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Gifts Given, Gifts Taken: The Behavioral Ecology of Nonmarket, Intragroup Exchange

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Behavioral ecologists combine evolutionary models of mechanism and ecological models of circumstance to analyze the origins and forms of intragroup exchange among social foragers, a category that includes primates, hominids, and recent and modern hunter-gatherers. Evolutionary mechanisms encompass individual, sexual, reciprocal, kin, group, and cultural selection; models of circumstance include tolerated theft, scrounging, marginal value, trade, show-offs, and risk reduction. After a critical review, I develop a partial synthesis of these models. The results show that exchange behaviors have multicausal origins and they likely will be diverse due to differing combinations of mechanism and circumstance. They also help explain seemingly unique features of foraging economies, including constrained production and routine demand sharing.

KEY WORDS: foraging theory; exchange; sharing; risk.

INTRODUCTION

What combinations of ecological circumstance and evolutionary cause might give rise to the routine exchange of food, other goods, information, or services among the adult members of a group of hominids or modern humans? The participants in exchange may be related or unrelated; I presume that they live in a nonmarket society. They may be known to us through prehistoric archaeology, ethnohistory, or ethnography. They may be hominids or members of diverse nonmarket societies of the recent past or present. The patterns we seek to explain in distant populations also may

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be present in muted, localized, or personalized forms within market economies, where they otherwise are subordinate to commodity exchange (Polanyi, 1944). Their analogues and perhaps their antecedents are evident in a variety of primates, and other species.

Trafficking in food, tools, materials, and obligations of effort or support is not unique to early hominids and their descendants. Creatures as diverse as vampire bats (Wilkinson, 1990), ravens (Heinrich and Marzluff, 1995), and chimpanzees (Stanford, 1995) share food. But we are notable in the extent of these activities, in the varied forms they take, and in their impact on social life. This observation of evolutionary continuity demands that our theory and models be applicable to nonhuman organisms as well as to ourselves and our ancestors (Cartmill, 1990). They must be capable of illuminating likeness as well as interspecific divergence and intersocietal variety. We look for general causes capable of producing diverse and uncommon results. In parallel we must move smoothly from biological to economic and social theory, asking to what extent neo-Darwinian analysis can inform about issues more usually reserved for social theorists as diverse as Hobbes, Mauss, and Sahlins.

Some of the concepts or models I review describe the ecological circumstances that might foster exchange behavior. These include tolerated theft, marginal valuation, scrounging, risk minimization, trade, by-product cooperation, and showing off. I follow with the evolutionary mechanisms that might promote the evolution of exchange: individual, sexual, kin, reciprocal, and interdemic (group) selection, as well as dual-inheritance models that incorporate the differential transmission of cultural information. I then attempt to assay the degree to which these ideas add up to a comprehensive theory of nonmarket, intragroup exchange and to identify where there are gaps. Finally, I argue that evolutionary ecology models place nonmarket exchange among modern humans in a more comprehensive and analytically promising framework than that developed in Sahlins' (1972) still influential *Stone Age Economics*.

These materials pertain to work of archaeologists and anthropologists curious about (a) the origins and form of exchange behavior, whether among foraging primates, hominids, or extant hunter-gatherers (b) the ecological bases of premarket economies (e.g. task-group formation, gender-based division of labor, risk minimization, work effort, and original affluence); and (c) methodological advances in the use of neo-Darwinian and microeconomic concepts for the study of nonmarket economies and their evolutionary transformations (see also Kelly, 1995). The models help explain the procurement and movement among individuals of materials that comprise part of the archaeological record. We are well short of a synthesis, but in the work of evolutionary biologists and anthropologists we now have

key elements of a comprehensive theory of the evolution of hominid exchange behavior. The reviewed materials should command the attention of anthropologists, economists, and other social scientists who ponder the manner and context in which neo-Darwinian self-interest becomes expressed in cooperative social behaviors (Arnhart, 1995).

EVOLUTIONARY ECOLOGY MODELS OF EXCHANGE

For the evolutionary ecologist it is not enough to identify the net adaptive benefits of a behavior as these might be envisioned in specific environmental circumstances. A complete hypothesis requires that the benefits be capable of acting causally within neo-Darwinian processes to generate the behavior. This dual obligation—to describe the ecological setting and the evolutionary process—obviates some of the problems that otherwise inhere in functionalist or adaptationist analyses (Elster, 1983; Smith and Winterhalder, 1992). Evolutionary ecology methodology entails both *models of circumstance* and *models of mechanism*.

The methodology for models of circumstance is straightforward and well described in the literature (Smith and Winterhalder, 1992; Winterhalder and Smith, 1992). An optimization premise (Foley, 1985) guides the construction of simple models (Richerson and Boyd, 1987) designed to assess the cost-benefit trade-offs of some restricted set of behavioral possibilities. Fitness or some proximate currency (e.g., net acquisition rate of energy) is used as the measure of relative success; the model embodies the environmental and other constraints thought most important to the analysis (Maynard Smith, 1978). Hypotheses produced by such models typically relate a range of behavioral options to a range of quite specific conditions in the biotic or social environment. Ideally, they are evaluated by hypothetico-deductive standards, and the outcome used to reflect on the adequacy of the premises, constraints, the model itself, and the preferred hypothesis.

Models of mechanism direct our attention to the processes by which natural selection is brought to bear on the evolution of behavior. They help assess how and to what degree the identified costs and benefits are likely to have causal salience. Neo-Darwinian mechanisms can be represented through simple optimization models when the relevant environment does not respond strategically (or with frequency dependence). Evolutionarily stable strategy (ESS) models are required when the environment alters tactics in response to an organism's actions (Maynard Smith, 1976; Winterhalder and Smith, 1992, pp. 8-9). An ESS is one that cannot be supplanted by a feasible alternative tactic. As in the prisoner's dilemma (below), it need not be the best tactic for any or all individuals.

Recent review articles explain the evolutionary ecology approach more fully and describe advances in empirical studies that it has stimulated (Borgerhoff Mulder, 1991; Cronk, 1991; Smith, 1992a, b; Smith and Winterhalder, 1992a, b; Winterhalder and Smith, 1992). Kaplan and Hill (1985b) and Smith (1988) have authored earlier reviews on hunter-gatherer exchange.

In the material that follows, I depart somewhat from conventional terminology in using "value" rather than (reproductive) fitness, utility, or some more specific currency (Blurton Jones, 1987, p. 34). The term value acknowledges microeconomic parallels, and it readily encompasses the non-reproductive forces that might guide the evolution of behavior in a cultural species (Boyd and Richerson, 1985). I also use resource "transfer" or "exchange" as neutral terms for the movement of goods among individuals, not implying any particular mechanism or motive (such as would be the case for "sharing" or "trade").

MODELS OF CIRCUMSTANCE

Tolerated Theft

Blurton Jones (1984, 1987) has proposed that food transfer may have its origins in tolerated theft. He observes that hunter-gatherers or other foragers encounter and harvest food items in natural units that can be called *packets*. Some of these may be resource items that are larger than can be immediately consumed, a surfeit to the individual making the discovery. If members of a group forage separately, acquisition of such packets is likely to be rare, sporadic, and out of phase.

Food packets of increasing size are likely to trace a curve of diminishing marginal returns, measured in terms of their value. If partial consumption of a large packet begins to sate the nutritional needs of the individual acquiring it, he or she has little to gain in defending the remaining, low-value portions. In contrast, companions less fortunate in the food quest that day have strong incentives to acquire what for them will be high-value portions. Interest in the marginal units of a large packet is strongly asymmetric between the replete and the hungry. As everyone gains by avoiding conflict that does not enhance fitness, or by threatening conflict that does, the holder of a large packet should relinquish portions and the supplicants take them until there is an equilibrium of their individual interests. Blurton Jones (1987, p. 35) designates this transfer as passive sharing or tolerated theft, and he likens it to Glynn Isaac's description of chimpanzee sharing as tolerated scrounging. For reasons explained below,

I refer to *contested*, rather than large packets, understanding them to be of at least intermediate size relative to the array of potential foods.

The repetition of giving and taking suggested by persistent tolerated theft opens the possibility that a slacker might regularly seize the benefits but avoid the effort and cost of securing contested packets, enhancing his or her net advantage. Through simple simulations using different group sizes and handicaps for active foragers, Blurton Jones reaches these conclusions about such cheating: (1) a scrounger stands to benefit by convincing other scroungers to become active foragers, thus “[e]ven in this possibly *primaevae* context, the gift of prestige to the active forager would be a self-serving deceit by the scrounger” (1987, p. 45); (2) full-time scrounging is unlikely in small groups but its probability grows with group size (1987, p. 45); (3) the (self-interested) decisions of active hunters to become scroungers strongly depresses the average harvest rate of a group, creating “a mechanism by which individuals maximizing their selfish interests come to under-produce” (1987, p. 47; see also Winterhalder, 1993); and, (4) particularly good hunters will have little incentive to leave or avoid groups with scroungers. Offenders can follow, and “although good hunters will not receive the advantage that may appear due to them . . . an equal share of their own greater returns will be greater than an equal share of a poor hunter’s lesser returns” (1987, p. 47). As well, there may be other, overriding advantages to group living.

Kaplan and Hill (1985b) provide the clearest ethnographic test of the tolerated theft hypothesis. Consistent with the prediction, larger packets, asynchronously acquired, are more widely distributed among the Aché of South America. However, Kaplan and Hill note that food often is saved for individuals absent at its distribution and that distribution does not appear to correlate with differences in the presumed ability of men to defend larger shares. In effect, food distribution does not appear to be the *contest* presumed by the model (although such contests need not be overt, and could be missed in behavioral observations). Most importantly, the unequal distribution of food—hunters receiving less than others—appeared to them to rule out the tolerated theft hypothesis. Because the original model emphasized its possible importance in the origins of food sharing, not its sufficiency to explain the mature practice that is observed ethnographically (Smith, 1992b, p. 53), this negative evidence does not necessarily diminish the significance of the proposal.

In tolerated theft an equilibrium among self-interested individuals compels (re)allocation of contested packets to avoid the costs of strife. Tolerated theft has the potential to produce regular, patterned exchange even in the absence of reciprocity. Over time in a small group with stable membership, the repetition of these purely self-interested interactions could

prime the evolution of reciprocal cooperation. This shift to a more socially embedded form of exchange does not necessarily eliminate resource contests. In fact, the continuing threat of tolerated theft—subtle or overt—may be at play in exchange behavior right into the modern context (Hirshleifer, 1991).

Marginal Analysis

Winterhalder (1996) has expanded on a key premise of tolerated theft: marginal valuation. His model shows more formally how the costs and benefits of resource transfers affect individual and collective value.

The basic situation is depicted in Fig. 1. The forager who relinquishes portions of a contested packet is designated G, the *giver*; T is the *taker*, the one to whom portions are ceded. When they meet, T has no food ($Quantity_T = 0$) and zero value ($Value_T = 0$), but G has pursued and captured the resource packet that will be contested ($Quantity_G = Quantity_p$, where p signifies a packet) with value ($Value_p$). Because of the disparity

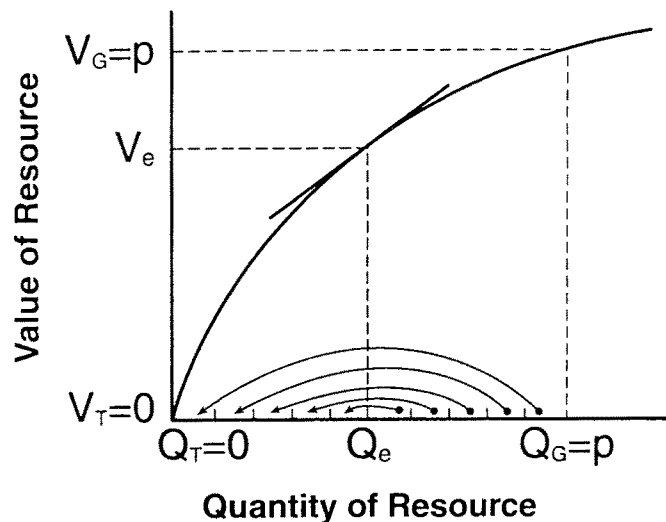


Fig. 1. Marginal value and the exchange of resources. The horizontal axis shows the quantity of a divisible, contested packet or patch; the vertical axis shows its value to an individual (in terms of fitness, utility, or some other currency). Tolerated theft will cause a giver (G) to cede portions and a taker (T) to acquire them until their marginal values equalize. At this point, the incentive for T to demand another portion is balanced by G's incentive to resist relinquishing it.

in their resource holdings, marginal units of the packet are much more valuable to T than to G. We can envision tolerated theft as a reallocation in which a taker acquires one portion of the packet for each that a giver cedes. The first portion transferred leaves a residual imbalance (marginal portions remain more valuable to T than to G) as does the second through fifth, to the convergence on $Quantity_e$ (e signifying the equilibrium). At this point, transfers cease. With their marginal utilities equalized, the incentive for T to demand is precisely balanced by that of G to resist relinquishing. The two individuals end with the same quantity of food (Q_e) and the contested packet has been equally divided [$Quantity_e = Quantity_p/2$]. The loss of value suffered by the giver is less than the gain to the taker; the *summed* value for the two individuals after tolerated theft ($2V_e$) is greater than before the transfer ($V_G + V_T$).²

The equilibrium at which marginal transfers cease has left the participants with equal resources and equal allocations of the packet, but the taker gains considerably greater value than the giver relinquishes. The number of portions taken is the same as that ceded, and portions change hands only so long as they are of greater value to T than to G. The transfer enhances the joint value of the resource.

By varying elements of this graphical model we can generate a series of insights about transfers under the circumstances of tolerated theft (or reciprocity cooperation). For instance, the same conditions that make contested packets subject to reallocation through tolerated theft—rare, unpredictable, and asynchronous encounter—mean that a forager must also be harvesting more reliable and regularly encountered food items, those occurring in smaller packets with relatively low daily variance. To add this element of realism, assume that T has acquired a limited catch of small packet resources, while G has been engaged in the pursuit and capture of a larger and more valuable contested packet. In this case the taker acquires one portion of the contested packet resource to add to its preexisting catch for each that the giver cedes. At the marginal equilibrium G and T hold the same amount of food, but the packet will have been unequally divided. T's share supplements his or her preexisting resources, while G retains the larger portion. Conversely, if the giver has the advantage in nonpacket resources in addition to the contested packet, T will be able to secure more than half of the packet. Because G and T are likely to come to their tolerated theft transfer with modest but dissimilar quantities of resources or levels of hunger (representing endogenous reserves), the packet itself most likely will be un-

²For any deaccelerating (concave downward) value curve the tangent at Q_e on the arc will always be above the intersection of Q_e with the chord. Thus $V_e > (V_G + V_T)/2$ or $2V_e > (V_G + V_T)$.

equally divided. This possibility has not been understood in some empirical tests of hypotheses about resource transfers (below).

The analysis can accommodate multiple (n) takers if we envision tolerated theft occurring in n -portion units until the equilibrium is reached at Q_e . For $n > 2$, the giver will relinquish more than half of the contested packet (but retain as much as any one of the takers has received). G's total loss in value may be greater than the gain to any individual taker but less than the gain to all takers. Summed over all the participants, the value enhancement arising from transfer grows with the group size. This occurs because with each increase in n more of the low-value portions relinquished by a giver concentrate on the highest increments of marginal value that can be gained by a taker.

The latter observation becomes important when the model is used to assess the potential costs and benefits of reciprocity-based transfer, such as gift giving or food sharing. If a recipient is indebted by the value he or she derives from receipt of such a resource, then the giver will achieve the greatest gain by distributing small portions as widely as possible and to the neediest of potential recipients. A behavior with the appearance of generosity may actually be one of heightened self-interest by the giver.

We also can modify the shape of the marginal return curve according to the properties of the resource and the potential of individuals for satiation. Due to a variety of factors (see analytic discussion, below), the marginal value curve of a rare but large food packet may climb steeply and have a long horizontal run along the asymptote. In this case a taker might well acquire portions up to the asymptote without any lessening of the value that the giver can derive from the balance of the resource. Both T and G gain their maximum value from the packet while leaving a surplus that neither has incentive to take nor defend. In a strict sense there has been no "theft" because the individual discovering the packet has suffered no loss of value from its partial appropriation. Two hominids can consume only so much giraffe before it is apparent that a glut has made dispute over the balance superfluous. The likelihood of such a surplus diminishes as n increases. Nonetheless, a small group confronting a quite large packet raises the possibility that there is no contest, thus no theft and no unique, equilibrium distribution.

Scrounging

Behavioral ecologists have adopted the term, "scrounging," to identify the constellation of behaviors that Blurton Jones designated as tolerated theft. Their work (Caraco and Giraldeau, 1991; Giraldeau *et al.*, 1990; Vick-

ery *et al.*, 1991) is based in game theory and ESS analysis. It carries the subject further into issues of evolutionary mechanism than has either of the approaches surveyed so far, revealing in more detail the complicated social dynamics of intragroup exchange.

Put simply, social foraging invites scrounging, just as particular economic situations invite free riders. Imagine a group composed of *producers* who expend energy to locate resources and *scroungers* who avoid those search costs by appropriating part of what a producer already has found (e.g., by tolerated theft). If scroungers are rare, their feeding costs are low and their scrounging opportunities many. They will flourish and increase in relative frequency. However, if producers are rare, chances to scrounge are scarce and, when they occur, intrascrounger competition is intense. Despite their reduced search costs, scroungers in a world of scarce producers will do poorly and decrease in frequency. This situation generates frequency dependent selection—each tactic has the advantage when rare—and thereby acts to create a stable mixture of producers and scroungers. At equilibrium each tactic does equally well and no individual can gain advantage by switching its role. This qualifies as an ESS.

We can complicate the situation slightly and increase its realism by adding an *opportunist* to the behavioral options. The opportunist produces or scrounges as the occasion presents, but may do so with a slight handicap—the cost of generalizing—in one or both of these activities relative to producers and scroungers. Vickery *et al.* (1991) show that the equilibrium mix of these tactics is determined by three factors: (1) the opportunist's handicap in detecting either production or scrounging opportunities, relative to the pure producer or scrounger, (2) the producer's advantage (or priority) in consumption of a food item or patch that it locates, and (3) group size.

Opportunist's Handicap. By dividing its attention between producing and scrounging, the opportunist may fail to detect all of the feeding opportunities that would be available to a single-minded producer or scrounger. If we take c ($0 \leq c \leq 1$) as the proportional ability of the opportunist to detect production opportunities, and h (same range) as the proportional ability to detect scrounging opportunities, then the opportunist's handicap may vary between 2 and 0. If $h + c = 2$, there is no detection handicap. Complete compatibility in search tactics allows the opportunist to double its feeding possibilities relative to the pure scrounger or producer. By similar reasoning, $h + c < 1$ assigns a detection penalty. In the author's terms, "overcompensation" ($h + c > 1$) gives the opportunist a feeding advantage, and "undercompensation" ($h + c < 1$) assigns a feeding penalty.

Producer's Priority. The second variable measures the degree to which the resource is disproportionately consumed by the producer who locates

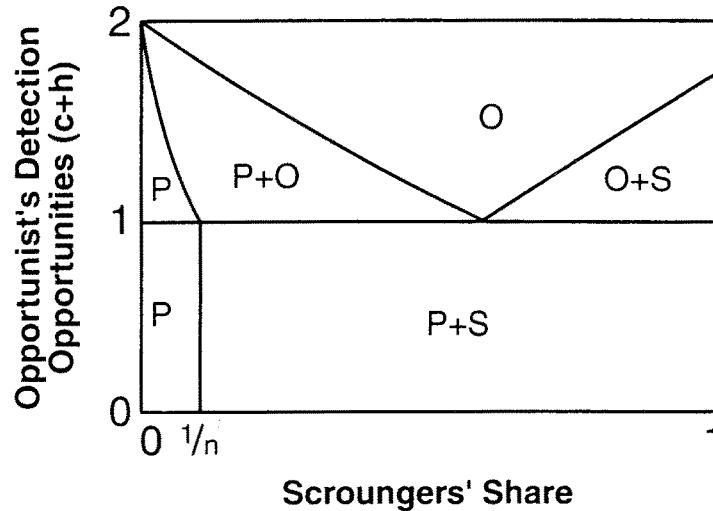


Fig. 2. A transition diagram for evolutionarily stable combinations of producers (P), scroungers (S), and opportunists (O). The horizontal axis is the scroungers' share; the vertical axis measures the opportunists' detection opportunities. Increasing producer priority in the consumption of a packet or patch diminishes the share available to scroungers, shifting the equilibrium to the left. Increases in the ability of an opportunist both to detect the feeding opportunities that would be available both to pure scroungers and also those available to pure producers shifts the equilibrium up the vertical axis. A population comprised solely of producers will be most likely if the group size (n) is small. Further details in text. [After Vickery *et al.* (1991, p. 855); used with permission.]

it. A producer might already have partially consumed the patch before scroungers can detect or reach the site. Producer priority will be high if food encounters are difficult to detect, travel distances between individuals are long, and/or the patch or food item is small.

Figure 2 shows an ESS mix of tactics as a function of these two variables and group size (n). All three tactics can coexist only in the presumably rare case of exact compensation ($h + c = 1$). Undercompensation ($h + c < 1$) eliminates opportunists from the equilibrium. A mix of producers and scroungers is stable unless the scroungers' share drops below the inverse of group size ($1/n$), in which case the population will be comprised of producers only. Overcompensation progressively restricts the range of conditions favoring pure producers and enlarges that favoring opportunists. In general, increasing the scroungers' share shifts the population from producing toward scrounging; increasing the opportunist's advantage moves it from scrounging toward opportunism. Whatever the degree of detection handicap, groups of pure producers will be uncommon unless group sizes

are small. Opportunism will dominate at high levels of compensation (low detection handicap).

In a related analysis, Caraco and Giraldeau (1991) examine equilibrium mixes of producers and scroungers whose goal is that of risk minimization. The frequency of scrounging is diminished by: (1) high scrounging costs; (2) high producer priority; (3) small group size, (4) infrequent producer discovery of food patches; and (5) high metabolic requirements. Conditions 1) and 5) elevate the energy needs of scroungers or exacerbate their sensitivity to risk while 2, 3, and 4 lower the profitability or frequency of scrounging opportunities. Producer priority has a stronger effect than other factors.

In both of these models scrounging extracts a penalty in terms of overall production. The equilibrium frequency of scroungers lowers the average food acquisition rate, sometimes to the point that all individuals, whether producer or scrounger, are more likely to starve than survive. Caraco and Giraldeau (1991) address this by speculating about countervailing selection pressures for either solitary foraging or greater within-group cooperation. Risk minimization as an advantage of exchange is examined below.

Spice finches (*Lonchura punctulata*) form egalitarian foraging groups in which individuals adopt mixed strategies of producing and scrounging. Experimental manipulation (Giraldeau *et al.*, 1994) has shown that individual finches readily shift their frequency of tactics as predicted by simple producer-scrounger games. Although scrounging is widespread in mammals, birds, and other organisms (Packer and Ruttan, 1988), this is the first demonstration that individuals have the sophisticated behavioral plasticity to adjust their behavior as a function of experience with local foraging conditions and the tactics of other group members.

The scrounging literature provides an ESS analysis of individual foraging tactics in a setting of tolerated theft. These models confirm the earlier observations of Blurton Jones (1984, 1987; above). They add an important dimension to that earlier material by showing how key variables (compensation, producer priority, and group size) affect behavioral transitions among different mixes of these tactics. In particular, groups of moderate or larger size will likely contain scroungers among the producers, or opportunists either alone or paired with one of the other tactics.

Group living typically has been analyzed for its benefits [e.g., enhanced hunting success (see Bertram, 1978; Smith, 1992a, b)], but scrounging draws attention as well to the costs of sociality. The spread of self-interested scroungers and (scrounging) opportunists in a population may lower the average rate of food acquisition with disastrous effects for all. If these behaviors appear too calculated or cunning to be feasible for primates or hominids, it is worth emphasizing that experimental research shows them

to be not beyond the capacities and the proclivities of songbirds. In fact, scrounging models have some novel implications for hunter-gatherer economics (below).

Risk Minimization

Risk minimization models give explicit ecological form to an ethnographic commonplace: hunter-gatherer sharing reduces the day-to-day variability in the food intake of cooperating band members (see Cashdan, 1985; Kaplan and Hill, 1985b; Wiessner, 1982). The more successful of the day's foragers return to a home base where they distribute their bounty widely in the anticipation that they will receive like consideration when they are among the empty-handed. Long-term fluctuations in resource availability affecting the whole range of a foraging group can be buffered with a regional variant of sharing: group mobility and reciprocal access to allopatric foraging areas (Smith, 1988; Smith and Boyd, 1990; Wiessner, 1982).

The risk minimization approach to local exchange encompasses three component models: (1) the z-score model for characterizing risk; (2) a stochastic variant of the diet breadth model for assessing the risks specific to resource choice decisions; and (3) a model relating the risk-minimizing effectiveness of sharing to properties of the environment.

(1) The z-score model (Stephens and Charnov, 1982; Stephens and Paton, 1986) represents the day-to-day food capture of an individual, non-sharing forager by a normal distribution. Risk minimization means avoiding to the extent possible the rare instance of a food shortfall severe enough to put the individual below a *starvation threshold*. In statistical terms this is achieved by choosing the foraging option (say, a particular combination of resource items) with a yield mean and variance that minimize the lower-tail value of the standard normal deviate (z), thus the probability of falling below (to the left of) the threshold. Three variables affect this choice: the starvation threshold of the forager, and the mean and variance of the capture rate for each possible choice of resources.

(2) Winterhalder (1986) analyzed the mean-variance properties of encounter-contingent foraging choices (Schoener, 1974). For each possible diet breadth, his computer simulation repeated calculations of foraging efficiency for a hunter-gatherer facing stochastically assigned distributions of encounter rates and pursuit costs. Several observations emerged from this exercise. First, in most circumstances, the optimal risk-minimizing diet will be either the same as the rate-maximizing diet or somewhat more generalized. Adding stochasticity increases realism but may not greatly improve the predictions of the simpler, deterministic (or rate-maximizing) analysis.

Stephens and Charnov (1982) reach a similar conclusion about the foraging model predicting movement among patches, the marginal value theorem. Second, even the best selection of resources may not be particularly good at avoiding severe shortfalls. In one simulation the optimal, risk-minimizing diet produced a harvest below the starvation threshold in 10% of the foraging intervals—not terribly attractive odds. Production choices for lowering subsistence risk may be of limited effectiveness.

(3) Faced with this result, Winterhalder (1986) undertook analysis of the risk-minimizing effectiveness of distribution practices, adapting a model developed by the economic historian Donald McCloskey for studies of field dispersion (references in Goland, 1993; Winterhalder, 1990). The model evaluates variation in the day-to-day food intake of a participant in food sharing, as a function of (a) the daily consumption variance experienced by the lone forager, dependent solely on his or her harvest; (b) the number of individuals who forage separately but participate in the pooling; and, (c) the average interforager correlation in daily harvest rates. For a wide range of plausible conditions, sharing is highly effective at reducing consumption variation. It is ineffective only if there is a high degree of synchrony (strong positive correlation) in the daily success rates of individual foragers. Most of the benefits that can be obtained from pooling and redistribution accrue to quite small groups of foragers (six to eight producing individuals).

Consistent with a risk minimization interpretation, Kaplan and Hill (1985b) show that package size and asynchrony are strong predictors of which resources are shared. They also use their Aché data to calculate improvements in the nutritional status of individuals practicing sharing:

Sharing of honey alone increased nutritional status by 20%, whereas sharing of meat alone increased nutritional status by a full 40%. Sharing of all food provided an 80% increase in nutritional status. This is consistent with the observed pattern, in which meat is shared most, followed by honey and then by other collected items. (p. 233)

Observations such as these give quantitative substance to qualitative ethnographic reports that sharing reduces risk.

Same-day or concurrent sharing reduces risk as a result of spatial averaging. Winterhalder (1986) also considered the effectiveness of short-term temporal averaging, saving by an individual from days of surplus to cover days of shortfall. Statistically, the individual forager averaging consumption over seven foraging trips achieves the same effect as seven foragers who pool from their individual trips. But go-it-alone temporal pooling entails runs of days with scant consumption, it incurs preservation costs, and it invites losses due to spoilage and tolerated theft. The forager carefully husbanding proceeds from a streak of luck is hoarding them in the

eyes of hungry companions; providential insurance to the one is stinginess to the others. Temporal pooling is most likely if harvest surpluses are synchronized (e.g., acorns, salmon, or other of the highly seasonal resources of some North American Indians).

Hegmon's (1989) analysis of Hopi exchange adds an important dimension to the study of resource pooling. Hopi are obligated to share food among households, lineages, and clans. They rely on corn produced in fields dispersed among several microecological zones. Hegmon simulated variation in agricultural production as a function of rainfall and damage from floods, hail, and grasshoppers. She then compared the effectiveness of three distribution regimes: (1) no sharing, or complete household independence; (2) restricted sharing, in which households meet their own needs first, redistribute as much of their surplus as is needed into a pool that aids neighbors who have fallen short, then store any remainder; and, (3) unrestricted sharing based on full pooling of the harvest and equal division among all neighbors. Only 46% of the independent households (regime 1) survive 20 years. If households practice unrestricted sharing (regime 3), 73% survive that duration. With restricted sharing (regime 2) the number increases to 92%. Restricted sharing is the most successful tactic because it protects at least some households from a series of years in which the spectacular failure of a few would obligate the marginally successful to dip below their household requirements in order to meet pooling obligations.

Hegmon concludes that "a little sharing is better than a lot" (p. 112), and indeed there is ethnographic precedent among hunter-gatherers for restricted sharing. Wiessner (1982, p. 77) observed that, in an extreme case of environmental failure, localized "[s]haring broke down and those who found something to eat consumed it discreetly. . . ." This lasted until the group dispersed to reside with regional *hxaro* partners less affected by food shortages (see also Feinman, 1979, pp. 709–712).

By solving risk minimization problems at the level of the group, foragers can make production choices that maximize capture rates. And they avoid the liabilities associated with temporal averaging by an individual, including tolerated theft. Two more advantages can be cited: sharing allows hunter-gatherers to avoid suboptimal task group sizes when foraging cooperatively (Smith, 1985; 1992b, p. 52), and it creates conditions in which individual foragers can specialize (Dwyer and Minnegal, 1993). Brief elaborations follow.

Smith (1985) has examined task-group formation using a simple optimization criterion: individuals choose a foraging group size that maximizes the net per capita return under different hunting conditions. But actually achieving the optimum comes into conflict with social reality. It may be to the advantage of a joiner, faced with foraging alone at very low efficiency,

to crash a group even if it lowers the efficiency of existing members. If such conflicts arise, group sizes typically will be larger than optimal. Smith notes, however, that such conflicts of interest can be eliminated if central place sharing extends to all members of a band. Task groups then can be adjusted to the optimum size, with everyone benefitting.

Likewise, Dwyer and Minnegal (1993, p. 54) observe that for Kubo foragers “[a]t Gwaimasi, community-wide sharing of both plant and animal foods, without concern for balanced exchanges, was usual” They cite an “absence of sanctions, positive or negative, associated with performance” (meaning how much or little a forager contributes; p. 67), and they add that “a hunter increases likely returns by specialization . . . [because] . . . [d]iversity of species is relatively high but, within species, abundance is relatively low and distributions are patchy” (p. 67). The Kubo apparently seek effective production through specialized geographic knowledge and hunting skills and then pool the harvest so as to be more secure and generalized consumers.

Potent benefits are associated with sharing. Provided that it can be shown compatible with evolutionary mechanisms, selection for risk minimization may have been a strong force in the origin, maintenance, and form of exchange.

Trade

Kaplan and Hill (1985b; above) use nutritional calculations to show that various groups of Aché (single adults, single adults with children, families) benefit significantly from sharing patterns. However, some individuals and families benefit disproportionately. Not only are individuals highly variable in their foraging effort, skills, and success, but family consumption of shared foods among the Aché correlates more strongly with the number of dependents than with family production. Unequal transfers appeared to Kaplan and Hill to be at variance with reciprocity, leading them to ask, “Why do better-than-average producers give away more food than they receive?” (p. 234).

They offer three possible answers. First, “food sharing benefits the group as a whole and individuals [those giving more] sacrifice their own fitness interests for the good of the group” (p. 236). This idea is rejected because of theoretical difficulties with group selection. Second, “even above-average foragers may be willing to give more than their share in order to avoid the risk of long stretches without food” (p. 237). Hunting intake is sufficiently unpredictable that all gain from pooling even though some gain more than others. This possibility also is rejected: “Above-aver-

age hunters would quit once they had acquired the mean amount acquired by others because they only benefit slightly from the additional food they would acquire from extra labor" (p. 237). Better foragers (measured by capture rate) also hunt longer, another observation taken to be unfavorable to this proposition. Third, because "there must be some payoff for acquiring more food than one consumes" (p. 237), Kaplan and Hill tentatively suggest that disproportionate production gains the hunter "trade" opportunities (pp. 226–227), perhaps through reproductive advantages in the form of higher offspring survival rates and more mating opportunities. There is some evidence of such effects (Kaplan and Hill, 1985a), but this idea arises also because the authors feel that something must be flowing opposite to disproportionate food contributions in order to balance accounts. Beyond this suggestion, trade (immediate or delayed, not-in-kind transfer) has received little attention from evolutionary ecologists, and we are yet without formal models.

By-product Cooperation

Imagine an organism performing a necessary task for itself in a manner that redounds to the benefit of another individual as an incidental by-product. For instance, when initiating pursuit an individual signals the presence of a large, elusive prey item to a conspecific. If joint pursuit has a significantly higher likelihood of success, the signal giver and receiver both benefit and the receiver that fails in future instances to reciprocate does so at its own expense. Or, if severe predation can be minimized by the cooperative vigilance of two individuals, cheating by either one risks loss of the partner and the danger of solitary exposure to predators. Two conditions are sufficient to produce these situations (Dugatkin *et al.*, 1992; Mesterton-Gibbons and Dugatkin, 1992): environmental adversity and a "boomerang" factor that makes a noncooperator the victim of its own cheating. Brown (1983, pp. 30–31) argues that this kind of mutualism may be common in nature. Connor (1995) terms these situations "pseudo-reciprocity"; Mesterton-Gibbons and Dugatkin (1992) use the term "by-product mutualism."

In by-product cooperation there is an immediate net positive benefit to an organism performing an action that will be augmented if the behavior is done cooperatively or is inadvertently cooperative. A donor to some collective good or activity has a higher fitness than a nondonor. The predator that fails to signal the presence of prey is less successful in pursuit; the prey that fails to be vigilant on behalf of a partner is more likely to be a victim itself. There are similar boomerang factors in foraging and exchange. Consider a medium to large packet, sure to be contested, which is normally

within the encounter-contingent diet of a social forager. The forager that shirks pursuing it (that is, fails to cooperate in providing some part of it to exchange) thereby reduces its own foraging efficiency.

Likewise, the hominid scavenger who locates a fresh lion kill and seeks the help of group members to displace other predators may be providing a collective good through by-product mutualism. Ethnoarchaeological study (O'Connell *et al.*, 1988) shows that such finds would have been valuable, but only if they were reached quickly and with enough group members that other predators/scavengers could be displaced. The hominid scavenger who locates a recent kill, then defects on by-product cooperation, garners only the very meager scraps that remain after predator/scavengers with better collective sensibilities have departed. Hominid scavenging mixes the by-product elements of foraging efficiency and predator avoidance found in the hypothetical examples of the previous paragraph. Heinrich and Marzluff's (1995) analysis of scavenging by ravens provides an analogous case. Common ravens depend for their winter feeding on cooperation quickly to locate, seize, and then defend the rare kills of larger predator/scavengers.

In their game theory analysis of the means by which punishing and retribution (social control) might stabilize reciprocity cooperation, Boyd and Richerson (1992, p. 185) state that "punishers collect private benefit by inducing cooperation in their group that compensates them for punishing, while providing a public good for reluctant cooperators." This also is an especially interesting instance of by-product cooperation, because it is embedded in and stabilizes a system of reciprocity cooperation.

Showing Off

A wide reading of hunter-gatherer ethnographies will show that typically men hunt game and women gather vegetable foods, even though encounter-contingent foraging theory indicates that each might do better by harvesting a mix of animal and plant resources (Hill *et al.*, 1987). With few exceptions, men preferentially target high-variance resources that when captured are distributed widely and consumed to a large extent beyond themselves or their families. Women preferentially harvest low-variance resources consumed primarily within the family unit. Hawkes (1991, 1992a) argues that the ethnographic regularity of this male-female difference invites explanation by processes of sexual selection. Male hunters, she believes, are seeking favorable "social attention" (1993a, p. 349) and public support by displays of food-sharing largess.

Hawkes considers two foraging practices available to males. *Provisioners* adopt reliable, low-variance foraging tactics that consistently provide

their family unit with adequate nutrition. In contrast, *show-offs* adopt a tactic of high-variance production that, although erratic in stocking the family larder, will generate “periodic bonanzas . . . visible to all” (1991, p. 32) and consumed widely within the group. If sexual selection is operating, females should prefer provisioners as mates but also should use favorable treatment to encourage their male neighbors to be show-offs. By doing so, they gain dietary benefits for themselves and their offspring. Sexual access or other rewards compensate the males, who otherwise would see their extraordinary efforts dissipated through uncompensated transfers. Self-interested males will supply a *public good* (Hawkes’s interpretation of large game packets) only if they have inducements apart from the modest portion they are able to consume. The advantages to be gained from large-game hunting are not direct or delayed consumption, risk minimization, or even trade, but less tangible matters of social influence.

Using Aché data and partial correlations, Hawkes (1991) demonstrates that sex of the producer accounts for somewhat more than half of the variation in sharing patterns, even with package size and unpredictability of the resource held constant. This relationship holds across food types, indicating that Aché men prefer to procure resources that are widely distributed whether or not they are game or plant foods (although the bulk is game). Hawkes argues that these patterns are consistent with the show-off hypothesis but not with any of the alternatives. Hawkes *et al.* (1991) show that, unlike many low-latitude foragers, Hadza males focus almost entirely on large game species (adult mass equal to or greater than 40 kg). By doing so they achieve average return rates two to four times higher than could be attained were they to focus exclusively on small game, but with highly variable day-to-day success. A lone hunter captures a large game animal approximately every 37 days. As large game is widely shared within the band, this evidence seems to support the risk minimization model: “Big game hunting and sharing provides more meat for everyone, just as the conventional wisdom would have it” (p. 247). Hadza foragers specialize their production optimally on the species that return high average capture rates and adopt distributional tactics to manage the resulting day-to-day variance to everyone’s advantage.

Despite its being self-evidently consistent with the data, Hawkes and her colleagues find the risk minimization explanation unsatisfactory. They cite ethnographic reports of differential contributions to exchange networks by unusually productive hunters. On this basis they argue that large game procurement is a collective action problem in which free riders undermine any advantage to be had through reciprocity: “[a] hunter may gain no consumption advantage from his own big game acquisition efforts” (Hawkes *et al.*, 1991, p. 243).

In a later paper, Hawkes (1993a) adds data from the !Kung to those on the Aché and Hadza, and she provides a sharpened account of her model: “goals that *compete* with family provisioning shape the foraging strategies of contemporary people who depend directly on wild foods” (1993a, p. 341; italics added). Tolerated theft makes large game collective goods. Males hunt large game to gain “deference in decisions about travel, support in disputes . . . and enhanced mating opportunities” (p. 349). Although elusive, Hawkes argues that such benefits might have significant fitness consequences for the successful show-off.

The reception given this proposal has been skeptical, not least so among those anthropologists who share Hawkes’ behavioral ecology framework (see comments in Hawkes, 1993a). Hill and Kaplan (1993) “disagree with her [Hawkes’] suggestion that current data allow [them] to accept or reject any particular explanation of food sharing” (p. 701). Their reservations center on three points. (1) Hawkes treats food transfers as due only to tolerated theft and then adds the show-off hypothesis to reconcile that possibility with her reading of the evidence. This belies the high degree of overlap among different food-exchange explanations (see below) and uncertainty about their relative importance. “We do not yet see any evidence that will allow us to determine in any human society what fraction of food sharing is attributable to which of the [potential] factors . . .” (Hill and Kaplan 1993, p. 702). (2) At critical junctures Hawkes goes beyond prudent empirical claims. Thus Hill and Kaplan reject as unwarranted her assertion that “the proposition that foragers share to reduce the risks posed by exploiting unpredictable resources is widely favored but lacks empirical support” (Hawkes, 1993a, p. 341), along with her claim that empirical evidence is inconsistent with reciprocal cooperation: “We have never seen any systematically collected data demonstrating this” (p. 703). (3) At critical points she advances her argument by overly restrictive interpretation of alternative hypotheses. Thus, according to Hawkes, reciprocity requires balanced flows. In contrast, Hill and Kaplan cite models of bargaining theory based on the Nash equilibrium to argue that “exchange imbalance does not constitute evidence against reciprocity designed to reduce daily intake variance” (p. 704).

Dwyer and Minnegal (1993) have tested four hypotheses derived from the show-off model with Kubo data, which they believe ideal for the purpose due to high variance in Kubo capture rates, intermale differences in subsistence success, and widespread sharing. Three tests are consistent with the model but are given alternative interpretations. The fourth and central prediction, that individuals classified as show-offs would have higher reproductive success (numbers of attributed surviving children), was not supported (see also Harpending comment, in Hawkes, 1993a, p. 354). Dwyer

and Minnegal also question Hawkes' interpretation of support from Aché data. They note that her cited association between reproductive and hunting success correlates reproduction with mean hunting returns. It thus is not necessarily supportive of her variance-based hypothesis: "good' and 'poor' foragers classed according to mean return rates need not correspond to competent and incompetent 'show offs' classed according to some combination of mean **and** variance in return rates" (p. 65; boldface in original).

The Hawkes proposal is attractive because it neatly answers three related questions with one idea (Why are large game pursued? Why predominantly by males? Why are the yields distributed widely?). But Kaplan and Hill can offer an alternative explanation for each of these three points. Foraging theory indicates that large game often are in the diet that optimizes production efficiency (as for the Hadza, see Hawkes *et al.*, 1991). Nutritional complementarity between vegetable and meat food sources suggests why both gathering and hunting are pursued. Women's child rearing constraints suggest why they specialize in foraging. Risk reduction or trade generates transfers. These are sufficient if less parsimonious explanations.

The show-off hypothesis has provoked a healthy, contentious debate. If the idea is correct, we face significant adjustments in our understanding of foraging economies: (1) Male and female foraging behaviors have divergent goals as a consequence of their dissimilar reproductive interests. (2) The notion of a hunter-gatherer (or hominid) family unit with common objectives achieved through a complementary, male-female division of labor is faulty. Males hunt not to provision their families but to gain extrafamilial fitness advantages. (3) Since resource transfers not perfectly balanced by like return are thought to be common ethnographically and imbalance is fatal for the evolution of reciprocal cooperation, we must discard arguments that sharing evolved to minimize risk.

These reinterpretations depend, however, on acceptance of the hypothesis in the strong form in which Hawkes states it: no alternative to showing off is logically or empirically credible as an explanation of exchange. A weak form of the hypothesis—one more tenable empirically—would recognize showing off as one among several models of circumstance and would focus on the novel elements it brings to the analysis of exchange: attention to indirect and intangible currencies of social prestige and the evolutionary mechanism of sexual selection.

MODELS OF MECHANISM

The recent history of behavioral ecology suggests that models of circumstance must be coupled to models of neo-Darwinian mechanism. Dis-

covery of a hypothetical benefit and the circumstances of its genesis and maintenance is not enough. A schematic rendering of this history in three stages sets the context for a summary of models of mechanism.

A *permissive* period preceded Williams' 1966 book, *Adaptation and Natural Selection*. Nearly any benefit could constitute a causal argument for the origin and maintenance of adaptation. These benefits were sometimes indiscriminately associated with units ranging from alleles to ecosystems. With respect to supra-individual units, this became known as naive or vulgar group selectionism to subsequent detractors. An example in anthropology would be the widespread belief that evolutionary processes produce mechanisms of reproductive self-restraint in hunter-gatherers, for the benefit of regulating their overall population density to a level comfortably below the carrying capacity (for a critique see Bates and Lees, 1979). Williams was not the lone reactionary to the analytical permissiveness of this stage, but his book set the tone for the following, *restricted* period.

Williams stated as "doctrine" the view that "adaptation is a special and onerous concept that should be used only where it is really necessary. When it must be recognized, it should be attributed to no higher a level of organization than is demanded by the evidence" (1966, pp. 4–5). He offered compelling arguments that many explanations of adaptive function not couched in terms of self-interest at the level of the gene or individual were inconsistent with neo-Darwinian mechanisms. By this view, low birth rates among hunter-gatherers and consequently their low population densities occur—if indeed they do—because they actually optimize a woman's net reproductive success, measured as surviving children (e.g., Blurton Jones and Sibley, 1978). Much that has been creative in the evolutionary study of social behavior (concepts of kin selection and inclusive fitness, parent-offspring conflict, sexual selection and parental investment, reciprocal altruism, ESS/game theory, etc.) has come from this narrowly conservative attitude.

However, a new, *cautiously expansive* era can now be discerned. This third stage is one of reconsideration and careful expansion in the range of mechanisms and conditions recognized as providing legitimate neo-Darwinian explanations for social behavior, particularly cooperation. Wilson and Sober (1994) entitle a recent review article, "Reintroducing Group Selection to the Human Behavioral Sciences." They state (pp. 585, 588), "It is no longer heretical for biologists to think of natural selection as a hierarchical process that often operates at the group level." Other examples can be found in recent developments in game theory and dual inheritance models (see below). The lessons of the restricted era remain vital, perhaps especially so for a social science such as anthropology in which permissiveness has flourished unabated. Nonetheless, in behavioral ecology one sees a

trend toward an expanded sense of possibilities for the evolution of social behavior.

Varieties of Selection

As it has grown in specificity and complexity, selection theory has produced a confusing and inconsistently applied terminology (Brown, 1983, pp. 22-31; Dawkins, 1979; Wilson and Dugatkin, 1992). To help sort this out (Table I), I distinguish here between *direct* fitness, achieved through effects on offspring and other descendants (e.g., grandchildren), and *indirect* fitness, achieved through effects on nondescendant relatives (Brown, 1983). Classic *individual fitness* is direct.

Kin or nepotistic selection and *inclusive fitness* properly refer to the aggregate effect of direct and indirect fitness (Brown, 1983, pp. 22-23; Hamilton, 1964a, b), although some authors use these terms to refer only to nondescendant fitness consequences. I distinguish these uses with the modifiers "broad" and "narrow," respectively. Narrow kin selection thus confers indirect fitness by extending to nondescendant relatives the types of aid that gain direct fitness when provided to offspring and other descendants. *Sexual selection* recognizes that males and females may diverge in the mating tactics that will give them the maximum reproductive success in the form of direct fitness (as in the show-off hypothesis). Male-female divergences in mating tactics follow from unequal parental investment (Trivers, 1972).

Biologists define four types of social interaction, depending on the net inclusive fitness effect (broad) on the donor (first position) and recipient [second position (see Brown, 1983)]: spite, --; selfishness, + -; altruism, -+; and cooperation, ++. In what follows, most of the attention is on mechanisms promoting cooperation among unrelated individuals. In this context, *cooperation* refers to a collective activity that has individual costs but produces a positive result for all members of a group (Mesterton-Gibbons and Dugatkin, 1992, p. 268). By these definitions, "reciprocal altruism" (Trivers, 1971) is more accurately called reciprocal cooperation, the term that is used here.

Reciprocal Cooperation

The Williams doctrine made cooperation among unrelated individuals a high profile problem for evolutionary theory. Gone were the vague covering arguments of group-level selection. What remained was an explanatory challenge that sometimes seemed to cast doubt on the very existence

Table I. A Schematic Association Between Models of Mechanism and Circumstance, Keyed to Primary Sources Mentioned in the Text

Models of mechanism	Source(s)	Models of circumstance	Source(s)
1. Direct fitness selection			
1a. Individual selection	Williams	Tolerated theft, scrounging	Blurton Jones, Packer & Ruttan, Giraldeau, Vickery, Caraco
		Marginal valuation	Winterhalder
1b. Sexual selection	Trivers	Trade	Kaplan and Hill
		Show-off	Hawkes, O'Connell, Blurton Jones
1c. Reciprocal cooperation	Trivers	Risk reduction	Stephens & Charnov, Kaplan & Hill, Smith, Winterhalder
1d. By-product cooperation	Brown, Mesterton-Gibbons, Dugatkin, Connor	??	
2. Indirect fitness selection			
2a. Kin/nepotism selection (narrow sense)	Hamilton	??	
3. Interdemic selection			
3a. Interdemic (or group) selection	D.S. Wilson	??	
4. Cultural selection			
4a. Dual inheritance	Boyd & Richerson, Durham	??	

of cooperation as a natural phenomenon. Self-interested individuals designed by selection always would undo any tendencies toward cooperation by taking the benefits of collective activity without forfeiting the costs of contributing. Since the influential work of Axelrod and Hamilton (1981), this issue has been associated with the game of "prisoner's dilemma" (PD). Its importance for us lies in the challenged but widely accepted view that sharing among human foragers is a form of reciprocal cooperation that has evolved to minimize risk (Table I).

The setting of the prisoner's dilemma (isolated suspects tempted to rat on each other due to a plea bargain offered by skillful authorities) might seem a puzzling context for studying social behaviors such as sharing. In fact, shorn of its dramatic setting it represents one of the most common dilemmas of collective action, extending well beyond the hazards of law-

breaking (Boyd, 1988; Smith and Boyd, 1990). Cooperation provides two individuals a handsome benefit (their highest combined score), but the temptation to defect and take the benefits without reciprocating the costs is individually yet more attractive. The dilemma is that each rational individual will yield to temptation and thereby produce an unhappy result for both.

A standard ranking of outcomes looks like this: DC (defect against cooperation) = 5 > CC (cooperate against cooperation) = 3 > DD (defect against defection) = 1 > CD (cooperate against defection) = 0. Twice CC must also be greater than DC + CD, as is true here, and the game must be symmetrical with respect to the two players. Note that to defect is always optimal for an individual (DC > CC and DD > CD), hence the dilemma that both will defect and earn the low score of DD = 1. Even if a player knew in advance the choice of an opponent, defection still returns the highest reward in a one-shot round of the game. This ranking of payoffs is thought to be common to social dilemmas ranging from the tragedy of the commons to free riders on public goods. It also characterizes the temptation to "cheat" on delayed sharing arrangements that might minimize risk.

It is important to distinguish carefully between reciprocity and by-product cooperation. In reciprocity cooperation the action has a net negative consequence for the individual performing it, relative to a nonperformer. This temporary cost is more than made up by the delayed benefits of reciprocation. In by-product cooperation the organism is rewarded directly for a cooperative move, whatever the other individual does. A donor benefits relative to a nondonor.

Axelrod and Hamilton (1981; Axelrod and Dion, 1988) organized computer tournaments from which they isolated an ESS for the iterated prisoner's dilemma: tit-for-tat (or TFT). TFT cooperates on the first round and then matches its opponent's previous move on all subsequent rounds; it is "a strategy of cooperation based on reciprocity" (Axelrod and Hamilton 1981, p. 1393). The success of TFT depends on an indefinite number of future rounds. TFT cannot establish itself in a population of pure defectors, but once initiated at low frequencies, it is robust and spreads to dominate the population. Axelrod and Hamilton suggested that narrow kin selection (nepotism) or an initial clustering of unrelated cooperators could provide the threshold frequency required for TFT to get a foothold. Tolerated theft is another potential starter mechanism. TFT succeeds because it is nice (cooperates first), provokable (meets defection with defection), forgiving (returns to cooperation after a defection), and clear (Axelrod and Dion, 1988, p. 1385). Cooperators meeting cooperators

thrive and increase in frequency despite small losses to inveterate defectors.

Modeling has shown that TFT cooperation is more likely if individuals encounter one another regularly (perhaps by being sedentary), face an indefinite number of future interactions, recognize one another and recall their last interaction, live in small groups, make few errors, and establish metanorms, such as the willingness to punish not only defectors but individuals who tolerate defectors (Axelrod and Dion, 1988; Boyd and Richerson, 1992).

Although it is dominant in computer tournaments, TFT is vulnerable to the errors that would occur in real life. A single mistaken defection sets up a run of retaliatory back-biting and low awards that will end only if there is a countervailing mistake. This liability shows the advantage of GTFT (Nowak and Sigmund, 1992). G (for "generous") TFT is a probabilistic tactic that meets a previous round of cooperation with cooperation and a previous round of defection with a certain probability (q) of cooperating anyway ($q = 1/3$ for the reward values given above). Because it usually allows two opponent defections before retaliating with its own defection, GTFT is forgiving of a partner's mistakes and does not get into long periods of disabling retaliations.

The newest successful entrant (Nowak and Sigmund, 1993a) in the cooperation derby is identified as "win-stay, lose-shift" (also called "Pavlov"). Pavlov responds to the joint outcome of the previous round by following this rule: stay with the last move if it generated a high reward (e.g., 3 or 5), change if it produced a low reward (1 or 0). Pavlov is generous (like GTFT) but it also exploits unconditional cooperators who might migrate or drift into a population of TFT or GTFT. By diminishing their frequency, Pavlov forestalls invasion by pure defectors. It is important to note that Pavlov and related strategies have complex dynamics with an overall tendency toward a high frequency of cooperation (Nowak and Sigmund, 1993b).

In evolutionary simulations, these models form a developmental sequence: In a world of selfish defectors seeded with these possibilities, TFT in threshold frequency gains a beachhead. It then is supplanted by GTFT, which subsequently will succumb to Pavlov. Says Sigmund (1993, p. 201): "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." Thus a modeling effort that began with a starkly restricted conception of the problem of cooperation (the one-shot PD) has arrived at a much more promising sense of cooperation's evolutionary possibilities.

Interdemic/Group Selection

Biologists today are giving greater attention to the possibility that group-level selection is an effective evolutionary force (Wilson and Sober, 1994). The basic requirement is spatial heterogeneity in the productivity of local groups, which has an indirect effect on the group member's productivity. This requires deme structure (the existence of partially differentiated subgroups). For example, if cooperation makes a subgroup more productive relative to others in the deme, natural selection will favor individuals resident in groups with more cooperators (Mesterton-Gibbons and Dugatkin, 1992). Pressures to cheat on cooperation locally (as envisioned in the prisoner's dilemma) are counteracted by competition among groups in the deme. The outcome will reflect the balance of these intra- and intergroup forces, but it occasionally should favor the group level. The intergroup variance necessary for this process may arise by chance (genetic drift), or it may be due to preferential association among cooperators, including group expulsion of cheaters.

The newer varieties of group selection acknowledge that the enduring units of selection are the genes, the *replicators* in Dawkins' (1976) terminology, but it also insists that groups along with individual organisms can be the *vehicles* that determine their relative fitness. The key is shared fate, obvious in the case of individual organisms, less obvious but still potentially important if it arises from the collective behavior of the individuals within a subgroup. In effect, "groups are like individuals by virtue of the adaptive coordination of their parts" (Wilson and Sober, 1994, p. 591): "As soon as we make vehicles the center of our analysis, group selection emerges as an important force in human evolution and the functional organization of human groups can be interpreted at face value—as adaptations that evolve because groups expressing the adaptations outcompeted other groups" (Wilson and Sober, 1994, p. 598).

The full details of the Wilson and Sober argument are beyond the present review. Suffice it to note that group-level selection can promote solutions to collective action problems if those solutions advance subgroup welfare.

Dual Inheritance

Dual inheritance models (Boyd and Richerson, 1985) explore how cultural information is affected by selective transfer among individuals (within and across generations), how these forms of transfer interact with genetic inheritance, and, especially, how the linked evolution of genetic and cul-

tural information might alter the results expected from genetic selection alone. Of particular importance here, dual inheritance models expand the possibilities for the evolution of cooperation.

Soltis *et al.* (1995) describe how this might occur, using the example of biased transmission. Biased transmission results when individuals adopt behavioral variants because their local attractiveness is frequency dependent, or because a “rule of thumb” prescribes adopting the most common local variant (say for those variants difficult to evaluate on their merits). It generates intragroup conformity and intergroup diversity in behavioral variants likely to affect group welfare. If the population is composed of partially isolated subgroups, biased transmission will maintain degrees of intergroup difference that can sustain cultural group selection.

More concretely, imagine that biased transmission produces intergroup diversity in the amount of time that individuals allocate to foraging. Groups that by chance invest a moderate number of hours per day exploit their resources around the maximum sustained yield and flourish, whereas those that forage long hours gain a short-term edge but eventually deplete resources to the levels that yield disproportionately small returns (see Winterhalder, 1993). The restrained groups flourish, grow, and divide to replicate themselves, the high-effort groups languish, perhaps eventually to collapse and disperse to surrounding units. Those units are likely to be among the relatively restrained, a pattern the minority of emigrants will now emulate by the mechanism of biased transmission (Soltis *et al.*, 1995). The result is group selection for the type of cooperation that avoids a collective action problem like the tragedy of the commons.

As yet there are no formal circumstance models or empirical studies of exchange behavior linked expressly to interdemec selection or to dual inheritance mechanisms. These appear to be especially promising venues for the study of cooperative behaviors.

Summary, Models of Mechanism

Purely selfish behaviors (+ -) arise from the direct fitness effects of individual and sexual selection (1a and 1b; Table I). Self-interested cooperation (+ +) among unrelated individuals only arises through mechanisms of reciprocal and by-product cooperation (1c, 1d), interdemec selection (3), and, for species with cultural inheritance, dual inheritance (4). Altruism and cooperation among nondescendent relatives are routinely attributed to (narrow) kin selection (2a), but aid-giving among this group also may be due to other of the mechanisms facilitating cooperation. Direct fitness effects (1a and 1b) explain aid given to offspring and their descendants. Co-

operation but not altruism is possible among nonrelatives; aid but not altruism can be directed by parents to offspring and their descendants.

Recent developments in game theory, interdemic selection, and dual inheritance characterize the cautiously expansionary stage of behavioral ecology. They identify new mechanisms capable of promoting cooperation among related and unrelated individuals. Especially, models of interdemic selection and dual inheritance promise to broaden the routes and the range of conditions under which evolution can shape cooperative, supra-individual social behavior. Models of circumstance that address issues of exchange are well developed for individual and sexual selection, reciprocal cooperation, and kin selection. However, they have yet to be formulated for interdemic and cultural selection. In general, conditions for the evolution of cooperative behavior, including sharing and other forms of exchange, no longer appear so stringent as they did in the decades immediately past.

OVERVIEW, ANALYTICAL ISSUES, AND PALEOECONOMICS

In this overview I assay the degree to which these models comprise a synthesis, show how they can be used to reflect critically on one other, and argue that they provide a more promising analysis of "primitive" exchange than Sahlins' widely accepted approach.

An Overview

The models depicted in Table I are notable for their complementary, sequential, and frequently overlapping roles in the analysis of exchange. Individual (1a) and narrow kin (2a) selection are primary mechanisms, operating through aid to offspring, through nepotistic altruism if ecological circumstances encourage proximity of extended family groups (Brown, 1983), and through tolerated theft or by-product cooperation in groups of social foragers, some members of which are unrelated. Any of these along with clustering might serve as a starter mechanism for reciprocity-based cooperation (1c), which in the right circumstances will tend to develop through a self-reinforcing sequence of individual tactics (e.g., TFE, GTFI, and Pavlov). Sexual selection (1b) may also affect exchange behavior.

With the exception of food provided to infants and children, uneven or asynchronous individual harvesting of medium to large packets (or discovery of patches) within contiguous family groups or among unrelated social foragers lies behind each of these mechanisms. The high fitness benefits and thus the salience of risk avoidance can be accurately assessed only if

food resources are appraised through marginal valuation. By turns, a given unit of food may be relatively inconsequential or it may represent survival itself. Sequential relationships among these factors do not necessarily mean that one fully replaces another. Tolerated theft does not disappear simply because it helped to initiate a well-established pattern of reciprocal cooperation. Some of these linkages have been unrecognized; few have been formally analyzed.

There also are lacunae. Game theory analyses of reciprocity have used deterministic, nonmarginal reward schedules that may not adequately represent the costs and benefits of food exchange. Additionally, most of these models are sufficiently novel that they've received insufficient empirical attention. Finally, it probably was salutary that behavioral ecology analyses of exchange began with the mindset of the restricted era (note the fullness of the upper right portion of Table I relative to the lower right). But we now should anticipate that models of interdemic selection and concepts of dual inheritance will significantly expand the range of mechanisms and circumstances enabling the evolution of exchange and other social behaviors with group-level benefits. I now elaborate on some of these points.

Evidence and Notes on Models of Circumstance

Tolerated theft and scrounging provide a starter mechanism, based in direct individual selection, for sharing through reciprocal cooperation. If harvest of asynchronous, intermediate-sized packets becomes routine in a small, stable group, tolerated theft likely will be transitory as the dominant cause of exchange. The large bonus of marginal value that can be garnered by participants fosters the shift to reciprocity cooperation, perhaps through a sequence like that now established within game theory. Nonetheless, tolerated theft does not exhaust its influence in some primal context. Ephemeral as an evolutionary catalyst, it remains a potential influence on every transaction: "If we include among the threats to a possessor not simply violence but punishment, reprobation and perhaps ostracism from the group, this model [tolerated theft] may well be relevant to explanations for sharing in some human groups *if* membership of a group is advantageous for other reasons" (Borgerhoff Mulder, 1991, p. 75; original italics). Risk minimization, perhaps initially an incidental benefit of tolerated theft, likely becomes a more prominent causal force with the shift to reciprocity-based exchange.

The widespread ethnographic phenomenon of "demand sharing, or mutual taking" (Peterson, 1993, p. 861; other examples in Ingold *et al.*, 1988) is consonant with a continuing role of tolerated theft or its threat in

maintaining reciprocity among hunter gatherers. Here is Peterson, summarizing observations by Hiatt:

Below the melody line in praise of generosity among the Anbara people of Arnhem Land, a grumbling about their stinginess, neglect and ingratitude also was evident. Public pressure on individual Anbara to share was virtually irresistible, so various counterstrategies were adopted by the diligent to prevent exploitation by the lazy or manipulative. The most effective of these . . . was eating during food collection, so that the greater part of a person's produce was in an advanced state of digestion by the time he or she returned to camp (Peterson, 1993, p. 860).

Ethnographically, it will not be easy to distinguish the threat or actuality of tolerated theft from the monitoring and threat of sanction that secures reciprocity-based cooperation.

Scrounging models suggest that a group of social foragers often will contain a mix of producers, scroungers, and opportunists, their respective proportions determined by group size, producer priority, and resource detection constraints. Consider how this might apply to a common model of hunter-gatherer organization—radial foraging of individuals from a camp or home base, occupied by a small group engaged in reciprocity-based food sharing. The isolation of individuals during the food quest guarantees producer priority (as for the Anbara, above); that and small group size diminish the frequency of pure scrounging. Speaking analytically, these foragers likely will reside on the left side in Fig. 2. Home base sharing of food portions not eaten in the field promotes overcompensation. Foragers need not sacrifice active production opportunities in order to also engage in scrounging or reciprocity. We can locate these foragers in the upper left quadrant in Fig. 2. The prediction is that of a population of producers and/or opportunists in an ESS mixture, with pure scroungers absent. The unequal productive effort evident ethnographically (and cited by critics of reciprocity) may reflect just such an ESS of a few producers and many opportunists.

In this scenario reciprocity-based sharing removes the detection handicap of active foraging, thereby shifting the equilibrium mix from scrounging toward production and opportunism. This in turn would mitigate (but not eliminate) the tendency toward underproduction and increased risk noted by Caraco and Giraldeau (1991; above). Although speculative, evidence favors this scenario. Recall the Aché practice of saving portions for those absent at an initial food distribution (Kaplan and Hill, 1985b). The literature also contains frequent descriptions consistent with producer priority: “The only sure way of guaranteeing game to one’s immediate family is to be the successful hunter” (Altman, in Hawkes, 1993a, p. 352). Hames (cited in Hill and Kaplan, 1993, p. 702) estimates that producer’s families receive twice the portion of other families, and citing this and other examples, Hill

and Kaplan (1993, p. 703) state that: "In four of the six societies [for which there are data] there appears to be clear evidence that hunters keep disproportionate shares for their own families' consumption."

Generally speaking, scrounging models allow us to associate structural properties of radial foraging to the individual foraging tactics and group production efficiency of hunter-gatherers. In the absence of a full ethnographic appraisal, mixed production and opportunism (with the balance toward opportunism) seems an accurate characterization of hunter-gatherer behavior. Such a scenario has precedent for hominids and may have been common in prehistory. The more important point, however, is the dependence of behavioral outcomes on what were likely diverse local ecological conditions, hence an expectation of diversity in these behaviors. Note also that Hegmon's restricted sharing regime contains within it the agricultural analog of producer priority.

Marginal valuation gives us means of distinguishing among by-product cooperation, tolerated theft, and reciprocity cooperation. These hypotheses are nearly identical in terms of their empirically observable features: the ecological conditions they assume (asynchronous acquisition of medium to large packets by individual foragers who then congregate) and the manifest behaviors they predict (redistribution). The proposals differ primarily in features that are difficult to observe: the evolutionary processes they invoke (direct individual selection, selection for reciprocal cooperation) and subtleties of psychological motivation (i.e., the degree to which resource exchanges are coerced or voluntary, subtly taken or given). For good reason it has proven quite difficult to separate these factors using ethnographic data (e.g., Kaplan and Hill, 1985b).

Marginal analysis of resource value points up two distinctions. First, if a giver can count fully on reciprocity from group members, he or she should seek to distribute portions of a resource as widely as is possible. This tactic garners the maximum aggregate obligation of future return (Winterhalder, 1996). In contrast, if tolerated theft is generating transfers (or is mixed with reciprocity), the holder of a resource should seek to avoid (or limit) encounters with group members. As in the Anbara case (above), the ethnographic literature records both situations, the press of unwelcome gifts and the attempt to avoid unwelcome solicitation. In by-product mutualism the discoverer of a resource should be indifferent to the fate of surplus portions.

Second, transfers resulting from tolerated theft always lower the value of a resource to its discoverer, and may do so sufficiently that an otherwise profitable item would be dropped from the forager's encounter-contingent diet choices. In contrast, since reciprocity exchanges are provided with the expectation of equal or greater return in value, reciprocity-based exchange

will never cause the item to be dropped from the diet. In fact, the extra marginal value entailed in reciprocity cooperation might actually elevate the rank of a resource enough to move it into the optimal diet. If exchange causes a resource to be dropped from the diet, tolerated theft is indicated. If exchange causes an item to be harvested that normally would be ignored by the forager, then reciprocity cooperation is indicated. Hill and Kaplan (1993, p. 706) give other means of distinguishing tolerated theft from reciprocity cooperation.

Two claims anchor the strong form of the *show-off* hypothesis. Large game necessarily are collective goods (their full value lost to tolerated theft, the acquirer uncompensated), and unbalanced transfer is fatal to models based in reciprocity cooperation. The materials reviewed here provide reason to question these assertions.

- (1) If the direct, realized value to the forager puts an item in the optimal, encounter-contingent diet of a forager, then he or she is better off harvesting it no matter how much is ceded to tolerated theft or sharing. By-product cooperation is a sufficient initial hypothesis.
- (2) Imbalances by quantity or number of items are not fatal to tolerated theft or reciprocity (Winterhalder, 1996). Indeed, measures of quantity need not correlate with imbalance in units of value. For instance, if the potential value to the finder of a resource remains satiated after redistribution, then there has been no tolerated theft and the resource is not a collective good. What we need but do not yet have are means of identifying the degree of imbalance that subverts reciprocity cooperation.
- (3) Scrounging models show that a likely equilibrium for hunter-gatherers contains both producers and opportunists, a mix of individuals making quite different contributions to production.
- (4) Although they do not elaborate, Hill and Kaplan (1993, pp. 703–704) suggest that exchange analyses using the Nash equilibrium concept also can result in stable but unbalanced systems of exchange.

Contrary to Hawkes' analysis, self interested individuals might procure, use, and incidentally or tactically provide substantial parts of medium to large game animals to group members without the opportunity costs that would make them public goods. Imbalance is consistent with a wide range of possibilities, including tolerated theft and by-product and reciprocity cooperation. A simple tally of how much is given and gotten—and to date this is the form of our scant data (Hawkes, 1993a; Hill and Kaplan, 1993)—cannot tell us if gains and losses of value deviate from those expected of these various hypotheses.

Risk-minimizing approaches generally have attended more to ecological circumstances than evolutionary cause, leaving them open to the criticism that free-rider problems will undermine the evolution of sharing. Game theory analyses that find stable systems of reciprocity based on contingent tactics blunt this criticism.

In an early note, Schaffer (1978) recognized that reciprocal food sharing will be favored when environmental variability creates a simultaneous surplus for one individual and a deficiency for another, with a subsequent reversal in their roles. This oscillation must be recurrent and unavoidable; the individuals must have an ongoing interaction. Consequently, reciprocity is expected only for behaviors that occur frequently during the life span of individuals, giving TFT-like interactions a quality of indefinite duration.

Band-level food sharing among hunter-gatherers seems the ideal context for reciprocal cooperation to evolve. Food acquisition and consumption are routine, visible activities occupying a large percentage of the adult population. The fortuitous elements of the food quest generate a high probability of day-to-day imbalances in acquisition, and regular role reversals. Those with surfeit incur only a modest (marginal) cost in providing a large benefit to those in need. Those who are contributors one day will be among the recipients the next. Such commonplaces have made proponents of risk minimization confident that evolutionary processes can generate the behaviors that realize the advantages they ascribe to sharing (Borgerhoff Mulder, 1991, p. 74).

Social mechanisms by which individuals monitor and enforce reciprocity are prominent in ethnographies: "The literature bursts with accounts of the weight of reciprocity in egalitarian societies" (Beckerman, comments in Hawkes, 1993a, p. 353; Smith and Boyd, 1990). Among Australian Aborigines, "the positive valuing of the demand sharing of food is established at and reinforced from the moment of birth, and its potential as an index of the state of social relations is powerfully inculcated" (Peterson, 1993, p. 863). Or, from a Mamaindê informant: "For if one doesn't give, one doesn't get in return, and we want to make sure we remain in the good graces of those who will themselves be distributing later . . . some people are specifically excluded from most distributions, because they never or only rarely give any of their products to us" (Aspelin, 1979, p. 317).

The joint consideration of scrounging and risk minimization models reveals that food sharing at a central location by radial foragers acts to diminish risk arising from harvest variance through two independent routes: (a) it lowers the pooled production variance, hence the chance that any individual will suffer an intolerably low deviation from the mean intake (Winterhalder, 1986), and (b) it reduces detection handicaps [that is, it enhances overcompensation (Caraco and Giraldeau, 1991)], which mitigates

the tendency for scrounging to depress average production efficiency. Reciprocity cooperation acts favorably on both the variance and the mean of stochastic food harvests. Thus sharing becomes its own defense against free-riding scroungers.

By-product cooperation, like that associated with hominid scavenging, might have served as a catalyst initiating reciprocity-based sharing. If by-product cooperation is a sufficient evolutionary explanation for punishing defectors (Boyd and Richerson, 1992; quoted above), then it may also lie behind the sanctioning required to sustain reciprocity. In both roles, by-product cooperation would lower the evolutionary hurdle to sharing. These two forms of cooperative behavior may interact in other contexts as well.

A hunter-gatherer will harvest a collective good so long as it has a realized value sufficient to put it in the optimal, encounter-contingent diet. This is simple by-product cooperation. But what of the initial decision to forage at all? Surely here is the true temptation to take the free ride. Perhaps not. If pure scroungers forgo the opportunity to detect some feeding situations available to foragers, and if there are modest degrees of producer priority, then pure scroungers pay a price that they might better avoid by active hunting and gathering (coupled with opportunistic scrounging).

Kin-selected cooperation (broad or narrow) will evolve by natural selection only if the benefit-to-cost ratio between the recipient and the donor is high and/or their degree of relatedness quite close (Feinman, 1979). These conditions are most readily met between close family members (high relatedness), between parents and offspring (high relatedness plus high benefit-to-cost ratio due to strong differences in competence), or when aid has very low opportunity cost to the food provider [as when adults have no alternative reproductive options (see Feinman, 1979; Kaplan and Hill, 1985b)]. While the nepotism hypothesis identifies an evolutionary mechanism for sharing and a favored class of recipients, it does not tell us what ecological conditions will produce the needed cost-benefit ratios (Borgerhoff Mulder, 1991, p. 74). These must be specified by appropriate models of circumstance, which we do not yet have. O'Connell (personal communication) suggests that relatedness may be a good predictor of the distribution of small, low-variance packets (e.g., many plant foods) but a poor predictor of the exchange of larger packets.

Because reciprocity is catalyzed by nepotism and depends on group stability, there likely will be overlap in these sources of fitness benefits (Wilkinson, 1988, p. 85). Nonetheless, reciprocity cooperation may provide benefits to kin entirely apart from relatedness, and food-sharing patterns based on kinship may interact with or be swamped by those based on the proximity of nonrelatives. Marginal valuation of resources predicts the widest possible sharing within a group practicing reciprocity (see above).

Wilkinson (1988, p. 98) concludes that “repeated altruistic exchanges among animals in relatively large groups—such as lions . . . elephants . . . dwarf mongoose . . . brown hyenas . . . or tribal human cultures, among others—are likely to have an RA [reciprocity cooperation] component of inclusive fitness that exceeds the component due to kin selection.” Wilkinson (1987) explores means of discriminating the relative effect of reciprocity and nepotism in groups with overlapping kin and nonkin relations.

Statistical analysis (Kaplan and Hill, 1985b) shows that individual Aché within a foraging band are no more likely to receive meat and honey from close relatives (husbands, fathers, brothers) than from other individuals who acquire these items. Thus, the prediction that sharing will be directed preferentially to close kin is not supported. Qualitative ethnographic accounts by Lee (1968, p. 31) cite equitable distribution to all present in a camp of !Kung San. Woodburn (1968, pp. 106–107) observes that among the Hadza large game animals are shared widely, without reference to kin or other specific categories of individuals. For Feinman (1979, p. 713) these examples confirm that “individuals who reside in a local group are recipients of shared food regardless of kin relatedness.” On the other hand, Hames “estimates that the families of hunters receive about twice the portions received by other families and that there is a strong kin bias in redistribution” (Hill and Kaplan, 1993, p. 702). In her reply to Hill and Kaplan, Hawkes (1993b, p. 707) uses Hadza data to show that “even though most of these very large animals are eaten by others, hunters keep a special share for their families.” The sharing of medium to large packets is somewhat biased to relatives but by no means limited to them.

Nepotism supplies another link among the effects posited by the models under review: by acting to bias distribution to family members within a broader group, broad kin selection generates producer priority and thereby discourages unbridled scrounging.

Analytical Issues

The Primacy of Food. Rendered as value and compared to other stuff entangled in exchange, food has special qualities. Along with air and water, its value is exceptionally time-sensitive. It is needed almost daily; it often is perishable. Food value is extinguished in consumption and its immediate aftermath of metabolic activity. Consumption by one individual precludes that by others (except for pregnant or lactating females). Food is needed in regular, modest quantities, but it also stimulates rapid dietary satiation due to limited digestive capacity. These properties determine the marginal return curve for food. They establish the time-sensitivity of food value and

thereby establish the link between marginal analysis and risk. Much of the value bonus that arises from localized, short-term food exchange in daily life is a consequence of this temporal property. Because “[f]ood is life-giving, urgent” (Sahlins, 1972, p. 215) it is the primal stuff of sharing and probably the starting point for other forms of exchange.

Qualities of a Contested Packet (or Patch). To be subject to tolerated theft or scrounging, a resource item (packet or patch) must be of sufficient size to represent temporary overabundance for the discovering forager. It must be divisible and susceptible to being taken. We presume that its value is characterized by diminishing marginal returns and that its discovery by one will entail a contest with others. However, an item large enough to saturate the nutritional needs of those assembled does not fit within this definition because portions removed by takers do not diminish the maximum value available to the giver. If unallocated portions remain after all are sated, then there has been no theft (or scrounging) of the evolutionary currency that matters. Thus for any forager whose largest resource finds (hunted or scavenged) exceed the food needs of those assembled, we should conceive of contested packets or patches as *intermediate* in absolute size.

Production of Packets. Why should a self-interested forager expend the effort to harvest a packet (or locate a patch) if the greater part of its value is sure to be lost to tolerated theft or scrounging? In standard applications of encounter-contingent foraging theory (Stephens and Krebs, 1986), resource rankings have been calculated using their absolute values (measured, say, in kilocalories). Exchange makes it clear that the more relevant measure is the *realized* value of the resource to the individual deciding whether or not to procure it. If portions are lost to scrounging (or even if the item becomes inedible before it can be fully consumed), its realized value may be significantly less than its absolute size.

This creates three possibilities. (1) A resource of high enough rank may remain in the optimal diet of a forager irrespective of losses to tolerated theft. (2) A lower-ranked resource or one subject to relatively high degrees of loss, perhaps because of multiple scroungers, may drop out of the optimal diet. (3) It also is possible that a resource will enter the optimal diet only when its realized value can be augmented through reciprocity or trade. In each of these cases exchange affects realized value and resource choices in ways that have not been recognized previously in standard diet breadth models or empirical studies.

Balance. Various of the authors reviewed above have adopted a standard of balanced exchange, as either the starting point for elaborating hypotheses or a benchmark for falsifying them. Blurton Jones' (1987, p. 43) conclusions about scrounging are predicated on equal sharing. Kaplan and

Hill (1985b; but see Hill and Kaplan, 1993) presume that if transfer of foodstuffs is unbalanced, then not-in-kind utilities must be flowing opposite to food. Hawkes predicates her rejection of the tolerated theft and risk minimization hypotheses on evidence of departure from precisely equal flows: "The economics of defense will lead to even sharing" (1992b, p. 295). But the models reviewed here show that unbalanced flows may arise in a variety of circumstances. Without ancillary data to eliminate these possibilities, lack of balance cannot be taken as evidence against tolerated theft, reciprocity, or risk minimization.

Currency. To inform accurately about behavioral ecology trade-offs, cost-benefit accounting should encompass direct *and* opportunity costs, and whatever the actual quantities of stuff (calories, etc.), they must be assayed ultimately in terms of resource values. In situations of diminishing marginal returns, there may be large disparities between measuring units of resource and measuring units of value. To my knowledge, virtually all studies to date have considered only units of resource (Winterhalder, 1996). The determination whether a behavior is by-product or reciprocity cooperation could turn on this distinction, as these possibilities are differentiated only by subtle shifts in the reward structure of an interaction.

Multicausality. Although remarkable for their quantitative detail, existing data do not allow us to choose among the various hypotheses about food exchange (Hill and Kaplan, 1993). Attempts by Hawkes to test various exchange models show the influence of hypothetico-deductive procedures on human evolutionary ecology (see also Winterhalder and Smith, 1992). A standard (e.g., the balance requirement) is identified; if quantitative evidence fails to match precisely, that hypothesis is rejected: reciprocity-based explanations are faulty (e.g., Hawkes, 1991, p. 37). But there are two shortcomings with this procedure. It now is apparent that the empirical standard of balanced flows does not have this degree of discriminating power. And the hypotheses being compared are not mutually exclusive. Rather, they describe causes that interact and must be evaluated for their situation-specific contribution to the *variability* among exchange systems. We cannot rule out any one factor because it fails to predict fully the observed behavior. "[W]hat is striking about foragers is the very diversity and complexity of these practices" (Speth, 1990, p. 172).

Paleoeconomics

In anthropology mention of exchange conjures Sahlins (1972) for his interpretation of Mauss and his social analysis of material reciprocity in primitive or stone-age economies. Sahlins' model is based on a correlation

between the character of exchange events and degree of social relationship. Exchange moves from a pole of *generalized reciprocity* (disinterested concern, “assistance freely given . . . [without] open stipulation of return” (p. 191), where “the material side of the transaction is repressed by the social” (p. 194)], through *balanced reciprocity* (mutuality, careful reckoning of equivalent return without significant delay, social and material aspects equal), to *negative reciprocity* [self-interested appropriation, gained by hard bargaining, chicanery or force, with the social inclinations repressed by the material: “the most impersonal sort of exchange . . . the most economic” (p. 195)]. This is a moral axis, positive to negative, altruism to maximization of “net utilitarian advantage” (p. 195). The chief clue to the character of an exchange event is material: “The stipulation of material returns . . . the “sidedness” . . . would be the critical thing” (p. 193).

The factor that determines (*impels* is Sahlins’ wording) the character of an exchange event is the “span of social distance” between the participants: “close kin tend to share, to enter into generalized exchanges, and distant and nonkin to deal in equivalents or in guile” (p. 196). The continuum is demarcated by “intervals of sociability” (p. 191), with social distance based on both kinship and residence. One shares with close kin and neighbors and practices sharp dealing with strangers and distant folk. For Sahlins, the social constitutes the economic; the economic measures the social. Although he also considers relative rank and wealth, and differences between comestibles and other exchange items, these enter the analysis as modifiers of the social dimension.

Sahlins’ analysis is resolutely social; his economy “is conceived as a *component of culture* rather than a *kind of human action* . . . as the process of (materially) provisioning society and [thus as a] definition opposed to the human act of satisfying wants” (1972, pp. 186–187; original italics). In contrast, evolutionary ecology begins from the very terms that Sahlins excludes: the wants and actions of interacting but self-interested individuals. And by an odd turn, these terms will better explain what Sahlins observes as well as some of the things he neglects.

Consider first Sahlins’ well-documented continuum between the character of reciprocity and the degree of social distance. One dimension of motivation (generosity to chicanery) is a product of one dimension of social life (near to distant relationship), facts and their cause reduced each to single parallel axes. But so reduced, the Sahlins approach has no means of incorporating need, quantity, value, or occasion. It cannot tell us—as frequently evolutionary ecology can—what types of things are exchanged, how much and to what benefit or loss, when (in what circumstances), or, in fact, why.

Even within its own restricted terms, Sahlins’ analysis begs the fundamental question: Why deal easily with kin and rather more shrewdly with

strangers if not that self-interest takes a different form in the unlike circumstances of the two cases? Kinship, community, and contiguity, and the social interaction they enjoin, give assurance of reciprocity. Sahlins' model can be recast as the observation that self-interest is correlated with degree of biological and social relatedness in just the manner that would be predicted by nepotism and reciprocal cooperation.

By predicating exchange solely on the social realm, Sahlins must restrict "net utilitarian advantage" (p. 195) to the pole of negative reciprocity and to decidedly amoral vocabulary: haggling, chicanery, and theft are among the words used. Here, as in his analysis of production, where the "Zen" forager is the binary opposite of economic man (see Winterhalder, 1993), structuralism determines the form of relationship: "The economic relation tends to be a simple negation of kinship reciprocities . . ." (Sahlins, 1972, p. 197). But it is not so simple. We might also presume that self-interest is ever present but its economic expression can take on diverse forms depending on specifics of the social and environmental context. Selfishness or generosity, individualism or cooperation arise from like impulses in different socioecological settings.

Sahlins (1972) also touches on exchange of food and sharing:

" . . . There is the principle that one does not exchange things for food, not directly that is, among friends and relatives. (p. 216) . . . About the only sociable thing to do with food is to give it away The implication is not only a rather loose or imperfect balance in food dealing, but specifically a restraint on exchanges of food for other goods. . . . (p. 217) Food has too much social value—ultimately because it has too much use value—to have exchange value. (p. 218)

But things *do* sometimes exchange against foods (Kaplan and Hill, 1985a; Wiessner, 1982), even among friends. Evolutionary ecology can identify the conditions under which this is expected, and they rest in material terms (unbalanced flows) that Sahlins' analysis omits. While we must reject the categorical social principle Sahlins states as wrong in fact and unlikely in theory, at the same time evolutionary ecology models suggest that his observation has an important kind of generality. Marginal exchange analysis (Winterhalder, 1996) makes it evident that the disadvantageous terms of trade between food and other items often will limit this type of transaction in foraging economies.

Sahlins' discussion of sharing and the special status of food is more congenial to the present approach:

That scarcity and not sufficiency makes people generous is understandable, functional, "where everyone is likely to find himself in difficulties from time to time." It is most understandable, however, and most likely, where kinship community and kinship morality prevail. . . . (p. 211; internal citation from Evans-Pritchard) The vulnerability to food shortage can be met by instituting continuous sharing within the local community. (p. 212)

Food sharing might be instituted by social action. However, evolutionary ecology models direct our attention more comprehensively and concretely, not only to kinship and community but also to specific models of circumstance showing the material or ecological conditions under which sharing might evolve.

Sahlins concludes his chapter on exchange with this statement: "Here has been given a discourse on economics in which "economizing" appears mainly as an exogenous factor! The organizing principles of economy have been sought elsewhere (1972, p. 230). Earlier in the text he is more circumspect: "Simply to demonstrate that the character of reciprocity is contingent upon social distances . . . is not to traffic in ultimate explanation, nor yet to specify when exchanges will in fact take place" (p. 202). The latter Sahlins expects to find in the "larger cultural structure and its adaptive response to its milieu" (p. 202). But the archaeologist or anthropologist who does wish to traffic in ultimate explanation and to know when exchanges occur might better approach the analysis through the very behavioral ecology factors that *Stone Age Economics* tries to expunge, including economizing. Because it is dedicated to polemics against formalist economic methods, Sahlins' analysis is deflected from the possibility of explaining what it so successfully characterizes about early, nonmarket economies.

Nowhere is the ambiguity of nonmarket exchange, truck in gifts, more evident than in Mauss [1967 (1925)].

The form usually taken is that of the gift generously offered; but the accompanying behaviour is formal pretence and social deception, while the transaction itself is based on obligation and economic self-interest. (p. 1)

Mauss documents the obligation in premarket societies to give, receive, and repay. He describes the social ambivalence hovering about these transactions. Personal history adheres to the item through its exchanges among individuals; the gift may be welcomed, onerous, or both; obligations linger long after the event. Acceptance of a gift can be dangerous (p. 58). Generosity may be magnanimity or a weapon of social advantage. For Mauss, exchange expresses the social confusion of "objects, values, contracts and men" (p. 24).

It is a complex notion that inspires the economic actions we have described, a notion neither of purely free and gratuitous prestations, nor of purely interested and utilitarian production and exchange; it is a kind of hybrid. (p. 70)

None of this is surprising if we view the impulse to exchange as having arisen from a complex mix of tolerated theft, nepotistic (kin-selected) generosity, pervasive and watchful reciprocity, and not-in-kind transactions, in which causes and motives are never entirely separate and always tethered to the ambiguities of social relationships. What is given might have been

taken; altruism is measured; reciprocity is attended by uncertainty and the need to *attend* and possibly to sanction to ensure the return; lavish generosity can put recipients into debt they might rather avoid; these qualities mingle. "If we understood [the obligation to give] . . . we should also know how men came to exchange things with each other" (p. 11). Mauss cites the dead and the gods as among the first groups with whom men made contracts. In our account, obligations to give would arise first with the foods exchanged by foraging/scavenging hominids who were seeking a more secular kind of security.

Mauss lamented the depersonalization of modern economic theory, its utter separation from the social realm. But the evolutionary ecology reviewed here—a kind of hybrid—returns the interpersonal to the core of economic analysis. Kin and charged social affinities with neighbors are central. Behavioral ecology also neatly transcends the focal and unresolved problem of the formalist–substantivist debate in economic anthropology (LeClair and Schneider, eds., 1968) by showing how neoclassical premises and methods can produce economic analyses of production and distribution that are nonetheless embedded in social and kin relations. The material value of things transferred and the nature of the exchange are constituted in part by the social relationships among the parties to the transaction. As an evolutionary matter, it is no wonder exchange is socially charged.

CONCLUSION

Evolutionary or behavioral ecology can claim a promising and diverse but incompletely synthesized and tested family of models on the subject of exchange. It is encouraging that we now have models of circumstance to match several of the known evolutionary mechanisms that could affect this behavior. Future work must engage the problem of making appropriate distinctions among existing possibilities. As with any rapidly developing set of ideas, it has not always been clear what we should be predicting or what we are in fact observing. Another promising area will be the elaboration of models that draw on the possibilities of interdemic selection and cultural inheritance.

Nonetheless, juxtaposition of the extant models illuminates several new structural relationships characterizing the foraging mode of production and its evolution. Besides by-product mutualism, we now can suggest several mechanisms capable of initiating reciprocity cooperation and the circumstances in which they might work. Individual selection for tolerated theft of resource packets or patches and/or nepotistic selection for providing aid to nondescendant relatives in a group of social foragers would provide the

starter mechanism for reciprocity-based cooperation. In small groups with continuing interactions, it is evident that reciprocity would develop from TFT or by-product mutualism to more stable and cooperative tactics, based in social monitoring and sanction.

Recurrent, unsynchronized discovery of intermediate-sized patches or packets of food, with regular role reversals among givers and takers, is the circumstance common to these mechanisms. The benefits of reciprocity—chief among them minimization of subsistence risk and provision of a more balanced and regular diet—are best shown through measurement of marginal values. Risk minimization benefits are achieved with a small number of participants, and, thus can be gained in the small groups in which reciprocity is most likely to evolve.

In small groups of kin and nonkin, sharing and group cooperation in the food quest evolve under the joint influence of several evolutionary mechanisms. Within this mix, nepotism selection somewhat biases distribution to the successful forager and his/her family, thus generating a situation of producer priority. Radial foraging from a camp and end-of-day pooling remove detection handicaps. Together nepotism and groupwide reciprocity cooperation—favored by marginal rewards—produce a pattern of sharing that eliminates pure scrounging from an ESS mix of producers and/or opportunists. This mitigates the problem of free riders, the chief impediment to risk minimization models based in reciprocity.

It now is also evident that food sharing reduces risk through two routes, first by reducing day-to-day variance in consumption and, second, by controlling the tendency of scrounging (free riding) to depress mean harvest levels. Wide reciprocity assures a high level of food security, and the ESS balance of opportunistic foraging and demand sharing (scrounging) results in constrained but sufficient levels of production. In the opportunist's balance of production and scrounging also lies an explanation for the much debated problem of hunter-gatherer avoidance of underproduction (see Blurton Jones, 1987; Sahlins, 1972; Winterhalder, 1993).

In concluding I wish to emphasize the dependence of this account on the combination of evolutionary theory and ecological context, the linkage of a selection-based perspective with that approach to ecological study usually identified as functional or adaptationist. This is an old insight, captured nicely in Hutchinson's (1965) classic title, *The Ecological Theatre and the Evolutionary Play*. It is likely that several evolutionary forces—individual selection, inclusive fitness, reciprocal cooperation, and sexual selection—have interacted with the material and social environments of hunter-gatherers to produce the diverse exchange economies of foraging societies. Exchange has a multicausal origin, just as each instance of a gift has a mixed inspiration.

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