

UC Davis

UC Davis Previously Published Works

Title

Intra-group resource transfers: Comparative evidence, models, and implications for human evolution

Permalink

<https://escholarship.org/uc/item/14b6b6zk>

Author

Winterhalder, Bruce

Publication Date

2001

Peer reviewed

- Symons, D. 1979. *The Evolution of Human Sexuality*. Oxford: Oxford University Press.
- Tooby, J., and L. Cosmides. 1992. The psychological foundations of culture. In *The Adapted Mind* (J. Barkow, J. Tooby, and L. Cosmides, eds.), pp. 19–136. New York: Oxford University Press.
- Trivers, R. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.
- von Neumann, J., and O. Morgenstien. 1953. *Theory of Games and Economic Behavior*. Princeton, NJ: Princeton University Press.
- Washburn, S., and C. Lancaster. 1968. The evolution of hunting. In *Man and the Hunter* (R. Lee and I. Devore, eds.), pp. 293–303. New York: Aldine Press.
- West-Eberhard, M. 1975. The evolution of social behavior by kin selection. *Quarterly Review of Biology* 50:1–33.
- Whiten, A., and R. Byrne, eds. 1997. *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge: Cambridge University Press.
- Winterhalder, B. 1986. Diet choice, risk, food-sharing in a stochastic environment. *Journal of Anthropological Archaeology* 5:369–392.
- Winterhalder, B. 1997. Gifts given, gifts taken: the behavioral ecology of nonmarket, intra-group exchange. *Journal of Archaeological Research* 5:121–168.
- Wrangham, R., and D. Peterson. 1996. *Demonic Males*. New York: Houghton Mifflin.

Intragroup Resource Transfers Comparative Evidence, Models, and Implications for Human Evolution

Bruce Winterhalder

Introduction

The notion that early hominid social groups might have engaged in routine sharing of meat or other highly valued food-stuffs apparently is seen by paleoanthropologists as a bit romantic and wholly naïve. The site-level empiricism that fueled Isaac's (1978a, 1978b, 1984) promotion of the idea has given way to taphonomic caution (Binford 1985). Alternative interpretations—such as the putative living sites may have been stone caches used briefly for secondary processing of animal parts removed from kill sites (Potts 1984)—have become available. The ethnographic analogy with extant hunter-gatherers that seemed to Isaac and others to offer decisive comparative confirmation is now viewed with skepticism. Prehistorians no longer willingly suffer the “tyranny of the ethnographic record” (Wobst 1978).

The rejection of sharing as an important feature of hominid socioecology is unfortunate. I say this even as one who endorses the cautionary, methodological lessons of taphonomy and who applauds certain kinds of skepticism about ethnographic analogy. Binford and other critics almost certainly were correct about weaknesses in Isaac's argument (see Blumenshine 1991). However, they almost certainly were mistaken in their negative appraisal of his emphasis on sharing. There are other and ultimately much better reasons than those offered by Isaac to think that routine sharing might have characterized hominid subsistence adaptations. Those reasons, their linkage to archaeologically visible patterns of food selection (e.g., consumption of meat versus vegetable items), and some of their implications are the subject of this chapter. The topic is important because it is central to socioecological reconstruction of hominid subsistence behavior and evolution, the larger subject of this volume.

I begin with the presumption that hominids, whatever their species, were *social* foragers, living in relatively stable, multiadult units. The size, composition, and turnover in the residential group, the subgroups that formed for task-specific activities, and other features of social organization presumably were no less diverse than those known from primate studies or ethology more generally. I also begin with some semantic conventions. I will use *transfer* as a generic, inclusive term for movement of food and other goods or services among individuals. Transfer thus refers broadly to behaviors described as scrounging, sharing, giving and taking, distribution, exchange, trade, etc. A key lesson of recent behavioral ecology work is that such transfers can take various behavioral forms for diverse evolutionary reasons. We can no longer think of food movement within a group as one, undifferentiated behavior; the food-sharing hypothesis has become a bundle of analytically distinct possibilities. We will be unable to talk intelligibly about hominid socioecology unless more specific terms become aligned with the variety of particular forms transfer behaviors can take (Winterhalder 1996c; Hames 1998). Throughout the remainder of this chapter I will use quotations ("sharing") when I refer to the broad and undifferentiated use found, for instance, in most ethnographies.

Evolutionary Concepts and Models Explaining Transfers

Through the same period that paleoanthropologists grew wary of the "sharing" hypothesis, behavioral ecologists were developing a variety of tools for analyzing transfers. They show that most evolutionary mechanisms have the potential to generate intragroup food allocation (reviews in Kaplan and Hill 1985b; Winterhalder 1996b, 1996c). I begin with these models rather than case studies because concepts and terminology developed in this literature are necessary to accurately and succinctly describe and interpret the examples that follow.

Tolerated theft

One of the most basic of these models is tolerated theft (Blurton Jones 1984, 1987), or scrounging (Giraldeau et al. 1990). Tolerated theft and the subsequent models reviewed here begin with an assumption about the resource environment. One or more food items important to a social forager occur in divisible *packets* of intermediate size, susceptible to transfer. In physical terms a packet is an item or patch larger than can be consumed in a few mouthfuls. It also must be smaller than would sate all members of the group. In analytical terms, it is a resource unit large enough to be subject to diminishing marginal value (fitness or utility) to an individual consuming it. Holders of a packet garner a weak form of possession (Kummer 1991). Possession itself implies a further constraint on size; a packet must be a resource that can be clutched, carried, or otherwise defended or sequestered from group members. For hominids, a 6-kg mammal meets this condition. Ripe fruit scattered throughout the canopy of a large tree that is encountered by the entire group while foraging together probably does not. However, the same fruit located by an individual and carried in quantity back to a residential camp in a string basket presum-

ably would meet it. Encounters with this type of resource are likely to be unsynchronized and unpredictable to greater or lesser degree.

From the perspective of the fortunate individual who located and is growing sated from consuming a packet, its surplus or residual portions rapidly diminish in value. Those same residual portions have a high value to a hungry onlooker. The possessor has little incentive to defend what the other has high incentive to contest and acquire. The fitness of both individuals is enhanced if harmful conflict without compensating benefits can be avoided. Evolutionary self-interest is expressed in this circumstance as willingness to hazard forceful acquisition of high value food portions and as reluctance to mount a defense of portions with limited value. Holders of a packet will cede low-value portions, and supplicants will take them until there is an equilibrium of their interests. Winterhalder (1996a) uses marginal analysis to show in greater detail how the balance of costs and benefits affecting tolerated theft are affected by resource availability and qualities, individual procurement behavior, and group size.

Producing, Scrounging, and Opportunism

Behavioral ecologists have given tolerated theft, or scrounging in their terminology, close analysis using game theory (Giraldeau et al. 1990; Caraco and Giraldeau, 1991; Vickery et al. 1991). This technique aids in understanding the complex social dynamics that can arise when the optimal behavior of an individual depends on how others in the group respond (Smith and Winterhalder 1992).

In a representative model there are three tactics (Vickery et al. 1991). *Producers* expend the time and energy to locate the food packets they consume while *scroungers* avoid these costs by appropriating portions of the packet that a producer has already located. Scroungers will do well as long as they are rare. However, as they increase in frequency, more and more of them compete for the take of fewer and fewer producers, and their relative advantage disappears. This creates frequency-dependent selection—each tactic has the advantage when it is uncommon—generating a stable equilibrium mix of producers and scroungers in the group. A third, *opportunist* tactic produces or scrounges as the occasion arises but with a slight handicap relative to the two pure options. This handicap arises because the mixed or generalist tactic likely entails extra costs or compromises in conceptual skills. Three variables determine the equilibrium mix of the three tactics: producer priority (the degree to which the individual locating a resource can monopolize its consumption), opportunists' handicap, and group size.

If the opportunist handicap is substantial, opportunists will be eliminated from the equilibrium. Producers and scroungers will occur together as long as the scroungers' share of a packet is greater than the inverse of group size (or, $1/n$). If the scroungers' total share is less than $(1/n)$, producers will eliminate scroungers. There are two important effects of these conditions. Greater producer priority in the consumption of a packet lowers the likelihood that scroungers will occur alongside producers. Larger group size increases the likelihood they will occur. On the other hand, if the opportunists' handicap is not substantial, then they enter the equilibrium mix, either alone or in combination with producers or scroungers. As the opportunist handicap diminishes to zero, opportunists will come to dominate the group.

The boundary conditions that mark shifts among these combinations of tactics are best appreciated graphically (see Vickery et al. 1991, Figure 2; Winterhalder 1996c, Box 2). Generally, the model makes the important point that groups of social foragers will evolve to contain opportunists and/or scroungers along with producers. They will do so under a wide variety of conditions. The mix may be expressed in two ways: (1) by the relative proportion of individuals in a group, each of whom practices one tactic exclusively (e.g., three producers and three scroungers); or (2) by the frequency with which all group members practice each tactic (e.g., each is a producer 50% of the time and a scrounger 50% of the time).

Risk Sensitive Subsistence

In the ethnographic literature on hunter-gatherers, it is commonplace to see the proposal that intragroup food transfers lower the likelihood of subsistence shortfalls. Group members who pool and divide their catch consume a daily ration of food that is subject to much less variance than the daily yield of their individual foraging efforts. The importance of pooling (or "sharing") grows as the group becomes increasingly dependent on large, unpredictably acquired packets. Its effectiveness can be quite high in small groups, as long as encounters with packets are not synchronized among group members (Winterhalder 1986, 1990; Winterhalder et al. 1998). Unpredictability in the subsistence quest sharply increases the marginal value of food to the temporarily unlucky, heightening the benefit-to-cost differentials that promote food transfers.

Pseudo-reciprocity or By-product Mutualism

In pseudo-reciprocity (Connor 1995), individual A undertakes a behavior for benefits that will be enhanced if, intentionally or inadvertently, individual B can be induced to cooperate and share in it. Mesterton-Gibbons and Dugatkin (1992; Dugatkin et al. 1992) call this situation by-product mutualism. Pseudo-reciprocity differs from altruistic reciprocity (Trivers 1971) in that the immediate structure of the situation guarantees that cooperation produces a relative gain to both the donor and receiver. There is no temptation to cheat (see "altruistic reciprocity," below) because a cheater who opts out of reciprocity when the occasion arises does so at its own expense. For example, when initiating pursuit of a large prey item a predator might signal the prey's presence to an unrelated conspecific. If joint pursuit has a significantly higher likelihood of success, the signal giver who shares this opportunity realizes a net gain along with the benefactor. Brown (1983: 30–31) argues that by-product mutualism may be common in nature; Alvard (this volume) provides a more complete review.

Altruistic Reciprocity

In reciprocal altruism (Trivers 1971) individual A performs an action at some small cost to itself but at a greater benefit to individual B. *Should* B reciprocate, both individuals realize a net fitness gain from the paired actions and reciprocity will

evolve by natural selection. However, the structure of the situation offers no guarantee that B *will* reciprocate in the future when their roles are reversed. A self-interested B may do better by cheating; accepting the benefit but avoiding the reciprocity when A is in need. Such cheating will impede the evolution of reciprocally altruistic acts except under certain circumstances (see below). Because the classical ethnographic vision of hunter-gatherer "sharing" is one of reciprocal altruism, this problem of defection by cheaters or free riders has made behavioral ecologists skeptical of some ethnographic claims about it (Hawkes 1992a).

The literature on reciprocal altruism is large and highly technical. Classic papers by Axelrod and coauthors (Axelrod and Hamilton, 1981; Axelrod and Dion, 1988), and more recent reviews by Sigmund (1993) and Nowak et al. (1995), provide authoritative and accessible summaries. The tactic of tit-for-tat reciprocity enjoins cooperation as long as you encounter cooperation and defection on encountering defection. It will expand and sustain itself in a population only (1) after group members reach a certain threshold frequency of reciprocal (cooperative) interactions; and (2) under certain, narrowly defined environmental conditions. Initially, these restrictions appear to create a stringent impediment to the evolution of cooperation. However, it has been shown that tolerated theft (Blurton Jones 1984, 1987), kin selection (Axelrod and Hamilton 1981), and the "clustering" of reciprocators (Nowak and Sigmund 1992) all can prime the evolution of reciprocal altruism, thus obviating condition (1). With respect to point (2), the conditions required to sustain reciprocity are, in fact, common among social foragers. Individuals must: (a) encounter and interact with one another frequently; (b) experience regular role reversals between giver and taker; (c) face an indefinite future of such interactions; (d) recognize one another and draw on memory to exclude or sanction cheaters; (e) live in a small group; and (f) make few errors (see Axelrod and Dion 1988; Wilkinson 1988). The ability to establish social norms leading to punishment of defectors (and of individuals who tolerate them) helps as well (Boyd and Richerson 1989, 1992). For instance, Nettle and Dunbar (1997) use a simulation to show that stable reciprocity evolves much more easily when reciprocators are able to use language dialect differentiation to recognize one another and to exclude cheaters.

Since the triumph of tit-for-tat, more effective and more cooperative tactics have been identified (Nowak and Sigmund 1992, 1993). Once tit-for-tat reciprocity establishes itself in a population, it will be supplanted in sequential fashion by these more effective tactics. Self-interest can "turn the table" on cheating. Under the right conditions, "Cooperation evolves even in a totally selfish population. . . . Reciprocity flourishes in a variety of environments, and it even acts to create an environment to its taste. It is a self-promoting policy" (Sigmund 1993: 201).

Trade/Exchange and Showing Off

Transfers of food might also represent flows within exchange networks involving other (not-in-kind) resources or services. If individuals hold different resources or capacities subject to diminishing marginal returns, such exchanges will occur because they are advantageous to both parties. Transfers completed simultaneously in both directions are relatively straightforward. Both parties presumably gain an

immediate advantage. If there is a delay before a return completes the transaction, then analysis must take account of the possibility of cheating and that of discounting (Rogers 1994).

Hawkes (1991, 1992b, 1993a, 1993b, this volume; see also Dwyer and Minnegal 1993; Hill and Kaplan 1993; Thiel 1994) has developed an exchange proposal within the rubric of sexual selection: the "show off" hypothesis. According to Hawkes, the potential for reproductive advantages will lead some male foragers to seek high-prestige, high-variance game resources. Although obtained sporadically, these game represent bonanzas of highly desired foods. When distributed widely, they capture social attention for their provider. Hawkes argues that this attention can be exchanged for enhanced fitness. In effect, some males trade a willingness to provide a public good—the capture and group wide distribution of an especially attractive food—for indirect, diffuse, and sometimes delayed social advantages accorded them by the group members. This show off proposal has the advantage that it collects under one model three routine observations about hunter-gatherers. It helps explain (1) why large game is pursued, (2) why some males might find it advantageous to contribute more resources to transfer networks than they receive from them, and (3) why males typically hunt and females gather (when both most likely could increase their foraging efficiency by mixing these activities to a greater extent; see Hill et al. 1987).

Kin, Interdemic, and Cultural Selection

A complete behavioral ecology explanation undertakes a dual obligation to describe (1) the ecological setting in which a behavior is expected and (2) the evolutionary process(es) thought to generate it. The first obligation generates models of circumstance. These specify how environmental constraints determine the costs and benefits of various behavioral tactics. Meeting the second obligation requires models of mechanism. These specify the processes by which selection acts on the evolution of the behavior. Attention to mechanisms is especially important because not all costs and benefits that might be cited in a functionalist argument (Elster 1983) are likely to have causal salience in an evolutionary analysis.

In a separate article (Winterhalder 1996b), I provide a concordance between models of circumstance and mechanism that have been proposed for explaining food transfers. It reveals that we do not yet have models of circumstance specifically associated with some potentially important evolutionary mechanisms. Among them are kin or nepotistic selection, group-level or interdemic selection (Wilson 1998), and cultural selection or dual inheritance models like those developed by Boyd and Richerson (1985) and Durham (1990).

Empirical Evidence: Ethological and Ethnographic

From bats to killer whales to extant human hunter-gatherers, field and experimental evidence indicate that food transfers are common in social foragers. Transfers take a variety of species- or population-specific forms. In the survey that follows, I have two reasons for beginning with cases taxonomically distant from our own

order (Table 14.1). The minor one is that these cases draw attention to an ethological literature full of unrealized comparative possibilities. The major reason is that they give substance and specificity to the theoretical models just examined.

The Ethology of Social Foragers

Songbirds

Colonial nesting cliff swallows (*Hirundo pyrrhonota*) forage in loose, widely spaced groups for compact aerial clusters of insects (Brown et al. 1991). Poor foraging conditions on cool, calm days stimulate a distinctive squeak call that individuals use to alert related and unrelated conspecifics that an insect swarm has been discovered. Experimentation shows that such calls increase when birds are presented with insect swarms (flushed from ground cover by investigators), and call playbacks quickly draw nonforaging birds to the source. By actively recruiting other birds to their discovery, individuals presumably are able to track the swarm longer, enhancing their own foraging success. If this interpretation is correct, use of the squeak call represents an instance of pseudo-reciprocity.

In two separate laboratory experiments with flocks of spice finches (*Lonchura punctulata*), Giraldeau et al. (1994) increased the proportion of scroungers in the group (treatment 1) and, separately, elevated the difficulty faced by producers in obtaining a food packet (treatment 2). Scroungers were conditioned to eat from the food discoveries of producers, as happens under natural conditions, but to avoid foraging themselves. Producers were conditioned to locate food packets. The authors found that birds would respond to the first treatment by shifting toward producing. They responded to the second by shifting toward scrounging. In effect, spice finches are able to opportunistically change their foraging tactics as a function of local socioecological conditions and the tactics of fellow flock members, as predicted by producer-scrounger models.

Bats

Vampire bats (*Desmodus rotundus*) exhibit one of the better studied instances of reciprocity "sharing" (Wilkinson 1987, 1988, 1990). Their feeding ecology—nightly foraging from a central roost for a mammalian blood meal—is unusually precarious. They will die from weight loss and metabolic collapse if they go more than 60 hours without a meal. Yet, individuals fail to secure a meal on 7% to 30% of nights, the higher figure characteristic of inexperienced juveniles. Based on the lower 7% nightly failure rate of adults, annual mortality should be about 82%. It actually is around 24%.

Food transfers forestall the predicted level of starvation in this species. Individuals that have fallen to a less than 24-hour metabolic reserve solicit and receive regurgitated blood from roost mates whose foraging was successful. Both relatedness and long-term prior association without relatedness lead to this transfer behavior. Unrelated individuals seem to form stable, dyadic relationships, "individuals who regurgitate almost exclusively to each other" (Wilkinson 1990: 80). Careful study

Species; Citation; Study Type	Effective Subsistence Environment	Social Organization	Transfer Behavior	Inferred or Known Evolutionary Mechanism
Common vampire bat (<i>Desmodus rotundus</i>); Wilkinson (1990); Naturalistic and field experiment.	High risk foraging conditions; bats cannot survive more than 2 consecutive nights without a meal, yet 7% to 30% fail to feed on any given night.	Long-term, fluid social associations among 8–12 females, comprising several matriline, and an equal number of offspring. Dyadic preferences among nonrelated females.	Unsuccessful foragers solicit regurgitated blood meal; sharing occurs preferentially among long-term roost mates who may or may not be related. Unrelated roost mates appear to develop a sharing "buddy system."	Transfers due to a mix of kin selection and reciprocal altruism, the latter predominating.
Killer whales (<i>Orcinus orca</i>); Hoelzel (1991); Naturalistic.	Coordinated group foraging on seals (2%) and sea lions (97%), with preference for restricted capture sites and efficiently captured prey, most often pups.	Three pods observed, 2–7 individuals, composed of two adults (male and/or female) and subadults. Close genetic relationship known for one pod; inferred for remainder.	Within-pod food-sharing could be confirmed for 27% to 86% of captures, depending on pod. One individual dominated the active hunting and capture, then provisioned others.	Transfers enhance inclusive fitness of related group members in an environment in which high quality feeding sites are limited. No discussion of other possible mechanisms.
Rhesus macaques (<i>Macaca mulatta</i>); Hauser and Marler (1993a, 1993b); Naturalistic observations and experimentation on free-ranging, provisioned populations, Cayo Santiago Island.	Although provisioned daily for over 50% of their diet, macaques also forage for coconut; small fruits such as berries; insects; and flowers.	Studies were conducted on 10 focal females and 12 focal males living in group "L," which totaled approximately 300 individuals.	Distinctive "calling" vocalizations (warbles, harmonic arches, chirps) given on discovery and possession of rare, preferred food patches; calls attract nearby individuals.	Kin selection suggested females call rate correlated (positively with number of nearby kin, who then may share in it or perhaps provide coalition defense of it); reciprocity altruism is suggested by social sanctions directed at hoarding.
Common ravens (<i>Corvus corax</i>); Heinrich and Marzluff (1995); Naturalistic and experimental field observations.	Difficult winter scavenging of partially consumed moose or deer carcasses, an unpredictable and short lived but very rich feeding opportunity.	Normally territorial, during the winter ravens actively communicate location of such a feeding opportunity, aggregating up to 100 or more unrelated individuals from distances as great as 30 miles.	Juvenile and vagrant ravens exchange information about feeding sites through communal roosts and soaring displays.	Reciprocal altruism: "... food-sharing turns out to be a successful strategy for maximizing survival in an environment where food is sparsely and unevenly distributed in space and time, and where young birds must cooperate in order to defend and feed on a carcass at the same time" (p. 342).
Cliff swallow (<i>Hirundo pyrrhonota</i>); Brown et al. (1991); Naturalistic and experimental field observations.	Signaling behavior during breeding season more likely if foraging conditions for aerial insect swarms are poor (calm, cool, sunless days), those in which insect swarms are relatively inactive.	Colonial nesting, social pair-sines; kin relationships in the foraging groups that practice squeak calls are unknown.	A vocal "squeak call" is used exclusively to recruit conspecifics to food discoveries when foraging in flocks spread over a wide area, away from the colony. This call augments passive information transfer at the colony itself.	Pseudoreciprocity: individuals issuing a call probably benefit from enhanced foraging success, as conspecifics make it easier to track or reestablish the position of the erratically flying swarms.
Chimpanzee (<i>Pan troglodytes</i>); Stanford (1995, 1998); Naturalistic field.	Hunting of small mammals (red colobus monkeys make up 80% of the prey) and meat consumption focused on relatively lean, dry-season months, when food shortages lead to weight loss.	Loosely structured, fission-fusion residential groups, in which hunting parties may vary from 1 to 35 individuals, predominantly male.	Meat may be "exchanged" for political support and/or sexual access; production of surviving offspring may be greater for females receiving more meat.	Exchange of valuable food for indirect and direct fitness-enhancing benefits.
Chimpanzee (<i>Pan troglodytes</i>); de Waal (1989); Seminatralistic enclosure, provisioning experiments.	Provision of concentrated food bundles of medium attractiveness.	24 m x 30 m outdoor colony of one adult male and eight adult females with subadults, totaling 19 animals, adults predominantly unrelated.	Of 4,653 food interactions observed, 50.4% were food transfers. Most transfers resulted from relaxed claims and cofeeding.	Reciprocity of food-for-social favors, such as grooming, indicating a concept of "trade." Food transfers (selective relinquishment) among adults showed a high level of long-term symmetry. Short-term transfers were mediated by social relationships (e.g., were not necessarily tit-for-tat reciprocity, from one event to the next). Tolerated theft not supported.
Spice finch (<i>Lonchura punctulata</i>); Giraldeau et al. 1994; Laboratory, experimental.	Experimenters manipulated either (1) the proportion of scroungers in a feeding flock, or (2) the cost of being a producer.	Spice finches form egalitarian social groups, in which they "scramble" to take advantage of each other's food discoveries.	Birds adjusted their use of producing and scrounging, as predicted, in response to local foraging conditions.	Individual-level selection, creating behavioral plasticity sensitive to rate-maximizing options under local socio-ecological conditions.

Table 14.1. (continued)

Species; Citation; Study Type	Effective Subsistence Environment	Social Organization	Transfer Behavior	Inferred or Known Evolutionary Mechanism
Lion (<i>Panthera leo</i>); Packer et al. (1990); Naturalistic observations.	Seasonally abundant migratory game (Thomson's gazelle, wildebeest, zebra) alternating with scarcity (warthog and buffalo); high levels of inter-pride competition.	Stable, territorial prides of related females, with fission-fusion formation of situation-specific subgroups (foraging groups, reproductive crèche, etc.).	Egalitarian consumption of prey by members of foraging groups, irrespective of participation in pursuit.	Cooperative hunting apparently a secondary consequence of reproductive patterns and grouping for defense of cubs and territory among related individuals.
White-faced capuchin monkey (<i>Cebus capucinus</i>); Perry and Rose (1994), Rose (1997); Naturalistic observations	Tropical dry forest; seasonal rainfall and differences in food and water availability between sites; occasional nest predation on squirrels and coatis pups.	Stable multimale, multifemale social group; female bonded, without exclusive male-female consortships.	At Santa Rosa, a low food site, the acquirer generally consumed all of a coatis pup; at a richer subsistence site, Lomas Barbudal, the capturing capuchin became sated and residual portions were subject to transfer.	Begging (tolerated food transfer to "theft") by individuals attracted to the kill; weak or nonexistent kin or dominance effects on likelihood of meat transfer.

documents that this species meets the conditions necessary for the evolution of reciprocal altruism: stable, long-term association among reciprocators; regular, donor-recipient role reversals; high short term benefit-to-cost ratio for transfers; and the ability to detect and control cheaters.

Ravens

Common ravens (*Corvus corax*) survive the New England winter feeding as scavengers from deer and moose carcasses (Heinrich and Marzluff 1995). Such feeding opportunities are rare and quite difficult to locate. They may be camouflaged by predators or covered incidentally by snowfall. Daylight is short, and ravens have the further handicap that they can eat only after the hide of a moose or deer has been breached by larger carnivores. Once located, a feeding opportunity usually is massive relative to an individual raven's requirements, but it may be ephemeral. In a scene observed repeatedly by Heinrich and Marzluff, one or two juvenile ravens flying alone will locate a dead deer or moose. Without eating, they fly off to a communal roosting site. From this assembly location, they return a few days later at dawn, leading a company of 40 to 100 other ravens who feed cooperatively for several days to a week.

It is telling that individual ravens forgo immediate feeding in order to actively communicate the location of the opportunity to a large number of nonkin. DNA studies show that such aggregations have no higher degrees of relationship than randomly captured individuals. High rates of turnover at the feeding site, the large numbers of birds involved, and their wide range reduce the odds that instances of "sharing" are reciprocated between individual pairs of birds. The roost assembly is not an ongoing social group. Heinrich and Marzluff propose that self-interested reciprocal altruism—principally for the benefits of risk minimization in an unpredictable feeding environment—operates here without stable social associations among the participating individuals. The cost of "sharing" is minimal, as an individual raven can eat its fill and scarcely dent the supply. The benefits—chiefly reduced uncertainty of subsequent meals—are great. Further, the subadults that most readily engage in this behavior must arrive at a feeding site with the force of numbers to overcome its defense by adult ravens.

Whales

Killer whales (*Orcinus orca*), observed at Punta Norte on the Argentinian coast, live in loosely structured "pods" (Hoelzel 1991). These social groups are composed of two adults (males, females, or both) and a variable number of subadult individuals (maximum observed = 5). Southern sea lions (*Otario flavescens*) constitute 97% of observed prey captures. Whales focus their hunting effort at spatially restricted sites where shallow water and bottom relief enhances success rates, and they selectively pursue sea lion groups containing pups, the most readily captured prey type. Within each pod one individual makes 70% to 100% of the active hunts and captures. Other pod members mill nearby. The hunter then joins pod mates before the group consumes the catch. Conservative estimates, based on cases observable on

the surface, indicate that between 27% and 86% of the captured prey were transferred in this manner.

Hoelzel infers that transfers occur because of genetic relationships, some of which are known and some inferred, among pod members. Subadults may be fed by a parent until they gain the experience required to effectively strand seal pups themselves, raising the inclusive fitness of the provider. Provisioning may be extended to less direct relations because good hunting sites are rare, and competition for them is more costly than cooperation in their use.

Rhesus Macaques

On Cayo Santiago, troops of rhesus macaques (*Macaca mulatta*) separate to forage. Frequently they are out of sight of one another in the foliage. Individuals, especially females, give food calls that signal discovery of a particularly rich patch of food to macaques in the surrounding area (Hauser and Marler 1993a, 1993b). Females' call rates are positively correlated with the number of kin in the vicinity, but nonkin are among those responding. When a macaque that did not signal is detected eating in one of these patches, she is aggressively punished. Hauser and Marler are able to show that, because of this punishment, nonsignalers who are detected eat less from their discoveries than those who call and share it with their fellows. However, in the rare case of a discoverer that did not call and was not detected, he or she eats more than discoverers who were joined by surrounding macaques.

The rare instance of successful hoarding shows that it is a cost-benefit temptation. The more common instances of unsuccessful hoarding (detection despite failure to call) show that social sanctions can effectively eliminate the immediate benefit and help to control frequency of cheating. Although Hauser and Marler do not explicitly compare causal possibilities, it would appear that both kin selection and reciprocal altruism are operating here.

Macaques are not unique among monkeys in these types of behavior. White-faced capuchins (*Cebus capucinus*) "share" portions of coatis pups captured from their nests (Perry and Rose 1994; Rose 1997, this volume; Table 14.1; see also de Waal 1997b on food transfers in brown capuchins). Adult, buffy-headed marmosets (*Callithrix flaviceps*) share large insects and vertebrate prey with nondescendent infants and juveniles (Ferrari 1987).

Lions

Group living, cooperative hunting, and food "sharing" in the social carnivores has made them attractive models for hominid adaptations (e.g., Thompson 1975, 1976). The same species have been subject to extensive study by behavioral ecologists (e.g., Packer and Rutan 1988). Lions make an instructive case, with a long interpretive history (see Packer et al. 1990). When game is seasonally abundant, per capita consumption and consumption variance are unrelated to foraging group size. Cooperative hunting itself provides no subsistence advantage. However, during the period of seasonal food shortages two group sizes optimize hunting success, measured as per capita intake. Lions do best either by foraging alone or by foraging

cooperatively in a group of five to six. Groups of two to four, by contrast, suffer significantly reduced intakes. Per capita success rates with different size classes of prey create this bimodal pattern.

Observations show that actual foraging group size deviates from these two optima in an interesting pattern. Individuals in prides whose total membership exceeds five or six adults can do equally well by foraging alone or with four to five others, but they very rarely are seen hunting alone. Individuals living in prides whose membership is four or fewer would do best hunting alone but nearly always are found hunting in the largest group allowed by the size of the pride (e.g., two, three, or four). In both cases, solitary hunting is avoided in favor of cooperation, even if, as in small prides, it means suboptimal capture rates. In light of this, Packer et al.'s (1990) present data indicate that female lions hunt in groups primarily to better defend themselves, their territories, and their cubs. They hunt in groups of a size that optimizes success only when that goal is consistent with defense, that is, in the larger prides. Cooperative hunting and food transfer in lions are secondary to other adaptive constraints.

Chimpanzees

Group hunting, meat-eating, and meat transfer are common among Gombe National Park chimpanzees (Stanford 1995, 1998, this volume; see also Boesch-Achermann and Boesch 1994). Hunting episodes peak during the dry season months of August and September, a period of vegetable food shortage when chimpanzees normally lose weight. Males do 90% of the hunting. Capture success grows with the size of the hunting group, from 30% for the lone individual to 70–80% for groups of 10 or more. Presence of an estrous female increases the likelihood of a hunt and, independently, an increase in the number of estrous females present increases the size of the hunting group. Meat transferred by males to females in exchange for sexual access appears also to increase female reproductive success by elevating offspring survivorship in ways not yet understood. Anecdotal evidence hints that meat transferred to other males gains their political support. Food transfers in this species appear to be sexually and politically charged matters of exchange, like those posited in the show off hypothesis. Stanford notes that one male, Frodo, was an especially prolific hunter. Like killer whales, individual chimpanzees may vary in the intensity and success of their hunting efforts.

Experimental provisioning studies by de Waal (1989) confirm the potential of chimpanzees for reciprocity. Adults provisioned with medium sized, moderately attractive plant food bundles transfer portions to others. These food movements are regular, symmetrical in frequency within dyads, and generally peaceable instances of "selective relinquishment." On a short-term basis, turn taking in such relationships frequently intersperses social favors, such as grooming, with transfers of vegetable foods. Sanctioning also occurs. "Stingy" individuals are subject to significantly more aggression from group members. Because of the not-in-kind nature of the transfers, de Waal describes them as "trade" (1989: 454).

In a follow-up study, de Waal (1997a) confirmed that reciprocity in these exchange partnerships is not due to simple frequency of dyadic association. Rather, a

applicant meets lessened resistance to a food transfer if he or she has earlier engaged in grooming the possessor. Reciprocity is contingent on earlier service from the partner. Chimpanzees apparently are keeping mental records of favors received and acting in response to a particular history of interaction. In the absence of a significant cost to the donor, de Waal stops short of calling these interactions reciprocal *altruism*, preferring instead to speak of “social exchange.”

The Ethnography of Social Foragers

The ethnographic literature on hunter-gatherer food transfers (“sharing”) is large, predominantly qualitative and, in many cases, anecdotal. It also is well known to most anthropologists. For these reasons, and because of my introductory claim that a strong argument for prehistoric food transfers can be made in the absence of ethnographic analogy, my summary of this literature will be brief. Key review articles on human food “sharing” include Price (1975), Feinman (1979), Gould (1981), Woodburn (1982), Kaplan and Hill (1985b), Smith (1988), Peterson (1993), Winterhalder (1996b, 1996c) and Hawkes (this volume). Representative ethnographic case studies of foragers and horticulturalist/foragers include those for the Pilagá (Henry 1951), the Mamaindê (Aspelin 1979), the !Kung San (Wiessner 1982), the Nata River Basarwa (Cashdan 1985), the G/wi, G//ana and Kua Basarwa of Kutse (Kent 1993), and the Kubo (Dwyer and Minnegal 1993).

The rationales for food “sharing” given by most ethnographers fall into two categories. There are functionalist claims that it enhances social solidarity or promotes egalitarianism. And, there are adaptationist arguments that it lowers the “risk” of a diet dependent at least partially on the acquisition of unpredictable resources, especially game. Only the latter possibility is clearly consistent with behavioral ecology. Although we can confidently claim that food transfer behavior is ubiquitous within extant hunter-gatherer groups, few ethnographic studies provide the kinds of data needed to evaluate specific behavioral ecology models. Most anthropological studies were conducted under the theoretical sponsorship of group-level functionalism and well before behavioral ecology models, with their more exacting data requirements, were available. I elaborate on a small set of recent studies (Table 14.2) that explicitly address one or more of the possible causal circumstances and mechanisms of behavioral ecology.

The Aché of Paraguay were mobile foragers until the mid-1970s, when they aggregated around mission settlements and took up swidden agriculture (Hill and Hurtado 1996). Periodically, they resume hunting and gathering on forest treks of several weeks’ duration, some of which were documented by Kaplan, Hill, Hawkes and Hurtado (Kaplan et al. 1984; Kaplan and Hill 1985a, 1985b; Hill et al. 1987). As predicted by scrounging, reciprocity, and risk-minimization models, the frequency of Aché transfers correlates positively with specific food qualities. Larger and more valuable foods, asynchronously and unpredictably acquired, are more frequently shared. Despite this consistency, these researchers reject tolerated theft or reciprocity as explanations because food transfers are not overtly contested or evenly balanced (cf. Winterhalder 1996a, 1996c). Instead, indirect evidence indi-

Table 14.2. Ethnographic case studies.

Group; Citation; Study Type	Effective Subsistence Environment	Social Organization	Transfer Behavior	Inferred or Known Evolutionary Mechanism
Aché Kaplan et al. (1984); Kaplan and Hill (1985a, 1985b); Naturalistic/ethnographic	Lowland subtropical forest, eastern Paraguay. Non-domesticated resources include game, honey, fruits, plant foods, and insects.	Now living in a residential settlement, Aché were until the mid-1970s mobile, band-level foragers. Data gathered from task groups of 15–28 individuals, on 1- to 2-week treks away from the settlement for hunting and gathering.	Sharing is common for highly valued resources acquired asynchronously and in packets (game, honey) and uncommon for plant foods.	Transfer behaviors are not patterned by kinship (relatedness), and while consistent with reciprocity and variance reduction, are unbalanced to a degree, suggesting delayed trade for social or reproductive benefits.
Ifabuk Betzig and Turke (1986); Naturalistic/ethnographic.	Pacific islets (western Carolines); predominantly a subsistence economy based on fishing and horticulture (taro, breadfruit, coconuts).	Fifty-six households belonging to ranked clans.	Routine interhousehold transfers of prepared foods.	Kin selection; transfer patterns generally follow expectations based on relatedness and cost-to-benefit ratios between givers and receivers.
Meriam Bliege Bird and Bird (1997); Naturalistic/ethnographic.	Small volcanic islands in the Torres Strait, subhumid tropical savanna zone; maritime foraging for marine fish, turtles, and mammals. Supplemented by yam, banana, and manioc, plus small amounts of domestic animals.	Formerly dispersed kin-based groups have coalesced to a single permanent village of 400; shortages of land put a premium social status and political alliances.	Distribution of low cost, nesting season turtles to nearby households; donation of high cost mating season turtle to public feasting.	Distribution of turtle meat consistent with tolerated theft, suggesting that males seek this resource in exchange for socio-political or reproductive benefits in a competitive resource environment.
Yanomamö Hames (1998); Naturalistic/ethnographic.	Egalitarian, horticultural/foraging population living in lowland Venezuela.	Village level, tribal social organization, 50 to 100 residents.	Interhousehold exchange of foodstuffs, predominantly among subvillage sets of families who cultivate dyadic relationships (their kinship relationships not analyzed).	Exchange patterns more consistent with self-interested reciprocal altruism and risk reduction than with the “egalitarian” exchange model of social anthropology.

cates that food donors gain reproductive benefits through more frequent mating and higher offspring survival rates. This would make Aché transfers a form of trade.

The horticulturalist/foragers of Ifaluk (Western Caroline Islands) regularly prepare food in greater abundance than can be consumed within the family. Portions are then allocated to other households. Betzig and Turke (1986) analyzed these transfers from the perspective of Hamilton's (1964a, 1964b) kin selection equation. They found that cost-benefit ratios and degree of relatedness correlated in the expected ways with transfer patterns. For instance, households transferring food had higher degrees of relatedness than would be found between randomly chosen household pairs, and the threshold relatedness necessary for transfer grew as transportation costs increased. Because Betzig and Turke (1986) examined only the predictions of kin selection, we do not know the importance of other evolutionary mechanisms in this case.

Bliege Bird and Bird (1997) use seasonal changes in the acquisition costs of turtles among the Meriam horticulturalist/foragers (Torres Strait) to analyze distribution patterns for evidence of evolutionary causation. Turtle hunting occurs in two circumstances, each with its associated distribution pattern. Open ocean encounter hunts during the feeding/mating season (May to September) are costly. They also are dangerous and physically demanding. Participation is limited to younger males, success is uncertain, and synchrony of captures is low. When turtles are captured in this season, their meat is consumed in public feasting. Because of this wide distribution, the hunter receives at most an individual share of the meat. By contrast, in the nesting season (October to April) Meriam foragers intercept egg-laying turtles on the beaches. This is a much less demanding and dangerous procedure, and it involves a broader sex-age segment of the population. The catch is larger and more synchronous. Nesting turtles are butchered and portions are parceled out to neighbors (who may be represented only by a bucket left at the butchery site).

Bliege Bird and Bird argue that hypotheses derived from kinship and reciprocity (risk) models of food transfers are not supported by this evidence. Trade/exchange could not be securely tested. By contrast, tolerated theft is supported, leading the authors to suggest that benefits like those predicted in the show off hypothesis must be the motivating factor in much male turtle hunting. This is especially evident for the ocean hunts, for which the catch is distributed at public feasts.

Hames (1998) compares two "sharing" hypotheses using data from four Yanomamö villages. Under the *egalitarian* model common in sociocultural anthropology, transfers in unranked societies are thought to be determined by the capacity to give and the need to receive. Because food producers are not equally skilled, and households exhibit different dependency ratios, this hypothesis predicts unbalanced flows among households. By contrast, under a model of reciprocity altruism, donations are given in the expectation of compensation through delayed return. Outflows should be independent of a household's productivity and inflows independent of a household's needs. By examining Yanomamö distribution patterns with respect to their frequency and balance, the demographic features of donor and recipient households, and village size, Hames shows that transfer patterns are more consistent with the reciprocity/variance reduction model. Despite their egalitarian tendencies, Yanomamö households do not preferentially transfer from high-production to high-consumption households.

Discussion

Given this summary of models and cases, the following inferences seem sound.

Intragroup food transfers are common among social foragers. They regularly occur in nonhuman as well as human populations. These include various songbirds, whales, ravens, bats, social carnivores, macaques, chimpanzees, and other primates. At least within vertebrates, the examples are not confined to advanced evolutionary grades.

This fact greatly expands the comparative possibilities for hypothesis generation and testing. Vampire bats offer a working instance of the traditional view that hunter-gatherer "sharing" is a case of risk minimizing based on reciprocal altruism. Ravens give us a behavioral ecology model of transfers by a wide-ranging scavenger that depends on group behavior to usurp more adept predators. Killer whales show us how physically constrained sites for harvest opportunities may lead to transfers. Lions demonstrate that cooperative hunting and food transfers may be suboptimal but occur anyway as a result of other selective pressures for group living. Swallows and ravens force us to confront the critical but subtle differences between pseudo- and altruistic-reciprocity. Studies of free-ranging macaques and chimpanzees may help us to understand how certain foraging behaviors combine with plant or animal properties to make resources act as packets.

Among primates, Boesch (1994) compares chimpanzee cooperative hunting and meat "sharing" at Gombe Stream and Taï National Park, Côte d'Ivoire. The reviews by Rose (1997, this volume) of capuchin, chimpanzee, and human predation and food transfer are a model for the comparative approach. Paleoanthropologists will have to immerse themselves in behavioral ecology to a degree not apparent in the contemporary literature on hominid evolution if they are to realize the analytical potential of this kind of evidence (O'Connell 1995; Winterhalder 1996c).

Intragroup food transfers are ubiquitous among social foragers having in common a particular suite of socioecological features. Asynchronous harvesting and weak possession of intermediate-sized food packets by members of relatively stable and contiguous social units is common to nearly all of the models and examples cited. Marginal valuation and risk sensitivity add to evolutionary pressures for transfers. The disparity between a raven-sized stomach and a moose-sized banquet highlights the potential significance of the former; the metabolic urgency of bat foraging points to the importance of the latter. Where this suite of resource conditions pertains, intragroup food transfers appear to be common. Because the generating conditions are material, well identified, and fairly limited in number, they should be observable archaeologically. However, it is important to add that packets are sometimes defined by their functional qualities (see also Winterhalder 1996a). A roost-mate's stomach, distended with a recent blood meal, is a packet to a vampire bat. A swarm of insects is a packet to a swallow. Fruit may or may not qualify as a packet depending on how it is harvested by macaques.

In evolutionary terms, food transfer behavior among social foragers is subject to multiple causation. Within the suite of subsistence features cited immediately above, food transfers can come about through a variety of evolutionary mechanisms (Tables 14.1 and 14.2; Winterhalder 1996b). Transfers are likely to result from overlapping

causes; more than one of these mechanisms can operate concurrently. In fact, multiple causation may in part be responsible for the ubiquity of transfers. The balance struck among the forces of tolerated theft/scrounging, marginal valuation, risk sensitivity, pseudo- and altruistic-reciprocity, exchange, and showing off presumably is determined by local features of social structure and environment. As the latter vary, the specific forms of transfer behavior are predicted to vary as well.

Wilkinson (1987) presents methods for discriminating between kin selection and reciprocal altruism. His evidence on vampire bats points to mixed causation, with reciprocity predominating: "the increase in individual survivorship due to reciprocal food-sharing events in this species provides a greater increase in inclusive fitness than can be attributed to aiding relatives" (Wilkinson 1988: 85). This finding echoes a preliminary result from ethnographic studies: in foragers, it typically has been difficult to show that intragroup distribution patterns are directed preferentially to relatives (compare Betzig and Turke 1986, and Kaplan and Hill 1985b). Reciprocity can dominate the concurrent operation of kin selection in the evolution of transfers.

Each of the four ethnographic cases attributes primary causal influence to a different evolutionary mechanism: individual selection for trade in the Aché, kin selection in the Ifaluk, tolerated theft and showing off in the Miriam, and reciprocity selection among the Yanomamö. Even if we treat these conclusions as preliminary—the data required to reliably assess the importance of differing causes exceed what is available in the best of studies—it is nonetheless suggestive in that they invoke nearly the full range of possible models as primary determinants.

Food transfer behavior takes diverse forms. Transfers can be active, passive, or both. Swallows in the field alert distant flock members to insect swarms with a special squeak call. They also use passive observations at their colonial nesting site to follow successful foragers to bountiful feeding sites (see Brown et al. 1991). Transfers may entail food and/or information about food. Food may transfer against itself (in-kind) or against other resources, social allegiance and political support, reproductive access, or other services or benefits (not in kind), as is seen in captive (de Waal 1989, 1997a) and wild (Stanford 1995) populations of chimpanzees. In the Stanford (1995) study, meat appears to be a rudimentary exchange commodity, at least in the spheres of sexual relationships and political alliances. Transfers may be symmetrical or asymmetrical, immediate or delayed. They may be embedded in social events that range from barely disguised thievery to gifts, forcibly given. Risk may be high (bats) or low (macaques). Transfer may involve related or unrelated individuals living in relatively stable social groups (e.g., bats), or it may occur among unrelated individuals with no ongoing associations (e.g., ravens) (Table 14.1).

Ethnographic studies show similar intergroup diversity among extant hunter-gatherers. As with other species, this diversity presumably arises from environment (e.g., degree of dependence on resource packets, the stability and size of the social unit, etc.) and from differing balances among the evolutionary mechanisms operating in each case. To repeat an introductory observation, "sharing" is no longer just sharing.

Intragroup diversity may also characterize the evolution of transfers. Models of scrounging and evidence from spice finches show that groups of social foragers might well contain stable mixes of different tactics. Producers and opportunists may exist

alone, producers may coexist with scroungers or with opportunists, and opportunists may coexist with scroungers. At equilibrium no individual can gain by switching its tactic (or the frequency with which it uses various tactics). We can predict that groups of social foragers will contain individuals who adopt unlike economic roles or who switch among economic roles. This indicates that differential foraging efforts by males may also be multiply caused by some balance between evolutionary tendencies for showing off and those for producing/scrounging.

Conclusions

The food "sharing" hypothesis was rejected in part because paleoanthropologists were made to feel uncomfortable projecting "modern" human behavior onto the Plio-Pleistocene past (Binford 1985). At the time, this was a laudable caution. However, we now know that in wider comparative perspective it has the unfortunate and indefensible consequence of denying to hominids the socioecological transfer capacities of ravens and bats. While we may be obliged to avoid seeing "signs of modern humanity in the activities of these early ancestors" (Potts 1984: 347), we are not under any similar analytical compulsion to treat our hominid ancestors as less behaviorally sophisticated in their food production and allocation than other vertebrates.

Along with Rose and Marshall (1996), I believe it is time to revive the food "sharing" hypothesis. My approach nonetheless differs from Rose and Marshall in at least three respects. I think it is evident that: (1) we must look to nonprimate as well as primate species and extant foragers for ideas and comparative information. Primate and ethnographic examples are too limited in number and confounded by phylogenetic association to trust as our only source of comparative evidence; (2) careful taphonomy is not enough for behavioral reconstruction. The archaeological and other evidence must be interpreted through the variables and models of behavioral ecology, that is through conceptual models (Tooby and DeVore 1987; O'Connell 1996). Glynn Isaac was prescient in this as well; he argued that, to imagine what cannot be directly observed in prehistoric archaeology, we will need "a knowledge of ecology and an understanding of alternative strategies for exploiting the economy of nature . . ." (1986, quoted in Blumenshine 1991: 321); and (3) one step in that direction will be recognizing that transfer behaviors in groups of social foragers are common, linked to clearly specifiable environmental circumstances, diverse in their behavioral manifestations, and caused by a variety of evolutionary mechanisms, some of which we are beginning to understand through analyses using behavioral ecology models.

REFERENCES

- Aspelin, P. L. 1979. Food distribution and social bonding among the Mamaindê of Mato Grosso, Brazil. *Journal of Anthropological Research* 35:309–327.
- Axelrod, R., and D. Dion. 1988. The further evolution of cooperation. *Science* 242:1385–1390.

- Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. *Science* 211:1390–1396.
- Betzig, L. L., and P. W. Turke. 1986. Food-sharing on Ifaluk. *Current Anthropology* 27:397–400.
- Binford, L. R. 1985. Human ancestors: changing views of their behavior. *Journal of Anthropological Archaeology* 4:292–327.
- Bliège Bird, R. L., and D. W. Bird. 1997. Delayed reciprocity and tolerated theft: the behavioral ecology of food-sharing strategies. *Current Anthropology* 38:49–78.
- Blumenschine, R. J. 1991. Breakfast at Olorgesailie: the natural history approach to Early Stone Age archaeology. *Journal of Human Evolution* 21:307–327.
- Blurton Jones, N. G. 1984. A selfish origin for human food-sharing: tolerated theft. *Ethology and Sociobiology* 5:1–3.
- Blurton Jones, N. G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information* 26:31–54.
- Boesch, C. 1994. Cooperative hunting in wild chimpanzees. *Animal Behaviour* 48:653–667.
- Boesch-Achermann, H., and C. Boesch. 1994. Hominization in the rainforest: the chimpanzee's piece of the puzzle. *Evolutionary Anthropology* 3:9–16.
- Boyd, R., and P. J. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Boyd, R., and P. J. Richerson. 1989. The evolution of indirect reciprocity. *Social Networks* 11:213–236.
- Boyd, R., and P. J. Richerson. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171–195.
- Brown, C. R., M. B. Brown, and M. L. Shaffer. 1991. Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour* 42:551–564.
- Brown, J. L. 1983. Cooperation—a biologist's dilemma. *Advances in the Study of Behavior* 13:1–37.
- Caraco, T., and L.-A. Giraldeau. 1991. Social foraging: producing and scrounging in a stochastic environment. *Journal of Theoretical Biology* 153:559–583.
- Cashdan, E. A. 1985. Coping with risk: reciprocity among the Basarwa of Northern Botswana. *Man (N.S.)* 20:454–474.
- Connor, R. C. 1995. Altruism among non-relatives: alternatives to the 'prisoner's dilemma.' *Trends in Ecology and Evolution* 10:84–86.
- de Waal, F. B. M. 1989. Food-sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution* 18:433–459.
- de Waal, F. B. M. 1997a. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior* 18:375–386.
- de Waal, F. B. M. 1997b. Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology* 111:370–378.
- Dugatkin, L. A., M. Mesterton-Gibbons, and A. I. Houston. 1992. Beyond the prisoner's dilemma: toward models to discriminate among mechanisms of cooperation in nature. *Trends in Ecology and Evolution* 7:202–205.
- Durham, W. H. 1990. Advances in evolutionary culture theory. *Annual Review of Anthropology* 19:187–210.
- Dwyer, P. D., and M. Minnegal. 1993. Are Kubo hunters 'show offs'? *Ethology and Sociobiology* 14:53–70.
- Elster, J. 1983. *Explaining Technical Change: A Case Study in the Philosophy of Science*. Cambridge: Cambridge University Press.
- Feinman, S. 1979. An evolutionary theory of food-sharing. *Social Science Information* 18:695–726.
- Ferrari, S. F. 1987. Food transfer in a wild marmoset group. *Folia Primatologica* 48:203–206.
- Giraldeau, L.-A., Hogan, and M. J. Clinchy. 1990. The payoffs to producing and scrounging: what happens when patches are divisible? *Ethology* 85:132–146.
- Giraldeau, L.-A., C. Soos, and G. Beauchamp. 1994. A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behavioral Ecology and Sociobiology* 34:251–256.
- Gould, R. A. 1981. Comparative ecology of food-sharing in Australia and northwest California. In *Omnivorous Primates: Gathering and Hunting in Human Evolution* (R. S. O. Harding and G. Teleki, eds.), pp. 422–454. New York: Columbia University Press.
- Hames, R. In press. Reciprocal altruism in Yanomamö food exchange. In *Human Behavior and Adaptation: An Anthropological Perspective* (N. Chagnon, L. Cronk, and W. Irons, eds.).
- Hamilton, W. D. 1964a. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1–16.
- Hamilton, W. D. 1964b. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7:17–51.
- Hauser, M. D., and P. Marler. 1993a. Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behavioral Ecology* 4:194–205.
- Hauser, M. D., and P. Marler. 1993b. Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology* 4:206–212.
- Hawkes, K. 1991. Showing off: tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology* 12:29–54.
- Hawkes, K. 1992a. Sharing and collective action. In *Evolutionary Ecology and Human Behavior* (E. A. Smith and B. Winterhalder, eds.), pp. 269–300. Hawthorne, NY: Aldine de Gruyter.
- Hawkes, K. 1992b. On sharing and work. *Current Anthropology* 33:404–407.
- Hawkes, K. 1993a. Why hunter-gatherers work: an ancient version of the problem of public goods. *Current Anthropology* 34:341–361.
- Hawkes, K. 1993b. Reply. *Current Anthropology* 34:706–710.
- Heinrich, B., and J. Marzluff. 1995. Why ravens share. *American Scientist* 83:342–349.
- Henry, J. 1951. The economics of Pilagá food distribution. *American Anthropologist* 53:187–219.
- Hill, K., and A. M. Hurtado. 1996. *Ache Life History: The Ecology and Demography of a Foraging People*. Hawthorne, NY: Aldine de Gruyter.
- Hill, K., and H. Kaplan. 1993. On why male foragers hunt and share food. *Current Anthropology* 34:701–706.
- Hill, K., H. Kaplan, K. Hawkes, and A. M. Hurtado. 1987. Foraging decisions among Ache hunter-gatherers: new data and implications for optimal foraging models. *Ethology and Sociobiology* 8:1–36.
- Hoelzel, A. R. 1991. Killer whale predation on marine mammals at Punta Norte, Argentina: food-sharing, provisioning and foraging strategy. *Behavioral Ecology and Sociobiology* 29:197–204.
- Isaac, G. 1978a. Food-sharing and human evolution: archaeological evidence from the Pliocene-Pleistocene of East Africa. *Journal of Anthropological Research* 34:311–325.
- Isaac, G. 1978b. The food-sharing behavior of protohuman hominids. *Scientific American* 238(4):90–108.
- Isaac, G. 1984. The archaeology of human origins: studies of the lower Pleistocene in East Africa 1971–1981. *Advances in World Archaeology* 3:1–87.

- Kaplan, H., and K. Hill. 1985a. Hunting ability and reproductive success among male Ache foragers: preliminary results. *Current Anthropology* 26:131–133.
- Kaplan, H., and K. Hill. 1985b. Food-sharing among Ache foragers: tests of explanatory hypotheses. *Current Anthropology* 26:223–246.
- Kaplan, H., K. Hill, K. Hawkes, and A. Hurtado. 1984. Food-sharing among Ache hunter-gatherers of eastern Paraguay. *Current Anthropology* 25:113–115.
- Kent, S. 1993. Sharing in an egalitarian community. *Man (N.S.)* 28:479–514.
- Kummer, H. 1991. Evolutionary transformations of possessive behavior. In *To Have Possessions: A Handbook on Ownership and Property* (R. W. Rudmin, ed.), pp. 75–83. Corte Madera, CA: Select Press.
- Mesterton-Gibbons, M., and L. A. Dugatkin. 1992. Cooperation among unrelated individuals: evolutionary factors. *The Quarterly Review of Biology* 67:267–281.
- Nettle, D., and R. I. M. Dunbar. 1997. Social markers and the evolution of reciprocal exchange. *Current Anthropology* 38:93–99.
- Nowak, M. A., and K. Sigmund. 1992. Tit for tat in heterogeneous populations. *Nature* 355:250–253.
- Nowak, M. A., and K. Sigmund. 1993. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* 364:56–58.
- Nowak, M. A., R. M. May, and K. Sigmund. 1995. The arithmetics of mutual help. *Scientific American* 272(6):76–81.
- O'Connell, J.F. 1995. Ethnoarchaeology needs a general theory of behavior. *Journal of Archaeological Research* 3:205–255.
- Packer, C., and L. Ruttan. 1988. The evolution of cooperative hunting. *The American Naturalist* 132:159–198.
- Packer, C., D. Scheel, and A. E. Pusey. 1990. Why lions form groups: food is not enough. *The American Naturalist* 136:1–19.
- Perry, S., and L. Rose. 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. *Primates* 35:409–415.
- Peterson, N. 1993. Demand sharing: reciprocity and the pressure for generosity among foragers. *American Anthropologist* 95:860–874.
- Potts, R. 1984. Home bases and early hominids. *American Scientist* 72:338–347.
- Price, J. A. 1975. Sharing: the integration of intimate economics. *Anthropologica* XVII:3–27.
- Rogers, A. 1994. Evolution of time preference by natural selection. *American Economic Review* 84:460–481.
- Rose, L. M. 1997. Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology* 18:727–765.
- Rose, L., and F. Marshall. 1996. Meat-eating, hominid sociality, and home bases revisited. *Current Anthropology* 37:307–338.
- Sigmund, K. 1993. *Games of Life: Explorations in Ecology, Evolution and Behaviour*. London: Penguin.
- Smith, E. A. 1988. Risk and uncertainty in the "original affluent society": evolutionary ecology of resource-sharing and land tenure. In *Hunter-Gatherers, Volume I: History, Evolution and Social Change* (T. Ingold, D. Riches, and J. Woodburn, eds.), pp. 222–251. New York: Berg.
- Smith, E. A., and B. Winterhalder. 1992. Natural selection and decision-making: some fundamental principles. In *Evolutionary Ecology and Human Behavior* (E. A. Smith, and B. Winterhalder, eds.), pp. 25–60. New York: Aldine de Gruyter.
- Stanford, C. B. 1995. Chimpanzee hunting behavior and human evolution. *American Scientist* 83:256–261.

- Stanford, C. B. 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Cambridge, MA: Harvard University Press.
- Thiel, B. 1994. Further thoughts on why men share meat. *Current Anthropology* 35:440–441.
- Thompson, P. R. 1975. A cross-species analysis of carnivore, primate, and hominid behaviour. *Journal of Human Evolution* 4:113–124.
- Thompson, P. R. 1976. A behavior model for *Australopithecus africanus*. *Journal of Human Evolution* 5:547–558.
- Tooby, J., and I. DeVore. 1987. The reconstruction of hominid behavioral evolution through strategic modeling. In *The Evolution of Human Behavior: Primate Models* (W. G. Kinzey, ed.), pp. 183–237. Albany, NY: State University of New York Press.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.
- Vickery, W. L., L.-A. Giraldeau, J. J. Templeton, D. L. Kramer, and C. A. Chapman. 1991. Producers, scroungers, and group foraging. *The American Naturalist* 137:847–863.
- Wiessner, P. 1982. Risk, reciprocity and social influences on !Kung San economics. In *Politics and History in Band Societies* (E. Leacock, and R. Lee, eds.), pp. 61–84. Cambridge: Cambridge University Press.
- Wilkinson, G. S. 1987. Altruism and co-operation in bats. In *Recent Advances in the Study of Bats* (M. B. Fenton, P. Racey, and J. M. V. Rayner, eds.), pp. 299–323. Cambridge: Cambridge University Press.
- Wilkinson, G. S. 1988. Reciprocal altruism in bats and other mammals. *Ethology and Sociobiology* 9:85–100.
- Wilkinson, G. S. 1990. Food-sharing in vampire bats. *Scientific American* 262(2):76–82.
- Wilson, D. S. 1998. Hunting, sharing, and multilevel selection: the tolerated-theft model revisited. *Current Anthropology* 39:73–97.
- Winterhalder, B. 1986. Diet choice, risk, and food-sharing in a stochastic environment. *Journal of Anthropological Archaeology* 5:369–392.
- Winterhalder, B. 1990. Open field, common pot: harvest variability and risk avoidance in agricultural and foraging societies. In *Risk and Uncertainty in Tribal and Peasant Economies* (E. Cashdan, ed.), pp. 67–87. Boulder, CO: Westview Press.
- Winterhalder, B. 1996a. A marginal model of tolerated theft. *Ethology and Sociobiology* 17:37–53.
- Winterhalder, B. 1996b. Gifts given, gifts taken: the behavioral ecology of nonmarket, intragroup exchange. *Journal of Archaeological Research* 5:121–168.
- Winterhalder, B. 1996c. Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology* 5:46–57.
- Winterhalder, B., F. Lu, and B. Tucker. 1999. Risk-sensitive subsistence tactics: models and evidence from subsistence studies in biology and anthropology. *Journal of Archaeological Research* 7:301–348.
- Wobst, H. M. 1978. The archaeo-ethnology of hunter-gatherers or the tyranny of the ethnographic record in archaeology. *American Antiquity* 43:303–309.
- Woodburn, J. 1982. Egalitarian societies. *Man (N.S.)* 17:431–451.

THE HUMAN EVOLUTION SERIES

Editors

Russell Ciochon, University of Iowa
Bernard Wood, George Washington University

Editorial Advisory Board

Leslie Aiello, University College, London
Alison Brooks, George Washington University
Fred Grine, State University of New York, Stony Brook
Andrew Hill, Yale University
David Pilbeam, Harvard University
Yoel Rak, Tel-Aviv University
Mary Ellen Ruvolo, Harvard University
Henry Schwarcz, McMaster University

African Biogeography, Climate Change, and Human Evolution
edited by Timothy G. Bromage and Friedemann Schrenk

Meat-Eating and Human Evolution
edited by Craig B. Stanford and Henry T. Bunn

MEAT-EATING & HUMAN EVOLUTION

EDITED BY

Craig B. Stanford & Henry T. Bunn

OXFORD
UNIVERSITY PRESS

2001