands became increasingly restricted. In this between-group selection environment, Plio-Pleistocene hominin trait groups that were composed of a greater proportion of food sharers could have outcompeted trait groups with lesser proportions of food sharers as well as trait groups that tried to make use of the more dangerous open grasslands to supplement their diet.

For Plio-Pleistocene hominins pre-adapted to the forest, sharing food obtained from fragmented but familiar closed habitat presents a more parsimonious strategy than expanding one's diet to include exotic foodstuffs endemic to more dangerous open environments (Kingdon 2003). That is, sharing woodland resources would solve many of the dietary stresses associated with woodland fragmentation while requiring fewer behavioral and physical adaptations than a strategy based on open grassland foraging. Up to a point of extreme forest degradation, successful altruistic hominin trait groups could export their offspring to other forest patches previously abandoned by less fit selfish foragers (but see Wilson et al. 1992). By the time forest patches finally became uninhabitable (exactly when this might have occurred cannot be addressed directly with SHARE), some (and possibly all) of the extant hominin groups might have possessed a new behavioral tool that allowed them to survive in open grasslands, the one place they previously had not dared to go. Just as survival on land probably could not have been possible for Romer's fish without the legs they originally developed to maintain contact with evaporating pools of water, hominins might not have survived the final move out of the trees without the altruistic food sharing traits that were initially selected to maintain contact with shrinking closed habitat resources. Ironically, this reconstruction proposes that it was those hominins whose ancestors had been better at avoiding open habitats by sharing food in woodlands that were best equipped to survive in the brave new world away from trees.

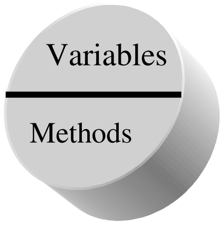
In sum, I propose that as open grasslands encroached upon and fragmented the preferred closed habitats, Plio-Pleistocene hominins were increasingly segregated into trait groups. Ecological patchiness facilitated assortative interactions between those hominins utilizing the same "island" of closed habitat resources while also fixing a shared biological fate among those dependent on the sustainability of their common food source. These environmental conditions shifted the balance of selective pressure from *within-group* to *between-group*. This allowed for the spread of altruistic traits, like food sharing, at the level of the metapopulation through differential trait group fitness. The physical environment comprises only one component of this equation, and one must not forget that hominin behavior and demography play equally important roles. In the terms of cultural niche construction theory, those groups whose members frequently shared food would construct their own behavioral and ecological niches by passing altruistic traits *and* sustainable resource patches to subsequent generations. Altruists provided their offspring not only with a suitable food resource but also the behavioral strategy to maintain it. In contrast, the members of those groups that did not regularly share food passed selfish traits and badly depleted local environments to their offspring. Such trait groups could not adequately survive the dietary stress triggered by ecological fragmentation and were often forced to search for other woodland patches or to forage for supplemental calories in open components of the savanna. According to this scenario, it was only after the closed patches had all but disappeared that hominins armed with a new behavioral adaptation—altruistic food sharing—committed fully to a more terrestrial lifestyle in the treeless grasslands.

4.3 Specifying SHARE

Models are tools used to learn more about one's simple ideas about processes operating in a complex world. The notion that models somehow simulate reality is hubristic; reality is too complicated and subtle to emulate. Rather, it is our ideas about reality that can be explored, modified, and disproved through the systematic application of well-designed models. Elegant, or minimal, models concern themselves only with addressing the essential properties of the system or process(es) in question. They actively exclude superfluous variables that could obfuscate causal relationships between initial conditions and observed outcomes. In this light, it is important to reiterate that the agent-based model presented in this section tests my ideas about how food sharing behaviors *could have* evolved among hominin trait groups in patchy Plio-Pleistocene environments. It does not purport to model every detail of that prehistoric reality. To construct an elegant model to test this theoretical scenario, only those properties of hominin foragers and their environment that are essential to the research question need be included. As Richerson and Boyd (2005:98) state in their most recent book, "in order to actually make progress with theoretical or empirical work, you have to be willing to simplify, simplify, and then simplify some more" (but see Edmonds and Moss [2005], who advocate a slightly different approach).

Critics might argue that this agent-based model does not do justice to *all* of the complex and subtle details of the Plio-Pleistocene paleolandscape, and they would be correct in saying so. However, any elegant implementation of a model is the result of a purposeful and difficult compromise between completeness and simplicity. The goal of this particular project is not to recreate every detail of Plio-Pleistocene sub-Saharan African savanna ecological communities, but rather to capture the *essence* of the biosocial evolutionary process in question. Stated as clearly as possible, the purpose of this agent-based model is exploration, not emulation.

Digital agent-based models are composed of *object* classes. Each *instance* of an object, referred to as an individual agent, is imbued with a suite of internal *state variables* and behavioral rules, called *methods* (Figure 4.1). State variables and methods particular to SHARE appear below in **`boldfacePrint`**.



An Agent

Figure 4.1. The two basic components of an agent. Agents contain internal values called state *variables*, which may or may not be modified through simulated time, and *methods*, which allow them to manipulate their environment and to change the values associated with their own state variables.

Agents may possess two distinct types of state variables: static and dynamic. As their names imply, values of static state variables do not change through the course of an agent's lifetime, while values of dynamic state variables can be (and usually are) modified through the course of a simulation run. An example of a static state variable in an evolutionary model is sex, while age is an example of a dynamic state variable. The following paragraphs and figures briefly describe the agents, state variables, and methods employed in SHARE. SHARE's spatial world is a two-dimensional grid, wrapped into a torus to avoid edge effects. Each regularly-shaped and regularly-spaced cell of this grid can contain four classes of agents: plants, meat, artifacts, and hominins. Each of these agent classes is described below.

Plant agents and patches

Plant agents are sessile; once created at the start of a simulation, they cannot move. Nor can plants reproduce or die. Plant agents have a dynamic state variable called **`currentEnergy`**. Plant energy is represented by a floating-point value that corresponds to the amount of energy available to any hominin forager. Each plant's **`currentEnergy`** is modified after each time step according to one of two methods, **`growLogistic`** and **`beEatenTo`**. If a plant is not eaten, then its energy value will increase according to a logistic growth rate ($r = 0.2$). If let uneaten for even a few time steps, each plant's **`currentEnergy`** will approach (but never reach) a fixed maximum limit of 10 energy units (Figure 4.2). If a hominin agent does feed upon a plant agent, then the **`beEatenTo`** method will decrease that plant's **`currentEnergy`** value by the amount consumed by a forager (note: all hominin foragers consume 90% of available energy from plant and meat agents).

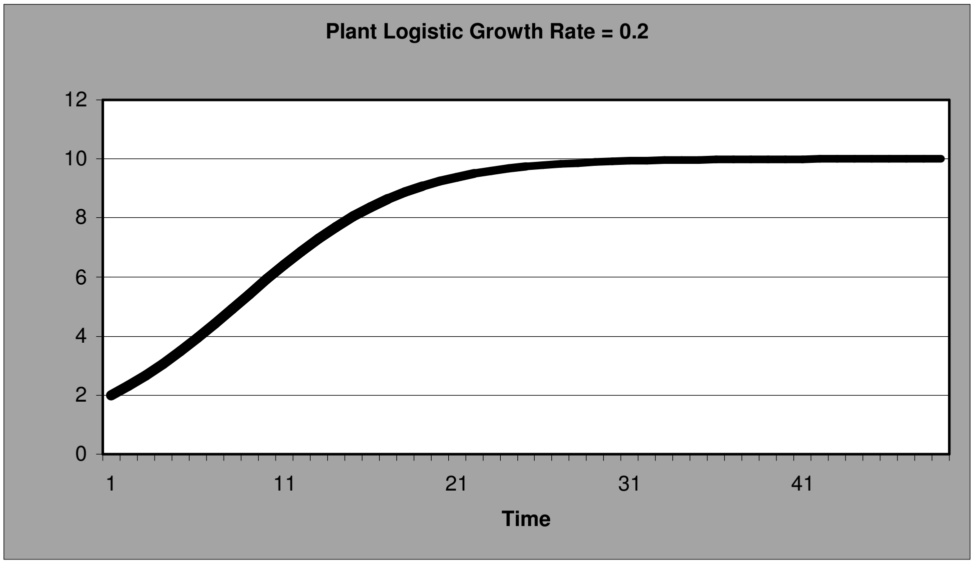


Figure 4.2. Logistic growth in the energy level of a hypothetical plant agent in SHARE. This plant agent began with an energy level of two units, but after only 50 time steps its energy had grown very close to the maximum limit of 10 units because it had not been fed upon by a forager. Note: plant `currentEnergy` can never reach 10 units.

Plant agents are clustered into patches. Each patch embodies an area of closed habitat/woodlands, while the absence of plant agents represents open grassland. Considering that the very name "grassland" refers to plants, to model it as lacking plant foods might seem counterintuitive. Indeed, grasslands do support many edible grasses, herbaceous perennials, and tubers that could have supplemented hominin diets. But because paleoanthropologists do not widely believe that these particular plant resources were important food staples to early hominins (but see Jolly [1970] and Tanner and Zilhman [1976]) they are not stressed in my model.

Because the plant agent distribution represents ecological patchiness, it must be controlled as a primary experimental variable. Following Pepper and Smuts' (2000, 2002) methodology, at the start of each simulation run, plant agents are systematically distributed into regularly shaped and spaced patches as designated by Patch Size (a proxy for patch area) and Gap Size (distance between patches), respectively (Figure 4.3). In a general sense, as the value for Patch Size decreases and the value for Gap Size increases, closed habitat shrinks and open habitat expands. Gap and Patch Sizes do *not* vary during the course of any single simulation run, but by running a suite of runs, each of which uses a different combination of these variables, one can quantify differences due to an increasingly fragmented ecological setting.

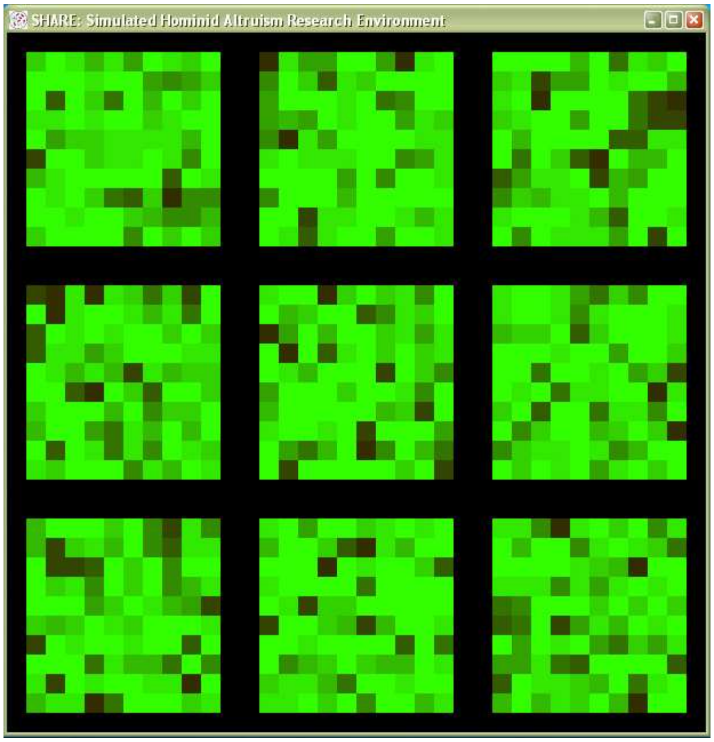


Figure 4.3. Plant agents arranged in patches at the start of a SHARE simulation run (Patch Size = 10 and Gap Size = 2). Plant energy level varies between 0 and 10 units; greater values are depicted with a brighter shade of green. This ecological setting is relatively homogeneous.

State Variables		Methods
Static	Dynamic	
growthRate	currentEnergy	growLogistic
startingEnergy	patch	beEatenTo
maxEnergy	newGrowth	
x		
y		

Table 4.1. Plant agent state variables and methods.

Meat agents

Meat agents represent the larger, less predictable, and more ephemeral food packages often associated with both open and closed components of African savanna environments. These are the carcasses of mid-to-large-sized savanna mammals. Like the plant agents described above, meat agents also possess the dynamic state variable **`currentEnergy`** and the **`getEatenTo`** method, and they are stationary. However, unlike plant agents, which grow logistically, the energy provided by meat agents quickly diminishes from a high initial value to a low minimum value according to a logistic decay rate ($r = 0.02$) (Figure 4.4). This rapid drop in energy value emulates scavenging by other savanna carnivores. Also unlike plants, which are arranged in permanent patches at the start of each simulation run, meat agents are “randomly” instantiated over space and through time. The probability that a new carcass will be added to each available cell (i.e., one not already occupied by a meat agent) per time step is set by a primary experimental variable that one can vary in order to investigate how the presence of large, unpredictable food packages impacts the evolution of early hominin food sharing. New carcasses are randomly assigned a starting energy level between 75 and 100 units, thereby varying the size of the carcasses while making sure that any single carcass provides far more food than any single plant agent.

State Variables		Methods
Static	Dynamic	
decayRate	currentEnergy	step
minEnergy	newDecay	getEatenTo
maxEnergy		decayLogistic
x		
y		

Table 4.2. Meat agent state variables and methods.

Figure 4.4. Logistic decay of a hypothetical meat agent in SHARE. This meat agent was created with an energy level of 100 units, but after only 49 time steps (white arrow) it was removed from the model because its energy level had decayed below the minimum. While the minimum energy level for meat agents is 10 units, carcasses are automatically removed when they fall below 15 units (dashed line) because the logistic equation never allows their energy level to reach 10 units.

Artifact agents

The probability that each hominin forager will “drop” an artifact per time step is also a user-defined experimental variable. When a random number between 0 and 1 is less than **`artifactDropProb`**, a hominin agent will drop an artifact at its current cell on the torus. The probability of dropping an artifact does not vary among time steps in a simulation run. In addition, the likelihood of dropping an artifact is not related in any way to a forager’s activity, so a forager that finds a plant or meat carcass at time *t* is just as likely to drop an artifact as a forager that does not find food at *t*, and that probability does not deviate from time *t* to *t* + 1. Artifact agents are fairly straightforward objects, as each has only one dynamic state variable called **`artifactCount`**. When a forager drops an artifact in an empty grid cell, a new artifact agent is created with an **`artifactCount`** equal to 1. When a forager drops an artifact into a cell that is already occupied by an artifact object, that object’s **`artifactCount`** is incremented by 1 to include the recent addition. In this way, artifact agents keep track of the number of artifacts that are deposited by foragers at various locations through time. This artificial archaeological landscape data is regularly reported to an output file that is used in spatial analysis.

State Variables		Methods
Static	Dynamic	
x	artifactCount	setArtifactCount
y		getArtifactCount

Table 4.3. Artifact agent state variables and methods.

Hominin forager agents

SHARE's fourth and final agent class—hominin forager—is more complex than plants, meat, and artifacts. For starters, each hominin agent must run through a lengthy `step` method during each time step of a simulation run (Figure 4.5). Forager agents have a greater number of internal state variables and methods, though they are still drastic simplifications of actual Plio-Pleistocene hominins. In a general sense, hominin foragers move about the model's torus following simple spatial search rules in seek of the energy provided by plants, meat, or food shared by other hominin agents. Those who are successful in this search reproduce more often than those who are unsuccessful in obtaining sufficiently large amounts of food.

State Variables		Methods
Static	Dynamic	
type	age	step
startingEnergy	timeSinceReproduction	reproduce
metabolism	currentEnergy	die
fertilityThreshold	progeny	getOlder
color	lastMeal	move
lifeSpan	myPatch	eat
birthInterval	cooperatorList	acceptFood
foodShare	defectorList	dropArtifact
lowerShareThreshold	x	predatorDanger
dropArtifactProb	y	shareFoodWith
offspringDispersal		reciprocalShareFoodWith
searchType		omniscientShareFoodWith
foodShareType		matchCooperator
		matchDefector
		reportFitness
		decideWhetherToPunish
		acceptPunishment
		acceptCostOfPunishment

Table 4.4. Hominin forager agent state variables and methods.

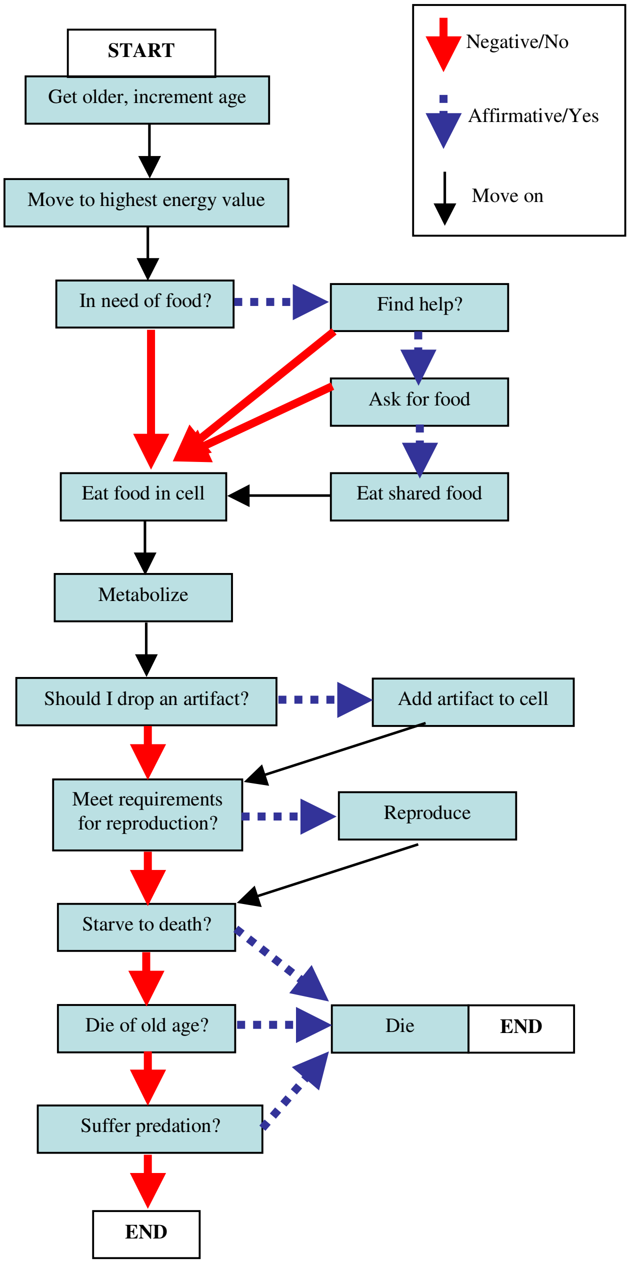


Figure 4.5. Flowchart of a hominin forager `step` method. Each forager agent executes this method (and the methods it may call) during each iteration of the simulation.

Each forager agent opportunistically procures both plants and meat (when included) as an individual only. That is, mutualistic group hunting is not included in the model. Like plants and meat agents, hominin forager agents also store energy. But unlike plant and meat agents, forager **`currentEnergy`** can be replenished by feeding upon plants and/or meat. Also unlike plants or meat, hominin foragers must pay a metabolic cost of living that subtracts a fixed amount of energy (two units) during each time step regardless of the actions taken by the agent during that time.

Foragers decide where to move by first scanning the energy values of plant and meat agents located within their immediate Moore neighborhood of cells (n = 8). Foragers then move toward the highest available value that can support the metabolic cost of one time step. Ties for the highest value in the search radius are broken randomly. If adequate food resources are not found (i.e., energy values within the search radius are not large enough to support the hominin agent for at least one time step), then the forager employs one of two search techniques. A secondary experimental variable determines which search technique is employed. In the case that a forager has no information about the global structure of the resource distribution, it embarks on a random walk to find better resources. That is, it moves to one of the eight possible cells with equal probability (note that this assumes that there is not an agent in any of the cells surrounding it—two foragers cannot inhabit one cell simultaneously). This simple foraging rule effectively models hominins using individually retrieved, proximate spatial information to exploit locally available resources. When information about resource distribution is included in the model, foragers search for new patches by traveling "diagonally," as this provides the most reliable route to a new patch of plant agents given their global spatial structure (see more on the importance of global information in Chapter 5).

A hominin forager that repeatedly procures food resources will quickly amass a large store of energy. If a successful forager's **`currentEnergy`** value breaches the fertility threshold (100 units) and it has satisfied the condition of a birth interval (not reproducing for at least 20 time steps), then it may sacrifice a sizable amount of its energy (50 units) to asexually reproduce an offspring with similar heritable traits in the nearest available grid cell. 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 (note: mutation is not included in this model, unless specifically noted). Obviously, Plio-Pleistocene hominins did not reproduce asexually, but because I am interested in studying the evolution of a behavioral trait (one that may or may not have a direct genetic connection), a haploid model is sufficient if it can be assumed that offspring learn how to behave socially from their parents. Thus, SHARE uses asexual haploid reproduction to model genetic transmission implicitly and to model vertical cultural transmission explicitly.

When a forager repeatedly fails to obtain adequate food resources, metabolic costs quickly deplete its energy store. When a forager's **`currentEnergy`** value reaches zero, it dies of starvation. Foragers can also be removed from the simulation if they fall prey to a savanna carnivore or when they reach their maximum age (100 time steps). The probability of predation per forager per time step is a primary experimental variable that can vary between forager types and/or between resource types. It is commonly assumed that closed habitats were safer than open grasslands for early hominins adapted to escaping up trees, so the rate at which foragers are exposed to mortal predation is three times (3x) greater in the open grasslands than it is in the woodland patches.

To make possible the act of sharing food, it is also assumed that each forager is capable of carrying a limited amount of food that has been procured but not yet consumed. Whether food is carried "by hand" or with the aid of cultural material such as bladders, skins, trays, baskets, or woven leaves, is not addressed in this model. To study the evolution of food sharing traits in the context of SHARE, each forager is imbued with an additional state variable, called **`foodShare`**, and one of three sharing methods. The state variable **`foodShare`** is a real number (i.e., floating-point value) that can vary between 0 and 1, where 0 indicates extreme selfishness and 1 indicates extreme altruism. Hominin foragers will share excess food with needy agents at a probability equal to their **`foodShare`** value. For example, an extremely selfish hominin with **`foodShare`** = 0 will never share food, while a highly altruistic hominin with **`foodShare`** = 0.9 can be expected to share in roughly 90% of the instances that it has excess food when asked for aid by a forager in need. A forager is considered to be "in need" when its **`currentEnergy`** level drops below a certain threshold (50 units). A forager in need (the prospective recipient) may ask another forager in its immediate Moore neighborhood (the prospective donor) for help. A prospective donor's decision to share some of its energy will trigger its food sharing method. Because each of the food sharing methods implies something different about the intelligence and/or cultural savvy of the foragers that possess it, it is important to describe each in order of increasing social sophistication.

According to the simplest food sharing method, **`shareFoodWith`**, a prospective donor will decide to share food if two conditions are met: (1) it possesses food in excess of its own lower food share threshold ("excess food" is defined as the amount of energy that is left after subtracting the lower food share threshold from one's **`currentEnergy`** value) and (2) a random number between 0 and 1 is less than or equal to its **`foodShare`** value. If either of these conditions is not met, the prospective donor will refuse to share with the prospective recipient. Note that sharing by this method is based entirely upon probabilities represented by **`foodShare`** values. Thus, **`shareFoodWith`** models interactions between "unintelligent" foragers who have neither memory of past actions nor the ability to recognize or otherwise recall the identity of others. In short, this method represents a null model of food sharing behavior because it includes the least assumptions of any of the behaviors modeled in SHARE.

The second food sharing method operationalizes Trivers' (1971) mechanism of direct reciprocal altruism. Recall that Trivers' research on direct reciprocity was aimed at finding a mechanism by which biologically altruistic traits could evolve by individual selection in groups composed of unrelated individuals. Trivers found that altruism could evolve in populations composed of non-kin if recipients of altruistic acts regularly repaid donors in kind at some point in the future. Unlike the simple null model of sharing presented in the paragraph above, reciprocal altruism requires some "intelligence" on the parts of individuals, each of whom must store details about who helped them and be able to match correctly identified individuals with their appropriate socio-economic "memories." Individual memory is a crucial component of reciprocal altruism, and this is why **`reciprocalShareFoodWith`** provides each forager the ability to remember and retrieve the unique individual identities of foragers who cooperated with or defected against it in past socio-economic interactions. Dynamic lists of social cooperators and social defectors operationalize individual memory in SHARE. Each agent maintains its own personally unique lists by updating them after each interaction in which it functions as the prospective recipient. Prospective donors rely upon their memory to make food sharing decisions on a forager-by-forager basis according to the following "tit-for-tat" 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 a prospective donor with excess food and a prospective recipient have not met before and, hence, there exists no "memory" of a previous interaction on which to base a decision, then the former will decide whether or not to share with the latter based on the simple **`shareFoodWith`** method described above.

The third possible food sharing method, **`omniscientShareFoodWith`**, assumes that a prospective donor can accurately identify a prospective recipient's **`type`**. Here, each forager's **`type`** functions very much like a tag. Hales (2005:89) recently defined tags as "markings or social cues that are attached to individuals (agents) and are observable by others." Tags have been used in many agent-based models of the evolution of altruism since John Holland (1993, 1995) pioneered this technique. Note that there is one important way in which my use of **`type`** in SHARE differs from a tag:

the former is a static state variable while the latter is traditionally modeled as a polygenic phenotype that can evolve over time. However, despite the fact that `type` is modeled here as a neutral discrete trait (either selfish or altruistic), that it is visible to all other hominin agents means that it has the same effect that full-fledged tags have had in previous models (Hales 2000, 2002, 2005; Holland 1993, 1995; Riolo 1997; Riolo et al. 2001)—it allows each agent to mediate its response to a prospective recipient based on perfect knowledge of that recipient's food sharing phenotype, which is ultimately a reflection of how likely an individual is to reciprocate an altruistic act in the future. As previous studies have shown, tag recognition provides altruists with a two-fold benefit. First, tags allow altruists to preferentially bestow benefits on individuals they recognize as fellow altruists; thus, only altruists enjoy the benefits associated with altruistic actions. Second, tag recognition provides altruists with a failsafe method of protecting themselves against incurring personal costs while unknowingly benefiting a social cheater that is not likely to reciprocate the act in the future. Tags also do away with the need for individual learning and memory because each individual's character is not concealed. Thus, it turns out that the ability to recognize another agent's phenotype, or its social "tag," allows altruists not only to concentrate benefits among individuals possessing the same `type` but also to eliminate the oft-significant costs associated with being the sucker in social interactions with cheaters. In addition, these benefits can be had without relying on individual memory, which is expensive to maintain and almost always incomplete at the individual level.

Depending on one's theoretical proclivity, **`omniscientShareFoodWith`** either explicitly models the situation in which there exists a reliable phenotypic signal for cheaters, cooperators, or both or it implicitly models the scenario in which foragers use shared information about past social interactions to correctly identify altruists and cheaters from their very first meeting. It is for this reason that **`omniscientShareFoodWith`** is the most socially sophisticated of the three methods modeled in SHARE. According to this method, altruistic donors with excess food will share only with the prospective recipients they recognize as altruistic (i.e., likely to share with them and others in the future) and choose not to share with those they identify as social defectors (i.e., those likely not to share with others). Selfish foragers will never share their excess food, and no foragers will ever share with them.

Regardless of which food sharing method is employed, when a prospective donor decides to behave altruistically, its **`currentEnergy`** value is decreased by the amount provided to the recipient, which is equal to the amount of food that the donor has amassed in excess of its own lower food share threshold. This can be a sizable amount of energy depending on how much excess food was being carried at the time. Herein lies the biological altruism of food sharing—each donor's energy store, which is used to meet somatic costs and to fuel reproduction, can incur a serious detrimental cost in order to benefit the fitness of a conspecific in need; a conspecific that may or may not be related to the donor and may or may not be able (or willing) to repay the altruistic act at any time in the future.

An experimental design for exploration

Agent-based computer simulations can substitute for Gould's divine tape player. ABMs can collect data from thousands, even millions, of different cultural histories—simulation runs characterized by different social and ecological conditions and stochastic events. To explore any dynamic system's state space effectively, it is important that one varies experimental variable values systematically. The practice of repeating simulation runs with different values for a particular parameter is referred to as a parameter sweep. By sweeping each parameter both independently and in parallel with other parameter sweeps, one is able to gain an understanding of how each primary experimental variable influences the dynamics of the system in question. Systematic parameter sweeps essentially rerun the tape of history by running one's agent-based simulation with values taken from a large realm of possibilities.

To explore how a variety of socio-ecological contexts affect the evolution of the food sharing strategies described above, 101 simulation runs—each initialized using the same set of standard variable values (Table 4.1) and a unique random number seed—were executed for each possible combination of primary experimental variables (for example, Patch Size = 4, Gap Size = 8, sharing rule = **`shareFoodWith`**, meat probability = 0.0001, predator danger = 0). Each possible combination was achieved by sweeping through all of the possible values for each parameter. At each parameter combination, all 101 runs were initialized with an equally mixed starting population of altruistic and selfish foragers. Each run was discontinued after one of the alleles (either selfish or altruistic) evolved to fixation in the metapopulation. Six weeks of computer time was required to execute and collect data from each of the resulting 30,300 simulation runs. Additional, but less exhaustive, sweeps were conducted to investigate the effects of secondary experimental variables.

Parameter	Value(s)
Minimum number of plants	500
Plant maximum (energy units)	10
Plant logistic growth rate *r*	0.2
Meat maximum (energy units)	100
Meat minimum (energy units)	10
Meat logistic depletion rate *r*	0.02
Starting number of foragers	40 (20 of each allele type)
Forager starting energy (energy units)	50
Forager metabolic rate (energy units)	2
Forager fertility threshold (energy units)	100
Forager birth interval (time steps)	20
Cost of reproduction (energy units)	50
Forager maximum life span (time steps)	100
Forager maximum (energy units)	110
Forager food share threshold (energy units)	50
Probability of sharing food (*s*)	
(when modeled as a binary discrete trait)	0 (selfish), 1 (altruist)
(when modeled as a polygenic trait)	$0 \leq s \leq 1$
Probability of artifact drop (per forager/time step)	0.1
Primary 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
Meat probability (per cell per time step)	0, 0.0001
Predation danger (per forager per time step)*	0, 0.0001
Food sharing method	`shareFoodWith`, `reciprocalShareFoodWith`, `omniscientShareFoodWith`
Secondary Experimental Variables	
Patch search method	`randomSearch`, `diagonalSearch`
Punishment penalty (energy units)	0, 20
Punishment cost (energy units)	0, 5

* Predation danger in woodland patches only, value is 3 times greater when foragers are in open grasslands.

Table 4.5. The standard and experimental variables (and their values) used in SHARE.

Data collection

Agent-based models are capable of yielding an extraordinary amount of quantitative data. Theoretically, one could gather data on hundreds of different variables from tens of thousands of agents for every time step of a simulation run. Over the course of a few hours, a relatively involved ABM can provide more data than one could hope to analyze in a week. Thus, collecting an appropriate amount of data from an ABM is like panning for gold in a swiftly flowing stream of information. One must have a clear data collection plan for filtering the important nuggets of information out of the model as they zip past in simulated time, else one's pan quickly fills with deposits that obfuscate the sometimes subtle patterns of interest. Of course, the data types of interest will vary with each model, but the collection scheme should always remain as streamlined yet comprehensive as possible so as to minimize processing time while allowing one to address tangential research questions without rerunning thousands of simulations solely to collect data from a previously overlooked variable.

The challenges one faces when *collecting* data are dwarfed by those encountered when *analyzing* the output produced by agent-based simulations. I have already stressed the importance of historical contingency in agent-based research. Axelrod (1997) notes that because history plays a crucial role in most ABMs (i.e., multiple runs of a model might produce very different outcomes given slight changes in initial conditions and/or the order or impact of stochastic events due to different random number seeds), it is possible to use the data collected from each simulation run to reconstruct the particularistic history of the artificial society it supported. Such path-dependent data, he explains, can be described in three ways. First, one can describe the events of any one simulation as they occurred in chronological order (e.g., in run #495 there was a population explosion, followed by the spread of disease and a marked decrease in population size…). While this tactic 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 *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 around us, it does not insure a representative description of the dynamical system in question, for not every agent experiences all there is to experience during the course of a simulation run. Third, one can explain trends in ABMs by tracking the values of large-scale, global variables through simulated time. This technique yields great explanatory power but sacrifices particularistic detail. Depending on the nature of one's research questions, there might be valid reasons to analyze data at any (or all) of these levels. The purposes of my research, however, are served best by the global-scale approach, which allows me not only to compare "identical" models with different histories generated by different random number seeds, but also to systematically contrast the results of models that use the same random number seed and different parameter values. In this way, effects due to historical contingency and controlled experimentation can be considered independently. Two different types of data were collected to assess the effect of this experimentation: population genetic and spatial data.

Population genetic data

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). It assumes that a metapopulation with an allele frequency of P is divided into a number of trait groups i, each of which has an initial population n_i and an initial allele frequency of p_i and will have a population of n'_i and an allele frequency of p'_i after selection. When the allele in question corresponds with a biologically altruistic behavior, like food sharing, the gene will increase the size of the group ($n'_i > n_i$) even though its frequency will decline within each group ($p'_i < p_i$). The following equations can be used to calculate the global frequency of the altruistic allele before selection:

$$P = (\sum n_i p_i) / (\sum n_i) = p + \mathrm{cov}(n,p)/n \qquad (1)$$

and after selection:

$$P' = (\sum n'_i p'_i) / (\sum n'_i) = p' + \mathrm{cov}(n',p')/n' \qquad (2)$$

where p equals the average allele frequency, n equals average group size, and the covariance term measures the association between the two. Price demonstrated that change in metapopulation allele frequency through time ($\Delta P = P' - P$) could be expressed by what became known as the Price Equation:

$$\Delta P = \mathrm{ave}_{n'}(\Delta p) + (\mathrm{cov}_n(s,p) / \mathrm{ave}_n s) \qquad (3)$$

where s is a measure of the group benefit provided by the altruistic allele. The two terms that are summed in this elegant equation capture the relationship between within-group and between-group selection, as Sober and Wilson (1998:73-74) explain:

> “The first term is the change in gene frequency within the average group, weighted by the size of the group after selection (n'). It serves as a

> measure of within-group selection. The second term includes the covariance between group benefit (*s*) and the frequency of altruists in the group (*p*) before selection (when group size was *n*). It measures between-group selection…The two levels of individual and group selection seem to literally jump out of the Price equation."

By employing patch membership as a reliable proxy for trait group affiliation in SHARE, the Price Equation can be used to partition the overall change in allele frequency so that one can track selection *within* subsistence-related trait groups (i.e., individual selection) and *between* subsistence-related trait groups (i.e., group selection). Values for both of these terms in the Price Equation, the percentage of altruistic foragers present in the metapopulation, and the total number of foragers in the metapopulation were collected during each run of SHARE at a rate of once per 25 time steps. These data were analyzed to confirm that altruistic alleles increased in frequency due to relatively high levels of between-group selection and not by other means (Figure 4.6).

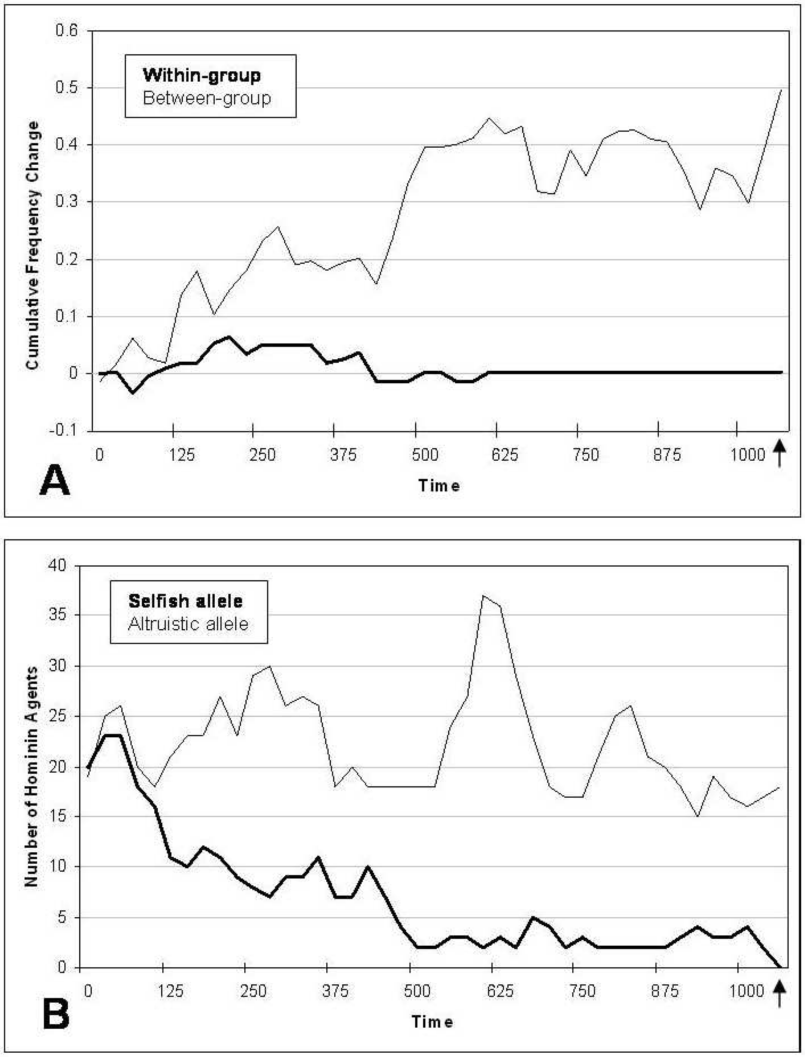


Figure 4.6. The Price Equation quantifies multilevel selection in one run of SHARE (Patch Size = 4, Gap Size = 6). **A**: Cumulative change in the frequency of the altruistic allele due to within-group selection (bold line) and between-group selection (thin line). **B**: Selfish and altruistic hominin 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 change in the frequency of altruistic allele (ΔP) from the start of the simulation run (P = 0.5) to the end (P' = 1).

Spatial data

As hominin agents articulate with their environment and interact with others according to individualized needs and food sharing behaviors, they also occasionally deposit artifacts on the spatial grid. As a result, each simulation run provides a unique artificial material assemblage that serves as the archaeological record of the hominin agents' locational behaviors. To document the development of the each run's artificial archaeological landscape, artifact agents are prompted to report their **`artifactCount`** values to their respective Cartesian coordinates on a two-dimensional array at the rate of once per 100 time steps. Each array is time-stamped with a uniquely descriptive name and saved as a space-delimited text file (Figure 4.7a). At the conclusion of a simulation run, any or all of the resulting text files can be imported into GIS software as continuous (raster) surfaces for the purpose of spatial analysis (Figure 4.7b).

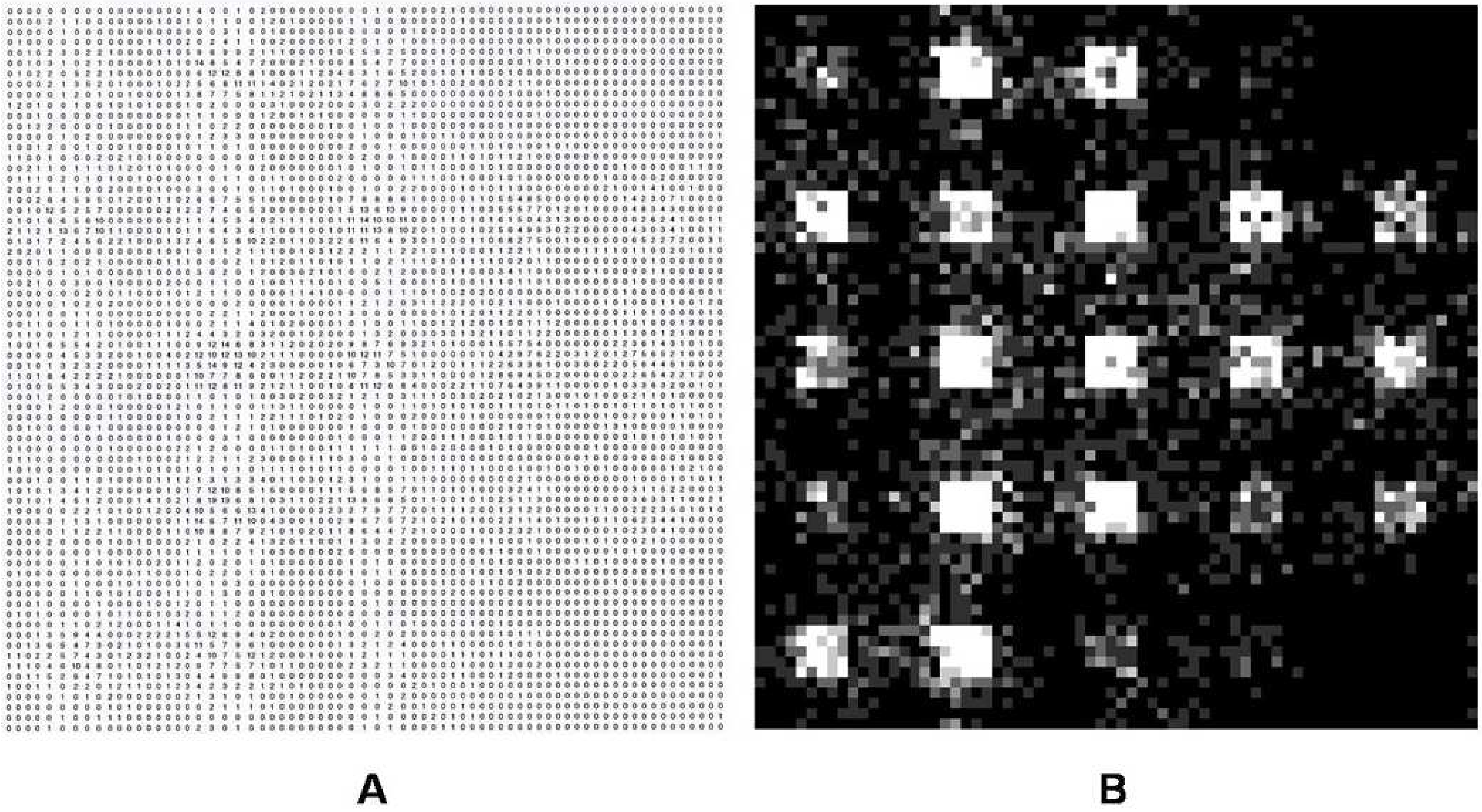


Figure 4.7. An example of spatial data collected from SHARE. **A**: Spatial output in the form of a space-delimited text file. **B**: The same data set converted into a raster surface. Artifact counts are integers and represented by grayscale: light shades are high values and dark shades are low values. Either data set can be used to calculate spatial statistics like local Moran's I_i or G_i^*, but the raster offers an important visual component that that the raw data does not.

Hominin interaction histories

In some cases, it is also important to gather data on the social interactions between different types of hominin agents. For example, when trying to elucidate why the sharing strategy based on direct reciprocity did not enjoy a larger basin of attraction (i.e., evolve to fixation in wider range of ecological initial conditions) than its simpler counterpart, it was necessary to track the cumulative interactions between different types of agent pairs (altruist/unknown, altruist/known altruist, and altruist/known egoist) in order to quantify how often altruists were able to employ their memories of past interactions to refuse the selfish individuals who had defected against them in the past. These interaction history data were crucial in recognizing why personal memory did not pay larger dividends in SHARE (see detailed discussion in Chapter 5).

4.4 Conclusion

> "A moral of the story is that models that aim to explore fundamental processes should be judged by their fruitfulness, not by their accuracy." [Axelrod 1997:6]

Archaeologists might not be entirely comfortable with Axelrod's view. After all, the ultimate goal of our research is to use archaeological data to reconstruct past behaviors as accurately as possible. Many archaeologists lean towards highly detailed models to aid them in these efforts because they share the belief that complicated models yield more accurate results than less detailed models. But an accurate reconstruction is the product of sound inferences, and sound inferences often come from fruitful models, which need not portray every detail of the empirical world with precision. An elegant model, which includes only those characteristics that are essential to the system in question, can be quite fruitful in that it can better inform our inferences by allowing us to observe a wider range of behavioral conditions and their archaeological consequences than is possible empirically.

Additionally, when using agent-based models to *explore possibilities*, rather than to *emulate observations*, it is often impossible to distinguish "accurate" parameter settings from "inaccurate" parameter settings. In fact, when the goal of a model is to better understand the ways in which essential components interact under a variety of conditions, the primary focus should be on the overall *behavior* of the dynamical system, not on the *accuracy* or *precision* of its variables or its output. The question concerning which of the modeled worlds most closely resembles the real world declines in importance as each possibility provides just one of many hypothetical socio-ecological environments, each of which is as interesting and important as the next. When exploring fundamental processes with an agent-based model, the majority of one's results often will not approximate anything in the observable world. Therefore, a measure of how accurately an experimental ABM approximates reality cannot be used to evaluate its utility in generating archaeological inferences.

In light of these statements, I must restate what SHARE is (and is not) designed to accomplish before moving on to an analysis of my simulation results in the chapters that follow. Recall the first of my primary research questions: By what means could food sharing have evolved in Plio-Pleistocene hominin populations? SHARE is designed to identify socio-ecological avenues through which biologically altruistic food sharing traits might have possibly evolved to fixation in Plio-Pleistocene hominin populations. To this end, the baseline version of SHARE explores how the spatial and temporal patchiness of food resources affect the evolution of food sharing among hominin foragers that possess no information about the distribution of food (save for that which they can sense in their immediate surroundings), no memory of past interactions with other foragers, and an inability to recognize kin, known cooperators, or known defectors. A demonstration that ecological patchiness can facilitate the evolution of altruistic food sharing among such "unintelligent" hominin foragers (as it did for feeding restraint and alarm-calling in Pepper and Smuts [2000, 2002]) serves as a null model for research on early hominin food sharing.

Many paleoanthropologists would rightly argue that, given the relatively sophisticated sociality observed among our living hominoid cousins such as *Pan* *troglodytes* and *Pan paniscus*, to model Plio-Pleistocene hominins as socially-inept would be a disservice. Thus, to investigate how added layers of social intelligence (i.e., memory, gossip, and recognition) affect the range of ecological environments in which food sharing evolves (i.e., altruism's basin of attraction) it is necessary to add new behaviors and variables to the baseline model: Just how much does memory of past interactions or gossip concerning social defectors expand or constrict the range of ecological settings in which food sharing can evolve to fixation? In the following chapter I use simulation data to address this central question, among others.

The second of my primary research questions addresses the ambiguous Plio-Pleistocene archaeological record. How can we recognize a behavior like food sharing in the inherently incomplete archaeological record of the Lower Paleolithic without turning Plio-Pleistocene hominins into !Kung hunter-gatherers? How can we recreate a detailed history of closed habitat patch use when the temporal resolution afforded by archaeological reconstructions is so coarse-grained (*à la* Stern 1993, 1994)? As discussed in earlier chapters, previous reconstructions have employed archaeological inferences borrowed from observations of modern hunter-gatherers. But SHARE is different in that it offers a tool with which inferences can (literally) be generated rather than borrowed. A null model of early hominin food sharing can strip away all of the behaviorally modern human strategies that have been "mapped onto" Lower Paleolithic remains previously, thereby allowing one to test just how little is actually required to produce artificial archaeological assemblages that share essential characteristics with those that have been excavated at some of the most famous Plio-Pleistocene sites in the world.

In addition, each simulation run produces a unique experimental assemblage to which global and local spatial statistics can be applied in an attempt to devise a methodology for identifying the multi-scale spatial signatures left by different food sharing behaviors. It is important to note that, because hominin agents are capable of depositing only one type of artifact in SHARE, the artificial archaeological record they produce during each run is not composed of a variety of tool types, and tool deposition is equally associated with all activities. Thus, SHARE treats individual archaeological artifacts as "trace fossils"—evidence of hominin presence but little else; certainly not evidence of specific behaviors like sleeping, eating, or sharing food. Though unrealistic, the presence of only one artifact type allows one to more easily compare the patterns of spatial dependence in distributions resulting from different behavioral processes. It is possible to include a wider range of artifact types and associate the deposition of each with a different activity (butchering, stone working, etc.) in future versions of SHARE. Finally, in the spirit of middle range research, one should hope that the quantitative techniques that show promise in analyzing artificial material assemblages might be applied to field assemblages with some success. In the following chapters, I hope to demonstrate that SHARE is indeed a fruitful model.

CHAPTER 5. EXPLORING THE EVOLUTION OF ALTRUISM IN *SHARE*

> "Much of evolutionary science can be boiled down to estimating the strength of various effects on the trajectory of evolution in a sufficiently large number of cases to obtain some empirical generalizations. The gold-standard study of organic evolution is one in which the investigator estimates the strength of natural selection and other forces in an evolving population. In the case of culture, such studies are still very few." [Richerson and Boyd 2005:252]

This poignant statement provides the perfect starting point for this chapter. One might consider my research project a response to Richerson and Boyd's implication that there exists a need to conduct behavioral research in the same vein as that which is standard in evolutionary biology. The manner in which I framed my investigation of the evolution of food sharing among early hominins will seem more familiar to theoretical biologists than to anthropologists, not because of the jargon used or the data collected, but because of the approach taken and the analyses conducted. The main goal of this research is to measure how various social and ecological conditions affect the trajectory of the evolution of food sharing in a large number of experimental cases. It is from this large set of experiments that I draw some empirical generalizations concerning the conditions under which altruistic food sharing traits *could* have evolved to fixation in Plio-Pleistocene hominin populations. To this end, I am less concerned with the outcome of any single experimental run and more interested in the trends that are properties of the larger collection of simulation runs. As Richerson and Boyd correctly identify, there are few cultural evolutionary studies like the one presented here.

Before presenting the population genetic results and their implications for behavioral reconstructions of Plio-Pleistocene hominins, it is first necessary to discuss a few of the techniques that were used to verify SHARE and test the sensitivity of its arbitrarily-defined parameters (section 5.1). My presentation of SHARE's population genetic results follows a premeditated course from simple to complex; one that purposefully emulates Epstein and Axtell's (1996) crystal clear discussion of Sugarscape's results. It begins in section 5.2, where I explore the impact of food sharing alleles in pure and mixed populations of hominin foragers in uniform environments. The next section (5.3) presents the results of a large set of simulation runs conducted to address the central research question of how variations in resource distribution and in the sophistication of social behaviors affect the evolution of altruistic food sharing. These experiments involve mixed starting populations of foragers and non-uniform environments of various patchiness levels. The effects of predator danger and the presence of meat packages (carcasses) are also addressed in section 5.3. Section 5.4 tackles the issue of why there is not a significant difference between the population genetic results of reciprocal food sharing and those of its simpler counterpart, which does not include memory. Section 5.5 explores how the knowledge of global resource structure affects the evolution of altruism. Section 5.6 discusses some preliminary data generated by a version of SHARE that includes the punishment of social cheaters. Because punishment requires each punisher to pay an individual cost for enforcing group norms, it is referred to as a form of secondary altruism. The chapter closes with a discussion of how the population genetic results provided by the agent-based model inform traditional behavioral reconstructions of Plio-Pleistocene hominins.

5.1 Model verification and validation

> "Model verification and validation are critical in the development of a simulation model. Unfortunately, there is no set of specific tests that can easily be applied to determine the 'correctness' of a model. Furthermore, no algorithm exists to determine what techniques or procedures to use. Every simulation project presents a new and unique challenge." [Sargent 2003: 46]

Given the apparent importance of verification and validation, one might be surprised by the amount of confusion surrounding these terms. Verification and validation refer to two different processes (Sargent 2003). Model verification refers to the process by which a programmer ensures not only that the code is bug-free but also that the computerized model (i.e., the program) correctly specifies all of the components of the associated conceptual model. Verification only concerns the computerization of a conceptual model; it does not address the validity, or utility, of that conceptual model. Thus, a *verified* agent-based model is one that correctly implements a conceptual model as a computerized model. In contrast, validation refers to the process by which one assesses whether a computerized model possesses the range of accuracy that is necessary to address the research questions it was designed to answer. A *valid* agent-based model is one that faithfully captures the process(es) in question to the extent that its results are applicable to the model's intended purpose. On a related note, one can consider a verified and validated model *credible* only when the members of a larger research community are also confident in the quality of the information derived from that model.

Agent-based modelers face unique challenges in both verifying and validating their models (Grimm 2002). One of the most significant obstacles to verifying agent-based models is caused by the presence of emergent properties. As Grimm explains, debugging a program is easiest when one can compare what a program *is doing* to what the program *should be doing*. For example, because we all know what word-processing software is supposed to do, we would be able to identify a bug in an application if, say, typed words failed to show up on the computer screen. However, because most agent-based models exhibit emergent properties, the way in which they should behave is not as apparent as the way in which word processing software should behave. It is often unclear to the programmer if unexpected model behavior is due to a logical error in the program or an emergent property resulting from interactions of many independent agents. There are many stories of interesting research papers resulting from projects that spent weeks tracking down "bugs" only to find out that the "bugs" were actually previously undiscovered emergent properties of complex systems.

Model verification is an iterative process that begins as soon as one begins programming and does not end until one sees it fit to begin collecting data. Sargent (2003:41) lists a number of techniques that researchers have used to verify and validate simulation models, all of which are also applicable to agent-based models. He includes brief descriptions of the following in his review: visual debugging (animation), comparison to similar models, degenerate tests, event validity, extreme condition tests, face validity, comparison to historical data, internal stochasticity tests, parameter variability (sensitivity) analyses, tests of predictive value, traces, and Turing tests. The subset I used to verify SHARE includes: visual debugging, agent traces, extreme condition tests, and sensitivity analyses.

I employed the visual debugging technique—sometimes alone, sometimes in conjunction with other methods—to accomplish the bulk of the verification work with SHARE. Grimm (2002) explains that visual debugging allows modelers to perform conventional debugging exercises (i.e., controlled experiments designed to expose possible deficiencies in a program) while watching for aberrations in real time visual displays such as line graphs and bar charts, or raster maps that depict the positions of the agents on virtual landscapes. Because human perception relies so strongly on our sense of vision, it seems especially germane to use Graphical User Interfaces (GUIs) as tools for debugging computer code. With the aid of continuously updated raster maps and line graphs even casual observers can spot errors that might otherwise require sophisticated statistical techniques and hundreds of hours of data collection to identify. By systematically stepping through a simulation run one time step at a time while tracking the movements of one agent on a raster map, any abnormalities in that agent's movements are surprisingly easy to recognize. Without a visual display of the agent's landscape and its position therein, however, logical errors in movement methods would be very difficult to identify.

The visual debugging technique becomes even more powerful when it is paired with agent traces. Traces prompt one or more agents to print informative messages to the screen (or to a text file) as they engage in an activity that the modeler is monitoring. Tracing an agent is a quick and inexpensive way to track its every movement and decision during a simulation run. By saving the messages that each agent prints to the screen for the duration of a simulation run, a modeler essentially collects a diary of each agent's "life." These traces can be used to identify abnormalities in agent behavior, such as when an agent's trace message does not match what actually happened (e.g., an agent says it has accepted shared food, but it does not increase its `currentEnergy` by the amount of energy shared).

Extreme condition tests provide modelers with another useful verification tool. As Sargent (2003) explains, models should be structured so that they can accommodate extreme settings, even if such settings are highly unlikely to be encountered during the intended research. Extreme condition tests can highlight serious implementation errors that could otherwise go unnoticed. For example, in SHARE when maximum forager life span is equal to one, I expect to see all foragers die after one time step. Obviously, if any foragers had lived past one time step this "silly" test would have identified a serious programming error in my model. If maximum forager life span equals 100 but forager birth intervals are set to the extreme value of 1,000, then I would expect not to see any new births because foragers cannot possibly live long enough to satisfy the birth interval requirement. Again, had there been new births occurring under these extreme conditions, this "silly" test would have identified a grievous error in the logic of the program. I conducted similar extreme condition tests for many of the state variables in SHARE. Such tests provide quick and easy ways to test the internal structure of an agent-based model before wasting valuable time and energy collecting data from it.

All modelers should strive to use as few arbitrarily defined parameters as possible. If arbitrarily defined parameters are unavoidable, then one must at least test how sensitive the model is to different values. Because SHARE is a heuristic model, some of its parameters are arbitrarily defined (refer back to Table 4.1). For instance, I did not use an empirically derived value for the logistic growth rate or maximum energy level of East African woodlands plants. For these variables I simply used values that had been used in previously published reports of a similar model, called ECO (see Pepper and Smuts 2000; 2002). Although defined arbitrarily, the values of SHARE's parameters are purposefully scaled to one another. For instance, although maximum forager life span might be set arbitrarily to 100 time steps, forager birth intervals are purposefully set to be one-fifth the length of that life span value. Nevertheless, it is necessary to test whether SHARE's behavior is altered when different values are substituted for parameters like maximum life span, fertility level, and lower share threshold. For illustration, I will now discuss one such sensitivity analysis in detail.

Pepper and Smuts' (2000, 2002) published an elegant multilevel selection agent-based model called ECO, which served as the foundation for SHARE. As a result, SHARE and ECO contain many of the same parameters, although they are not always used in exactly the same way. One of the shared parameters they do use in the same way is called **`foragerFertility`**. This parameter sets the energy threshold for forager reproduction; a forager is not eligible to reproduce unless its **`currentEnergy`** is greater than or equal to **`foragerFertility`**. Pepper and Smuts set **`foragerFertility`** equal to a value of 100 in ECO, but before using the same value in SHARE, it was necessary to see how sensitive the model was to variation in **`foragerFertility`**. To do so, I collected data from a small number of simulation runs (*n* = 7) at each of 9 different Patch Size, Gap Size combinations using three different values for **`foragerFertility`** (75, 100, 125) (Table 5.1). Only the simplest sharing method, `shareFoodWith`, was tested in this sensitivity analysis. As you can see in Table 5.1, there was little difference in the results of the model when compared between the three settings for `foragerFertility`. Because varying the value of `foragerFertility` did not result in qualitatively different model results one can conclude that the evolutionary dynamics of SHARE are not sensitive to some variability in the threshold for forager reproduction. The results of this particular sensitivity analysis provide confidence that the same `foragerFertility` value that had some precedence in the literature also works well with my model. Similar parameter variability tests were performed for a number of the arbitrarily defined parameters. If SHARE showed sensitivity to parameter variability, care was taken to use values that diminished the parameter's influence on model dynamics.

	A			**B**			**C**		
	Gap Size			Gap Size			Gap Size		
Patch	3	5	8	3	5	8	3	5	8
3	1	3*	2*	1	2*	4*	2	4*	3*
5	0	0	2	0	0	1	0	0	1
8	0	0	0	0	0	0	0	0	0

Table 5.1. Sensitivity analysis results of `foragerFertility`. Integers designate the number of simulations runs (out of 7) in which the altruistic allele evolved to fixation for each Patch Size, Gap Size combination. A: `foragerFertility` = 75. B: `foragerFertility` = 100. C: `foragerFertility` = 125. * Not viable populations, average population size at time of fixation is less than 10.

The last few paragraphs explain the techniques I used to verify that my code works properly. However, whether or not SHARE is *valid* is less clear than whether or not it is *verified*. Are the agents in my computerized model true implementations of the agents in my conceptual model? Is SHARE structured appropriately to address the research questions I started with? It might be easier to answer these questions if SHARE could be compared to other agent-based models that attempt to explain the same process in slightly different ways. However, because no other agent-based model of Plio-Pleistocene hominin food sharing exists at the moment, SHARE's validity can be judged only through a comprehensive understanding of its agent classes and scheduling. Frankly, this means that any verbal description of SHARE's validity—short of the code itself—will be woefully incomplete.

After months of verifying, testing, and reassessing the model, I have concluded that it is fit for its intended purpose. However, it is ultimately up to the reader to either accept my assessment of the model's validity and move on or assess it for one's self. Agent-based model validation functions best when it is organized as a group activity, one in which a community of programmers (and non-programming modelers alike) contribute towards a common goal of creating and maintaining a set of validated models that can reliably be used for comparison. It is in this spirit of community that I invite anyone who is interested in getting one's hands dirty with model validation to contact me for a freely-available version of SHARE's source code. Working with other researchers' models in an attempt to replicate their published results is an activity that must quickly become "old hat" for members of the social science agent-based modeling community, just as replicating someone else's laboratory experiment is commonplace in chemistry. If such "validation by committee" does not soon become the norm, then anthropologists can expect to see a large number of flawed models as the popularity of the agent-based modeling technique grows faster than the standards required to facilitate fruitful research.

5.2 Experiments with foragers in uniform environments

This initial experiment is designed to illustrate how selfish and altruistic food sharing alleles serve forager populations in a uniform environment. For this reason, the spatial variability of food resources is held constant. Woodland resources are clumped into one large “mega-patch” rather than distributed into a number of regularly shaped and regularly spaced patches. In this uniform environment there is no open grassland—woodland plants cover the entire landscape. In order to concentrate solely on the effects of altruistic alleles in a uniform environment, neither carcasses nor predator danger are included in these initial experiments. Within this uniform environment, I evaluate the success of selfish and altruistic food sharing alleles, first in pure populations and then in mixed populations. In a pure population, all foragers display the same phenotype (selfish *or* altruistic), while mixed populations contain hominin foragers of both phenotypes (selfish *and* altruistic)

Pure populations of selfish foragers

Thirty runs were executed with pure starting populations of 40 selfish foragers. These runs were allowed to continue for up to 5000 time steps, unless populations went extinct in fewer. The runs for this experiment were initialized using the default parameter settings (see Table 4.1) with Gap Size = 0, Patch Size = 30, and 30 unique random number seeds. Not surprisingly, forager population size and food availability are related in a manner reminiscent of the Lotka-Volterra predator-prey cycles (Lotka 1925; Volterra 1926). As a growing forager population skyrockets, it depletes once-abundant food resources at an increasing rate and forces the amount of edible energy to plummet. While over-used resources are replenishing themselves, the once healthy forager population is reduced by starvation. Population size continues to decrease until another cycle of food resource abundance begins. The period during which plant resources regenerate is a crucial time for hominin agents in SHARE because this is when food resources are most scarce and when forager populations are still fairly large. Due to the vagaries of foraging decisions and the timing and location of births, hominin agents amass unequal amounts of energy—some foragers procure large stores of excess food while others are ill prepared for the lean period of plant regeneration. As a result, the former are far more likely than the latter to survive periods of resource scarcity.

In the case of binary **`foodShare`** values, selfish foragers (**`foodShare`** = 0) avoid all of the costs associated with sharing food because they always refuse to aid prospective recipients. Even when in possession of excess food, a selfish forager will choose to hoard it. Thus, when in a pure population of other hoarders, starving selfish foragers can count on not receiving any food from other forager agents. Because a pure population of selfish foragers has no method for redistributing procured food more equally among its members, the majority of the foragers have little chance of living through extended periods of food scarcity. Only those few selfish foragers who are lucky enough to procure amounts of food near their maximum energy level have a reasonable chance of surviving the lean period of plant regeneration. In effect, each generation of a pure population of selfish foragers produces a few, well-prepared individuals to serve as seeds for the next generation.

There are selective regimes for which this strategy is suited. For instance, in the absence of predation or stochastic death (as was the case in this experiment with uniform environments), the strategy of relying on a few well-endowed individuals is adequate for overcoming periods of scarcity. As you can see in Table 5.2, in 14 of 30 simulation runs, pure populations of selfish foragers survived for at least 5000 time steps. Thus, despite an inability to redistribute common resources more equally among a larger number of individuals, pure populations of selfish foragers were "successful" in roughly 47% of the runs conducted in uniform environments.

Allele Type	# Runs Survived	# Total Runs	% Runs Survived
Selfish	14	30	47
Altruistic	21	30	70

Table 5.2. Success of pure populations in uniform environments (Patch Size = 30, Gap Size = 0). # Runs Survived = number of simulation runs in which the forager population survived greater than 5000 time steps. # Total Runs = total number of simulation runs. % Runs Survived = percentage of simulation runs in which the forager population survived greater than 5000 time steps.

Pure populations of altruistic foragers

As was done with their selfish counterparts, 30 simulations of up to 5000 time steps were run with pure populations of altruists. Each of these runs was initialized with the default parameter settings (see Table 4.1) with the following exceptions: Gap Size = 0, Patch Size = 30, and all 40 starting foragers were altruistic. The same 30 random number seeds that were used to run the selfish experiments described above were employed here, too. Because altruistic foragers (**`foodShare`** = 1) will part with excess food to benefit anyone who asks, they are constantly exposed to the individual costs associated with sharing. However, foragers that are members of pure populations of altruists are guaranteed to receive food in times of need as long as they can locate a conspecific in possession of excess food. Therefore, although altruists in pure populations frequently pay the individual cost of sharing when they have excess food, they are also often beneficiaries of sharing during times of scarcity. Remember that this is not the case in pure populations of selfish foragers, whose members do not have to worry about paying costs when they are doing well but also can count on receiving no aid when they are starving.

Altruistic forager population size and food resources vary through time in the same way that was described for selfish forager populations. The same particularistic reasons for the unequal distribution of food resources among group members hold in this case as well. However, in contrast to selfish foragers, altruistic food sharers have a method for redistributing resources among themselves. As a result, energy is more equally distributed among members of pure populations of altruists than it is among members of pure selfish populations. The majority of the sharing events that occur during a simulation run take place during the scarce period—the time marked by widespread plant resource regeneration. This might initially seem counterintuitive: why would foragers share more frequently when food is harder to come by? In fact, foragers are not in need of assistance during times of plenty, when each has little problem procuring enough food to keep its energy level above the lower threshold. During the lean periods, a sizable proportion of the altruistic foragers can be seen redistributing food even as the heavily depleted resources around them have not fully grown back. Keep in mind that each individual must try to outlast the shortage in food resources (the duration of which is unknown to any agent) on its stored energy. Thus, from an individual perspective, sharing a portion of one's food resources during this particular time is not only biologically altruistic, but also incredibly risky. The behavior is less risky from the group-level perspective than it is from that of each individual because it yields a larger number of foragers that are equally equipped to survive the lean period. In this sense, a pure population of altruistic foragers provides a larger number of individuals, in none of whom an extraordinarily large or small amount of resources has been "invested," to serve as seeds for the next generation. From the group's perspective this strategy is more resistant to predation and other stochastic processes than its selfish counterpart because it produces a larger founding population. However, in the absence of predation or accidental death the success of a pure population of foragers employing the altruistic strategy is inversely related to the duration of the lean period. *Ceteris paribus*, slower resource regeneration rates (down to some limit) will favor the better prepared individuals provided by the selfish strategy.

Given the lack of predation and accidental death in these experiments, one might predict that pure populations of selfish foragers would survive to the arbitrary threshold of time steps (5000) more often than pure populations of altruists. However, this was not the case. As you can see in Table 5.1, pure populations of altruistic foragers were "successful" in 21 of the 30 (70%) runs conducted in uniform environments. Compare this to only 14 of 30 (47%) for pure populations of selfish foragers. Keep in mind that both sets of experiments were initialized with the same set of 30 random number seeds. Because the amount of time that elapsed between crests in food resource abundance is relatively brief in comparison to the amount of time a forager can live on procured energy alone, this set of experiments did not provide a strong selective pressure for individuals with exceedingly large energy stores. One might prompt the strong selective pressure needed to select for extremely well prepared individuals by simply increasing forager metabolic rate or lowering the logistic rate at which plants grow. However, given the default parameter settings, a larger number of altruists were able to survive multiple lean periods despite the fact that their energy stores were on average relatively smaller than those of fewer selfish founders. This observation explains why pure populations of selfish foragers did not have a significant evolutionary advantage in this particular ecological scenario, but it still does not address why the altruists did.

To address this issue we must first recall that this is a spatial model. Not only do individuals have to survive the temporal duration of the lean period, they must also quickly find newly regenerated food on the virtual landscape as soon as it becomes available. Depending on the foraging decisions and/or deaths of other foragers, some areas will regenerate sooner (but not more quickly) than others. Although these “early” resources are not located randomly, no hominin agent can predict the locations of these early resources given the limited amount of local environmental information available. The successful foragers that serve as founders for the next generation often survive on stored energy just long enough to find one of these newly regenerated areas. It follows that if finding fresh resources soon after they become available is an unpredictable (and in this sense, a “random”) process, whichever strategy provides a greater number of possible seeds—i.e., lean period survivors—possesses a better chance of placing at least one of them in the vicinity of early resources. Here, then, is the selective advantage of the pure population of altruistic foragers: they produce a greater number of individuals with food stores that are sufficiently large enough to outlast relatively brief periods of scarcity even though they are smaller than those of selfish survivors. Having a greater number of possible seeds increases the probability that at least one of them will find “randomly” distributed, “early” resources in the spatial model, and this is why pure populations of altruistic foragers are more often successful than pure populations of selfish foragers in the uniform environments tested here.

Figure 5.1 illustrates the success of the altruistic strategy in pure populations in uniform environments by highlighting some data from just 20 of the 60 simulation runs. All ten of the altruistic populations in the figure survived indefinitely while not one of their selfish counterparts “succeeded” in surviving at least 5000 time steps in the uniform environment. In other words, all ten of the selfish populations went extinct and all ten of the altruistic populations survived, despite the fact that each pair of runs was instantiated using exactly the same set of random number seeds and initial conditions (aside from the sharing allele used, of course).

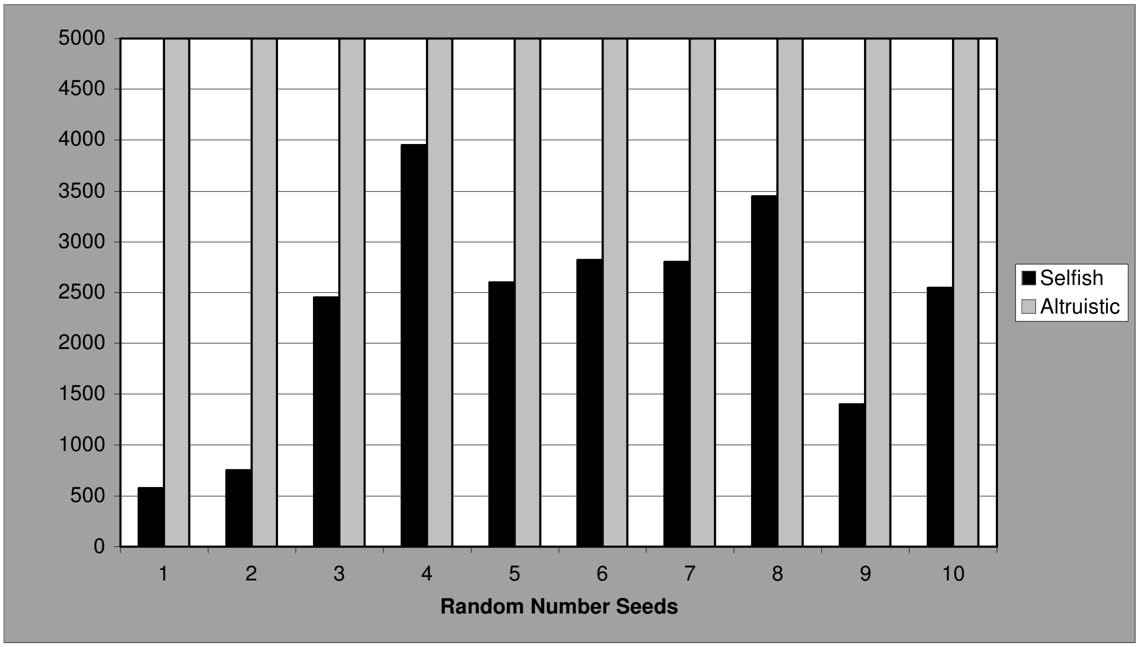


Figure 5.1. Comparing the success of ten pure populations of selfish (black) foragers and ten pure populations of altruistic (grey) foragers in uniform environments. Although the sizes of all populations fluctuate through time, each of the selfish populations goes extinct and each of the altruistic populations survives past 5000 time steps.

Experiments with pure populations of foragers are useful for comparing sharing and hoarding strategies. The results presented above simply demonstrate that altruistic foragers provide their groups with a greater benefit than selfish foragers, and that pure populations of altruists are more successful than pure populations of egoists in uniform environments. This news should come as no surprise. In fact, it is to be expected when dealing with biologically altruistic traits. However, it is important to keep in mind that the data collected so far have come from groups composed entirely of either altruistic *or* selfish foragers. The next logical question is: How does the altruistic version of the food sharing allele fare in mixed populations of altruistic *and* selfish foragers in uniform environments?

Mixed populations

Answering this question requires a set of experiments similar to those described above: the uniform environment is composed of one mega-patch of woodland resources, no predation is allowed, and carcasses are not included. However, unlike the experiments with pure populations, each starting forager population is composed of an equal mix of selfish and altruistic individuals (20 of each type). And because the level of social sophistication displayed by sharing traits is also of interest, the three different sharing behaviors (**`shareFoodWith`**, **`reciprocalShareFoodWith`**, and **`omniscientShareFoodWith`**) are tested with 30 runs each.

Recall that the simplest food sharing behavior in SHARE (**`shareFoodWith`**) involves neither memory of past interactions nor the ability to identify the phenotypic character of foragers. Altruistic foragers share excess food with a probability of 1, and selfish foragers share excess food with a probability of 0. As was the case with pure population experiments, selfish foragers avoid all costs associated with sharing food. However, unlike in the pure population experiments, when present in mixed populations, selfish foragers also have the opportunity to benefit from the selfless deeds of altruists. In other words, in mixed populations selfish foragers become social cheaters in addition to non-sharers.

The news is not so good for altruistic foragers. As in pure populations, altruists are able to benefit from the selfless deeds of other altruists. However, when present in mixed populations, altruists are exposed to the detrimental costs associated with sharing their hard-earned resources with free-riding egoists. The data collected from experiments with pure populations show that altruistic foragers benefit the groups in which they belong, and of course this also holds true for the mixed population experiments. An altruist always benefits the trait group to which it belongs. However, given the fact that selfish individuals have a higher relative fitness *within* mixed groups because they accept the benefits of altruistic acts without paying the associated costs, altruists always will be selected *against* at the level of the individual. Because a uniform mega-patch facilitates strong within-group selective pressures, one should expect to see the selfish allele evolve to fixation in the vast majority of the runs in this particular experiment.

Indeed, this is exactly what we see. The selfish `shareFoodWith` allele evolved to fixation in 28 of the 30 (93%) runs that were initiated with equally mixed populations of foragers in uniform environments. In the two cases (7%) in which the altruistic `shareFoodWith` allele evolved to fixation in the metapopulation, neither survived 5000 time steps. Obviously, this simple version of the altruistic food sharing allele was regularly out-competed by its selfish counterpart within the megapatch. This demonstrates that when foragers lack any behavioral method to segregate themselves into trait groups, within-group selection is by far the more powerful force in a uniform environment. In other words, there can be no between-group selection when there is only one trait group. In cases such as this, when the metapopulation and the trait group describe the same set of individuals, all selection takes place within-group and is focused at the level of the individual.

Recall that the second food sharing behavior, `reciprocalShareFoodWith`, allows forager agents to create, maintain, and apply their own memories of the interactions they have had with others. When acting as prospective recipients, foragers update personal lists of selfish and altruistic donors. These lists are consulted whenever one is asked to share excess food. A prospective donor will not share excess food with a prospective recipient that appears on its personal list of defectors (i.e., when the donor “remembers” that it was denied by the prospective recipient). Of course, a prospective donor will share excess food with those that appear on its personal list of cooperators (i.e., when the donor “remembers” that it received aid from the prospective recipient in the past).

Theoretically, the fact that a prospective donor has the ability to refuse to share with an agent it recognizes as a cheater allows altruistic foragers to protect themselves from being exploited after as few as one interaction. However, this one interaction must take the form of an altruistic prospective recipient asking a selfish prospective donor for food. Because information used in updating memory is passed unilaterally (from donor to recipient) rather than bilaterally (from Player 1 to Player 2 *and* from Player 2 to Player 1), this memory system differs somewhat from the strategies used in the iterated Prisoner’s Dilemma (Axelrod 1980a, b). In other words, updating one’s memory in SHARE requires *a certain type* of interaction (asking for food as a prospective recipient) rather than just *an* interaction (participation as either the donor or the recipient). Because a forager must ask another for food before it gains information that can be used in future interactions with that individual, it is possible for social cheaters to take advantage of altruistic foragers for an extended period, even in cases where all foragers possess personal memories. For example, a selfish forager could repeatedly and indefinitely receive aid from an altruist as long as that altruist never asks the selfish forager for help.

Once a selfish forager refuses to share food with an altruist, however, the cheater can expect to receive no further benefits from that jilted hominin agent.

To gain any benefit from personal memory, then, an altruistic forager must use it to refuse social cheaters. But this only occurs when an altruistic forager is asked to share with a selfish forager that it recognizes as a cheater. In other words, *memory benefits foragers only in interactions where they can deny a forager that previously refused them.* Under conditions that facilitate high frequencies of this type of interaction, memory is invaluable to food sharers because it is used to avoid a large number of sharing events that would be detrimental to altruists and beneficial to social cheaters. However, when this particular type of interaction is rare—if altruists rarely interact with selfish foragers that have previously denied them—stored information is far less valuable. Strategies that retain information for later use cannot be used to their full potential if that information is never utilized. In other words, regardless of its accuracy, *unrecalled* information is of no value. Thus, one should expect the success of the altruistic **`reciprocalShareFoodWith`** allele to surpass that of the simpler altruistic **`shareFoodWith`** allele only under environmental conditions that increase the frequency at which selfish foragers proposition the very same altruists they previously denied. This requires a scenario that facilitates a large number of repeated pair-wise interactions.

By tracking the number and type of interactions between altruistic donors and prospective recipients, it is possible to test whether the failure of reciprocal altruism in this case is indeed due to a lack of repeated interactions. Figure 5.2 provides the cumulative altruistic interaction history of one simulation run (Patch Size = 30, Gap Size

= 0). Of the nearly 300 interactions in which an altruistic forager functioned as the prospective donor, the vast majority (*n* = 175) resulted in the altruist sharing its excess food with an unknown forager. In this run, altruists refused to share with recognized cheaters only about 60 times and agreed to share with foragers they recognized as altruists only about 35 times. It is obvious from this figure that the largest proportion of cumulative altruistic donor interactions involves unknown foragers (approximately 65%), many of which are social cheaters and some of which could even be repeat offenders. Interactions in which altruistic foragers used memory to protect themselves accounts for only 20% of the total. This relatively low frequency of interactions equates to an equally low value for the information retained by foragers.

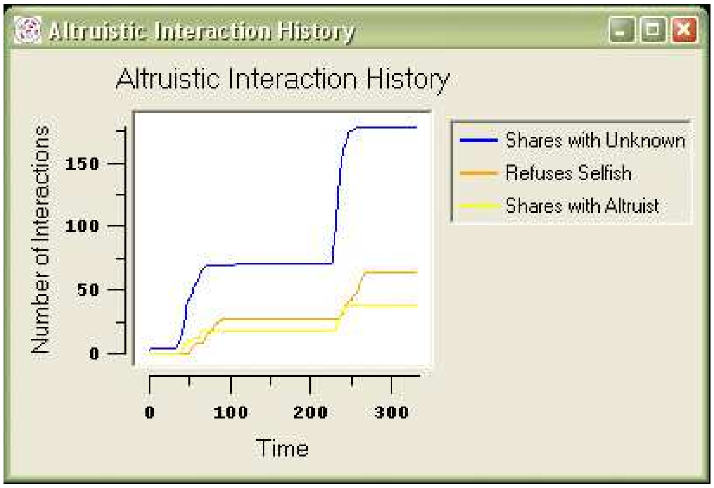


Figure 5.2. The cumulative altruistic interaction history of a simulation run in a uniform environment (Patch Size 30, Gap Size 0, selfish allele evolved to fixation in the 290th time step). The most common interaction for altruists is to share with individuals whom they have never asked for help.

Data collected from the altruistic interaction histories of all 30 **`reciprocalShareFoodWith`** simulation runs demonstrate a similar trend (Tables 5.3 and 5.4). In all of these runs, the most common interaction for an altruistic donor is to share with an unknown recipient, who may be either selfish or altruistic. The average proportion of interactions in which altruistic donors shared with unknown recipients for the 27 simulation runs in which selfish allele evolved to fixation (56.0%) is only slightly higher than both that for all 30 runs (55.9%) and that for the three runs in which the altruistic allele evolved to fixation (55.3%). The second most common interaction for an altruistic donor in a mega-patch is to refuse to share with a known cheater. As one might expect, the average proportion of interactions in which altruistic donors denied known cheaters is highest for the runs in which the altruistic allele evolved to fixation (33.5%), but this is only slightly higher than that for the runs in which the selfish allele evolved to fixation (32.9%). The fact that there is not a greater disparity between these average probabilities when comparing runs in which the selfish allele evolved to fixation to those in which the altruistic allele evolved to fixation is surprising and interesting. This might be a function of inappropriately averaging unique histories, but it is more likely a sign that the ultimate success of either allele hinges on just a small proportion of the total interactions. The latter is a provocative proposition worthy of further investigation with a greater sample size of simulation runs.

Sharing Behavior	# Altruistic Fix	Total Runs	% Altruistic Fix
`shareFoodWith`	2	30	7
`reciprocalShareFoodWith`	3	30	10
`omniscientShareFoodWith`	17	30	57

Table 5.3. Population results from mixed populations in uniform environments. # Altruistic Fix = number of simulation runs in which the altruistic allele evolved to fixation. Total Runs = total number of simulation runs. % Altruistic Fix = percentage of simulation runs in which the altruistic allele evolved to fixation. Row 2 is expanded in Table 5.4.

`reciprocalShareFoodWith`	ASU	ARS	ASA
Selfish evolved to fixation (n = 27)	0.560 (0.060)	0.329 (0.069)	0.111 (0.029)
Altruist evolved to fixation (n = 3)	0.553 (0.040)	0.335 (0.076)	0.112 (0.038)
Total runs (n = 30)	0.559 (0.058)	0.330 (0.069)	0.111 (0.029)

Table 5.4. Summary statistics on altruistic interaction histories of 30 simulation runs with mixed populations of selfish and altruistic reciprocal food sharers in uniform environments. Cell values report the mean (and standard deviation) of the cumulative frequencies of three particular types of agent interactions (ASU = altruist shares with unknown recipient. ARS = altruist refuses known selfish. ASA = altruist shares with known altruist).

According to the results of this experiment, while the uniform mega-patch does facilitate repeated interactions, it does not provide a scenario conducive to type of symmetrical relationships that reward altruists for memory. This is demonstrated by the fact that altruistic versions of the two least sophisticated food sharing alleles experienced comparable levels of success. Although more sophisticated than **`sharefoodwith`**, which evolved to fixation in only 2 or 30 runs (7%), the altruistic **`reciprocalShareFoodWith`** allele evolved to fixation in only 3 of 30 runs (10%). Further, of those three reciprocally altruistic populations, only one survived beyond the 5000 time step threshold. Thus, the selfish version of the **`reciprocalShareFoodWith`** allele was more successful than the altruistic counterpart in the vast majority (90%) of runs involving mixed populations in uniform environments. This is due in part to the fact that selfish foragers can reap the benefits of accepting food from altruists while rarely encountering those they have wronged in the past. If an altruistic donor rarely gets the chance to use stored information to avoid sharing valuable resources with an agent who has already refused to share with it in the past, that stored information is rendered nearly worthless. When the information stored is nearly worthless, as in the case discussed above, memory does little to improve one's position over those who have no memory at all.

The **`omniscientShareFoodWith`** strategy does not include personal memory, *per se*, but rather includes the ability to identify the phenotypic character of other foragers upon the first interaction between two "strangers." This means that, when employing **`omniscientShareFoodWith`**, each prospective donor is able to recognize its prospective recipient's phenotype without the benefit of information gathered individually from previous interactions. This ability substantially improves the position of those displaying the altruistic phenotype in three ways. First, by recognizing selfish prospective recipients for the cheats they are, altruists eliminate all of the debilitating personal costs they pay when they share their "hard earned" resources with social parasites. Second, altruists become the sole beneficiaries of all altruistic actions. Because they are the only ones who can receive shared food, the benefits conferred by food sharing events are concentrated among altruistic foragers only. Third, selfish foragers can no longer benefit from altruists when both are present in mixed populations. Together, all three have the combined effect of strengthening the fitness of altruists while simultaneously weakening that of the egoists.

Because **`omniscientShareFoodWith`** foragers possess a cultural tool for defining trait groups independently of the ecology, one should expect to see a different outcome with mixed populations of **`omniscientShareFoodWith`** foragers in uniform environments than we witnessed for the previous two food sharing methods. Namely, one should expect to see a sizable increase in the proportion of runs in which the altruistic allele evolves to fixation. Indeed, the altruistic **`omniscientShareFoodWith`** allele evolved to fixation in 17 of 30 (57%) runs of mixed populations in uniform environments. Though not a vast majority, this is a sizable increase over both of the less sophisticated food sharing behaviors. Because this occurred in a uniform environment, it is obvious that the increased success of this altruistic trait is directly related to the social sophistication of the food sharing strategy and not to ecological patchiness.

Summarizing the experiments in uniform environments

The results of these experiments with uniform environments demonstrate that pure populations of altruistic food sharers are quantitatively more successful than pure populations of selfish non-sharers in uniform environments. This is due to the fact that altruists provide a public good even though they pay an individual cost for doing so. These experiments also demonstrate that simple altruists do not fare as well in mixed populations as they do in pure populations because social cheaters are able to take advantage of their generosity without ever repaying the associated costs. This is exactly what we should expect of biologically altruistic traits, which must benefit the group's fitness at a cost to an actor's individual fitness. It is also worth noting here that the only social scenario in which altruists enjoyed regular success in uniform environments was when they could protect themselves from engaging in detrimental unilateral exchanges by recognizing the phenotypic tags of each prospective recipient from their very first interaction. The increased social sophistication of the **`omniscientShareFoodWith`** strategy was sufficient to weaken within-group selection and strengthen between-group selection, even when mixed populations of foragers inhabited one uniform megapatch. We shall return to this point in a longer discussion below.

5.3 Patchiness and prosociality

> "To understand the direction human social evolution has taken it is necessary to examine the ecological context in which it has occurred." [Foley and Lee 1996:57-58]

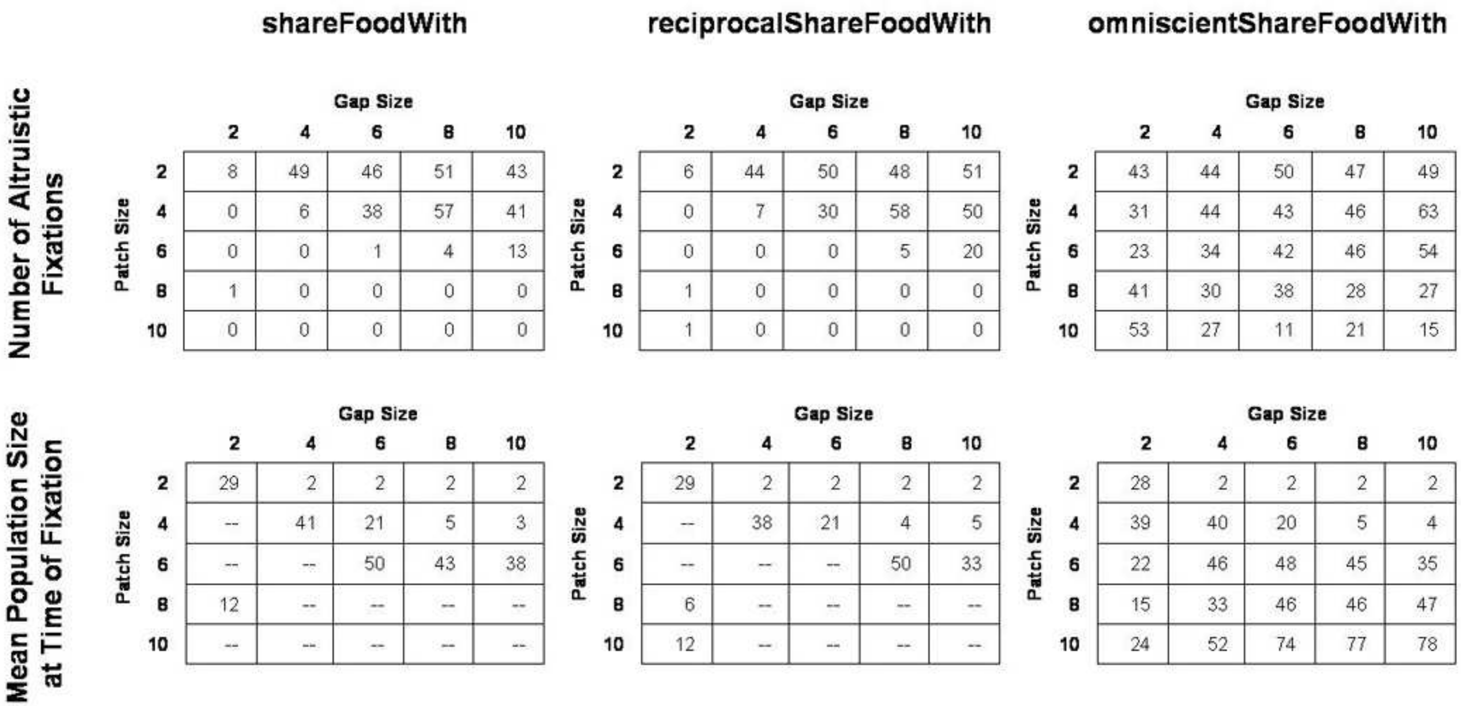
Now that we have sufficiently demonstrated that the food sharing behaviors in SHARE are biologically altruistic and outlined how the various food sharing strategies differ from one another, it is time to address one of the major research questions: How do variations in resource patchiness *and* cultural sophistication affect the evolution of food sharing in mixed populations of hominin foragers? The large suite of 30,300 simulation runs described in this section provides the most comprehensive look at SHARE's socio-ecological parameter space. For each of the three discrete food sharing methods, two possible settings for Predation Danger, and two possible settings for Meat Probability, 101 runs were executed within each of 25 possible Patch Size, Gap Size combinations (3 * 2 * 2 * 101 * 25 = 30,300). I initialized each of these runs with the default parameter settings (see Figure 4.1) and one of 101 random number seeds (see Appendix A). In addition to investigating the effects of variation in ecological patchiness and in social savvy, I also used this baseline suite to test the effects of predation danger and the presence of a temporally and spatially unreliable source of food (i.e., meat provided by carcasses). Thus, 30,300 runs are divided equally among four different scenarios: (1) neither carcasses nor danger is included; (2) carcasses are present, but danger is not; (3) no carcasses, but danger is present; and (4) carcasses and danger are both present. As was the case in the pilot study (Premo 2005), the population genetic results collected form this large parameter sweep display a distinctive pattern.

No carcasses or predation danger

This section summarizes the population genetic results of 7575 runs of SHARE, none of which included the presence of carcasses or predation danger. In considering the first and second columns of Figure 5.3, the effect of ecological patchiness is readily discernible—the altruistic alleles evolve to fixation predominantly in intermediate Patch Sizes (4 and 6) and intermediate-to-large Gap Sizes (4, 6, 8, and10). This pattern clearly echoes that which Premo (2005) found previously for food sharing and that which Pepper and Smuts (2000) found for feeding restraint and alarm calling, but why?

Recall that the evolution of altruism requires strong between-group selection. The strength of between-group selection depends largely upon how genetic variation is partitioned within and among trait groups. Resource patchiness can structure the genetic variation of a population in a variety of ways, many of which weaken between-group selection. For example, small patches succeed in creating trait groups that are too ephemeral to compete as evolutionarily meaningful groups; large patches support equally large trait groups that often contain a mix of forager types; and small gaps between patches do not pose deterrents for migration. Each of these conditions effectively increases both within-group heterogeneity and between-group homogeneity. As the first two columns of Figure 5.3 illustrate, between these extremes exists a *transitional* range of resource patchiness that provides the structure necessary to form internally homogenous and externally heterogeneous trait groups. It is under this rather restricted range of ecological conditions, which I will hereafter refer to as the transitional range, that ecological patchiness enjoys its most influential between-group selective power. Though theoretically possible, it is far less likely that altruistic versions of **`shareFoodWith`** and **`reciprocalShareFoodWith`** will evolve to fixation in ecological settings outside of this transitional range of resource patchiness.

The fact that altruistic alleles evolve to fixation less frequently than their selfish counterparts, even within the transitional range of patchiness, should not detract from the finding that ecological heterogeneity can effectively structure socially-inept foragers into evolutionarily meaningful trait groups. Here, it is important to remember that the significance of an event need not be directly related to its probability, for rare events often precipitate profound consequences. The quantitative results presented in these figures can also be interpreted at the qualitative level of presence versus absence. In other words, whether the altruistic allele evolved to fixation in 23 or 44 of the possible 101 simulation runs in any given patchiness level is immaterial. In this sense, what is important is that the altruistic allele evolved to fixation at all.



Number of Altruistic Fixations

shareFoodWith

Patch Size	Gap Size				
	2	4	6	8	10
2	8	49	46	51	43
4	0	6	38	57	41
6	0	0	1	4	13
8	1	0	0	0	0
10	0	0	0	0	0

reciprocalShareFoodWith

Patch Size	Gap Size				
	2	4	6	8	10
2	6	44	50	48	51
4	0	7	30	58	50
6	0	0	0	5	20
8	1	0	0	0	0
10	1	0	0	0	0

omniscientShareFoodWith

Patch Size	Gap Size				
	2	4	6	8	10
2	43	44	50	47	49
4	31	44	43	46	63
6	23	34	42	46	54
8	41	30	38	28	27
10	53	27	11	21	15

Mean Population Size at Time of Fixation

shareFoodWith

Patch Size	Gap Size				
	2	4	6	8	10
2	29	2	2	2	2
4	--	41	21	5	3
6	--	--	50	43	38
8	12	--	--	--	--
10	--	--	--	--	--

reciprocalShareFoodWith

Patch Size	Gap Size				
	2	4	6	8	10
2	29	2	2	2	2
4	--	38	21	4	5
6	--	--	--	50	33
8	6	--	--	--	--
10	12	--	--	--	--

omniscientShareFoodWith

Patch Size	Gap Size				
	2	4	6	8	10
2	28	2	2	2	2
4	39	40	20	5	4
6	22	46	48	45	35
8	15	33	46	46	47
10	24	52	74	77	78

Figure 5.3. Summary of population genetic results by food sharing strategy from runs that included neither carcasses nor predation danger. Tables in the top row provide the number of runs (out of a possible 101) in which the altruistic allele evolved to fixation for each possible patchiness scenario. Tables in the bottom row provide the mean population size at time of altruistic allele fixation; single digit values in these tables are indicative of non-viable populations.

Altruistic `shareFoodWith` and `reciprocalShareFoodWith` alleles evolve to fixation almost exclusively in small-to-medium sized patches (i.e., the upper right corner of the tables). However, a more subtle effect of ecological patchiness becomes apparent when one examines the average population size at time of allele fixation within the ecological range in which altruistic alleles are seemingly so successful. The first thing to point out is that half of these patchiness levels (Patch Size, Gap Size = 2, 4; 2, 6; 2, 8; 2, 10; 4, 8; and 4, 10) —those located in the upper right corner of the tables—do not support "viable" populations. I arbitrarily define a viable population as being at least 25% as large as the starting population to distinguish populations on their way to extinction from those that would be more likely to continue indefinitely if the simulation were continued past the point of allele fixation. It is obvious from Figure 5.3 that many of the values for "average population size at time of fixation" are well below 10. Low averages for population size at time of fixation imply that in a large number of cases in which the altruistic allele evolved to fixation, altruistic individuals "won out" *not* because they handily outcompeted selfish individuals or because they were selected over their egoist counterparts in any way, but simply because they happened to die out *less quickly*. In other words, altruistic populations composed of only two or three individuals would have also gone extinct had many of these runs been continued for only 10 – 20 additional time steps after the time of allele fixation (note: this was verified for a number of cases).

In addition, for these same ecological scenarios the number of simulation runs in which the altruistic allele evolved to fixation is near 50. The fact that the altruistic and selfish versions both evolve to fixation in roughly half of the 101 runs supports my hunch that each has an equal chance of fixing in these patchiness levels. Not only do very low average population sizes at time of fixation (regardless of whether the "successful" allele is altruistic or selfish) show that populations were going extinct in these areas, but low values for "average duration until fixation" indicate that these food resource distributions do not support forager populations for very long, usually less than the maximum life span of any single hominin forager. Thus, the large number of simulation runs in which the altruistic allele quickly evolves to fixation in very small populations in these particular patchiness levels are not as informative as those that are accompanied by much larger average population sizes at time of fixation. For this reason, data from the ecological scenarios that fall in the upper right hand corner of the patchiness parameter space are not considered equivalent to those from ecological conditions that support viable populations at time of allele fixation.

Patchiness levels that support viable altruistic populations are found along the boundary between uninhabitable levels (i.e., the upper right half of the tables) and those in which selfish alleles are almost always successful (i.e., the lower left half of the tables). These results can be found along the transitional diagonal, which is defined by the following patchiness levels: Patch Size, Gap Size = 2, 2; 4, 4; 4, 6; 6, 8; 6, 10). Along the transitional diagonal, the averages for population size at time of fixation are all greater than 20 as opposed to less than 6 and the averages for duration before fixation are at least ten times greater than those in the uninhabitable region of ecological patchiness.

The data collected from the 2525 runs involving **`omniscientShareFoodWith`** paint a different picture than those provided by either of the less sophisticated sharing strategies. Although these results bear the signature of the same uninhabitable region, they clearly show that altruistic versions of the **`omniscientShareFoodWith`** allele evolve to fixation more frequently and over a much larger area of the ecological parameter space. In fact, with the aid of this more sophisticated cultural behavior, the altruistic **`omniscientShareFoodWith`** allele evolves quite often not just in those areas along the transitional diagonal but also in each of the patchiness levels that can support viable populations. By refusing to share with individuals whom they recognize as non-cooperators, altruistic donors use their sense of prospective recipients' phenotypes to protect themselves and avoid suffering from the "sucker's payoff." These results illustrate an inverse relationship between ecological selective power and behavioral sophistication: *ecological patchiness plays only a minor role in the evolution of altruism when more sophisticated strategies are involved.*

A small number of **`omniscientShareFoodWith`** simulation runs have been deemed *incomplete*. In an incomplete run, neither allele had yet evolved to fixation after 25,000 time steps. Interestingly, the incomplete cases consistently occur in a region of the parameter space characterized by large patches and large gaps (lower right corner). Further study is required to assess whether selfish and altruistic **`omniscientShareFoodWith`** behaviors can act as Evolutionary Stable Strategies (ESS) in these patchiness levels.

Some of the results obtained from these baseline runs are surprising. The fact that even the least sophisticated form of food sharing (**`shareFoodWith`**) regularly evolved to fixation in at least one region of the ecological parameter space, 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. This scenario serves as the null model for our behavioral reconstructions of early hominin sharing behavior. It demonstrates that altruistic traits can regularly evolve to fixation in lieu of complex social behaviors *if* certain ecological conditions are present. It is no coincidence that simple altruistic food sharing strategies evolved to fixation most consistently in the transitional range of ecological patchiness. Less surprising, but still interesting, is the observation that the selective influence of ecological patchiness is inversely related to the social sophistication of food sharing strategy employed by foragers. The first and second columns of Figure 5.3 show that resource patchiness played a significant role in the evolution of the socially sophomoric food sharing behaviors (**`shareFoodWith`** and **`reciprocalShareFoodWith`**), both of which evolved to fixation only under the relatively restricted range of transitional ecological conditions. In contrast, the third column of Figure 5.3 shows that resource patchiness played an insignificant role in the case of the socially sophisticated **`omniscientShareFoodWith`**, which spread to fixation at least once under each and every ecological condition capable of supporting a viable population. Note that the frequencies at which the altruistic version of **`omniscientShareFoodWith`** evolved to fixation are greater than the others' frequencies, even in the transitional range of resource patchiness, and that altruistic **`omniscientShareFoodWith`** alleles evolved to fixation more frequently in a much larger range of ecological conditions than did either of the less sophisticated altruistic alleles.

Here, we see that sophisticated cultural rules can function like ecological patchiness in subdividing a metapopulation into evolutionarily meaningful trait groups.

Adding animal carcasses

Woodland patches are composed of plant agents. Plant agents represent a temporally and spatially reliable food resource. In every SHARE run, plant locations do not change through simulated time. Though reliable, woodland resources do not provide large amounts of energy per unit (maximum plant energy = 10 units). In order to test what kind of impact a different type of food resource, like animal carcasses, might have on the evolution of the various food sharing behaviors in SHARE, I included meat agents in half of the baseline runs. Unlike the plant resource, these meat agents are temporally and spatially unreliable. That is carcasses appear "randomly" (i.e., with equal probability in each cell that does not already contain meat) through time and over space. Though unpredictable and therefore unreliable, carcasses can potentially provide much larger amounts of energy per unit (i.e., maximum energy is up to ten times greater than that of plants). A meat agent is also different from a plant agent in that its energy value *decreases* logistically. This means that the energetic value of a carcass depletes at a decreasing rate—relatively large proportions of the starting energy are lost in the first few times steps and increasingly smaller proportions are lost in subsequent time steps as the energy level converges on the theoretical minimum limit. Thus, meat agents represent potentially large windfalls of energy that are randomly distributed and deteriorate quickly.

I cannot directly address the idea that food sharing could not possibly have evolved before large and easily shared packages of food, like chunks of meat, were regularly obtainable by hominins with SHARE, because hominin agents are allowed to carry around the same maximum amount of energy regardless of from which type of resource it is procured. However, I hypothesize that the presence of meat will increase the fitness of food sharers, thereby expanding the basin of attraction for all of the altruistic alleles.

In the cases of **`shareFoodWith`** and **`reciprocalShareFoodWith`**, the results did not support this hypothesis (Figure 5.4). There is virtually no difference between the number of runs in which the altruistic version of the allele evolved to fixation in the absence of meat or in the presence of meat (the differences are less than 1% per 2525 runs) for each of these two behaviors. When the presence of meat did happen to change the results of SHARE it was only minimally and only in the case of **`omniscientShareFoodWith`**. The presence of meat increased the number of runs in which the altruistic version of the **`omniscientShareFoodWith`** allele evolves to fixation by just over 3%. There are a few possible reasons why the presence of meat did not have the expected effect on the evolution of altruistic food sharing in SHARE.

Number of Altruistic Fixations

shareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	2	57	48	55	47
4	0	0	21	43	59
6	0	0	2	2	6
8	0	0	0	0	1
10	1	0	0	0	0

reciprocalShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	4	52	47	58	56
4	0	3	30	52	44
6	0	0	2	6	4
8	0	0	1	0	2
10	2	0	0	0	0

omniscientShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	50	45	61	55	52
4	33	63	54	55	53
6	51	31	38	47	51
8	38	26	23	36	35
10	44	27	22	24	24

Mean Population Size at Time of Fixation

shareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	27	2	2	2	2
4	--	--	31	7	4
6	--	--	52	39	42
8	--	--	--	--	54
10	14	--	--	--	--

reciprocalShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	28	2	2	2	2
4	--	49	30	7	4
6	--	--	45	51	43
8	--	--	43	--	50
10	19	--	--	--	--

omniscientShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	33	3	2	2	2
4	43	44	32	8	4
6	27	47	50	49	43
8	17	39	45	52	50
10	29	52	70	79	79

Figure 5.4. Summary of population genetic results by food sharing strategy from runs that included carcasses but not predation danger. Tables in the top row provide the number of runs (out of a possible 101) in which the altruistic allele evolved to fixation for each possible patchiness scenario. Tables in the bottom row provide the mean population size at time of altruistic allele fixation; single digit values in these tables are indicative of non-viable populations.

First, the maximum limit of transportable food may be too low to allow big carcasses to be fully procured by individuals. This particular problem would only hold in instances when a relatively successful forager in possession of a large store of energy would have the opportunity to procure a recently deposited carcass. According to the relatively low maximum limit for stored energy, this forager would not be able to carry all of the energy it had procured (i.e., much would be "wasted"—not shareable with others and not procurable by others). This would be analogous to trying to pour 12 oz. of good bourbon into a shot glass. According to my observations of the model, this particular scenario does not occur very frequently, though it still might have a slight but important effect on the results.

Second, the probability that a carcass will be deposited per cell per time step might not be high enough to provide a resource that can be found very often by foragers. In other words, meat might be *so rare* in this implementation of SHARE that it is not a significant component of the model. After tracking the number of meat agents that were procured by foragers throughout a number of simulation runs, I can say that the probability I used in baseline runs does provide a resource that—while rare—is frequently found and utilized by hominin agents. Systematic sweeps of meat probability (while keeping forager population size constant) would provide a better idea of how it affects the total number of carcasses procured during an entire run. Nevertheless, the default value does provide a rare resource that is utilized less often than plant resources, which was the goal from the beginning.

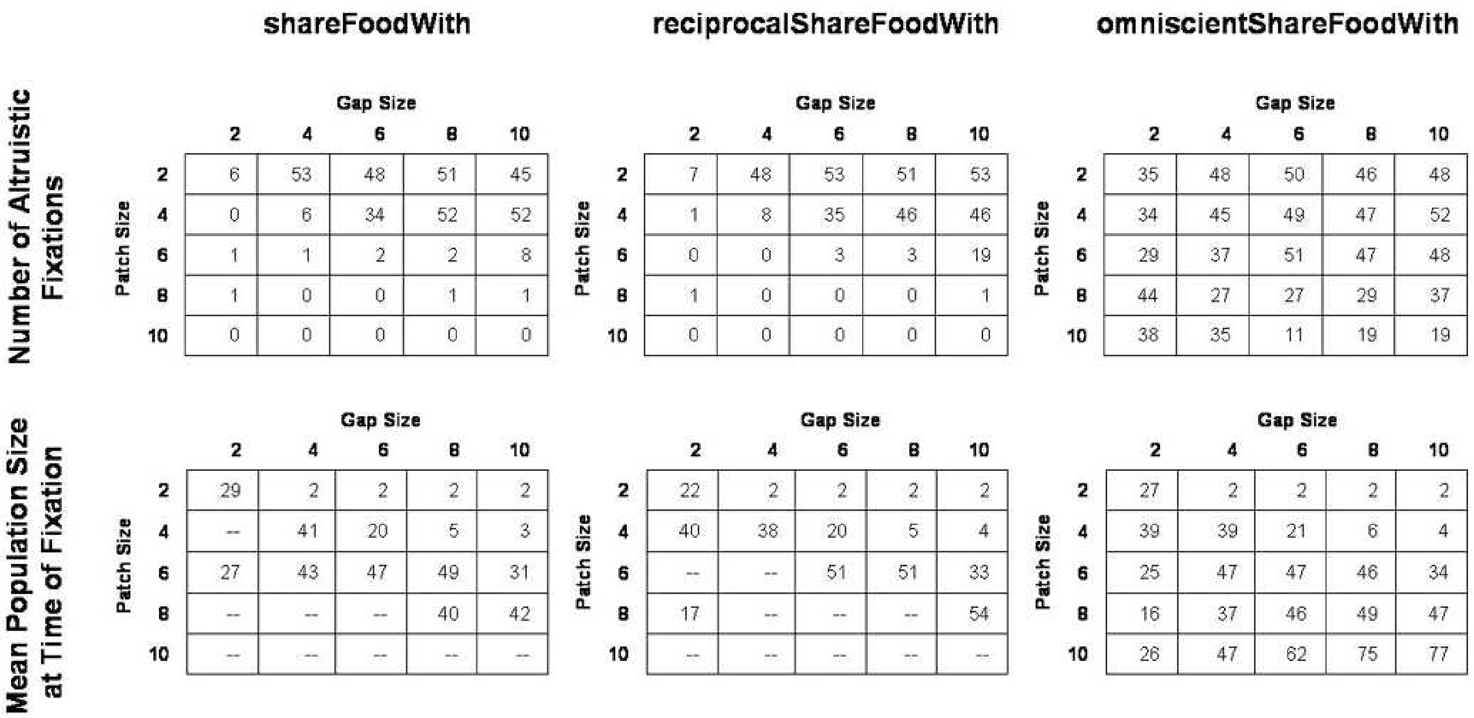
Third, there is the possibility that the presence of meat does not strongly affect the success of altruistic food sharing. If this is the case, then it provides an interesting counterexample to those very reconstructions that prompted the analytical modeling research presented in this dissertation. However, given the fact that package density—the characteristic of meat that might be most important to food sharing—is not considered in this version of SHARE, it would be ill-advised at this point to make a strong statement based on the findings that the presence of carcasses does not significantly aid altruistic food sharing in this agent-based model.

Having stated those caveats, however, there may be some interesting dynamics to talk about if we take a closer look at the results for the 2525 runs involving **`omniscientShareFoodWith`**. When carcasses were added to landscapes inhabited by these socially sophisticated foragers, the total number of runs in which the altruistic allele evolved to fixation increased by 3%. This implies that the presence of meat might have an appreciable effect on the evolution of food sharing when altruistic foragers possess the ability to protect themselves from sharing their large spoils with individuals that will not return the favor. Of course, as one's average energy store increases with the introduction of an additional food resource, so do the costs of sharing and (maybe more importantly) the benefits to cheaters. However, if altruists can successfully identify cheaters and abstain from sharing with them, these large benefits are at least concentrated among other altruists. If there is any truth to this preliminary observation, one could argue that if meat did play a vital role in facilitating the evolution of altruistic food sharing, as previous models of circumstance have implied, then the earliest food sharing behaviors must have been fairly complex (involving gossip, etc.) because the presence of meat did very little to aid the sophomoric sharing methods in this model. This implies that either the earliest sharing behaviors were socially sophisticated or that meat's role was not as important to the earliest version of hominin food sharing as some have argued. It is worth stating unequivocally that in SHARE the altruistic versions of all three food sharing behaviors evolve to fixation without the presence of meat and that there are still modeling issues that need to be worked out before I feel comfortable making more generalized statements about the how the presence of meat affects the success of altruistic food sharing traits. Nevertheless, these results have opened interesting tangential avenues of research.

Adding differential predation danger

The previous sub-sections describe only those 15,150 runs of the baseline model that do not include predation. Here, predation is included in the model under the assumption that open grassland habitat is three times (3x) more dangerous for hominin foragers than closed woodland habitat. That is, the probability that each hominin agent could become prey when in open grasslands is three times higher than when in closed woodlands. Given this assumption, one might hypothesize that those hominin agents that spend a larger proportion of their time in closed patches will have a higher fitness than those who spend comparatively more time in the riskier open environment. I hypothesized that a homogenous group of altruistic foragers would have to spend less time outside of closed habitats than a homogenous group of selfish foragers (and probably a heterogeneous group), because on average they would more evenly distribute limited food resources among all members through sharing. Because of this added benefit of sharing resources, in the presence of predation altruistic foragers should enjoy a higher fitness than they did in the scenarios without predation. In short, if membership in a group of altruistic food sharers reduces one's risk of falling prey to grassland predators, then altruism's basin of attraction should also expand in ecological scenarios that include differential predation.

The results collected from SHARE do not support this particular hypothesis (Figure 5.5). The difference in the total number of runs in which the altruistic allele evolved to fixation between the scenarios that include differential predation and the scenarios that do not is less than 1% in the case of each of the three sharing strategies. This implies that both the altruistic and selfish versions of the food sharing allele are affected similarly by predation, regardless of the cultural sophistication of the phenotypic behavior. Initially, this outcome was perplexing, but I can think of at least two possible reasons for why differential predation did not have the proposed effect on the evolution of altruism in SHARE.



Number of Altruistic Fixations

shareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	6	53	48	51	45
4	0	6	34	52	52
6	1	1	2	2	8
8	1	0	0	1	1
10	0	0	0	0	0

reciprocalShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	7	48	53	51	53
4	1	8	35	46	46
6	0	0	3	3	19
8	1	0	0	0	1
10	0	0	0	0	0

omniscientShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	35	48	50	46	48
4	34	45	49	47	52
6	29	37	51	47	48
8	44	27	27	29	37
10	38	35	11	19	19

Mean Population Size at Time of Fixation

shareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	29	2	2	2	2
4	--	41	20	5	3
6	27	43	47	49	31
8	--	--	--	40	42
10	--	--	--	--	--

reciprocalShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	22	2	2	2	2
4	40	38	20	5	4
6	--	--	51	51	33
8	17	--	--	--	54
10	--	--	--	--	--

omniscientShareFoodWith

Patch Size \ Gap Size	2	4	6	8	10
2	27	2	2	2	2
4	39	39	21	6	4
6	25	47	47	46	34
8	16	37	46	49	47
10	26	47	62	75	77

Figure 5.5. Summary of population genetic results by food sharing strategy from runs that included predation danger but not carcasses. Tables in the top row provide the number of runs (out of a possible 101) in which the altruistic allele evolved to fixation for each possible patchiness scenario. Tables in the bottom row provide the mean population size at time of altruistic allele fixation; single digit values in these tables are indicative of non-viable populations.

First, the value used for the probability of predation might be too low relative to the maximum forager life span. A very low value would render `predationDanger` an insignificant component of the model, because when very few individuals die of predation very little selective advantage is placed on any behavior that keeps foragers in safer places. This possibility could be tested further by running a suite of simulations in which `predatorDanger` is varied systematically from a lower value than that used here to one that is at least two orders of magnitude higher.

The second possibility is that sharing food with other altruistic "patchmates" simply *does not* allow altruists to enjoy the hypothesized secondary benefits associated with limiting the amount of time one spends in areas characterized by higher predation rates. In other words, my original thinking was incorrect, altruists and egoists actually spend equivalent amounts of time in dangerous open grasslands. It would be possible to test this alternative by comparing the average amount of time altruists spend within (or outside of) patches to the average amount of time selfish foragers spend within (or outside of) patches in pure and mixed populations in uniform and patchy environments.

These are two very different alternatives—the first is specific to my model parameter values and the latter may have something more general to say about food sharing in spatial models. Future experiments with SHARE will involve parameters sweeps designed to collect data that will be used to tease apart these possibilities. This remains an important issue to address with further research because the likelihood that a rather simple form of altruistic food sharing could have evolved to fixation is increased if it can be shown that the behavioral trait not only aids individuals with resources but also decreases the frequencies at which they fall prey to predators in an environment comprised of “safer” and “more dangerous” components. However, as it stands, predation has little or no selective impact in this implementation of SHARE.

Adding carcasses and predation

In the final 7575 runs, carcasses and predation were both included in the same ways that they were incorporated separately above. There appears to be no combinatorial effect of these two experimental variables, as the results of this suite of simulations closely approximates that in which only carcasses were included (Figure 5.6). Specifically, the only case in which the total number of runs in which the altruistic trait evolved to fixation is even minimally higher than that found in the sweep that involved neither carcasses nor predation is **`omniscientShareFoodWith`**. Again, this difference is approximately 3%, just as when carcasses were added without predation.

Number of Altruistic Fixations

	shareFoodWith					reciprocalShareFoodWith					omniscientShareFoodWith				
	Gap Size					Gap Size					Gap Size				
Patch Size	2	4	6	8	10	2	4	6	8	10	2	4	6	8	10
2	6	55	45	58	52	7	56	48	58	57	36	47	67	51	49
4	1	1	20	52	59	0	4	28	51	45	36	54	55	63	60
6	0	0	0	1	5	0	0	0	2	11	49	46	42	41	52
8	1	0	0	0	0	0	0	0	0	1	36	28	36	38	41
10	1	0	0	0	0	0	0	0	0	0	44	28	15	19	25

Mean Population Size at Time of Fixation

	shareFoodWith					reciprocalShareFoodWith					omniscientShareFoodWith				
	Gap Size					Gap Size					Gap Size				
Patch Size	2	4	6	8	10	2	4	6	8	10	2	4	6	8	10
2	32	2	2	2	2	33	3	2	2	2	32	2	2	2	2
4	35	42	26	8	5	--	36	33	7	4	43	44	32	8	4
6	--	--	--	58	45	--	--	--	60	40	27	48	50	49	41
8	11	--	--	--	--	--	--	--	--	45	19	34	45	50	50
10	21	--	--	--	--	--	--	--	--	--	28	49	71	79	78

Figure 5.6. Summary of population genetic results by food sharing strategy from runs that included carcasses and predation danger. Tables in the top row provide the number of runs (out of a possible 101) in which the altruistic allele evolved to fixation for each possible patchiness scenario. Tables in the bottom row provide the mean population size at time of altruistic allele fixation; single digit values in these tables are indicative of non-viable population.

5.4 Taking a closer look at reciprocal food sharing

At first blush, it should seem surprising that the altruistic version of `reciprocalShareFoodWith` did not evolve to fixation more frequently in the transitional range of patchiness and/or in a greater area of the ecological parameter space than its simpler counterpart. In iterated Prisoner's Dilemma experiments, the act of granting players the ability to remember past interactions often allows them to cultivate cooperation in scenarios in which players without memory cannot. Why was this not the case here; why are the `shareFoodWith` and `reciprocalShareFoodWith` results so similar? This section concerns itself with trying to answer that question.

Robert Trivers (1971) described how memory might affect the success of altruistic alleles in his seminal paper entitled "The Evolution of Reciprocal Altruism." According to his definition, reciprocal altruism can be viewed as a symbiosis between two partners who take turns helping each in the short term while helping themselves in the long term. Unlike byproduct mutualism, reciprocal altruism involves a time lag—one partner must provide a benefit to another and then wait an undisclosed duration for the altruistic act to be reciprocated by that recipient. This important time lag requires that recipients remember who helped them in the past so that they may repay those particular individuals when the chance to do so arises. For reciprocal altruism to evolve to fixation in a population, the "exchange" must also be characterized by an unequal benefit/cost ratio: the cost to the donor's fitness must be less than the benefit to that of the recipient. In environmental scenarios that facilitate this type of exchange, Trivers (1971:37) argues that reciprocal altruistic alleles will enjoy the greatest success when three conditions are met:

> "(1) when there are many such altruistic situations in the lifetime of the altruists, (2) when a given altruist repeatedly interacts with the same small set of individuals, and (3) when pairs of altruists are exposed 'symmetrically' to altruistic situations, that is, in such a way that the two are able to render roughly equivalent benefits to each other at roughly equivalent costs."

Further, Trivers argues that these conditions are in fact functions of larger biological parameters, three of which are important to the present discussion: length of life span, offspring dispersal rate, and degree of social interdependence. First, Trivers reasoned that the number of altruistic interactions in which an organism can be involved is directly related to the length of its lifetime. Thus, long-lived species should have a greater likelihood of satisfying the first condition, and so it follows that extending one's life span should increase the total number of altruistic interactions in which one can expect to be involved. Second, Trivers stated that reciprocal altruistic alleles would do best when individuals interact repeatedly within small groups. Of course, there is a greater chance that this will occur when offspring do not disperse quickly and/or far from their parents and siblings. Hence, species with low dispersal rates are more likely than those with high dispersal rates to interact with the same small set of spatially proximate individuals. Third, organisms that exhibit a high degree of mutual dependence (i.e., sociality) are more likely than nonsocial organisms to interact repeatedly with a small set of others (Trivers 1971). In the case of highly social organisms, interdependence on others for aid in defense, foraging, child rearing, etc. is a cohesive force that keeps small groups of individuals together for extended periods. This closeness greatly enhances the potential for repeated pair-wise interactions. Highly social species are also more likely to display the kind of consistency in subgroup membership that is necessary for the development of symmetrical altruistic relationships. The influence that these three biological parameters have on SHARE's results is discussed in more detail in the subsections that follow.

Regardless of conditions that may facilitate a greater number of repeated altruistic situations between a small set of individuals, the strategy that yields the highest individual fitness in all cases is to accept the benefits from altruistic neighbors and refuse to repay the favor. The time lag between *being helped* and *helping* makes defection an easily employable and effective strategy. However, Trivers had a good answer to the painfully obvious question: Why not cheat?

> "Selection will discriminate against the cheater if cheating has later adverse affects on his life which outweigh the benefit of not reciprocating. This may happen if the altruist responds to the cheating by curtailing all future possible altruistic gestures to this individual." [Trivers 1971:36]

In the act of curtailing all future altruistic gestures, an altruist must use personal memory in a different manner. We have already discussed how being able to store information about the individuals who have acted altruistically in the past is crucial to being able to repay them in the future, however, in order for an altruist to punish cheaters for accepting the benefits associated with altruistic acts without repaying the associated costs, it must remember the cheaters in addition to the altruists. Thus, memory is used not only to direct future altruistic acts towards individuals that are known cooperators, but also to punish cheaters by refusing to help them ever again. In scenarios where altruists are able to make cheaters pay a large cost for choosing to defect, cheating will be selected against. In this way memory plays a central role in the evolution of reciprocal altruism.

As Axelrod (1984) explains, memory is more likely to pay dividends when the "shadow of the future" is large—that is, when it is highly probable that there will be many (the exact number must be unknown to either player) interactions between the same two individuals through time. One might also think of this in terms of the *value* of the information contained within a player's memory. If a player repeatedly interacts with the same individual, it will often rely on its memory of previous actions to make decisions about whether to act altruistically or selfishly. When memory is used frequently, a high value is conferred upon stored information. On the other hand, when a player remembers the previous actions of individuals with whom it will never again interact, the stored information, though accurate, has a very low value because it will not be used. Therefore, as the number of interactions between players increases so too does the value of the information they remember and, hence, the general importance of memory to the evolution of reciprocal altruism. Conversely, memory plays a much-diminished role when the average number of repeated interactions between individuals is low; the ultimate example being a single iteration game in which two individuals do not interact more than once. Single iteration, or one-shot, games render memory worthless.

In order to assess why memory does not significantly enhance the evolution of reciprocal food sharing in SHARE, it was necessary to track individual interactions. Plots of the cumulative number of times that all altruistic foragers (blue) shared with an unknown forager, (yellow) shared with a known cooperator, and (orange) denied a known defector (see Figure 5.6) made it possible to study the relative frequency of all of the interactions in which the prospective donor was an altruist. Only this type of interaction was targeted for study because, when using binary phenotypes (0, 1) for selfish and altruistic alleles, only interactions in which altruists protect themselves by withholding resources from selfish foragers that previously refused to share with them distinguish `reciprocalShareFoodWith` from `shareFoodWith`. After tracking forager encounters during simulation runs that include reciprocity, it quickly became apparent that the vast majority of altruistic donors' interactions are with unknown recipients (foragers whom they have not yet asked for help). Interactions with known altruists (resulting in sharing) and known cheaters (resulting in withholding excess food) each occur far less frequently (Figure 5.7). Furthermore, except in cases where large patches are separated by small gaps, altruistic donors interact with known selfish recipients less frequently than with known altruists. The fact that in most simulation runs altruistic foragers enjoy very few opportunities to deny known selfish recipients—thereby conferring little value upon stored information—is the key to understanding why the basin of attraction for reciprocal food sharing is not significantly larger than that of `shareFoodWith`.

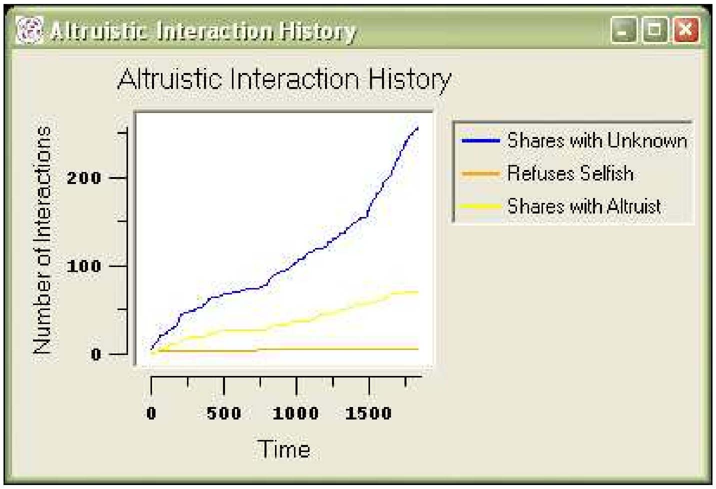


Figure 5.7. The cumulative altruistic interaction history of one simulation run in a heterogeneous environment (Patch Size 4, Gap Size 6, altruistic allele evolved to fixation in the 1849th time step). The most common interaction for altruists is to share with individuals whom they have never asked for help and the least common is to refuse known cheaters.

These observations raise a number of interesting questions. Is there a threshold in the proportion of times that altruistic foragers deny known defectors that will provide altruistic **`reciprocalShareFoodWith`** alleles an advantage that altruistic **`shareFoodWith`** alleles cannot enjoy? If so, what are some of the social and ecological factors that raise the proportion of these interactions past that threshold? How is the frequency of this type of interaction affected by increased rates of offspring dispersal? Answers to these questions might open new avenues of research on reciprocal sharing, memory, and spatial models. A couple of these avenues were explored here, and some results are presented below.

Extending life span

My initial hunch as to why the population genetic results of `reciprocalShareFoodWith` and `shareFoodWith` were so strikingly similar was that pairs of foragers did not often interact more than once—more specifically, that altruistic foragers did not get the opportunity to act on the information they gained concerning the identities of selfish foragers. If this hunch did indeed identify the problem—that altruistic foragers rarely got the chance to deny someone who had refused them in the past because symmetrical repeated interactions were relatively rare—then, according to the first of the biological parameters Trivers defined, increasing forager maximum life span might provide them a better chance of interacting with the same individuals more frequently. A reasonable hypothesis is that extending life spans would essentially extend Axelrod's "shadow of the future," thereby increasing the value of stored information and providing a stronger selection for reciprocal altruism.

Contrary to this hypothesis, however, extending forager life span did not significantly increase the number of pair-wise interactions between altruistic donors and recognized recipients. As you can see in the example illustrated in Figure 5.8, doubling the maximum forager lifetime did not significantly increase the proportion of interactions in which altruistic donors dealt with foragers they recognized (note: this is slightly different from pair-wise interactions), it simply allowed the longer-lived foragers to accumulate a larger number of total interactions. Quadrupling maximum lifetime from 100 to 400 time steps showed some of the desired effect—interactions with known agents comprise a larger proportion of the total interactions than in previous models. Yet, in this case, repeated symmetrical interactions are in the minority. Thus, in SHARE, an increase in the maximum life span of foragers does not significantly increase the proportion of times altruistic donors interact with recipients they recognize. So, after discovering that extending forager life span did not aid reciprocal altruism in SHARE, the question remains: Why are the **`shareFoodWith`** and the **`reciprocalShareFoodWith`** results so similar?

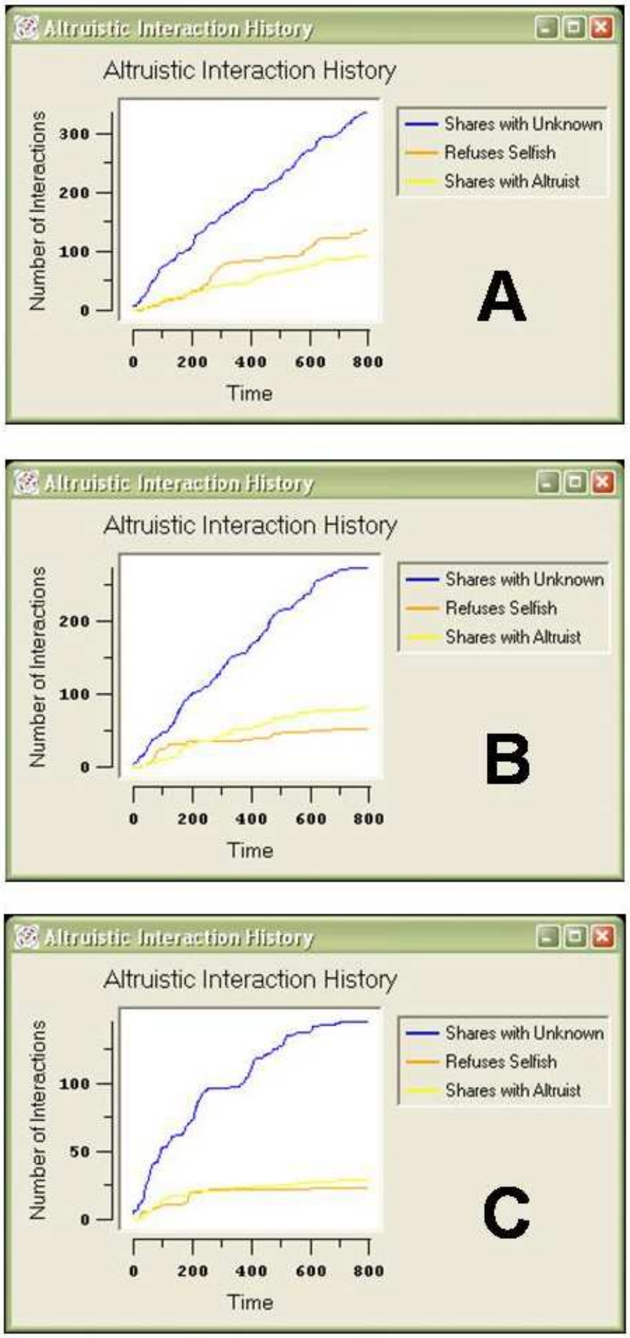


Figure 5.8. Tracking cumulative altruistic interaction histories while varying `lifeSpan`. A: `lifeSpan` = 400, B: `lifeSpan` = 200, C: `lifeSpan` = 100. All three simulations were initiated with Patch Size = 8, Gap Size = 6, and random number seed = 12345.

Increasing offspring dispersal rate

The second biological parameter discussed above has to do with offspring dispersal. *Ceteris paribus*, one can expect the number of repeated pair-wise interactions between individuals to decrease if offspring quickly disperse from their parent(s) and siblings. The default offspring dispersal method in SHARE is to place a newborn hominin agent in the nearest available cell to its parent. Slowing the rate of dispersal by placing offspring near their parents allows them the chance to begin to develop a history of social interactions. However, what happens if this assumption is relaxed and newborn hominin foragers are placed randomly in any patch of woodland resources? When random offspring dispersal is employed, it is far more likely that offspring they will begin their lives close to agents that are not their parents or siblings. So, if Trivers' second biological parameter is a significant condition for the evolution of reciprocal altruism, then we should expect to see a decrease in the success of the altruistic version of **`reciprocalShareFoodWith`** when random offspring dispersal is employed in the model. To test this hypothesis, I collected data from 101 runs of **`reciprocalShareFoodWith`** in three different patchiness scenarios—one in the transitional range and two below the transitional range. Table 5.5 compares the summary statistics for these 303 runs conducted with proximate offspring dispersal with 303 runs conducted with the same initial conditions but with random offspring dispersal.

Proximate Offspring Dispersal

Patch Size	Gap Size	# Altruistic Fix	Mean Pop Size	Mean Duration
4	6	30	21	1653
8	2	1	6	285
8	8	0	--	--

Random Offspring Dispersal

Patch Size	Gap Size	# Altruistic Fix	Mean Pop Size	Mean Duration
4	6	8	48	774
8	2	3	10	403
8	8	2	47	1253

Table 5.5. Summary statistics for 303 simulation runs involving proximate offspring dispersal (top) and an equal number of runs involving random offspring dispersal (bottom). # Altruistic Fix = total number of runs in which the altruistic allele evolved to fixation, Mean Pop Size = average population size at time of altruistic fixation, and Mean Duration = the average duration until altruistic allele fixation.

Let us compare the **`reciprocalShareFoodWith`** results between proximate and random offspring dispersal. In the transitional range of ecological patchiness (Patch Size = 4, Gap Size = 6), the total number of runs in which the altruistic trait evolves to fixation dropped substantially from 30 to 8 when offspring were dispersed randomly. There are no significant quantitative changes in either of the other patchiness levels under random dispersal—altruism is still quite unsuccessful in these regions of the ecological parameter space. At first glance, one might assume that these results support Trivers assertion that offspring dispersal has a measurable effect on the evolution of reciprocal altruism, and this could very well be the case. However, the fact that the simplest food sharing method also shows the same trend (38 with proximate offspring dispersal and 5 with random offspring dispersal in the transitional range of patchiness), even though it does not involve memory, illustrates the point that regardless of reciprocity, random offspring dispersal weakens between-group selective pressure by increasing the variation within trait groups while decreasing the variation between trait groups. To disentangle these two possible causes one could compare the average number of times that altruists reject known cheaters when offspring are dispersed randomly with the average number of times that altruists reject known cheaters when they are dispersed proximally. But because these types of interactions occur so infrequently in both conditions, I would argue that, contrary to Trivers' general statement, the differences we see here in the reciprocal food sharing strategy are not directly attributable to the increased rate of offspring dispersal, but rather to an increase in the rate of migration between trait groups.

Facilitating symmetrical relationships with continuous traits

Trivers (1971) also mentions that the establishment of symmetrical relationships is a key to the evolution of reciprocal altruism. A symmetrical relationship is one in which each partner benefits equally from their exchanges over the length of a reciprocal relationship. A relationship in which one partner (a scrounger) always benefits at the expense of another's generosity (a producer) is an asymmetrical relationship. The scrounger-producer relationship is not conducive to the evolution of reciprocal altruism.

As you may have already deduced, using binary values (0 or 1) to define a hominin agent's probability of sharing food makes scrounger-producer relationships possible in runs that include either **`shareFoodWith`** or **`reciprocalShareFoodWith`**. Selfish foragers with **`foodShare`** values of 0 can scrounge off of altruistic foragers with **`foodShare`** values of 1 indefinitely in the case of **`shareFoodWith`** and until the altruist asks the scrounging egoist for food in the case of **`reciproalShareFoodWith`**. As the results presented above (see Figures 5.7 and 5.8) clearly demonstrate, in simulations that include reciprocal food sharing, altruists share most frequently with foragers they do not "know" (i.e., have not asked for help). This implies that the asymmetrical scrounger-provider relationship is not only possible, but also present, and maybe even *pervasive*, in SHARE.

Symmetrical relationships require repeated pair-wise interactions, but they also require that partners alternate between the roles of prospective donor and prospective recipient. One way to try to facilitate symmetrical relationships is to use continuous values in place of binary values for **`foodShare`** phenotypes. In lieu of a technique for enforcing increased repeated interactions (like group living), one might get a population of foragers to engage in a greater number of symmetrical relationships if a large proportion of the total forager population has some chance of starting reciprocal relationships. When binary values are used for forager sharing phenotypes, only altruists can possibly begin reciprocal relationships. However, if the probability of sharing food is modeled as a continuous trait with real numbers ranging between zero and one, then every hominin agent in the population has at least a small chance of beginning reciprocal relationships. For instance, each first interaction with a potential donor that possesses extra food and a **`foodShare`** value of 0.5 has a 50% chance of resulting in an altruistic act which would begin a reciprocal relationship, as opposed to the 0% chance that holds if that same potential donor's **`foodShare`** value is 0. An increase in the number of reciprocating dyads does not guarantee a greater number of symmetrical relationships, but it makes them more likely.

An additional experiment was undertaken to test whether using continuous traits in place of discrete ones would influence the evolution of reciprocal food sharing in SHARE. Under the socio-ecological conditions of **`reciprocalShareFoodWith`** with a Patch Size = 4 and Gap Size = 6, I reran 101 simulation runs for each of five different combinations of selfish and altruistic **`foodShare`** values. The results of these 505 runs are presented directly below the results from the version of the model that uses two binary values for forager **`foodShare`** (Table 5.6). None of these runs included differential predation or the presence of carcasses. Of particular interest is the significant jump in the success of reciprocal food sharing between binary values (0, 1) and the next nearest continuous pair (0.1, 0.9). Allowing all foragers the chance to start a reciprocal relationship—even if that chance is very slight for half of the population—increases the number of runs in which the altruistic allele evolves to fixation by 150%.

Selfish **`foodShare`**	Altruistic **`foodShare`**	# Altruistic Fix	Mean Pop Size	Mean Duration
0	1	30	21	1653
0.1	0.9	45	20	1928
0.25	0.75	46	20	1928
0.49	0.51	58	21	1773
0	0.51	37	21	2300
0.49	1	51	23	1492

Table 5.6. Testing various combinations of continuous **`foodShare`** values with **`reciprocalShareFoodWith`** (Patch Size = 4, Gap Size = 6). # Altruistic Fix = number of runs (out of 101) in which the altruistic allele evolved to fixation, Mean Pop Size = average population size at time of fixation, and Mean Duration = average time of altruistic allele fixation.

The number of altruistic fixations continues to increase as the difference between selfish and altruistic phenotypes decreases. Interestingly, there is another significant jump in the success of the altruistic reciprocal trait when the continuous **`foodShare`** values for each type are nearly equivalent. When only 0.02 separates **`foodShare`** phenotypes, the altruistic allele enjoys its highest level of success. The altruistic **`foodShare`** value of 0.51 is lower in this case than in any other scenario, meaning that one would expect altruists with this value to miss out on a greater number of possible reciprocal partners (by denying them food the first time they meet them) than altruists with a **`foodShare`** value of 0.9. However, because the **`foodShare`** value of selfish foragers is nearly equivalent (0.49), altruists have about an equal chance of starting a reciprocal relationship with any forager they ask for help, regardless of its type. Because foragers do not often interact repeatedly with the same individuals in SHARE, this scenario of having roughly an equal chance of receiving food *and* starting a reciprocal relationship with anyone you run into might actually be more fertile for the evolution of reciprocity.

However, this scenario might be fertile for the evolution of food sharing even if memory is not involved in the method. When selfish and altruistic **`foodShare`** phenotypes are nearly equivalent and near 0.5, all foragers enjoy a reasonable shot of receiving food from each of the many individuals with which they interact only once or twice. Indeed, when this pair of continuous values were used for forager **`foodShare`** in 101 simulation runs with the simplest food sharing method, **`shareFoodWith`**, the number of runs in which the altruistic allele evolved to fixation also jumped from 38 (with binary values) to 53. This implies that using this particular combination of continuous traits significantly increases the likelihood that even unsophisticated food sharing behaviors will evolve to fixation in the transitional range of ecological patchiness.

Regardless of whether the **`foodShare`** values are binary or continuous, an altruist does not directly benefit by sharing with any agent it is likely not to interact with again. So, an alternative explanation for the apparent success of the (0.49, 0.51) setting might go like this: the low **`foodShare`** value of altruists in this case provides protection against frequently sharing resources with unknown recipients who turn out to be social cheaters. I test this hypothesis by rerunning a set of 101 runs with a **`foodShare`** combination of (0, 0.51). If the success of the altruistic allele is due entirely to the ability to limit the number of donations that altruistic foragers give to unknown recipients, then the results of this experiment should approximate those of the (0.49, 0.51) combination. Table 5.6 shows that this is not the case, the number of runs in which the altruistic allele evolves to fixation under this scenario is only 37, which is 36% fewer than was the case with the previous combination (0.49, 0.51). This implies that while lowering one's **`foodShare`** value helps protect altruists to some extent, they are most successful when they can also count on getting food from selfish donors some of the time.

This point is illustrated by the results of one final experiment, in which 101 simulations were run with the combination of (0.49, 1) to test whether altruists who could count on receiving food and starting reciprocal relationships with egoists 49% of the time, but could not stop themselves from sharing with all unknown foragers, would fare as well as those who had a better means of protecting themselves from sharing resources with foragers they were unlikely to meet again. The number of runs in which altruism became fixed in the population (51) is 38% larger than the previous combination, implying that reciprocal altruists do enjoy greater benefits from occasionally receiving food from “selfish” donors than from guarding against sharing with potential cheaters. In short, *according to this model of direct reciprocity with continuous traits, it is better to receive than not to give*. Obviously, gaining a more complete understanding of how continuous traits affect reciprocal altruism in SHARE will require collecting data from additional experiments with a larger set of selfish and altruistic **`foodShare`** combinations, something I plan to do in future work with this agent-based model.

Summary

It is important to note that researchers currently reconstruct Plio-Pleistocene hominin forager groups as small, cohesive bands. Although an average group size is impossible to predict, most would agree that the groups were small enough to facilitate many repeated pair-wise interactions among the same individuals, thereby facilitating symmetrical relationships that cast a “long shadow of the future” across early hominin food sharing interactions. Because SHARE does not force foragers to stay together in small groups (beyond the grouping structured by ecological patchiness), this model is not the best place to compare a reciprocal altruistic strategy with one that does not involve memory. This is due to the fact that memory is worthless in social scenarios that are characterized by a series of single iteration interactions, and this is exactly the scenario that occurs in SHARE most often. Thus, because the specific type of interaction in which a selfish forager asks an altruist that it previously jilted rarely occurs in SHARE (though it might have occurred more in the real world) we should not expect the memory afforded by **`reciprocalShareFoodWith`** to provide a significant benefit over the simpler **`shareFoodWith`** strategy.

Following Trivers' (1971) suggestions, a number of measures were taken to increase the likelihood that foragers would interact with the same individuals more frequently, but in all cases **`reciprocalShareFoodWith`** results did not differ significantly from **`shareFoodWith`** results. This implies that memory has little value in SHARE. I suspect that if group living were included in the model (e.g., by requiring hominin agents to remain within a minimal distance of at least three or four other hominins rather than allowing them to move to the highest possible food source), Trivers' biological parameters would have a more pronounced affect on the evolution of reciprocity. That is, if hominin agents lived in small groups maintained by cultural bonds rather than ecological circumstance, then the parameters tested in this section would have a greater effect on the selection of the altruistic strategy that involves memory than they would on the selection of the simple altruistic strategy that does not.

However, based on the findings of this research with solitary foragers, I argue that the biological parameters Trivers laid out in his 1971 paper should not be viewed as equivalents. As we have seen in the experiments with reciprocal altruism, without a high degree of mutual interdependence (sociality), variables like length of life span and offspring dispersal rate do not display the hypothesized effects, and alternative designs to facilitate symmetrical relationships through continuous traits have ambiguous results. A future version of SHARE, which will include an explicit definition of sociality in the form of group-living, will be used to test the interesting hypothesis that a socio-economic mechanism like central place foraging might be a necessary precondition to the evolution of food sharing based on direct reciprocity.

5.5 Assessing the effect of non-local information

All of the experiments described to this point include hominin agents that know nothing of the “global” distribution of food resources in their environment. In each of these simulation runs, when a forager cannot find adequate food supplies in its immediate surroundings, it embarks on a random walk because it lacks the global knowledge that might otherwise help in finding food outside of its local environment. Although random walks might be suitable for finding temporally and spatially unpredictable resources, they are not efficient methods for discovering sessile food patches, especially when they happen to be separated by large gaps. Thus, it is not surprising that many foragers starve to death in open habitat (i.e., gaps) while in the process of randomly searching for a patch. Because both selfish and altruistic foragers use random walks, this selective pressure does not directly favor one allele over the other—both types of hominin agents die of starvation in open habitat. Thus, gaps present spatial obstacles because they cannot be traversed easily or consistently with random walks. Although this characteristic does not directly benefit altruistic *individuals*, it does provide an ecological scenario in which between-group selection is strengthened at the expense of within-group selection, thereby favoring altruistic *groups*.

Random walks do not often result in successful migrations between patches. Initially, this might seem detrimental to all foragers—even altruists need to migrate to new patches once in a while. Indeed, a limited number of successful migrations are necessary for any trait (selfish or altruistic) to export itself to additional resources (Wilson and Dugatkin 1997). However, an overall increase in the number of migrations between patches increases the homogeneity among trait groups and the heterogeneity within trait groups, both of which strengthen within-group selection. In other words, because foragers are more likely to find new patches if they know where to look, a nonrandom search strategy results in a less viscous, more freely-mixing population, and trait groups on average will have equal frequencies of both forager types (more heterogeneous within groups) and there will be fewer distinctions between the compositions of the trait groups (more homogeneous among trait groups). Both of these characteristics favor within-group selection and selfish traits.

Given this relationship between migration rate and the relative strengths of within-group and between-group selection, one would hypothesize that nonrandom search methods between patches would decrease the frequency at which altruistic traits evolve to fixation in mixed populations. In order to test this hypothesis I ran 909 simulation runs, divided equally among the three usual patchiness levels and all three food sharing behaviors, this time equipping foragers with a nonrandom search strategy in place of the random walk method.

If one imagines a continuum of search strategies, random walks anchor the least sophisticated end and perfect knowledge of all patch locations represents the most sophisticated end. I chose to use a nonrandom search strategy that falls somewhere between the two poles of this spectrum. Foragers do not know the exact location of food patches but they do have an understanding of the global spatial structure of the resources. That is, they know that a most reliable strategy to use in this distribution of regularly shaped and regularly spaced woodland patches is to travel continuously in one "diagonal" direction

To test how this nonrandom search method affects the evolution of food sharing, one of four diagonal directions (i.e., SW, SE, NW, NE) was randomly assigned to each forager (regardless of forager type). A forager will travel in this direction in any situation that would have required a random walk in the previous version of the model. The results obtained for three patchiness levels provide some interesting insights into the effects of global spatial knowledge when compared with the same results from the version of the model that included random walks (Table 5.7).

Sharing Behavior	Search Method	# Altruistic Fix	Mean Pop Size	Mean Duration
`shareFoodWith`	Random	38	21	1948
`reciprocalShareFoodWith`	Random	30	21	1653
`omniscientShareFoodWith`	Random	43	20	1868
`shareFoodWith`	Diagonal	0	6	285
`reciprocalShareFoodWith`	Diagonal	0	47	1253
`omniscientShareFoodWith`	Diagonal	19	55	2249

Table 5.7. Assessing the effect of the nonrandom search strategy in population-level genetic results of simulations that included patchy conditions (Patch Size = 4, Gap Size = 6). # Altruistic Fix = number of runs (out of 101) in which the altruistic allele evolved to fixation; Mean Pop Size = average population size at time of fixation; and Mean Duration = average time of altruistic allele fixation.

Table 5.7 demonstrates that the nonrandom search method has a significant effect on the evolutionary success of altruism in the transitional range of ecological patchiness in the cases of all three sharing rules. Note that in **`shareFoodWith`** and **`reciprocalShareFoodWith`** the numbers of runs in which the altruistic allele evolves to fixation dropped from 38 and 30, respectively, to zero. Even in the case of **`omniscientShareFoodWith`**, the number of runs in which the altruistic allele evolves to fixation decreased by 56% from 43 to 19. Given this significant drop it is apparent that the nonrandom search method has increased the number of successful migrations to the extent that between-group selection is heavily outweighed by within-group selection in the cases of **`shareFoodWith`** and **`reciprocalShareFoodWith`**. The very patchiness level that supported the highest number of viable altruistic populations can no longer support any. It is also interesting that **`omniscientShareFoodWith`** is so significantly hampered; this is an unexpected result. Although altruists cannot be taken advantage of by invading selfish cheaters in the case of **`omniscientShareFoodWith`**, increased migration rates might make it more difficult for homogenous groups of altruists to share with each other, thereby squandering the benefits they once conferred only on each other.

In a more homogeneous ecological scenario, the effect of the nonrandom search strategy is not so dramatic, and the results are qualitatively similar to those yielded by the random walk method (Table 5.8). Because small gaps can be traversed rather easily, the nonrandom search method does not provide much of an advantage over the random walk method in this case. For this reason, we should not be surprised that the results are comparable. Instead, we need to recognize that the impact of global spatial knowledge varies with ecological parameters like Gap Size. Small gaps can be navigated successfully by random methods, but larger ones pose more significant obstacles. Thus, one can expect the importance of resource location information to increase as Gap Size increases—up to the point at which gaps become too large to cross regardless of the search method.

Sharing Behavior	Search Method	# Altruistic Fix	Mean Pop Size	Mean Duration
`shareFoodWith`	Random	1	12	288
`reciprocalShareFoodWith`	Random	1	6	285
`omniscientShareFoodWith`	Random	41	15	1482
`shareFoodWith`	Diagonal	0	--	--
`reciprocalShareFoodWith`	Diagonal	2	3	650
`omniscientShareFoodWith`	Diagonal	52	9	1291

Table 5.8. Assessing the effect of the nonrandom search strategy in population-level genetic results of simulations that included relatively homogeneous ecological conditions (Patch Size = 8, Gap Size =2). # Altruistic Fix = number of runs (out of 101) in which the altruistic allele evolved to fixation; Mean Pop Size = average population size at time of fixation; and Mean Duration = average time of altruistic allele fixation.

This principle is further illustrated by the results from the largest Gap Size tested (Table 5.9). There is little difference in the results of **`shareFoodWith`** and **`reciprocalShareFoodWith`** at this patchiness level, and why should there be? If the altruistic trait did not evolve to fixation in the random walk model, why would we expect it to now that the nonrandom search method has increased within-group selection? However, in the case of **`omniscientShareFoodWith`**, the number of runs in which the altruistic trait evolves to fixation decreased by 60%. Given the relationship between the influence of the search strategy and Gap Size, it is not surprising that we would see this drop in the success of the altruistic allele in conjunction with larger gaps. Note that even fewer **`omniscientShareFoodWith`** runs end in altruism than when Patch Size = 4 and Gap Size = 6. This is due in part because larger patches support more heterogeneous trait groups and in part because the larger gaps amplify the influence of the nonrandom diagonal search strategy. As was the case above, I think the precipitous drop in the success of the altruistic strategy is caused by the inability of homogeneous trait groups of altruists to form and/or remain secluded for long periods of time.

Sharing Behavior	Search Method	# Altruistic Fix	Mean Pop Size	Mean Duration
`shareFoodWith`	Random	0	--	--
`reciprocalShareFoodWith`	Random	0	--	--
`omniscientShareFoodWith`	Random	28	46	4637
`shareFoodWith`	Diagonal	0	--	--
`reciprocalShareFoodWith`	Diagonal	0	--	--
`omniscientShareFoodWith`	Diagonal	11	50	2329

Table 5.9. Assessing the effect of the nonrandom search strategy in population-level genetic results of simulations that included large patches and large gaps (Patch Size = 8, Gap Size =8). # Altruistic Fix = number of runs (out of 101) in which the altruistic allele evolved to fixation; Mean Pop Size = average population size at time of fixation; and Mean Duration = average time of altruistic allele fixation.

Although not tested here, it would be interesting to see how these results might differ if foragers had access to the specific coordinates of resource patches instead of generally effective search methods. If knowledge of resource coordinates was universal (i.e., all foragers had equal access to the information), its presence might further decrease the strength of between-group selective powers. However, if this locational information was learned through individual experience and *shared* according to rules not unlike those

SHARE employs for food sharing, the results could be quite different. In this scenario, instead of sharing food, altruistic foragers could share information that might lead to food. One would assume that sharing information would be less costly than sharing procured food, but there might be ecological conditions in which this assumption is false. And, as we have found for food sharing, one would expect that certain ecological patchiness levels would not favor altruistic strategies of information sharing. However, it would be interesting to see if the ecological range that favors sharing information pertaining to the location and condition of food resources would be comparable to that which favors sharing the food, itself. It is quite possible that the basin of attraction for sharing information would be different from the basin of attraction for sharing food. If it turned out to be true, this discovery would have interesting implications for early hominin behavioral reconstructions, but for now this shall be left to a later version of SHARE.

5.6 How does altruistic punishment affect the evolution of food sharing in SHARE?

In the case of **`shareFoodWith`**, cheated altruists cannot punish cheaters. But in two of the three food sharing methods employed thus far, **`reciprocalShareFoodWith`** and **`omniscientShareFoodWith`**, one could argue that social cheaters are "punished" for their selfish actions whenever an altruistic donor refuses to share with them. This form of punishment costs the altruistic donor nothing in terms of fitness: that is, so far altruistic donors in SHARE have not been required to pay personal costs for refusing to share excess food with known cheaters (in fact, I have already discussed some of the ways in which this behavior works entirely to their benefit). By the same token, simply withholding one's resources and not sharing them with an agent in need does not detract from the fitness of the cheater in any way: the cheater is not actively punished, it simply is not helped. Following an interaction in which an altruist refuses to share with a known cheater, the two merely go their separate ways and neither is better or worse off than they were before the interaction. As far as punishments go, refusing to help someone is quite different from (and less severe than) actively harming them.

In addition, up until now altruistic foragers have had no method by which they could *immediately* punish a selfish donor for refusing to share excess food with them. In the case of **`reciprocalShareFoodWith`**, jilted altruists must wait until the same selfish forager asks them for food in order to exact their "punishment" of withholding resources. As we have demonstrated above, the rarity with which such specific interactions take place when repeated pair-wise interactions are asymmetrical is one of the reasons why altruistic food sharing based on direct reciprocity does not evolve to fixation in a larger area of the ecological parameter space than its simpler counterpart. In the case of **`omniscientShareFoodWith`**, altruistic foragers are equally unable to punish selfish donors at the time of refusal.

In an article informatively entitled “Punishment allows the evolution of cooperation (or anything else) in sizable groups,” Robert Boyd and Peter Richerson (1992) review a number of ways in which altruistic cooperators can punish cheaters for their unacceptable behaviors. They mention withholding resources during future interactions as well as gossip, physical attack, and group ostracism. The practice of gossiping about the reputations of individuals and refusing to share with those held in low regard is implicitly modeled in SHARE by **`omniscientShareFoodWith`**. This version of punishment is especially popular among human societies precisely because it costs altruists so little to use. Talk is cheap, word spreads fast, and it is relatively easy for altruists to think of a legitimate excuse for not sharing if a cheater’s reputation precedes him by even just a whisker. However, the other methods of punishment that Boyd and Richerson mention are not as easily enacted by altruists because they involve some personal cost to the individual doing the punishing. The punisher, who physically attacks or actively expels a needy cheater, risks one’s well being in an effort to enforce a group norm. Unlike gossip and withholding resources, this type of retaliation requires that the punisher pay a personal cost to its own fitness in an attempt to exact a greater cost on the fitness of a cheater. Such forms of retribution are considered examples of altruistic punishment. This is a bit of misnomer; because one individual pays a cost to hurt another, altruistic punishment is actually an example of spiteful behavior.

As is the case with all altruistic behaviors, the most fit punishment strategy from the individual perspective is for one to let others pay the costs of enforcing one's group norms—that is, to defect by not punishing cheaters. After all, why risk getting injured in a physical battle with a cheater if someone else can pay that price for you? The within-group selective pressure to avoid punishing is analogous to the one to avoid sharing. But groups that contain a greater proportion of altruistic punishers will outcompete groups with a lesser proportion of punishers. Because it requires meta-punishers to punish those who do not punish cheaters, altruistic punishment poses what has been referred to as the problem of second order cooperation (Boyd and Richerson 1992; Oliver 1980; Yamagishi 1986).

Although the problem of second order cooperation is interesting its own right, in this experiment I am only interested in how the model dynamics are affected by adding a form of altruistic punishment, so I only include two types of hominin agents: (1) selfish foragers that do not share or punish and (2) altruistic foragers that share and punish. Absent from this model are foragers who share and do not punish as well as foragers who punish and do not share, because I am not investigating the second order problem here. Altruistic punishment is operationalized in SHARE by adding a second stage to interactions in which altruistic prospective recipients ask selfish prospective donors for help. After the selfish donor refuses to share excess food, the spurned altruist physically attacks the selfish donor. The reprimanded cheater must subtract 25 units from in its `currentEnergy` as a result of the altercation. The altruist must pay a personal cost for punishing the cheater, but this tax is much less—only 5 units of energy. This experiment includes only the simplest food sharing method, **`shareFoodWith`**, because it previously included no punishment at all—not even withholding resources. Table 5.10 provides the results of 303 simulation runs, 101 of which were executed for each of three Patch Size, Gap Size combinations: 4, 6; 8, 2; and 8, 8. To aid comparison, these results are presented above the results from the analogous sets of runs that included no punishment.

Altruistic Punishment

Patch Size	Gap Size	# Altruistic Fix	Mean Pop Size	Mean Duration
4	6	52	20	1684
8	2	27	18	861
8	8	7	51	2666

No Punishment

Patch Size	Gap Size	# Altruistic Fix	Mean Pop Size	Mean Duration
4	6	38	21	1948
8	2	1	12	288
8	8	0	--	--

Table 5.10. Assessing the effect of altruistic punishment in population-level genetic results across a range of ecological conditions. # Altruistic Fix = number of runs (out of 101) in which the altruistic allele evolved to fixation; Mean Pop Size = average population size at time of fixation; and Mean Duration = average time of altruistic allele fixation.

The results presented in Table 5.10 unequivocally demonstrate that the presence of altruistic punishment does indeed allow altruistic food sharing to evolve in quantitatively and qualitatively different ways in SHARE. In the transitional range of ecological patchiness, which facilitates the evolution of altruism even without the aid of altruistic punishment, the number of runs in which the altruistic version of **`shareFoodWith`** evolves to fixation jumps from 38 to 52, a 137% increase. This is quite a quantitative difference, especially in an area of the state space that was already conducive to the spread of cooperation. The results for the other two patchiness levels demonstrate just how significantly the presence of altruistic punishment expands the basin of attraction for food sharing. In the case of large patches and small gaps, the number of times that the altruistic allele evolved to fixation grew from 1 without punishment to 27 with punishment. The qualitative change in the results of large patches and large gaps also is impressive. When altruistic punishment was included in this ecological scenario, the number of runs in which altruistic food sharing was successful rose from zero to 7. Obviously, the ability to punish cheaters for refusing to share excess food provides the previously toothless altruists with the tool they needed to exact some retribution on social cheaters that continuously accept the benefits of altruistic acts without ever paying the costs. Although including altruistic punishment in this version of `shareFoodWith` allows altruists to punish cheaters who refuse to share with them, it does not allow altruists to withhold excess food from egoists. According to the results of this experiment, however, the ability to punish selfish donors is enough to drastically change the success of the altruistic allele in a number of patchiness levels.

As stated above, this experiment with altruistic punishment only involved the simplest food sharing method. Because the other two food sharing strategies already include a selfish version of punishment (withholding resources), one might hypothesize that adding altruistic punishment would make it even easier for the altruistic allele to evolve to fixation in an extended range of ecological conditions. This hypothesis could easily be tested in the future. It might also be interesting to test the influence of altruistic punishment when the costs of punishing and being punished are calculated as a percentage of one's `currentEnergy` rather than as fixed values, as they were here. Regardless of whether these costs are fixed values or percentages, it would also be interesting to test how variability in punishment costs to both parties affects the model's dynamics. And, although it was not the focus of this particular experiment, SHARE could be used to address the problem of second order cooperation by including foragers that can share food but not punish as well as those that can punish but not share food.

5.7 Conclusions

In the final analysis, one must consider how the population genetic results of SHARE inform our understanding of how altruistic food sharing *could have evolved* in Plio-Pleistocene hominin populations. In doing so, one must keep in mind that SHARE is a null model of early hominin behavior, and as such it purposefully excludes traits like group-living and central place foraging in order to test their relevance to the evolution of altruistic food sharing. The point in using a null model is to demonstrate that these assumptions are not necessary to the evolution of even the simplest altruistic food sharing alleles under certain ecological conditions. The fact that the population genetic results of the model would probably differ had I expressly included group-living and/or central place foraging is something I freely admit, but it does not detract from the utility of the null model, which gives us a tool for identifying superfluous presumptions and paring our assumption-laden narrative reconstructions down to elegant explanatory models.

First, we have learned that food sharing behaviors need not be overly complicated to evolve to fixation within the transitional range of ecological patchiness: *in certain* *ecological circumstances even socially-sophomoric food sharing strategies could have evolved to fixation in hominin populations during the Plio-Pleistocene*. The premise that early hominins displayed relatively simple food sharing strategies is more parsimonious than the traditional application of modern hunter-gatherer behaviors, and, according to these results, the more parsimonious hypothesis could also be more accurate in the face of environmental fragmentation. This finding yields an interesting and testable hypothesis: *if the earliest food sharing behaviors were indeed simple, a strong temporal correlation should exist between significant forest fragmentation and the spread of this altruistic behavior*. Of course, high resolution research on the timing and spatial structure of Pliocene forest fragmentation in East Africa as well as a methodology by which spatial signatures left by food sharing can be recognized in early archaeological assemblages are required to test for the presence of this correlation in the field.

Second, we have learned that cultural sophistication liberates food sharing from a narrow, transitional range of ecological patchiness, thereby allowing altruistic alleles to evolve to fixation at higher frequencies in a larger are of the environmental parameter space. This finding implies that *had early hominins been capable of a relatively complex version of food sharing, one which involved gossip and/or possibly even the punishment of social cheaters, woodland fragmentation would have played a greatly diminished role in the biosocial process.* Therefore, if the earliest food sharing behaviors were culturally sophisticated, paleoanthropologists should not expect to find a strong temporal correlation between the evolution of food sharing and the fragmentation of Pliocene forests in East Africa. The population genetic results of this instantiation of SHARE also demonstrate that the presence of differential predation, the presence of carcasses, or the presence of both does not significantly alter the success of either allele. In the cases of the two less sophisticated sharing strategies, altruists and egoists are affected in the same way by these additions. Only in the case of the most sophisticated strategy do altruists enjoy a slightly higher success rate (a 3% increase in the total number) when carcasses are included in the model. However, for reasons discussed at length above, SHARE does not provide a definitive test of the impact that the presence of meat has on the evolution of food sharing, *per se*. It merely tests how the addition of a temporally and spatially unreliable windfall resource affects the success of those that are willing to share their bounty.

Third, we found that reciprocal food sharing did not enjoy a larger basin of attraction than its simpler counterpart. Because I purposefully chose to leave group living out of this null model, it is no surprise that repeated pair-wise symmetrical interactions rarely occur. However, *it is rather surprising that despite efforts to follow Trivers' suggestions—extending maximum life span, increasing rates of offspring dispersal, and fostering symmetrical interactions with continuous traits—the kinds of interactions that would lend more value to the memory of past socioeconomic interactions could not be facilitated*. This is one case in which a more involved model, which includes some form of obligatory group-living, would be useful, and I hypothesize that the results of such a model would be quite different: **`reciprocalShareFoodWith`** probably would have a larger basin of attraction than **`shareFoodWith`**. I plan to pursue this issue with future versions of SHARE.

Fourth, we documented the effect that non-local knowledge of resource structure has on the evolution of food sharing in SHARE. In general, *the ability to easily move about patches decreases the likelihood that altruism will evolve unless sophisticated cultural strategies are used to help maintain trait groups behaviorally rather than ecologically*. The assumption that hominin foragers are entirely unable to remember details about the structure of their environment is most likely the null model's greatest oversimplification. Even the model's "sophisticated" nonrandom method of diagonal search is (probably) a gross oversimplification of Plio-Pleistocene foraging strategies. Nevertheless, a comparison of the random and nonrandom search methods' results illustrated that while non-local knowledge of resource structure has less of an impact in some ecological conditions (small gaps) than in others (large gaps), it significantly decreased the evolutionary success of altruism in all ecological conditions tested.

Finally, we briefly explored how the evolution of food sharing is affected by the presence of altruistic punishment. This experiment illustrated how altruistic punishment can effectively expand the range of social and ecological conditions that support the evolution of altruistic food sharing. *With altruistic punishment, the number of runs in which altruistic food sharing evolved to fixation increased in the transitional range of patchiness as well as in some patchiness levels that did not support cooperation in its absence.* Thus, had Plio-Pleistocene hominins been willing and able to pay a small individual cost to incur a larger one on the fitness of a cheater, one should not expect the link between the evolution of food sharing and ecological fragmentation to be as strong as in the scenario that lacks punishment. Ironically, the presence of spiteful behavior can sometimes facilitate the evolution of the altruistic trait to which it is linked.

CHAPTER 6. A NULL MODEL OF PLIO-PLEISTOCENE ARCHAEOLOGICAL LANDSCAPE FORMATION

Given the success enjoyed by Potts' (1984, 1988) early simulation work, Mithen (1991) predicted that computer models would play an important role in furthering our understanding of Plio-Pleistocene archaeological landscape formation processes. However, despite the promise of Potts' model and Mithen's optimistic outlook on the future of simulation work, few Paleolithic studies have employed computer models. In this chapter, I present the results of a long-overdue agent-based model of Plio-Pleistocene archaeological landscape formation. Because the goal of my research is to help generate a more rigorous and holistic theoretical framework for understanding Plio-Pleistocene landscape formation, this agent-based model purposefully excludes many of the untested assumptions that permeate previous reconstructions of early hominin foraging strategies, such as food sharing at centralized "home bases."

At first blush, it might seem as though I have inserted unrealistically simple assumptions in place of those traditionally borrowed from modern *Homo sapiens*. But the assumptions are kept minimal for a good reason: so that I may study the artificial archaeological results of an elegant model that purposefully eschews behavioral assumptions for which unequivocal independent evidence does not exist. By evaluating the artificial archaeological landscapes created in a null model, one can assess whether a more parsimonious model predicts the important characteristics of the archaeological record as accurately as more complicated models. It is necessary to preface a discussion of my artificial archaeological results with discussions of three issues: the use of null models in archaeology, temporal resolution in Lower Paleolithic data, and the landscape approach to Oldowan archaeology.

6.1 Null models in archaeology

What is a null model, and what does it do? A null (or neutral) model is merely the simplest-case version of a proposed explanatory model. Null models purposefully exclude the very assumptions that are central to more complicated explanations. For example, to test whether raw material abundance really affects forager mobility and stone procurement strategies in the ways described by current archaeological theory, Jeff Brantingham (2003) studied a neutral model of lithic raw material procurement. His model included the nontraditional assumptions that "foragers do not optimize any specific currency associated with movement, do not depend on any form of planning depth, and are risk insensitive to all their movement and procurement decisions" (2003:504). As surprising as it may seem, even though Brantingham's foragers employ random walks and make stone procurement decisions without considering raw material types—contrary to two central assumptions of an optimal lithic procurement strategy—characteristics of the artificial lithic assemblages they produce are qualitatively similar to empirical Middle Paleolithic assemblages from Europe.

It is precisely because Brantingham's agent-based model dispenses with the central assumptions of alternative explanations that it constitutes a null model. This type of analytical research agenda forces us to reassess whether there is any explanatory connection between our often-overbuilt behavioral models and the archaeological signatures they are proposed to explain. Further, it allows us to construct archaeological inferences "from the null up." The behavioral models yielded by this generative approach are tailor made for the earliest stone tool makers in a way that models borrowed from modern human hunter-gatherers obviously cannot be. The goal of any useful heuristic modeling project is to explain as much of a phenomenon as possible while making as few assumptions as feasible. This goal is more easily attained by constructing a model from a null starting point, rather than by sequentially subtracting individual assumptions, which need not have been included in the first place, from a complicated model. In other words, the default for inference building models should be simple, not complicated, and more sophisticated behaviors, like male provisioning of nuclear families at central places, should be invoked *only* when simpler assumptions fail to predict important characteristics of observed record sufficiently.

David Raup (1987:121) describes the main function of null models:

> "Neutral models are useful in testing hypotheses about process. In the typical case, a pattern is seen in empirical data and a mechanism is proposed to explain the pattern. A neutral, or null model is then constructed to answer the question, Would the same pattern have occurred in absence of the proposed mechanism?...If the pattern produced by the neutral model is indistinguishable statistically from the real world pattern, there is no compelling reason to accept the proposed explanation."

Thus, null models function like null hypotheses; they make the precocious assumption that alternative explanations of a phenomenon are incorrect. Only by disproving a null model—which requires demonstrating that it does not adequately predict an empirically observed pattern—does one lend some credibility to the alternatives. One or all of the so-called "proposed mechanisms" might be valid if the null model is disproved. However, if the null model adequately predicts the real world pattern on its own, then one need not accept any of the alternative models as a more useful explanation.

Here, I employ a tactic similar to that which Brantingham (2003) used to investigate lithic procurement strategies. I use a null model of Plio-Pleistocene hominin foraging strategies to explore the possibility that ecological patchiness alone can facilitate the creation of artificial archaeological data that are qualitatively comparable to Oldowan landscapes in East Africa. This null model purposefully does not include commonly held assumptions such as central place foraging, male provisioning, division of labor, or mutualistic hunting and/or gathering. Instead, hominin agents use the combination of solitary foraging and random walks to move through their environment, and they employ only the simplest version of encounter-based food sharing, which is operationalized by probabilities, not by memory of past interactions or by kin recognition. In short, this null model tests whether complicated assumptions, such as male provisioning and central place foraging, are necessary to explain the nature of Oldowan archaeological landscapes in East Africa, and it finds that they are not.

6.2 Lingering questions and the issue of temporal resolution

Nearly twenty years ago, Kathy Schick (1987:790) neatly summarized the major characteristics of Plio-Pleistocene archaeology in a brief list of five items. Nearly two decades later, relatively little needs to be added to her list to describe the state of the art:

(1) stone artifacts consist of simple unifacially-flaked stone core and flake tools, debitage, and enigmatic spheroids and anvils, all generally assigned to the Oldowan (Mode 1) tool tradition which dates to as early as 2.6 MYA in East Africa (Semaw 2000; Semaw et al. 1997);

(2) despite being made expediently, even early Oldowan tools show that their makers possessed a fairly sophisticated understanding of fracture techniques (e.g., bi-polar fracture);

(3) raw materials used for stone tools are generally those that can be found locally (within 5-10 km);

(4) stone artifacts may be found alone or with fossilized faunal remains, some of which display cut marks and/or fractures as evidence that they were processed by stone tools;

(5) fossilized animal remains with cut marks have been found without associated stone tools, from which some have inferred that the stones were exported from the locale after being used to process the carcass (de Heinzelin et al. 1999); and

(6) survey and excavations indicate that the Plio-Pleistocene archaeological landscape can be characterized as a “scatter and patches” distribution in which a widely-dispersed, low density scatter of artifacts is occasionally interrupted by high

artifact densities that are localized in relatively small concentrations (Isaac and Harris 1975; Kroll and Isaac 1984).

It is impressive that we know this much about Lower Paleolithic hominin behavior given the amount of time that separates us from our subject. However, it is safe to say that all of the basic questions concerning the behaviors of the earliest (stone) toolmaking hominins still lack unequivocal answers. For example: What did these Lower Paleolithic hominins eat, and what proportion of their diet was composed of meat? If meat was eaten regularly, was it obtained via hunting, aggressive scavenging, or passive scavenging? To what ends were Oldowan tools used? What was the social organization of Lower Paleolithic hominins? To what extent did conspecifics cooperate with one another to make a living off of the mosaic of fragmented woodlands and expanding grasslands? Which hominin behaviors are recorded in Oldowan artifact distributions?

We do not have definitive answers to any of these questions, but it is not due to a lack of trying. Previous archaeological work in and around the Great Rift Valley in East Africa has identified numerous localities containing Oldowan tools, faunal assemblages, and/or hominin fossils. Although it is beyond the scope of this chapter to recount the entire history of Plio-Pleistocene archaeological reconstructions—from “living floors” (Leakey 1971) and “home bases” (Isaac 1978a) to favored locales (Binford 1987; Schick 1987; Sept 1992) and safe refuges (Rose and Marshall 1996) (see Chapter 3)—suffice it to say that some Lower Paleolithic archaeological interpretations (e.g., living floors) require a greater number of more complicated assumptions than others (e.g., favored locales). A thorn in the side of all of these Lower Paleolithic research projects has been the issue of data resolution.

In the same way that contemporary hunter-gatherer residential camps often provide the best ethnoarchaeological information about a wide range of daily activities, Leakey's "living floors" (1971) were thought to lend significant insights into the daily activities of hominins living in East Africa as early as 1.8 million years ago. Isaac (1978a) also assumed that these artifact concentrations possessed high temporal resolution, and therefore provided the opportunity to reconstruct Plio-Pleistocene hominin land use and settlement systems on a regional scale. That Oldowan "living floors" and "home bases" formed as a consequence of a large suite of activities, performed at only certain places during relatively brief occupations, constitutes *just one of many* possible archaeological explanations, however. As Binford (1987:19) correctly states:

> "Dense aggregations of materials may be understood in several ways: They may be the result of a consistent use of a place for similar purposes over varying lengths of time; they may be the result of multiple and different episodes of use; or they may be aggregations of the traces of diffuse episodes caused by natural agencies, such as fluvial action. (And there are still other confusing possibilities.)"

Although paleoanthropologists agree that most Oldowan landscapes are largely the products of cultural processes and not other "natural agencies," the important issue of temporal resolution remains, well, unresolved. An archaeological assemblage that accumulates over the duration of a few weeks or months might faithfully reflect the characteristics of a "living floor" or "home base." An assemblage that accumulates at a locale that was used in the same way each time it was occupied may provide a palimpsest of successive “living floors.” However, a material landscape that accumulates over hundreds, thousands, or even tens of thousands of years cannot possibly represent one “living floor,” and probably not even a palimpsest of “living floors.” This diachronic data set is more likely to contain materials that represent a host of different activities performed by many individuals (each of whom possibly belonged to different hominin species), who utilized the same locale but in different ways at different times. Obviously, the questions an archaeological landscape can be used to address are determined by its temporal resolution. One must not analyze an archaeological landscape encompassing 50,000 years of cultural deposition as if it were created in one month, and vice versa. Violating this basic rule, by inappropriately using archaeological data to address questions they cannot possibly answer, invariably leads to nonsensical interpretations.

Frustratingly, reliable measures of temporal resolution are not easily gotten from Oldowan landscapes—even from “living floor” contexts. Some researchers have tried to quantify the temporal resolution of Oldowan faunal assemblages with analyses of bone weathering stages (Behrensmeyer 1978b; Bunn 1982; Potts 1986; 1988). But because bones usually deteriorate within 6 – 15 years of being exposed to the elements in East Africa, they cannot be used to quantify intervals of cultural deposition on the order of hundreds or thousands of years. Potts (1988:54) concedes this point: “[b]ones may well have been deposited on a single surface for longer than 15 years, but the evidence will probably not be preserved.” Acknowledging this methodological limitation and moving on, he concludes that:

> “If average rates of weathering are assumed, all of the Olduvai faunal assemblages signify *at least* a 5– to 10–year period of time...[this] interval

> represents a *minimum estimate* for bone assemblages from thicker deposits.” [Potts 1988:54, emphasis added]

In light of the possibility that Oldowan landscapes might encompass thousands of years of deposition (Stern 1993, 1994; see below), the conclusion that Olduvai faunal assemblages encompass *at least* 5–10 years of accumulation does little to help determine a maximum limit, let alone a measure of the actual duration. Furthermore, Bunn and Kroll (1986) question the utility of bone weathering studies, stating that differential burial of bones could obfuscate the archaeological signal to the extent that differential weathering actually reflects staggered times of *burial* and not the maximum temporal extent of *accumulation*. In lieu of a trusted methodology for quantifying the temporal resolution of Lower Paleolithic faunal and lithic deposits in East Africa, the default has been to assume that Oldowan landscapes provide approximately the same level of temporal resolution that contemporary hunter-gatherer ethnoarchaeological landscapes provide. As we shall see below, not only is this presumption inaccurate, it might also be misleading.

6.3 A landscape approach to Lower Paleolithic archaeology

I cannot continue without first introducing the landscape approach to Lower Paleolithic archaeology. Landscape archaeology draws from a number of disciplines including geography, ecology, Marxism, and postmodernist critiques of social science (Whittlesey 1997). This interdisciplinary birth has caused some confusion among archaeologists (Anshuetz et al. 2000). For instance, archaeologists have been known to use the term “landscape” to refer to the biophysical habitat in which their subjects lived (as in paleolandscape), to the socio-political world (as in a cultural landscape), and even to the conceptual space in which individuals influence each other’s fitness via adaptations (as in the adaptive landscape). None of these definitions corresponds to that used in landscape archaeology, where “landscape” refers to the material and spatial manifestations of the interaction between humans (hominins) and their biophysical and socio-cultural environments (Marquardt and Crumley 1987). To be crystal clear, archaeological landscapes refer only to cultural material distributions (artifacts and their contexts) and the information therein. They do not refer to ecological zones or geographic regions.

Paleolithic archaeological landscapes are dynamic records of the interface between hominins and their inherited environment, which is the product of past niche construction behavior (Laland and Brown 2006; Laland et al. 2000, 2001). Certain characteristics of material landscapes influenced hominin behaviors just as hominin behaviors modified landscapes through time. There is no such thing as a “pristine” or “completed” landscape because they are constantly modified and reorganized by agents’ behaviors through time. As a result of this recursive modification, landscapes are palimpsests that may exhibit traces of previous activities in areas where subsequent behaviors failed to efface extant archaeological signals. Because they reflect diachronic changes in hominin behavior, landscapes have particular life histories, which can be studied to learn how different societies organized their actions within their environment (Gramsch 1996; Anshuetz et al. 2000).

The holistic nature of archaeological landscapes holds great potential for helping archaeologists connect certain spatial signatures in cultural material with the emergent processes responsible for them. However, to realize this potential one must first deal with the spatial and temporal complexity of landscapes. This task is best accomplished with nonsite archaeological approaches, which treat space as a *medium* rather than as a *container* for behavior. Nonsite approaches view the artifact, not the "site," as the minimal unit of archaeological inquiry because, as Isaac recognized long ago, hominin actions almost invariably operated at a larger scale than that defined by the excavation units of an arbitrarily defined "site."

The pioneering nonsite work by Isaac and his colleagues in East Africa began the shift from traditionally vertical, excavation-based investigations of diachronic "mega-sites" to regional studies aimed at gathering horizontal data on pene-contemporaneous artifact distributions by means of lateral sampling of the Oldowan archeological landscape (Isaac and Harris 1975, 1980; Isaac et al. 1981). Robert Foley (1981a, 1981b, 1981c) furthered this nonsite archaeological approach by studying the ways in which postdepositional taphonomic processes modify ubiquitously distributed artifacts "off-site." Shortly thereafter, Kay Behrensmeyer (1985) and Rick Potts (1989a, 1989b) employed lateral sampling strategies in and around hominin localities in East Africa in seek of both paleontological and archaeological data at the regional scale.

Since the late 1980s, Robert Blumenschine has spearheaded the long-running Olduvai Landscape Paleoanthropology Project, aimed at refining "paleogeographic and ecological interpretations of synchronic hominid land-use in the Olduvai Basin" (Blumenschine and Masao 1991:460). To meet this goal, he and his colleagues have employed a new brand of nonsite fieldwork, one that employs a healthy mix of test-trenches and surface survey as the means to collect data from horizontally separated outcrops of targeted geologic horizons. Through a series of interesting publications, Blumenschine and his team have reported on the development of their nonsite approach and offered tantalizing glimpses at the types of questions that can be addressed when archaeological data is collected from different parts of a paleolandscape (Blumenschine and Masao 1991; Blumenschine and Peters 1998; Peters and Blumenschine 1995, 1996). Although this Paleolithic research should be applauded for taking the right direction and innovating long-overdue techniques for sampling the earliest archeological landscapes laterally, it has not been able to provide definitive answers to self-imposed questions concerning synchronic hominin land-use. But this failure is largely due to the fact that Oldowan artifacts recovered from horizontally separated outcrops of the same stratigraphic layer are not synchronous; they are, at best, pene-contemporaneous (see below).

In sum, archaeological landscapes are not simple entities. I do not doubt that this complexity is responsible for some of the confusion archaeologists have shown over the definition of an archaeological landscape as well as the utility of the landscape approach. To explain landscapes adequately one must have reliable control of the spatial and temporal processes responsible for the formation of material distributions at a regional scale. That is, one must be aware of the locations, the range, and the duration of activities necessary for landscape formation. This is a tall order for any archaeological data set, but especially so for the Oldowan (see Blumenschine and Masao 1991). For in the case of the Lower Paleolithic landscape, we are aware of some of the locations where hominins deposited cultural material, but we still do not have a good handle on the range of activities or the temporal resolution represented by Oldowan landscapes. Luckily, these are the variables that an exploratory agent-based model can help us better understand.

6.4 Making minimal assumptions in SHARE

Leakey, Isaac, and Lovejoy each made the same tenuous assumptions in their reconstructions of Plio-Pleistocene hominin behavior: (1) because cultural material found at Oldowan "sites" was deposited over short periods, these "sites" provide high resolution temporal records of hominin behavior and (2) Oldowan hominins exhibited a rather sophisticated foraging strategy called central place foraging. Obviously, these assumptions are closely related. If operating under the assumption that cultural deposits were laid down rather quickly, then one must address the issue of how so many non-local artifacts could be deposited at one place in such a short time. Central place foraging—the strategy of transporting widely-dispersed resources back to a predefined "place" on the landscape—provides a behavioral explanation for the archaeological pattern because it can effectively concentrate cultural debris in and around a residential locus in a relatively short time. This passage from Isaac's landmark publication neatly illustrates the connection between these two assumptions:

> It does not seem likely that all the animals of the different species represented among the KBS [Kay Behrensmeyer Site] bones could have been killed *in a short interval of time at this one place*. …The studies strongly suggest that the hominids carried animal bones (and meat) around and concentrated this portable food supply at certain places. [1978a:99-100, emphasis added]

The second part of Isaac's quote may be true—hominins probably did carry some resources around and they might have been responsible for concentrating them at certain "places" over time. But the validity of this conclusion does not require that both of the tenuous assumptions above be true. Hominins could have been responsible for these concentrations regardless of whether they were formed over weeks or over millennia, and regardless of whether Plio-Pleistocene hominins were sophisticated central place hunter-gatherers or simple routed foragers.

Consider for a moment what happens if we relax either of these presumptions. If we replace the unproven assumption that Oldowan archaeological landscapes provide high resolution “snapshots” of hominin activity with the more reasonable assumption that they are in fact time-averaged assemblages representing thousands of years of hominin activity (Binford 1987; Stern 1991, 1993, 1994, see below), then no longer must we invoke a sophisticated behavior like central place foraging to account for the “rapid” formation of dense concentrations of artifacts. In fact, many behaviors can account for spatial clustering in archaeological landscapes that encompass thousands of years of deposition.

The same holds true if we start with a much simpler assumption about hominin foraging savvy (Schick 1987). Assume for the moment that Plio-Pleistocene hominins were simple foragers, who only occasionally shared food (like chimps), not obligate central place food sharers (like modern humans). Starting from this minimal scenario allows one to explore which other social or ecological factors might influence hominin movements and/or artifact deposition rates such that Lower Paleolithic landscapes would display the distinctive “scatter and patches” pattern in lieu of central place foraging.

The main point is that there are many combinations of duration of occupation and behavioral strategies that could have resulted in the archaeological patterns we observe in East Africa. Dense concentrations could have been created by a large group of hominins in a few days, by lone hominins visiting the same locale infrequently over the course of a thousand years, something between these two extremes, or various combinations of these scenarios. The explanatory models posed by Leakey, Isaac, and Lovejoy are heavily influenced by their use of the two most complicated assumptions, which happen to be taken directly from observations of modern human hunter-gatherers. However, a more parsimonious approach, which involves making simpler assumptions about the nature of the foraging behaviors responsible for the Plio-Pleistocene archaeological record, makes possible a host of previously unexplored, yet entirely plausible, Lower Paleolithic interpretations. The latter describes the approach taken in this research.

Minimal Assumption #1: Oldowan landscapes are composed of time-averaged assemblages, and the discrete events each contains are merely pene-contemporaneous

Over a decade ago, Nicola Stern recognized a disconnect between the temporal resolution of Lower Paleolithic landscapes and the archaeological models proposed to explain them. As a result, she argued that the interpretive theory that Lower Paleolithic archaeologists had commonly applied to Oldowan landscapes was inappropriate. One problem was that it treated patterned associations of artifacts as proxies for actual observations of *individual* hominins (*a la* Isaac 1981). According to Stern, this paradigm propagates a false sense of security in the unproven presumption that horizontally discontinuous distributions of Oldowan artifacts “translate readily into a map of the movements of early tool-using hominids across an ancient landscape” (1994:89). In order to provide better interpretations of the complicated record from this time period, Stern admonished archaeologists to consider two important characteristics of all Oldowan landscapes: time-averaging and pene-contemporaneity.

Unlike Leakey, Isaac, and Lovejoy, Stern does not assume that Oldowan concentrations display frozen snapshots of Plio-Pleistocene hominin behavior. Her perspective differs markedly in that it considers both behavioral and geological agents of accumulation through relatively long periods:

> "Pleistocene sediments contain palimpsests of debris that accumulated over time spans ranging from 1,000 to 100,000 years. The variables that influenced the loss and discard of these material remains are not the same as those that created the patterned associations of debris that archaeologists study." [Stern 1994:202]

Stern (1991, 1993, 1994) focuses on the minimum archaeological-stratigraphic unit, "the smallest sedimentary package that can be used to study the distribution of archaeological debris across an ancient landscape" (1993:93). In the Turkana Basin, this minimum unit is the lower Okote Member (LOM) of the Koobi Fora Formation. Geologists use the term *scope* to describe the total time span required for a stratigraphic layer to accumulate. Similarly, archaeologists use the term scope to describe the maximum time span required for the accumulation of the behavioral evidence found within the archaeological-stratigraphic layer, or, in other words, to set the uppermost limit on the length of time possibly represented by cultural remains found within a stratigraphic layer. Thus, the scope of the LOM provides the highest possible temporal resolution (i.e., the shortest period of accumulation) for Oldowan assemblages found among its horizontally separated outcrops in Koobi Fora.

Paleolithic archaeologists interested in gathering data at a high level of temporal resolution dream of deposits characterized by a scope on the order of decades or even centuries. However, according to Stern, this is not what we have available to us in the case of Oldowan remains. She uses long term, average sedimentation rates to argue that the scope of the LOM is 65,000 ± 5000 years. This does not mean that material landscapes lack all evidence of isolated events (see below). Rather, it implies that—*as a whole*—the archaeological landscape contained within one stratigraphic unit must be considered a composite of cultural and natural processes that were at work sometime during the scope of that geologic bed.

Invertebrate paleontologists use a special term to refer to a biological assemblage that is defined by the scope of one sedimentary unit; they call it *time-averaged*. When a time-averaged paleontological assemblage is found in sediments that accumulated at a much slower rate than the lifespan of an organism it contains, the fossil assemblage does not accurately reflect the community structure of that organism *at any given time*. The same holds true for Oldowan assemblages. Granted, being an archaeologist, Stern's interests are behavioral rather than biological, but paleontological and archaeological concepts of "assemblage" are roughly equivalent in this case. Because behavioral strategies, ecological conditions, and deposition rates vary through time, the length of each archaeological-stratigraphic layer's scope is directly related to the number of different processes that contributed to the record it contains: the longer the scope, the greater the number of different natural and cultural variables involved (Stern 1993). And because behaviors vary categorically through time and/or over space, time-averaged archaeological assemblages do not present averages of behavioral strategies, just as the mean of a set of nominal values does not provide an interpretable measure of their central tendency. Further, because sedimentation rates vary through time and across space, and cultural deposition rates vary by behavior, one cannot assume that a time-averaged assemblage preserves the most common cultural strategy. In short, time-averaged archaeological assemblages preserve neither the mean nor the mode of the set of behaviors exhibited during the scope of their archaeological-stratigraphic unit. Instead, they embody an irregular, incomplete, and enigmatic palimpsest of past behaviors.

Although he focused more on the variability displayed by Oldowan assemblages in Olduvai Gorge than on sedimentation rates, Binford drew the same conclusion as Stern. In commenting on the striking similarities between vertically diffuse assemblages and "living floors," he went beyond simply stating that, within each stratigraphic layer, Oldowan assemblages provide temporal aggregates of unrelated events:

> "…there seem to be *no structural differences* in the composition of assemblages from living floors and from diffuse deposits. In the latter assemblage it seems clear that the deposition of tools was episodal and the assemblage represents a temporally averaged aggregate of discrete and nonintegrated events of tool manufacture, use, and discard…but on the stable land surfaces [responsible for the formation of 'living floors'] this palimpsest is vertically undifferentiated in the archaeological record." [1987:26, emphasis added]

To Binford, the only thing that distinguishes a "living floor" assemblage from a vertically diffuse cultural deposit is the presence of a geologically stable land surface. "Living floor" deposits happen to be thinner merely because the stable land surface on which they form records episodic use differently—as a conflated palimpsest rather than as a vertically diffuse scatter—not because the area was used any differently by hominins. In other words, if one could manually conflate a vertically diffuse deposit of Oldowan materials, this “flattened” landscape would have the same general archaeological characteristics as a “living floor.”

Both Stern and Binford conclude that Oldowan landscapes are aggregates, or composites, of past behavior that are characterized by low temporal resolution. Thus, contrary to the assumption made by Leakey, Isaac, and Lovejoy, Lower Paleolithic landscapes do not provide high-resolution temporal records of hominin behavior. Even “living floors,” once internationally lauded as precious snapshots of a large suite of hominin behaviors, actually present conflated palimpsests rather than “moments” frozen in time.

To be clear, to argue that the temporal resolution of Oldowan landscapes is generally low is not to say that they are void of spectacular examples of well-defined behavioral events. Refit studies, which conjoin flakes with the core, chopper, or flake tool from which they were struck, demonstrate that certain components of Oldowan landscapes can indeed preserve synchronic moments. Unlike the material landscapes to which they belong, each of these small sets of conjoining artifacts possesses an extremely high level of temporal resolution; presumably, each tells us something about an individual tool manufacturing event which may have lasted only ten minutes 2.5 million years ago. There is no question that Lower Paleolithic archaeological landscapes possess numerous subsets of artifacts such as this, and that these components provide valid information about well-defined events, like core reduction and tool sharpening.

However, information gleaned from isolated, high resolution events can be used to build inferences about higher-level adaptations, like daily movements within a settlement system or the division of labor, only if they are contemporaneous. Ethnographers and ethnoarchaeologists enjoy unparalleled success in studying land use strategies and the division of labor because they are able to document how a single group distributes behaviors across space *at the same time*; these researchers are privy to contemporaneous behavioral data. However, the task of reconstructing Plio-Pleistocene land use strategies is complicated by the fact that truly contemporaneous behavioral data is unavailable.

Although Paleolithic archaeologists are keenly aware of the fact that geologic sediments and archaeological materials accumulate at different rates, they find it less intuitive that archaeological deposits found in different outcrops of one distinctive bed are not necessarily contemporaneous. But Stern (1993, 1994) argues that because (1) Oldowan assemblages in Koobi Fora are characterized by poor temporal resolution and (2) deposition rates vary locally, horizontally separated outcrops should be viewed as containing *pene-contemporaneous* archaeological remains. Unfortunately for those interested in reconstructing settlement systems, two pene-contemporaneous archaeological data sets may be separated by tens of thousands of years. Although two distinct outcrops of one well-defined geologic bed might each contain evidence of a discrete behavioral event, such as sharpening a stone tool, Stern argues that there is no logical justification for associating these two pene-contemporaneous events any closer than the scope of the archaeological-stratigraphic unit they share. For example, even if evidence of two flintknapping events had been found in two outcrops of the LOM that are horizontally separated by only 500 meters, one could not reasonably argue that these well-defined events occurred within less than approximately 65,000 years of one another. Thus, due to the poor temporal resolution of the time-averaged assemblages that contain them, two discrete events cannot be linked as components of the same settlement system, even when they occur in horizontally separated outcrops of the same geologic bed.

Stern warns that the time-averaged structure of Oldowan landscapes preempts their use in reconstructing the daily activities of hominin foraging activities at any point during the scope of the archaeological-stratigraphic unit. She also forces us to consider whether pene-contemporaneous data can be used to reconstruct land use systems. At the very least, her provocative challenges admonish archaeologists to first obtain a better understanding of how archaeological landscapes are affected by changing rates of cultural deposition and sedimentation if they wish to use time-averaged Oldowan landscapes to reconstruct high-resolution details of daily life. Her perspective provides the minimal assumption about the content of Lower Paleolithic landscapes: *Oldowan assemblages are time-averaged composites of potentially nonintegrated behaviors whose actors may have been separated by tens of thousands of years, and the discrete events they contain cannot be assumed to be contemporaneous components of one group's land use system given only their co-occurrence in the same geologic bed.* Because the burden of proof rests on the shoulders of those who wish to argue the case of contemporaneity among Oldowan artifacts, Lower Paleolithic landscapes should be considered time-averaged and pene-contemporaneous until proven otherwise.

Minimal Assumption #2: Important spatial characteristics of Oldowan landscapes can be predicted by stone import-export pressures affecting niche geography foragers

By using the term "home base" to describe localized concentrations of Oldowan artifacts, Isaac implied that hominins regularly made a behavioral distinction between (at the very least) "camps" and "not camps." The ability to redefine and then modify certain parts of the natural environment into "camps," from which individuals exploit their surroundings so as to sustain themselves and their constructed infrastructure, is observable among a number of species—most notably, modern humans (Binford 1987). Humans culturally and physically construct "places," and their spatial structure in turn organizes the way in which we exploit the natural environment and, ultimately, the remains we leave behind. Las Vega$ is a great example of a culturally-constructed place. It attracts millions of people and tons of cultural material annually despite offering very little in the way of natural resources to justify such attention. Binford (1982, 1987) refers to such sophisticated behavior as interaction with a "cultural geography." He explains how cultural geography is fundamentally different from "niche geography," which involves mapping one's movements *directly* onto the resources necessary for biological success, rather than *indirectly* mapping them between culturally-constructed places or between culturally-constructed places and resource patches. Niche geography refers to a "pattern of differential placement, differentiation of behavior, and intensity of use within a habitat," which is "a *direct response to the structure of the natural environment* with regard to different locations of species-specific requirements" (Binford 1987:18, emphasis added). Chimps use niche geographies, but modern humans do not, and it is unknown when we made the switch to the seemingly more complicated system.

The interpretation that Plio-Pleistocene hominins lived at “home bases” requires that they exhibited the modern human behavior of organizing their behaviors within a cultural geography. Some researchers have cited “living floors” as the archaeological evidence of culturally constructed-places and, by extension, of the existence of a Plio-Pleistocene version of cultural geography. According to this reconstruction, then, early hominin settlement systems were centered on the creation and maintenance of “central places” rather than on sequential movements among resource-rich patches scattered throughout the paleolandscape. Plio-Pleistocene hominins were thought to closely resemble modern human foragers in this way.

Because the act of partitioning the natural environment into culturally-defined places has the effect of nonrandomly distributing human behaviors over space, one can expect different sets of behaviors to be reflected by archaeological material found at different locales (Binford 1972, 1980, 1987). However, when Binford looked at the “living floors” from Olduvai, he did not find material evidence of the kind of behavioral organization that would suggest the presence of a sophisticated settlement system, complete with cultural geography:

> “Associations at places [in Olduvai] do not appear organized...this behavior looks much more like a tool-assisted direct adaptation to the environment than like a modern human strategy…the associations among artifacts at early sites appear to be fortuitous responses to the organizational properties in the natural environment...” [Binford 1987:22]

Thus, in contrast to the two-part assumption that “living floors” serve as evidence of camp sites and that these camp sites serve as evidence of modern human-like settlement systems, he argued that:

> “the episodes standing behind the aggregates of material commonly considered camp assemblages were independent and nonintegrated. ...One can make the case that there are no camps in the Lower Paleolithic record —only archaeological landscapes varying in the frequency of episodal use at different magnet locations in the natural environment.” [Binford 1987:26]

This interpretation dovetails nicely with the behavioral model Kathy Schick (1987) proposed in a thought-provoking article concerning the formation of lithics concentrations in Koobi Fora. Her research questions are simple and direct: How did Oldowan artifact concentrations (and diffuse scatters) form, and what can they tell us about how Plio-Pleistocene hominins exploited the environment? After discussing why interpretations based on “home bases” and stone caches are inadequate, Schick proposes a much simpler model of landscape formation which explains the presence of large and small distributions of both vertically concentrated and vertically diffuse concentrations as a function of habitual stone transport and differential discard behaviors. In the presence of habitual stone transport, all lithic concentrations can be explained as locales where hominins simply imported more stone than they exported. Schick (1987) describes a number of reasons why the amount of stone exported from a particular spot might be less than the amount imported, including: (1) more important resources (like food) had to be carried away from the locale; (2) sudden, possibly forced, abandonment did not allow hominins to recollect all of their possessions before dispersing; (3) foraging activities planned for the immediate future either (a) did not require the use of stones or (b) were to take place in the vicinity of the existing scatter of stone tools; or (4) the next planned destination was known to contain plenty of stone resources. According to Schick's simple framework, each of these factors would decrease the pressure to "pack out" stone materials, which over time "would tend to produce a store of useful materials at some locations, not through a deliberate stockpiling motive, but as a by-product of the site-specific import-export imbalance" (1987:800).

For a modern day illustration of the import-export imbalance, consider the material record created by mountain climbers on Mount Kilimanjaro. The challenging trail to the peak is littered with thousands of empty oxygen canisters. Obviously, these tools were not cached in particular places for later use; they were discarded because there was very little pressure to export them from the spot where they were emptied. In other words, because there is high pressure to habitually carry oxygen canisters that are not empty and low pressure to export the extra weight of empty canisters, they will tend to accumulate solely as a by-product of habitual transport and import-export imbalances. Further, think about where empty oxygen canisters will tend to accumulate on Mount Kilimanjaro. Will they be scattered randomly about the mountainside, or will their distribution display spatial structure, perhaps even some level of patchiness? Obviously, one would expect the empty bottle concentrations to be densest along the trail, because hikers visit that area of the mountain is most frequently. Given the rise in elevation and canister capacity, one might also expect to find denser concentrations in some sections of the trail than in others.

An analogous scenario may apply to Oldowan concentrations. Holding deposition rates constant, it is obvious that artifact concentrations will tend to develop in locations that hominins used frequently. Schick concludes:

> "This cycle could promote the accentuated development of large-scale artifact concentrations (n > 1000) in locales where excellent food resource availability would draw large quantities of stone imports with numerous and/or frequent hominid foragers...the vertically diffuse deposits observed in some sites could represent areas frequently visited over extended periods of time, but where the rate of sedimentary deposition was very rapid relative to the rate of cultural deposition." [1987:801]

It is easy to identify Binford's "magnet locations in the natural environment" in Schick's locales of "excellent food resource availability," and to recognize that Schick would agree with Binford that "living floors" and vertically diffuse archaeological assemblages only differ in the sedimentation rates that accompanied them. Schick provides a simple behavioral mechanism to explain the archaeological pattern Binford described. According to Schick, the frequent use of favored locales by hominins, who reserve the right to discard stone when reduced export pressures make it beneficial for them to do so, can result in dense concentrations of lithic artifacts. It is important to point out that Schick's behavioral model does not require central place foraging or the organizing structure of cultural geography. Instead, she argues that the frequency at which locales are utilized can be determined to a large extent by the distribution of food resources. The type of land use strategy Schick envisions for early *Homo* would fall under the category of "tool-assisted direct adaptation to the environment" (Binford 1987:22). Thus, Schick's minimal model demonstrates that *important spatial characteristics of Oldowan artifact concentrations can be adequately explained as a* *function of fluctuating stone import-export pressures affecting foragers utilizing nothing more than niche geography.*

6.5 A null model of Lower Paleolithic landscape formation

Stern, Binford, and Schick raised difficult questions about Lower Paleolithic landscape formation, and they provided some plausible scenarios that can be tested formally. Contrary to early paleoanthropological thought on the topic, their work suggests that it is more parsimonious to assume that (1) Lower Paleolithic cultural deposits are time-averaged and that cultural materials found in similar deposits across a paleolandscape are pene-contemporaneous and (2) Plio-Pleistocene hominins need not to have exhibited modern human-like central place foraging strategies to have produced "scatter and patches" landscapes. Although my approach might seem counterintuitive at first, *this agent-based null model tests the validity of previous assumptions about the formation of Plio-Pleistocene landscapes by leaving them out*. Recall the principle of Occam's razor: when a simple model is equally capable of explaining a phenomenon, it should be preferred over unnecessarily complicated models. Although I will not argue that this simple null model uncovers the "Truth" about Plio-Pleistocene archaeological landscape formation, it certainly provides a more sensible place to begin the task of *building* (not *borrowing*) behavioral reconstructions via sound archaeological inference.

My null model is informed by Stern's perspective of time-averaged archaeological deposits and by Schick's ideas about the potentially influential role that favored locales can play in landscape formation. It is important to review the way in which artificial archaeological landscapes are created in the agent-based model before discussing the spatial results. SHARE models the archaeological landscape as something that develops over hundreds of generations, rather than over a few short weeks, months, or even years. Hominin agents do not drop artifacts in order to add another stone to a cache or because they just used it to procure food from a carcass; they drop artifacts stochastically. This operationalizes Schick's simple description of early hominin stone transport in which hominins habitually carried stone tools and/or cobbles of raw material during the course of daily foraging activities and occasionally deposited more stone than they exported at certain locales. SHARE simply "sums over" the possible factors influencing artifact import and export pressures by providing a probability (e.g., 0.1) that export pressures are reduced enough to deposit an artifact per forager/time step. This probability is held constant through time and over space for all hominin agents. Given this minimal assumption that import-export pressures do not vary with activity or proximity to different locales, artifacts serve only as trace fossils of hominin agent movements. Simple stone transport and foraging behaviors cause artifact counts to grow indefinitely in cells that are (re)visited frequently by hominins agents. In contrast, low artifact counts will result in cells that are visited infrequently by hominin agents. Thus, artifact accumulations in any cell are probabilistically related to the cumulative time hominin agents have spent in that cell over the entire course of a simulation run.

This null model does not include explicit representations of central place foraging or of cultural geography. Instead, hominin agents employ a very simple foraging rule: of the immediately proximate energy values that support the metabolic cost of at least one time step (i.e., ≥ 2 units), foragers move to that which is highest. Thus, agents nonrandomly move towards the highest value of food in their immediate surroundings without regard for culturally constructed “places.” In this way, hominin agents map themselves directly onto the resource rather than onto an intermediary cultural geography. If no suitable energy amount can be found in one’s local neighborhood, then a move will be made randomly to one of the available cells. Because hominin agents cannot “remember” locales where they previously sensed food, their foraging behavior is even less sophisticated than Binford’s (1984) definition of routed foraging. Could these extremely simple stone transport and niche geography foraging behaviors possibly produce the types of “scatter and patches” landscapes described above?

When a random number between zero and 1 is less than the probability of dropping an artifact, a hominin agent deposits an artifact agent (or increments the **`artifactCount`** of an extant artifact agent, see Chapter 4) at its current local on the spatial grid. To document the development of the each run’s artificial archaeological landscape, each artifact agent is prompted to report its current **`artifactCount`** to its respective Cartesian coordinates on a two-dimensional array at the rate of once every 100 time steps. Each array is time-stamped with a uniquely descriptive name and saved as a space-delimited text file. At the conclusion of a simulation run, any or all of the resulting text files can be imported into GIS software as continuous (raster) surfaces for the purpose of spatial analysis.

Like Stern, Binford, and Schick, I can think of no *behavioral* reason for distinguishing between “living floors” and vertically diffuse cultural deposits in either empirical or artificial contexts. As a result, each artificial archaeological landscape is modeled as if it has collected on a stable land surface. These artificial distributions contain only two spatial dimensions. I can study the ontology of each landscape by looking at how it evolves through time in 100 time step slices, but because artifacts are not assigned depth values and sediments are not continuously added through time, I am unable to address the vertical dimension of these artificial data. As a result, the spatial results provided by SHARE are palimpsests of all cultural deposition events that occurred during a simulation run, entirely unmodified by natural processes, loss, redistribution, or accumulation. Although they are modeled as if they are accumulating on a stable land surface, I would never call any portion of these artificial landscapes "living floors" or "home bases" *per se*, because of the behavioral baggage associated with those terms. Think of these artificial landscapes, instead, as providing plan views of regional-scale distributions of Oldowan artifacts as they would appear if we could make invisible the sediments that would normally separate most of them into vertically diffuse deposits.

Archaeological results of the null model

The spatial data collected from SHARE are appropriate for commenting on three central issues, each of which is addressed in this section.

Ecological patchiness strongly affects the structure of archaeological landscapes created by niche geography foragers

> "…a spatial focus for debris-producing activities...may have as much to do with the ecological attributes of the location as with the socioeconomic organization of the litterers." [Sept 1992:204]

As discussed above, previous explanations of Lower Paleolithic landscapes commonly identified sophisticated hominin foraging behaviors as the driving force behind artifact accumulations. Environmental structure was not thought of as a particularly important variable to consider in early models of the formation of Oldowan artifact concentrations because central place foraging strategies are capable of consolidating resources at certain spots on the landscape regardless of the level of spatial patchiness they might display. However, by directing our attention at this seemingly minor oversight, Sept (1992) asks the simple question that should have been addressed long before there was ever any talk Plio-Pleistocene hominins as central place foragers: What role does ecology play in structuring activities and, thus, the archaeological landscapes they leave behind?

Answering this question requires a spatial statistical method that can be used to characterize and compare the levels of "patchiness" displayed by multiple continuous, raster (i.e., distributional) archaeological data sets. Local spatial autocorrelation and "patchiness" refer to essentially the same spatial phenomenon: the nonrandom association between like values (i.e., clusters, concentrations, or patches of similar values). Elsewhere, I have introduced archaeologists to a combined local spatial autocorrelation technique (Premo 2004). This quantitative method makes use of two local spatial statistics (Anselin 1995; Getis and Ord 1992; Ord and Getis 1995), which together can be used to characterize multi-scale spatial signatures of patchiness in distributional archaeological data. Of the two spatial statistics introduced in the earlier paper, only one—Local Moran's I (I_i)—is discussed further here. In the interest of brevity, I refer you to the 2004 paper for details concerning I_i, including its algebraic expression. In short, Local Moran's I_i provides a measure of the degree to which each value (x_i) is similar or dissimilar to the values that surround it (x_j). Local Moran's I_i is large and positive when x_i is similar to x_j, and it is large and negative when x_i is dissimilar from x_j. In a general sense, positive I_i values are indicative of "patchiness" because they identify the presence of localized concentrations of similar values. Large, negative values are indicative of "overly mixed" distributions in which values are negatively autocorrelated. Random distributions yield Local Moran's I_i values near zero, which indicates no spatial autocorrelation between target values and those in their local neighborhoods.

Figures 6.1 – 6.6 illustrate how Local Moran's I_i can be used to quantify local spatial autocorrelation in distributional data. The top row of Figures 6.1 – 6.3 present the spatial data collected from three simulation runs, each of which used the same values for almost all of the initial conditions, including the random number seed, the number of starting foragers (40 altruists), and the probability that each forager will deposit an artifact per time step (0.1). However, the values for Patch Size and Gap Size were varied at the start of each run to test whether food resource patchiness alone could influence routed foragers to the extent that they might produce artificial landscapes that exhibit the same spatial signatures found in East Africa. The bottom row of Figures 6.1 – 6.3

present the standardized I_i results as calculated for each artificial landscape. These results were calculated in ESRI's Grid workstation with a custom made local spatial autocorrelation AML that is currently available upon request. In this particular case, I_i scores were calculated for each cell using only its eight immediate Moore neighbors. Those cells on the "edges" of the unwrapped torus were assigned NODATA values. Finally, standardized I_i values were transformed into z-scores by subtracting the mean and then dividing the result by the standard deviation.

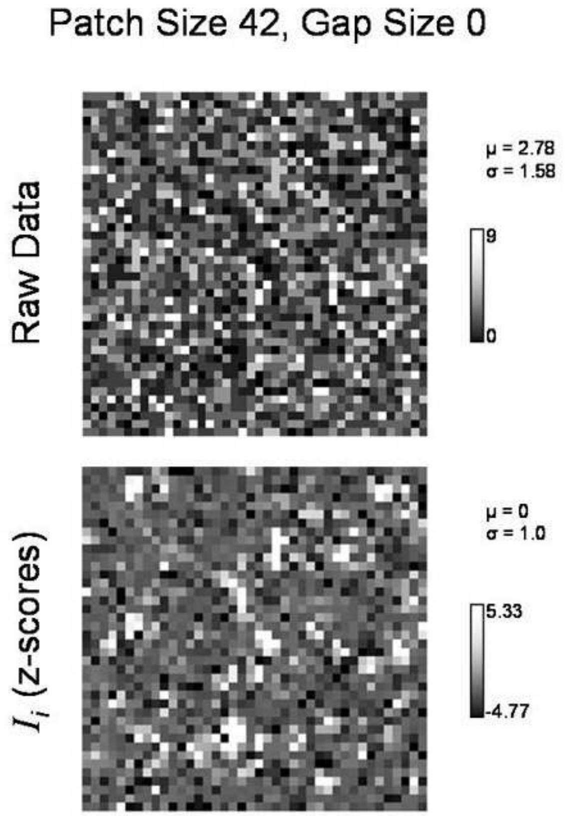


Figure 6.1. Local Moran's I_i quantifies the effect of ecological patchiness on the structure of the artificial archaeological landscape created in Patch Size = 42, Gap Size = 0. Top: raster map of the raw archaeological data created by the simulation run (integers represent the number of artifacts per cell). Bottom: raster map of resulting I_i z-scores (floating point values). Each appears with its summary statistics.

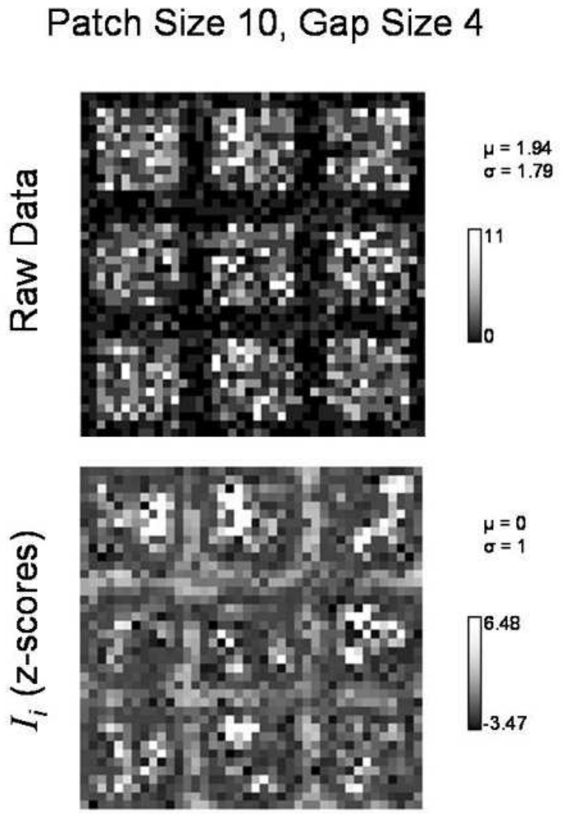


Figure 6.2. Local Moran's I_i quantifies the effect of ecological patchiness on the structure of the artificial archaeological landscape created in Patch Size = 10, Gap Size = 4. Top: raster map of the raw archaeological data created by the simulation run (integers represent the number of artifacts per cell). Bottom: raster map of resulting I_i z-scores (floating point values). Each appears with its summary statistics.

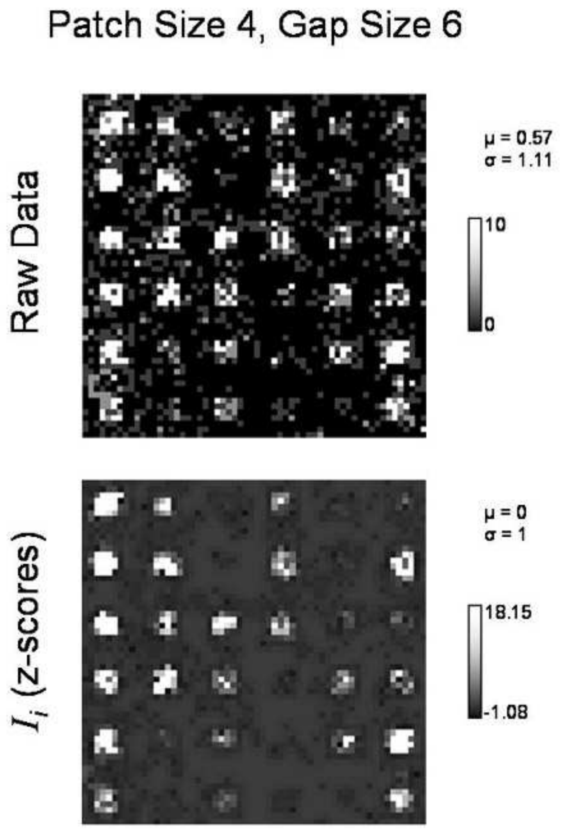


Figure 6.3. Local Moran's I_i quantifies the effect of ecological patchiness on the structure of the artificial archaeological landscape created in Patch Size = 4, Gap Size = 6. Top: raster map of the raw archaeological data created by the simulation run (integers represent the number of artifacts per cell). Bottom: raster map of resulting I_i z-scores (floating point values). Each appears with its summary statistics.

In the large homogeneous resource distribution (Figure 6.1), forager movements yield a diffuse scatter of artifacts, which lacks any sign of localized concentrations in the raw data or in the corresponding I_i scores. Figures 6.4 – 6.6 demonstrate, however, that as food resource patchiness increases, so too does the structure of the resulting archaeological landscapes. As many generations of artificial hominin agents search for energy via simple niche geography foraging strategies, a consistently patchy resource distribution influences the spatial structure of the resulting archaeological landscape such that concentrations of artifacts accumulate in the vicinities of diachronically reliable food sources. Local Moran's I_i can be used to identify this spatial signature. Although the raster maps of the z-scores seem to reflect an obvious trend from less structured to more "patchy" landscapes, the more reliable bits of evidence come from analyses of the *skewness* and *kurtosis* of the z-score distributions presented in Figures 6.4 – 6.6. Skewness characterizes the degree to which values are asymmetrically distributed around their mean. Positive skewness indicates a right-skewed distribution, which has an asymmetric tail extending toward positive values, while negative skewness indicates a left-skewed distribution, which has an asymmetric tail extending into negative values. Kurtosis, on the other hand, is a way of characterizing a distribution by comparing it to the proportional shape of the normal distribution. Positive kurtosis indicates a relatively peaked distribution in which many values are disproportionately concentrated within one small region of the total range (this would look like an extremely tall and skinny "spike-shaped" curve). Negative kurtosis indicates a relatively uniform distribution in which values are spread along the entire range more evenly than one would expect in a normal curve (a short, wide "box-shaped" curve).

Note that in the case of Figure 6.4, I_i scores are distributed normally about zero. More specifically, there are roughly equivalent numbers of positive and negative values and the mode is near zero. These are exactly the results one would expect to see under the assumption of random spatial assortment and homogeneous archaeological distributions. In fact, the homogeneity of this artificial archaeological landscape is not surprising given the homogeneity of its associated food resource. However, the z-score distributions of Patch Size 10, Gap Size 4 (Figure 6.5) and Patch Size 4, Gap Size 6 (Figure 6.6) are right-skewed. Unlike the distribution of I_i scores of the homogeneous landscape, which yields a relatively symmetrical normal curve and a correspondingly low skewness value of 0.24, the other distributions possess much higher skewness values (1.71 and 7.10) because their ranges expand farther in the positive direction. A trend toward high positive skewness values and extended positive ranges is exactly what we should expect to see as archaeological distributions display more patchiness.

In addition, as archaeological landscapes become patchier, one should expect their distributions to look less and less like the well-proportioned shape of a normal curve. In other words, because patchy landscapes tend to yield I_i scores that cluster disproportionately in only one or two bins of the entire range, they produce "spiked" rather than bell-shaped distributions. For example, in Figure 6.6, the bin that includes cells with z-scores ranging between -0.5 and zero contains 2860 cells, while the second most populated bin contains less than 150 cells. As expected, the kurtosis value for Patch

Size 10, Gap Size 4 (6.63) is nearly twice that of the more homogeneous Patch Size 42, Gap Size 0 (3.60); and the kurtosis value of the patchiest landscape, Patch Size 4, Gap Size 6 (70.32), is more than an order of magnitude greater than either of the others.

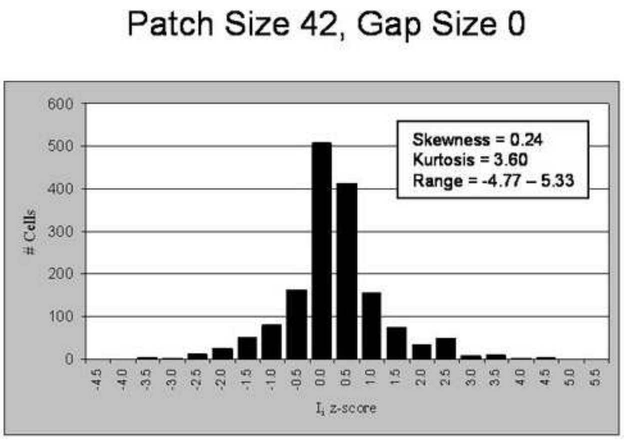


Figure 6.4. Histogram of the I_i z-scores presented in Fig. 6.1. Aside from some minor kurtosis near the mean, this distribution of I_i z-scores approximates a normal curve because the artificial archaeological landscape is homogeneous.

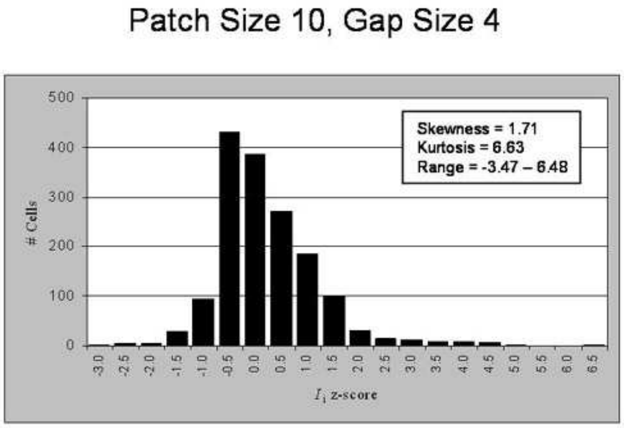


Figure 6.5. Histogram of the I_i z-scores presented in Fig. 6.2. Increases in skewness and kurtosis as well as the positively shifted range imply that the artificial archaeological landscape displays more spatial structure than its more homogeneous counterpart.

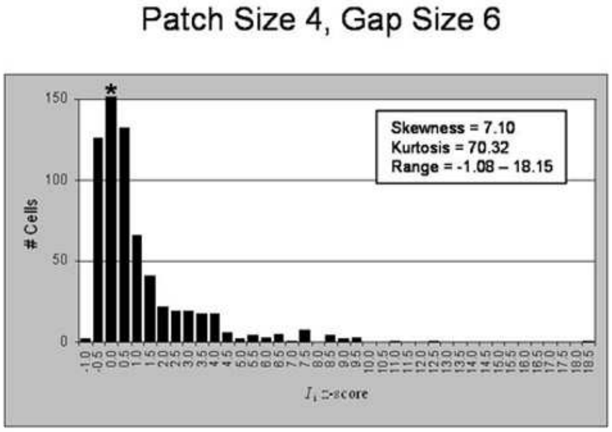


Figure 6.6. Histogram of the I_i z-scores presented in Fig. 6.3. This distribution is distinctly right-skewed, shows a high level of kurtosis, and has an expanded positive range because it is associated with an archaeological landscape characterized by a high degree of local spatial autocorrelation among its artifact count values. These are the statistical indicators of a patchy archaeological landscape. *2,860

The results of this spatial analysis with local Moran's I_i demonstrate that ecological patchiness can effectively facilitate the formation of "scatter and patches" landscapes, even in cases where hominin agents do not exhibit central place foraging behaviors. This finding is not completely unanticipated. Binford (1987), Schick (1987), and Sept (1992) each previously hypothesized that the presence of favored locales (i.e., areas (re)visited often, but not necessarily by the same individual) could produce highly structured material landscapes over time, with or without central place foraging. However, this agent-based research marks the first time that the dynamics of such a conceptual model have been studied analytically. The spatial data collected from a number of artificial landscapes created in different ecological scenarios demonstrate that foragers living in patchy environments need not display central place foraging strategies in order to leave behind equally patchy archaeological landscapes. Indeed, Sept's (1992) quote at the beginning of this section is correct: the spatial results from SHARE demonstrate that when one assumes that Plio-Pleistocene hominins were moving between patches not between "places," the ecological characteristics of an area have as much—or more—to do with structuring debris-producing activities as the socioeconomic organization of those dropping the artifacts.

Including carcasses does not drastically change the structure of artificial landscapes

> "Plant foods, in omnivorous scenarios of hominid evolution, play the role of low-risk, dependable foods with predictable locations and known processing efforts. By formally estimating the probabilities that specific archaeological assemblages formed in different plant food contexts, archaeologists may be able to elucidate aspects of assemblage patterning that have so far been overlooked." [Sept 1994: 315]

In this model, plant agents provide a temporally and spatially dependable resource, but individually they are not capable of yielding large amounts of energy. Meat agents, on the other hand, provide temporally and spatially unpredictable resources, but their energy payoffs can be quite large. Although Sept has argued that plant resources may play a significant role Lower Paleolithic landscape formation, carcasses have traditionally received the lion's share of attention in paleoanthropological models, simply because they yield meat. The presence of carcasses has played a large role in previous behavioral reconstructions, such as "home bases" and stone caches, but here they are included in the model only to test whether the presence of a second type of resource—one found unpredictably in both time and space—will drastically change the patterning observed in artificial records. *Because both plant and carcass agents yield energy that can be carried easily, SHARE cannot be used to test the hypothesis that carcasses were* *necessary for the evolution of food sharing because they provide larger and more easily shared packages of calories.* This is a known limitation of the current version of the model. However, by adding a very different type of food resource in the form of meat agents, SHARE's spatial results can be used to address the following question: Will the presence of a temporally and spatially unpredictable resource, available stochastically in both woodlands and grasslands, blur the resulting archaeological "patches" such that they form one large "scatter"?

To address this question with quantitative data I again employ Local Moran's I_i to compare the levels of "patchiness" exhibited by two archaeological landscapes—one created by hominin agents who did not have access to carcasses and one created by foragers who did. Both simulations were run for 1000 time steps, and both were executed with nearly identical initial conditions—the only exception being that one included carcasses and the other did not. The probability that a carcass could appear per cell/per time step was raised from 0 to 0.0001 in the "carcasses present" version. Figures 6.7 and 6.8 present the raw data raster maps and the standardized I_i z-scores for the artificial archaeological results of these two runs.

The raw data raster maps of these landscapes show some subtle differences. Although, they both show heterogeneous artifact distributions, the "carcasses present" landscape contains a greater number of localized concentrations as well as a seemingly greater number of artifacts in areas between concentrations than its counterpart, the "carcasses absent" landscape. Also note that although both runs were stopped after 1000 time steps the mean of the "carcasses present" landscape is almost twice that of "carcasses absent." Keep in mind that adding an additional food source to the total amount of food available increases the carrying capacity of the simulation run. Because the probability that an agent will deposit an artifact per time step is kept constant between these two runs, a larger population equates to a greater number of artifacts and a larger mean for the raw data.

Second, although the I_i z-score raster maps also look quite similar, in that they both display numerous localized "hot spots" of artifact concentrations separated by a sea of lower scores, note that the range displayed by the "carcasses present" results is much smaller than that displayed by the "carcasses absent" z-scores. On a related note, the kurtosis value of the "carcasses present" z-score distribution is nearly half that of the "carcasses absent" z-score distribution. These results imply that the "carcasses present" landscape is more homogeneous than the "carcasses absent" landscape, a fact that is reflected by a more normal distribution and a smaller range. However, one must not forget that, despite these subtle differences, both landscapes produce I_i scores that are obviously right skewed (skewness values of 7.10 and 5.46). These results demonstrate that while both landscapes are quite patchy, including an additional food resource that is not concentrated in patches does blur the ecological signal displayed by the archaeological landscape. Whether this is caused solely by the presence of a resource in the grasslands or by the presence of an additional food resource, which supports a larger forager population, requires further investigation.

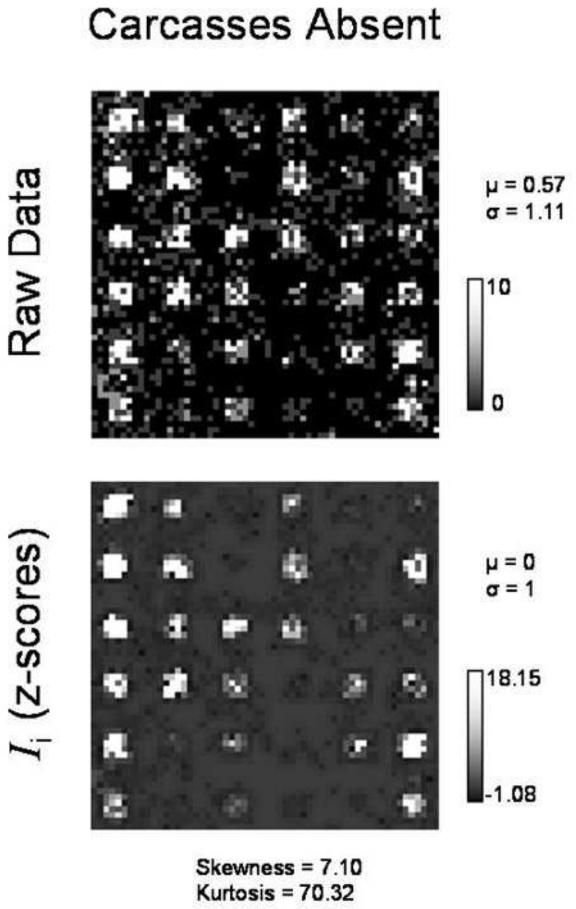


Figure 6.7. Quantifying the effect of carcasses on archaeological landscapes: carcasses absent. Archaeological data presented here were produced by a simulation run that did not include carcass agents. Top: a raster map of the raw archaeological data created during the simulation rum. Bottom: a raster map of I_i z-scores, complete with summary statistics.

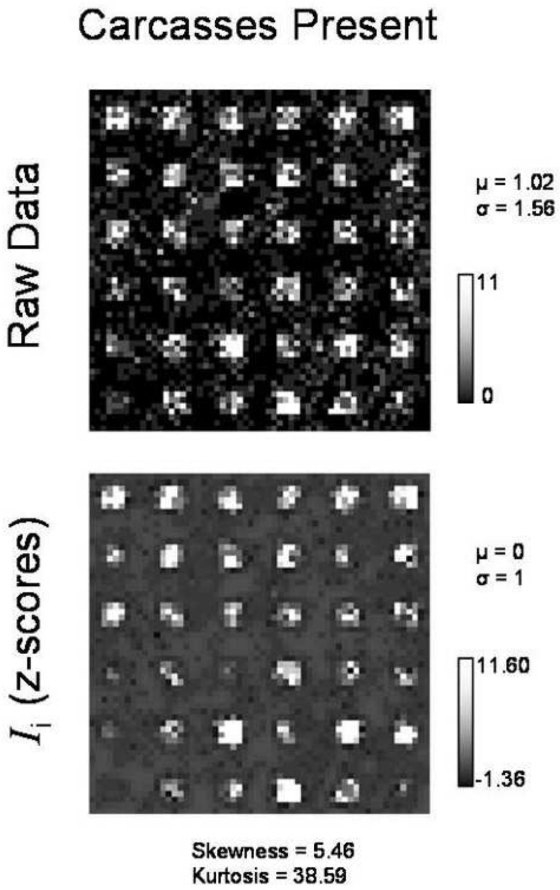


Figure 6.8. Quantifying the effect of carcasses on archaeological landscapes: carcasses present. Archaeological data presented here were produced by a simulation run that differed from the first only in that it included carcass agents. Top: a raster map of the raw archaeological data created during the simulation run. Bottom: a raster map of I_i z-scores, complete with summary statistics.

It is also interesting to think about how these spatial results might differ if stone export pressures were reduced only when associated with certain activities rather than kept constant over all behaviors. That is, would the subtle differences between the spatial signatures of "carcass absent" and "carcass present" landscapes be amplified if agents were more likely to drop artifacts after they had just eaten or after they had just procured food that needed to be carried than when merely moving across the landscape "empty-handed?" A related question is: How would increasing the probability of carcasses affect the spatial structure of the archaeological landscape? How prominent must carcasses become before their presence across both habitats swamps the spatial signature of woodland patches? Experiments designed to answer these (and other) intriguing questions about the role of multiple resource types in the formation of Plio-Pleistocene archaeological landscapes might provide the elucidation to which Sept refers in the quote that began this section.

Comparing apples and…artificial apples, or what artificial archaeological data can teach us about the behaviors responsible for patterns observed in the field

> "To explain the formation of the early archaeological record, a model must somehow account for the range of sites encountered, from the large concentrations of thousands of artifacts to the small scatters of only a few dozen…" [Schick 1987:795]

Schick draws a proverbial line in the sand with this quote. She believes that in order to be considered useful to Paleolithic archaeologists, an explanatory framework must account for the variability present in Plio-Pleistocene archaeological landscapes. The densities of artifact concentrations and the spatial extent of their boundaries both exhibit interesting variability. In the presence of simple foraging strategies, both of these archaeological characteristics could be affected by the spatial and temporal ecological patchiness of important resources in the following ways.

First, the scale of artifact concentrations are directly related to the scale of resource patches: expansive resource patches are likely to yield large concentrations of artifacts just as constricted resource patches are likely to yield small concentrations of artifacts. The spatial data collected from SHARE support this principle, time after time. As long as resources patches are separated by a Gap Size greater than 4, the average area of the dense archaeological concentrations can be predicted best by Patch Size. That is, assuming that each forager is navigating niche geography, the spatial extent of archaeological concentrations is positively correlated to the size of well-separated resource patches in SHARE.

Second, the number of artifacts found per unit of space (i.e., artifact density) is strongly correlated to resource availability. A temporally reliable resource, which remains productive over a long time (possibly thousands of years), will likely promote the accumulation of dense concentrations of artifacts if for no other reason than because its nearly constant availability provides a greater number of hominins the opportunity to locate and utilize it. Conversely, a transient resource that is available for only a brief period will promote the accumulation of few artifacts simply because few hominins will have a chance to locate and then utilize it before it disappears. The spatial results from SHARE support this principle. After looking at the figures presented above, it is obvious that the highest artifact densities regularly occur in woodland patches. Recall that woodland patches are not modeled as culturally-constructed "central places." Rather, they are composed of plant agents, which represent temporally reliable resources that regenerate quickly and can never be extinguished completely. The presence of these temporally reliable resources attracts hominins and, by extension, their cultural debris. In SHARE, sizable open grasslands (Gap Size > 2) are always characterized by much lower artifact densities than those found in woodland patches. Even when carcasses—a temporally unreliable resource—are allowed in the open areas, artifact densities in grasslands are still much lower than those recorded in the vicinity of the more stable sources of energy.

These two principles can be combined in a number of ways to form a variety of archaeological signatures. Depending on the characteristics of the resources provided by ecological patches, one can find small and large concentrations of artifacts characterized by either high or low densities. Resource patches that are small and transient (i.e., carcasses) can sometimes still yield small, dense clusters. On the other hand, one might expect resource patches that are large and transient (i.e., masting trees) to yield large, dispersed clusters. One should not expect that large, stable resource patches will always be associated with large, dense concentrations of artifacts. Large resource patches merely *facilitate* large, dense accumulations; they do not necessitate them. In the case of a meandering stream or fluctuating lake shore, where a large resource might not be fixed in space through time, we might actually expect to find large, diffuse "smears" of cultural material rather than well defined concentrations. In addition, because Plio-Pleistocene hominins probably would have been interested in a number of resources, many of which might not often co-occur in time and/or space, empirical archaeological landscapes will rarely be as cut and dry as predicted by these two simple principles. In my simple model, I control the spatial and temporal scales of the only two resources included, and, as a result, I have a good idea as to which behaviors are responsible for artifact concentrations. But in the real world, Lower Paleolithic palimpsests record behaviors that targeted many different resources, each of which might have had its own unique spatial and temporal scale. Although I do not attempt to emulate this more complicated scenario, by exploring the state space of a very simple socio-ecological scenario with SHARE I have (1) proven that some levels of ecological patchiness can structure the archaeological landscapes of routed foragers into "scatter and patches" landscapes and (2) begun to investigate the cultural depositional processes that affect the basic building blocks of the more realistic coupled hominin-environmental system that characterized Plio-Pleistocene hominins.

6.6 Conclusion

At the end of such a long discussion concerning the use of null models and modern analogues; the unnecessary complexity of previously held, untested assumptions and the elegance of minimal ones; and the explanatory power of a formal model like SHARE in contrast to the cloudy causal relationships implied by verbal models like the home base hypothesis, it is but customary to ask what can be learned from all this.

For one, we have learned that we can jettison many of the central assumptions of our cherished, highly detailed referential models without sacrificing much of their explanatory power. The spatial results of SHARE demonstrate that, when minimal assumptions are made from the outset, many of the behaviorally modern human "bells and whistles" that accompanied prior reconstructions are not required to predict the observed archaeological phenomenon of interest. For instance, central place foraging need not be invoked to explain an archaeological landscape characterized by "scatter and patches" of cultural material when foragers inhabit patchy environments. An elegant socio-ecological model, which includes only differential stone transport pressures, niche geography, and a patchy environment, can sufficiently predict variability in the sizes and densities of the empirical archaeological concentrations once thought to be explainable only by Plio-Pleistocene hominins exhibiting modern human-like behaviors. The take-home lesson here is not that Plio-Pleistocene hominins were asocial, solitary foragers, but, rather, that *previous paleoanthropological reconstructions include a number of behavioral assumptions that are not necessary to explain important spatial characteristics of Lower Paleolithic landscapes*.

In light of this revelation, it is high time we begin constructing archaeological inferences of Plio-Pleistocene hominin behavior “from the null-up,” which involves testing alternative scenarios against empirical data. This approach requires that we start with the admittedly few unequivocal things that we do know about hominin behavior, and test more complicated scenarios only when simpler models fail to predict archaeological patterns of interest. It is possible that the process of generating an explanatory model from the null-up might still result a complicated model like Isaac’s or like Lovejoy’s. But if it does, we at least will know why the complicated model is preferable to its simpler alternatives. However, as it stands now, Paleolithic archaeologists are stuck with bulky, “off the shelf” referential models, which cannot be reduced into simpler components because they are borrowed from contemporary hunter-gatherers as more or less complete packages. These ill-fitting models might provide sufficient “just-so stories” for Lower Paleolithic distributions, but they are not supported by a scientifically-validated justification for why any particular one should be considered the best possible explanation out of an almost infinite number of possibilities. The methodology introduced here—inference building via generative agent-based modeling—can imbue models with the legitimacy they need to replace such irreducible, *ad hoc* scenarios.

So, what are the archaeological implications of this exploratory agent-based model, how does it further our understanding of the formation of Plio-Pleistocene landscapes, and how can it be tested in the field? As discussed above, SHARE demonstrates that under fragmented ecological conditions, it is possible that even routed foraging could have produced the type of patchy archaeological landscape known from fieldwork in East Africa. Assuming for the moment that Plio-Pleistocene hominins were not central-place foragers, this nontrivial finding implies that the localized concentrations of archaeological material they left behind signal favored locales, which may have taken the form of ecological islands of closed habitat. High-resolution paleoecological reconstructions at locales marked by dense concentrations of Lower Paleolithic materials may elucidate environmental circumstances that played a role in archaeological landscape formation. However, to gain a statistical sense of whether archaeological concentrations are more commonly associated with certain types of local environments than with others, paleoenvironmental investigations comparable to those that have been conducted on “mega-sites” (i.e., deeply stratified localities marked by high concentrations of cultural material) must also be carried out on pene-contemporaneous geological deposits that contain very little to no archaeological material.

This approach calls for concentrating serious archaeological, paleontological, and paleoecological attention on locales that are poor in cultural resources. Concentrating our efforts in areas devoid of artifacts may at first seem counterintuitive, but this is vitally important to gaining an accurate sense of the relationship between ecological fragmentation and archaeological patchiness in the field (e.g., Blumenschine and Masao 1991). Studying the ecological conditions in the vicinities of archaeological concentrations might allow one to propose an explanation for why artifacts are found there. But without studying the ecological conditions in areas that lack archaeological remains, one has no data on which to propose an interpretation that also explains why artifacts are absent in other regions of a paleolandscape. Because the Plio-Pleistocene archaeological landscape is not randomly distributed (i.e., it has some structure), it is just as important to identify those microhabitats that lack artifacts as to identify those in which they are regularly found. In other words, because there are reasons for why we do not find equivalent artifact densities everywhere, an explanation as to why we find very few artifacts in some areas is just as important as an explanation as to why we find dense concentrations in others. Both are necessary for a holistic understanding of the behaviors responsible for Paleolithic landscape formation. Although the traditional task for archaeologists is to interpret the artifacts we find rather than those we do not find, rest assured that this perspective is not new to Paleolithic archaeology. In fact, this was a goal of Isaac's innovative approach to learning more about the "scatters-between-the patches" thirty years ago.

This discussion of locales that lack artifacts brings us to an interesting archaeological conundrum. As the old adage goes, absence of evidence is not evidence of absence. On the whole, this is good advice. For example, just because artifacts are not found at a locale does not necessarily mean that hominins never inhabited it. But keep in mind that what is of interest when studying the formation processes responsible for Paleolithic landscapes is not the record of one visit, or even a few visits, to one locale, but, rather, the repeated use of a resource patch or maybe even a "place" over the course of thousands of years. Blumenschine and Masao also made this distinction at the start of the Olduvai Landscape Paleoanthropology Project:

> We harbor no pretense of identifying traces of a hominid group's home range created over a seasonal or annual round. Rather we are attempting to reveal patterns in the distribution and character of archaeological occurrences that can be related to features of the biotic and physical

> landscape that remained relatively constant with the target horizon… [1991:454-455]

The archaeological signal left by such long-term use is not likely to be erased by the kinds of post-depositional processes that go unnoticed by trained professionals. So, it may be that, when dealing with archaeological landscapes that are the products of tens of thousands of years of deposition, the absence of archaeological evidence can and *should* be used as evidence that hominin behaviors responsible for artifact deposition were largely absent over that period. At any rate, I am of the mind that the "absence of evidence" mantra is less of a concern in this case than in others, and it should not hinder us from actively using locales that lack cultural material to aid our interpretations of Paleolithic landscapes.

In the end, SHARE provides a new hypothesis about the influence of ecological patchiness on archaeological structure which can be tested in the field by assessing the relationship between the density of artifact concentrations and the characteristics of the micro-habitats in which they are found. Given the null model of Plio-Pleistocene hominins moving through niche geography, dense archaeological concentrations should correlate positively with patches of closed habitat *and* negatively with open habitat. Note that this hypothesis test requires extensive sampling of both closed and open microhabitats, regardless of whether they contain archaeological material. Given what we have learned from SHARE, had early hominins been capable of more sophisticated foraging strategies, including travel among culturally-constructed "places," we would expect forest fragmentation to play a diminished role in the formation of Plio-Pleistocene landscapes. And, as result, we should not expect to see such strongly positive spatio-temporal correlations between the patchiness of Lower Paleolithic archaeological landscapes and dwindling patches of Pliocene forests in East Africa. Regularly finding large concentrations of Oldowan artifacts in open paleohabitats to the exclusion of closed habitats might be a sign that closed patches were less important to Plio-Pleistocene hominins than culturally-defined places in open grasslands.

CHAPTER 7. EXPLORING BEHAVIORAL *TERRA INCOGNITA*: A SYNTHESIS

While Glynn Isaac's name will forever be associated with the "home base" hypothesis, it must not be forgotten that this he forwarded as just one of many possible alternatives, all of which to his mind deserved—nay, *needed*—to be exposed to potential falsification against empirical data:

> "…in pursuing the archaeology of the very remote past we are exploring behavioral *terra incognita*. If we are to avoid simply creating our origins in our own image, we have ruthlessly to expose all important propositions, however obvious seeming to potential falsification." [Isaac 1983:16]

This simple, honest statement outlines a fruitful modeling approach, which many Paleolithic archaeologists have taken to heart. To wit, I have reported on the most recent attempt to ruthlessly expose to falsification some previously held, but analytically untested, assumptions concerning Plio-Pleistocene archaeological landscapes. I used a null model to question whether commonly held paleoanthropological assumptions are logically *necessary* to produce archaeological signatures in artificial archaeological landscapes that are comparable to those documented empirically in East Africa. SHARE's assumptions differ markedly from those which serve as the foundation of previous explanatory frameworks such as the "home base," "central place," and stone cache models. Major differences include a focus on woodlands patches, a study of the benefits of altruism at a level above that of the individual, and a minimalist instantiation of hominin foragers which does not include central place foraging.

Like in other Plio-Pleistocene reconstructions, expanding grasslands play an important role in SHARE. Unlike in most previous models, however, open grasslands are important here not because they provide a new ecological niche for hominins to conquer, but because their expansion is directly related to the fragmentation of the more crucial resources found in closed habitats. It is more likely that grassland expansion triggered serious ecological stresses for hominins better adapted to life in and around trees than to life in open grasslands. Morphological and paleoenvironmental evidence can be cited to support this statement. *Au. afarensis* fossils prominently display ancestral arboreal traits. In addition, many of the new, exciting Late Miocene and Early Pliocene hominin finds are associated with closed woodland environs, not open grasslands. These facts warrant a serious reconsideration of the role that woodland resources played in the evolutionary scenarios of Plio-Pleistocene hominins. It is probable that grasslands did not present a golden socio-economic opportunity for adventurous and highly capable pre-human populations (*contra* the Serengeti hypothesis). It may be that they presented dangerous hinterlands that were to be avoided by hominins if at all possible. SHARE reflects this reconsidered perspective, as it includes the more parsimonious assumption that in the face of significant environmental changes caused by a cooling and drying climate, Plio-Pleistocene hominins continued to evolve behaviorally in ways that enhanced their use of shrinking closed habitats rather than expanding open grasslands.

Paleoanthropologists have modeled Plio-Pleistocene food sharing variously over the last four decades. In a previous chapter I discussed some of the ways in which Plio-Pleistocene hominin food sharers have been characterized, ranging from reliable monogamous partners and family provisioners to reputation-aggrandizing show-offs. Although these explanatory models appear quite different superficially, each shares the same central tenet: because the “altruistic” behavior of sharing food is actually motivated by self-interest, it evolves to fixation via individual-level selection. Besides the fact that this assumption is flawed, as it requires that we redefine the altruism out of “altruism,” it requires of hominins rather sophisticated social capabilities including kin recognition, image-scoring, gossip, memory, and/or punishment. It is certainly possible that Plio-Pleistocene hominins possessed some or all of these traits, but until we identify unequivocal evidence for such behaviors in the archaeological record it is more parsimonious to assume that they did not. This is the tact I take with SHARE. As strange as this might seem, SHARE is unique in that it treats hominin food sharing as a biologically altruistic behavior that benefits the fitness of recipients at a cost to fitness of the donor. In its plainest clothes, SHARE models hominin foragers as unable to recognize their kin, gossip about cheaters, remember the results of previous interactions, consider reputations, or punish social defectors. Instead of being imported as parts of behavioral systems borrowed from contemporary hunter-gatherers, in SHARE each of these qualities remains to be demonstrated. In order to explain how the truly self-sacrificial version of food sharing evolves in mixed populations one must consider the benefits it bestows upon fitness at a level above that of the individual—hence, the importance of the multilevel selection perspective introduced in Chapter 2.

As Isaac recognized over two decades ago, the early assumption that Plio-Pleistocene “sites” could be evaluated by comparison to modern hunter-gatherer camps, which often serve as true central places, made it seem rather natural that the 2 million years old assemblages might also be explained by an analogous Paleolithic version of central place foraging:

> "Archaeologists have assumed that these commonplace accumulations are the residues of camps or settlements formed as the outcome of ethnographically observed processes that include as a quasi-universal behavior, the transport of food back to a "home-base" for collective consumption…Having, as it were, followed an apparently uninterrupted trail of stone and bone refuse back through the Pleistocene it seemed natural to all those involved in the first round of research to treat these accumulations of artifacts and faunal remains as being 'fossil home base sites.'" [Isaac 1983:3-4]

It is not surprising that paleoanthropologists saw in Plio-Pleistocene landscapes early glimpses of modern human behavior, because they were applying inferences borrowed from modern humans to explain these materials distributions. Who (or what) else could the data possibly have looked *like* when compared only to those yielded by modern humans? The conclusion that Plio-Pleistocene "home bases" serve as proof of central place foraging while, at the same time, central place foraging explains the presence of "home bases" is circular and uninformative. The previous chapter documents how the famous interpretations of Mary Leakey, Isaac, and Lovejoy were all imbued by the seemingly benign presumption that Plio-Pleistocene hominins regularly transported resources back to central places, or "camp sites." It also explains how researchers like Binford, Schick, and Sept questioned this proposition. Although it was once believed that dense concentrations of Lower Paleolithic artifacts provided evidence of "living sites"—to which hominins transported non-local materials via central place foraging—Stern's convincing work at Koobi Fora provides a strong argument against jumping to the conclusion that enigmatic, time-averaged concentrations provide clear evidence of the central places that served as domestic camp sites for hominins. In light of recent reanalyses, there are no archaeological data that unequivocally demonstrate that Plio-

Pleistocene hominins were central place foragers, and, until such data have been uncovered, we should error on the side of parsimony with the assumption that Plio-Pleistocene hominins were not much like modern humans in this respect (Binford 1987). Given this statement, it is not surprising that SHARE starts with a much simpler assumption about foraging savvy: Plio-Pleistocene hominins were routed foragers who navigated niche geography and only occasionally shared food; they were not obligate central place food sharers who made use of culturally constructed and maintained places.

7.1 Paleoanthropological contributions

SHARE was built to address two principal questions. First, what range(s) of ecological and social conditions facilitates the evolution of food sharing in artificial Plio-Pleistocene hominin populations? Second, is food sharing at central places necessary for the formation of the so-called “scatter and patches” archaeological landscapes that are characteristic of the Plio-Pleistocene record in East Africa? Previous studies of this nature relied heavily upon observations of living humans to address early hominin food sharing. But extant and historically documented hunter-gatherers, bound by their own historical, economic, and political contexts, represent only a small subset of possible forager societies. Here, artificial societies of hominin foragers were employed as behavioral laboratories to investigate the effects of a much wider range of plausible scenarios.

It is important to reemphasize that SHARE predicts a relationship between closed habitat fragmentation and the evolution of altruistic food sharing without including the unproven assumption that Plio-Pleistocene hominins *preferred* open habitats at this time. As a consequence, SHARE's results demonstrate the powerful role that resource patchiness can play in structuring an otherwise free-mixing population of socially inept foragers. For both of the less sophisticated sharing rules, the altruistic allele evolves to fixation in sizable populations predominantly in the so-called *transitional zone* of ecological patchiness. This transitional zone facilitates the evolution of altruism by increasing between-group selective pressures while decreasing within-group selective pressures. But resource patchiness plays only a minor role in the case of the most sophisticated sharing rule, which spreads to fixation at least once under each and every ecological condition capable of supporting viable populations. Because cultural behaviors can supersede ecological patchiness in structuring trait groups, the selective influence of ecological patchiness is inversely related to the social sophistication of food sharing behaviors. In addition, SHARE demonstrates that "scatter and patches" archaeological landscapes do not require central place food sharing in every experimental ecological scenario. Rather, under certain conditions—specifically, those marked by fragmented and patchy food resources—archaeological landscapes containing both concentrated patches and diffuse scatters can form over many generations as a result of solitary foraging routes that are not tethered in any way to culturally defined "central places."

So, how do the findings from this heuristic model better inform our ideas about food sharing and Plio-Pleistocene archaeology? For one, if Plio-Pleistocene food sharing behaviors were indeed simple, a strong temporal correlation should exist between forest fragmentation and the spread of this altruistic behavior. However, had Plio-Pleistocene 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 spatio-temporal correlation between the evolution of food sharing and the fragmentation of Pliocene forests in East Africa. It is possible to test these new hypotheses against empirical archaeological and paleoenvironmental data at some Plio-Pleistocene localities.

Further, it is no longer necessary to invoke central place foraging to explain an archaeological landscape composed of dense artifact clusters separated by diffuse artifact scatters. In certain ranges of ecological patchiness, routed foraging strategies are sufficient to produce artificial landscapes that resemble Plio-Pleistocene archaeological distributions in East Africa. In some ways, the most important conclusion is that the conventional assumptions upon which previous paleoanthropological interpretations rely are sufficient but not *necessary* to predict important spatial characteristics of Lower Paleolithic landscapes in patchy environments like those that have been reconstructed for this period in East Africa.

I agree that the results of SHARE do not (in fact, cannot) *prove* that altruistic food sharing spread through hominin populations due to the fragmentation of closed habitats nor that solitary routed foragers were responsible for the empirical archaeological record, and to think otherwise is hubris. However, the null model results demonstrate that ecological patchiness can facilitate the spread of even simple biologically altruistic food sharing behaviors. In addition, they demonstrate that, in many environments, routed foraging techniques are sufficient to form artifact concentrations that approximate "home base" localities.

Generating archaeological interpretations from the null-up

> "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]

A generative model, like SHARE, provides archaeologists with the valuable opportunity to act as their own informants in building better archaeological inferences. In this case, SHARE improves our understanding of how simple cultural formation processes influence archaeological landscapes under a large variety of behavioral and ecological scenarios. It also demonstrates how agent-based models can provide powerful tools for testing the validity of archaeological inferences via experimentation with artificial societies. When employed as behavioral laboratories, agent-based models can provide forums for not only generating new hypotheses, but also for testing their archaeological implications against the empirical record. To ignore received wisdom in order to explore alternative ways in which Lower Paleolithic landscapes *could* have formed within a behavioral laboratory is to better fit our ideas of the past to the data we recover in the present. Contrast this approach with the subtle practice of fitting the data we recover in the present to support our ideas about the past, or fitting our models in the present to support our ideas about the past. As Binford warns, archaeologists must not "approach the external world in search of verification for our ideas and slip into the trap of accommodating experiences to fit what we *believe* to be true" (1987:21, emphasis in original).

What I have described in the previous chapters is a methodology for testing the validity of our inferences with a theoretical tool that is largely independent of the archaeological record. When used to explore rather than to emulate, an agent-based null model provides a test that does not suffer from the same pernicious circularity that confounds studies which use the same set of archaeological data *both* to spark and to support hypotheses about the behavioral formation processes responsible for its formation. However, not all agent-based modeling approaches are immune to circularity; those used explicitly to imitate real world archaeological data or to instantiate preconceived notions and unquestioned assumptions sacrifice their independence in favor of a higher degree of "realism" (as if that can be measured). Because there are an infinite number of ways to program a computer model in order to produce artificial archaeological data that matches those we observe in the field, merely miming partially understood systems *in silico* is neither difficult nor particularly informative. For instance, it would not have been hard for me to create a more "realistic" agent-based model complete with hominin agents who share food at central places, but imagine how much less that model would have taught us about the relationship between ecological patchiness and the evolution of food sharing. The approach I used instead demonstrates that agent-based models are more informative when they are kept as elegant as possible, because these null models can teach us about the regions of behavioral and ecological state space that are not covered in overly detailed verbal models or represented by observations of contemporary hunter-gatherers. In this way, simple exploratory agent-based models can be used to generate new archaeological inferences and to build behavioral interpretations from the null-up.

Simpler interpretations of archaeological landscape structure

> "Can we conceive of patterns of behavior and adaptation that could lead to the formation of familiar-looking patterns of archaeological evidence, and yet which were behaviors unfamiliar to us in that they were structured differently from recent and present-day human ones?" [Isaac 1986:237]

Isaac's question provided the motivation for the modeling research reported here. Although there may be many patterns of behavior that could lead to the formation of "scatter and patches" archaeological landscapes, I started by exploring the most parsimonious. Traditionally, central place foraging has been championed as the most likely candidate, but its popularity among paleoanthropologists has been fueled more by visceral observations of modern hunter-gatherers than by analytical support. While a handful of researchers had written about other ways in which Plio-Pleistocene hominins *might* have gone about creating the patchy archaeological landscape we find today, only one actually tested his hypothesis analytically (Potts 1988). It was not until relatively recently that Jeanne Sept finally acknowledged that the lack of a basic understanding of assemblage formation was the proverbial elephant in the corner: "…the extent to which the concentration of debris at archaeological sites was conditioned by the interplay between habitat structure and socioeconomic organization remains an open question" (1992:204). While I would be the first to admit that this remains an open question, the results of SHARE better our understanding of the interplay between archaeological landscape structure and the structures of habitats and social systems.

The first step has been to strip away most of the unfounded assumptions borrowed from modern human analogues, including central place foraging, nuclear families, male provisioning, group hunting/scavenging, and division of labor. Despite these purposeful omissions, we still see examples of artificial artifact distributions that have the same *qualitative* characteristics as empirical Plio-Pleistocene archaeological distributions. Thus, SHARE demonstrates that the omitted modern human characteristics are not necessary to explain Plio-Pleistocene distributions in all cases. In other words, while central place foraging offers one possibility, it does not offer *the only* possibility. Given enough time and certain ecological conditions, even asocial foragers using routed foraging and random walks in place of central place foraging can create artifact concentrations that might otherwise be interpreted as hominin "sites."

When working in behavioral *terra incognita*, we must be vigilant to avoid applying to Lower Paleolithic landscapes "overbuilt" amalgamations of influential (and seemingly insightful) observations of modern human foragers, especially when a more parsimonious model predicts important characteristics of the archaeological record to the same extent. In short, the artificial archaeological results of SHARE should prompt Paleolithic archaeologists interested in interpreting Plio-Pleistocene distributions to sharpen Occam's razor (explanatory entities should not be multiplied beyond necessity) and put it to good use on their models of circumstance.

Ecological factors facilitate, but do not determine, the evolution of food sharing

> "To understand the direction human social evolution has taken it is necessary to examine the ecological context in which it has occurred." [Foley and Lee 1996:57-58]

It looks as if Foley and Lee were on to something, because the results of SHARE demonstrate that ecology can play an important role in social evolution, especially when hominins are modeled as relatively simple foragers. However, this statement is not meant to argue—implicitly, or otherwise—that ecological conditions alone *determine* the success of one trait over another. Rather, in the case of SHARE, certain levels of ecological patchiness *facilitate* the evolution of altruistic food sharing among socially-inept agents by structuring metapopulations into evolutionarily meaningful trait groups, or, in the parlance of nonlinear dynamical systems, it places them in a basin of attraction that often leads to the evolution of altruism. Of course, ecological patchiness is not the only variable of interest, and there are many ways to structure demes culturally. Boehm's research on the egalitarian syndrome (1999) and emergency decision making (1996) provide two examples of cultural mechanisms that can reduce within-group variability while increasing between-group variability. In addition, one of Boyd and Richerson's research interests, conformist cultural transmission, provides another potentially powerful cultural mechanism that can act independently of ecological patchiness to increase between-group differences while homogenizing the strategies displayed within any group (Richerson and Boyd 2005). For the time being, SHARE has purposefully left these sorts of sophisticated cultural abilities off the brief list of what were meant to be very simple assumptions. And yet, even without any of these cultural mechanisms (which may or may not have been important during the Plio-Pleistocene) we still see the evolution of altruistic food sharing in a number of scenarios in SHARE due in large part to the level of ecological patchiness. So, while I feel comfortable concluding that it is necessary to consider the role that ecology might have played in social evolution, I do not think ecology's role should ever be considered *deterministic*.

7.2 Future directions

In many ways, the version of SHARE discussed here marks only the beginning of a promising modeling endeavor that certainly does not lack for intriguing tangential research avenues. While this elegant model teaches us much about the significance of our own presumptions, it is limited in what it can address in its current incarnation. Therefore, before closing the book on the results of the initial version, I would like to briefly discuss a few of the related research questions this model will be used to address in the future.

Technology matters

> "To explain the formation of the early archaeological record, a model must somehow account for the range of sites encountered…Furthermore, such a model must not only explain the artifact densities encountered, but must also deal with stone transport systems indicated by technological evidence at individual sites." [Schick 1987:795]

The version of SHARE discussed here addresses the first of Schick's mandates—the range of artifact densities across space. However, it does not consider the technological evidence preserved in assemblages. The current version of SHARE cannot address this issue simply because artifacts are modeled as generalized objects that do not vary and do not have life histories. That is, in SHARE there is no representation of the variety in Lower Paleolithic artifact forms (manuports, choppers, flake tools, etc.). The artifacts deposited in SHARE are the same regardless of when they are dropped or what behavior the hominin agent is engaged in at the time of deposition. This means that a hominin agent will deposit the same type of artifact whether it is feeding on a carcass, asking for help, or wandering around aimlessly. In future versions of SHARE, I plan to allow for some diversity in artifact types and to correlate particular types of artifacts with certain behaviors, thereby setting the stage for an analysis of how tool function affects patterns in the diversity of artifact types across space and through time.

Currently, the generalized artifacts in SHARE do not undergo reduction from cobbles to choppers to flakes, for example, nor can they be "recycled" or moved to a secondary location. In short, each artifact agent has a very simple life history: it gets dropped, and that is all. But by coupling the abilities to reduce and reuse stone tools with a wider variety of artifact types in future versions of SHARE, it will be possible to compare measurable technological aspects of artificial assemblages with those of empirical, time-averaged concentrations. These additions to SHARE could satisfy the second half of Schick's two-fold mandate for a successful model of Plio-Pleistocene cultural material.

No bones about it

Following previous work by Schick and Potts, I have concentrated mainly on modeling the deposition of stone artifacts. Although the artifact agents in SHARE are generalized enough not to exclude animal bones, the model does not include any special rule to increase artifact deposition rates immediately after carcasses are encountered, for example. An explicit representation of bones would add much to SHARE, for what is distinctive about many Plio-Pleistocene “sites” is a strong spatial association between bones and stones. Thus, future versions of SHARE could be used to address the zooarchaeological consequences of ecological patchiness and of food sharing. For example, can a neutral model yield nonrandom spatial concentrations of both lithic and bone artifacts in excess of the background signal? Or must hominin agents employ specific transport rules in order to create an archaeological landscape that is qualitatively different from that formed by natural animal deaths and stochastic artifact deposition? If so, what are those transport rules and what spatial signature do they leave in the archaeological landscape? In so far as stone tools end up being associated with carcasses that occur in or near patches of closed habitat more regularly, a null model might adequately predict Type C assemblages, but this remains to be demonstrated. In any case, such a model would require some minimal assumptions about transport of animal parts, akin to those that I made for the transport of stone tools. However, in the case of carcass transport one would have to address to the issue of whether hominin agents should obtain meat by scavenging and/or by hunting. Regardless of the minimal assumptions one uses, it would be interesting to see whether these two procurement strategies (and all of their variants), which have been polarized in the anthropological literature, would yield distinguishable archaeological landscapes. It is quite possible that they might not, and this would be of great interest.

Natural site formation processes and Z

SHARE currently represents artificial archaeological landscapes in only two dimensions. Because SHARE does not model natural deposition or erosion processes of any kind, the artificial archaeological data it yields have no vertical extent, no depth below datum (Z). It is as if all of the artifacts deposited through each simulation run accumulate on just one constant paleosol, which is never buried by later sediments or eroded by wind or water. This characteristic makes SHARE useful for studying the formation of "living floors," but it does not allow the study of vertically diffuse distributions. Therefore, in order to learn more about how regional variations in natural deposition rates can concentrate artifacts *vertically*, it will be necessary to represent artificial landscapes in three dimensions. Conducting experiments with a future version of SHARE in which geologic deposition and erosion rates are varied either stochastically or regularly across space and through time will allow us to build inferences about the vertical distributions of Lower Paleolithic artifacts in much the same way that the present study has informed archaeological inferences of horizontal concentrations. In this way, I expect future work with SHARE to extend earlier simulation work on time-averaged assemblages by Behrensmeyer and Chapman (1993), but within an agent-based framework.

The selective influence of information sharing

> "…any group with members that were able not only to exchange food but also to exchange information would have gained a critical selective advantage over all the rest [of the groups]." [Isaac 1978a:106]

Here, Isaac provides yet another intriguing hypothesis worthy of testing with a formal model. The commodity that foragers share in the agent-based model discussed here takes the form of procured but unconsumed food—i.e., energy. However, things other than material goods can be shared among group members. One such commodity is information about the location and condition of food resources rather than food resources, themselves. Because information is more easily gotten than large stores of food, virtually everyone can participate in the sharing of information, even if the information concerns where *not* to forage or which strategy *not* to use. Theoretically, the costs associated with sharing information about the condition of food resources as well as the benefits of receiving that information will be quite different from those associated with sharing procured food directly. Sharing information about food might entail less of a cost on the donor than sharing food itself, but it might provide less of an immediate benefit to the recipient as well. As a result, the evolutionary dynamics of sharing information about both the location and condition of food resources would probably differ from those documented here for sharing procured energy. Isaac hypothesizes that those groups who could share both food and information would outcompete all other groups. While this seems like a reasonable hypothesis, it remains to be tested analytically. There might be some levels of ecological patchiness in which it actually hurts altruistic food sharers to know of food resources elsewhere, as travel to those locales might bring them into contact with selfish cheaters more often then if they stayed put. Although a finding such as this would seem counterintuitive, future versions of SHARE might elucidate how a higher level of mobility, fueled by the sharing of information about non-local resources, actually benefits the selfish alleles in a metapopulation.

7.3 Coda

> "It is healthful for anthropologists to tell biologists that their ideas are too simple to explain the really important qualities of human social behavior, and for biologists to tell anthropologists that they will never have a satisfying explanation of that behavior in the absence of evolutionary theory and population biology." [Wilson 1979:521]

This paleoanthropological modeling project provides addition by subtraction. The fact that even simple food sharing behaviors can sometimes evolve in a metapopulation of solitary foragers teaches us something new about the between-group selective power of ecological patchiness. Hence, SHARE elucidates an important coupled hominin-environmental relationship that could not have been discovered without the aid of null modeling. Likewise, the discovery that concentrations of artifacts which approximate "home bases" can be formed by solitary agents using only routed foraging (and random walk) strategies also would not have been possible without a null model of hominin behavior that, in the interests of exploration and experimentation, eschewed conventional assumptions such as central place foraging. Although arguing that our current behavioral reconstructions incorporate unnecessary components does not provide a better model of circumstance, it allows us to reengage a whole suite of questions previously overlooked by researchers who believed that evolutionary and archaeological explanations required more sophisticated behaviors on the parts of early hominins. As Wilson alludes, it is healthy for anthropologists to compare their models to those in biology, and to constantly question the elegance of their behavioral reconstructions. This is especially true for those of us working with the inherently fragmentary record composed of the earliest archaeological materials, for it is famously difficult to disprove complicated hypotheses with incomplete data sets. Using agent-based null models as behavioral laboratories not only serves as a way to test the logical necessity of our presumptions, but also provides a framework in which we can generate more parsimonious explanatory models "from the null-up." I have begun this process for one hominin behavior—altruistic food sharing—and I invite others to try their hands at this methodology. By further blurring the lines between anthropological and biological models we can provide paleoanthropological interpretations with more appropriate archaeological inferences; inferences *generated* from controlled, repeatable experiments, not *borrowed* from living primates. In the end, all of this exploring brings us back to the empirical archaeological record with which we started, this time with a better appreciation of the behaviors that *could* have been responsible for the formation of Lower Paleolithic archaeological landscapes.

> "And the end of all our exploring
> Will be to arrive where we started
> And know the place for the first time." —T. S. Eliot, *Little Gidding*

APPENDIX A

A list of the 101 nine-digit random number seeds used in the experiments presented in section 5.3.

480207697 387946597 562954596 706570560 153768594
107032492 291582303 847543645 223575322 515092991
211370273 993004240 829834582 114986308 294011848
570327055 199468767 824121821 168958591 697278728
914444276 460858606 901563124 862353590 341715842
879100302 427629052 824473689 414065985 149242076
479534983 952929870 977920184 707147854 340451649
150638273 208860618 473846591 226625016 412694009
643464910 397544150 436894948 645751139 324882399
276943583 454785306 492343373 717540840 513029084
817035617 420182937 517243686 698193080 562460280
892838231 608950182 909940158 566740409 163089824
786273456 165960130 369851757 875855019 856475327
466983559 326745981 675302925 570321321 997167932
798756187 524378601 835546058 973045583 850676593
129885712 996995045 972605026 614985284 966797062
656927695 391605438 993731485 223775709 607726695
371758121 616971089 823589027 305608612 204625424
384097197 310253808 307398660 358360113 245832693
628147733 456497627 280937154 381257091 896190312
561929304

NOTE: The source code for SHARE is freely available from the author, as are the object libraries used to run it (www.swarm.org). Please contact me directly if you are interested in running SHARE on your machine.

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