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Social Foraging and the Behavioral Ecology of Intragroup Resource Transfers

BRUCE WINTERHALDER

Two chimpanzees stalk, isolate, and kill a red colobus monkey. An attendant primatologist notes that parts of the prey are relinquished selectively to onlooking scroungers (Fig. 1). A human forager returns to camp mid-afternoon with a freshly killed, medium-sized ungulate. Later in the day, an ethnographer observes that shared portions of the animal have found their way into the cooking pots of most or all of those in the small band. Examining a prehistoric scatter of food residues, an ethnoarchaeologist wonders when early hominids began to scrounge or share food, and with what consequences for our evolution. All of these settings represent one problem: the analysis of intragroup resource transfers among social foragers. New studies in the behavioral ecology of transfers show them to be more commonplace in nature, more complicated and variable, and more subject to comparative analysis than has been appreciated.

Food sharing has been a routine observation in hunter-gatherer studies. Scrounging is a more recent, but not uncommon observation for some primates. At one time, the explanations for these practices seemed clear. Hunter-gatherers, living in small, stable groups, enact their social allegiances and secure a more regular diet through the institutionalized sharing of food. Obvious group benefits are served. For chimpanzees, prey transfer has been seen as something the

holder of a fresh kill could not prevent or control to benefit. This is nascent sharing at best, incidental to the rare instance of hunting. With chimps and modern foragers anchoring the endpoints of a presumed continuum, disputes about the evolution of hominid behavior often have turned on one

question: is sharing as practiced among modern foragers an early or late development in our prehistory?

The models of **behavioral ecology** (boldface indicates a term defined in the Glossary) described here emphasize the importance of intragroup resource **transfer** among social foragers, but give them different and more diverse explanations than those just cited. Among the key ideas are tolerated theft, marginal evaluation, scrounging, trade, by-product cooperation, reciprocity cooperation and risk-minimization, and showing off. I will describe each of these ideas, then return to a discussion of resource transfers among hominids, nonhuman primates, and extant foragers.

The premises and methodology of human evolutionary or behavioral ecology should be familiar to most

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Figure 1. Alpha male chimpanzee shares a colobus monkey carcass with members of the hunting party. Photo courtesy of Craig Stanford.

Keywords: Hunter-gatherers, primitive economics, risk, exchange, sharing, scrounging

GLOSSARY

Behavioral ecology — the field that applies natural selection theory to the study of behavioral adaptation in a socio-ecological setting. A subfield of evolutionary ecology.

By-product cooperation — individual A acts to its own fitness benefit. Individual B enhances the fitness of that action to A, and to itself, by cooperating in the performance of the task. Synonyms, by-product mutualism, pseudo-reciprocity.

Detection opportunity — the chance of securing access to a resource either by producing or scrounging it.

Encounter-contingent foraging — optimal diet selection model that assumes a concurrent search for randomly arrayed resource items. The decision to pursue an encountered item is contingent on its profitability relative to the efficiency of foraging for items of higher rank. Also called the diet selection or diet choice model; preferred to synonym, diet breadth model.

Evolutionarily stable strategy (ESS) — the tactic or mix of tactics that will evolve to an equilibrium that cannot be changed or "invaded" by any other options within the set. ESS analysis, based on game theory, is used to predict the evolution of phenotypes with frequency-dependent fitness.

Evolutionary ecology — the study of adaptation and biological design in an ecological context, using the theory and concepts of neo-Darwinism.

Exchange — the two-way flow of goods and services (e.g., trade and some forms of reciprocity-based sharing).

Marginal value — the value, in fitness, utility, or other currency, of the n th unit of a resource to an individual already holding $n-1$ units. See total value.

Models of circumstance — portrayals of an expected functional relationship between environmental factors and a set of phenotypic or behavioral options.

Models of mechanism — constructs that examine if and how neo-Darwinian evolutionary processes might generate hypothesized phenotypes.

Opportunity costs — the cost of a behavior, as measured by the benefits associated with alternative activities that it precludes.

Opportunist — one who acts flexibly either as a producer or a scrounger, depending on which opportunity presents.

Producer priority — the proportion of a resource packet consumed or otherwise held aside by the producer, which thus is not subject to the depredations of scroungers. See scroungers' share.

Producer — one who lives entirely from resources that she/he

makes the effort to locate and procure.

Realized value — the total marginal value of a resource to the individual procuring it, corrected for losses or gains arising through tolerated theft, reciprocity, or trade.

Reciprocal cooperation — individual A acts to the benefit of B at some cost to A, expecting that B will reciprocate in the future. The individual benefit is greater than the cost, providing a mutual benefit for the two-way interaction. Preferred to synonym, reciprocal altruism.

Risk — the likelihood of a resource shortfall and, consequently, a negative effect on fitness.

Scrounger — one who lives by appropriating resources from producers, who pay the costs of locating and procuring them.

Scroungers' share — the portion of a resource patch or packet remaining when scroungers show up and begin to consume it along with the producer.

Scrounging — appropriating part of a resource that another individual has located. Both opportunists and scroungers engage in scrounging. Synonym, tolerated theft.

Sharing — 1) the mutual, uncoerced, two-way transfer of portions of a like resource or service, sometimes with a delay, as in reciprocity-based food sharing; 2) a one-way transfer among kin without equivalent return in kind, as when a mother shares food with a child.

Trade — a voluntary, two-way transfer of unlike resources or services, with or without delay.

Tolerated theft — a resource transfer occurring when the holder of a packet relinquishes portions of low marginal value that are being contested by an individual to whom those portions have a high marginal value. Synonym, scrounging. Because theft connotes property rights, scrounging in most cases is a better label for this phenomenon.

Total value — the sum of the marginal values of x units of a resource.

Transfer — a neutral word for the movement among individuals of good and services, not presupposing a particular mechanism such as scrounging, sharing, or trade.

Unilinear evolutionism — the approach taken by social anthropology and archeology in the late nineteenth and early twentieth centuries, which portrayed societies as developing through a single sequence of stages graded by increasing complexity, technological prowess, or energy capture.

readers of this journal.¹⁻⁵ Earlier reviews on food transfers among humans have been written by Kaplan and Hill,⁶ Smith,⁷ and Hawkes.⁸ The primate literature has been reviewed by de Waal.⁹

MODELS OF CIRCUMSTANCE

Tolerated Theft

Individual-level selection should favor social foragers who contest the unequal possession of foodstuffs within a group. The holder of a temporary

surfeit has little fitness incentive in risking defense of low-value portions. The potential taker, less successful in the food quest and perhaps facing hunger, has a large fitness incentive in pressing a claim on what it sees as high-value portions. One gains by avoiding unnecessary strife, the other by threatening it. Transfers generated by this mechanism are known as **tolerated theft**.^{10,11} Such transfers are likely to occur if: i) the food item is discovered individually and sporadically (that is, not in phase among for-

gers); ii) the packet is larger than an individual can consume immediately; and iii) consumption of the packet is characterized by diminishing marginal returns. It does not matter whether the packet is from an animal or plant source. Assuming that competitors meet as equals, transfers from the replete to the hungry will occur until an equilibrium is established at which the last portion has an equal **marginal value** for the giver and taker.

Tolerated theft requires only indi-

Box 1. Marginal Valuation and Evolutionary Currencies

When King Richard III declares "A horse! a horse! my kingdom for a horse!" we can be reasonably sure he is engaging in marginal analysis. Misfortune on the battlefield can upend the relative value of an equine mount and continued sovereignty. In less than dramatic circumstances, humans make such comparisons all the time. Other species routinely behave as if they do so as well.

The **evolutionary ecology** hypotheses that explore these behaviors are formulated around cost-benefit accounting. The balance of accounts allows us to trace the likely fitness consequences of behavioral alternatives. However, tallying up these costs and benefits entails refinements in the way they are conceptualized and measured.

First, in behavioral ecology, all costs and benefits include **opportunity costs** and benefits. Any behavior should be assessed relative to the alternate fitness-enhancing options available to the organism. Direct measures of outcome for a particular behavior are subordinate to potential trade offs among behaviors. Thus, the fitness gains of foraging at a certain net yield must be assayed against the fitness gains associated with other activities that might occupy the same time.

Second, the value of an activity changes as it is performed or as a function of the time since it was last performed. Because of this, the decision to switch behaviors is a *marginal decision*. As hunger is sated, continued foraging returns less and less value for effort. Correspondingly, while attention is on the food quest, the demands of other fitness-enhancing activities grow more urgent. This linkage between opportunity costs and marginal analysis requires only that we postulate scarcity of time, resources, or both; organisms for which fitness depends on at least two mutually exclusive activities; and a nonlinear relationship between either the duration of an activity or the time since it was last performed and the contribution of that activity to fitness.

Ideally, we would focus our models and observations on marginal analysis of fitness in terms of opportunity costs and benefits. In practice, we compromise. We often settle for direct rather than opportunity cost measurements, measure proxy currencies instead of fitness, and assume a linear relationship between quantity and value. Each simplification has advantages. Direct measurement allows us to isolate one behavior for study. The desirability of a greater as opposed to a lesser foraging efficiency is a reasonable premise, whatever the opportunity costs. Because fitness rarely is amenable to direct measurement, we observe instead more tractable proxy currencies such as net acquisition rate of energy or number of items exchanged. Further, we assume that fitness is a constant function of units of proxy.

Often, this will not be the case. For example, a meal-sized portion of food makes a high contribution to well-being, but continued consumption of like increments adds less and less to well-being. Satiation sets an asymptote in the relationship between quantity and fitness value.

The above figure shows the fitness gain associated with food packets of increasing size. *G* (for *giver*) has a packet of quantity (Q_p) and (V_p). It is relinquished in small portions to a scrounger (*T*, for *taker*), who begins the transaction with no resources (Q_0, V_0). Under conditions of tolerated theft, the transfers will equilibrate at Q_e . With their marginal values equal, the incentive for *T* to acquire additional portions is precisely balanced by the incentive for *G* to resist ceding any more. Note that the packet has been divided equally, but that *G* has lost considerably less value ($V_p - V_e$) than *T* has gained ($V_e - V_0$). The aggregate value for the two of them is greater after the tolerated theft ($2V_e > V_p + V_0$), although the aggregate resource quantity has not changed. Variations on this graphical treatment allow for complications due to the holding of resources other than food packets, differing numbers of takers, and other factors.¹⁴

Several points in this paper turn on the appraisal of marginal values. Note that the holder of a very large packet (Q_{s2}) might relinquish much of it (Q_{s1}) with virtually no loss of value. Much is ceded; nothing of value is lost. Conversely, the small quantity propitiously gained by an individual with no resources may have extraordinarily high value. For example, scrounging models use constant units ("items") of food. However, with even a small degree of producer priority, the finder of a packet cedes much less value to scroungers than would be indicated by the amount scroungers might consume. Similarly, a hungry scrounger might obtain value that is disproportionate to the quantity it is able to secure.

vidual-level selection for its initiation. The conditions favoring it are less stringent than those that might produce reciprocity-based **sharing**. Blurton Jones makes the very plausible suggestion that sharing has its origins in tolerated theft, which became sufficiently routine in small, relatively stable groups that it could prime the evolution of reciprocity by meeting these additional conditions.¹⁰⁻¹³ Most important are regular role reversals among a small set of givers and takers, stable group membership, the prospect of an indefinite future of transfers, and a clear advantage to the interaction.

Marginal Analysis

Tolerated theft assumes that a resource packet has decreasing marginal value to its holder as it increases in size. Formal analysis of this premise with graphical models¹⁴ not only shows how resource transfer distributes costs and benefits among the participants, but also how such transfer can be affected by group size and ecological conditions, and can interact with models of production (resource selection).

In tolerated theft, the benefits to a taker are greater than the costs to a giver (see Box 1). This follows from the marginal nature of the transaction. Distribution does not change the amount of the resource, but does enhance its **total value** to the participants. This is the advantage required for the evolution of **reciprocal cooperation**. It underwrites the shift from tolerated theft to sharing.

This enhancement of a packet's value by its transfer grows with the number of recipients. With increasing "n," the low-value portions ceded by a giver concentrate on the highest increments of marginal value that can be realized by takers. If the situation is one of reciprocity, with a receiver indebted by the value derived from its portion, then a self-interested giver will distribute portions as widely as possible, and to the neediest among the supplicants. In sharing, a motive of maximum self-interest may well give the appearance of selfless generosity.

Marginal valuation also highlights the pitfalls of accounting for evolu-

tionary costs and benefits in terms of resource quantity. Consider two examples. First, much of a very large packet might be subject to appropriation without any loss of value to its finder. Graphically, we would envision the packet holder's value as lying along the horizontal asymptote both before and after redistribution (Box 1). Despite having a reduced portion, the holder has suffered no loss in the currency of

Producers expend energy to locate resource packets; scroungers avoid search costs by appropriating portions of a producer's packet; and opportunists produce or scrounge as the occasion presents.

evolutionary significance. Second, central to resource choice models is a ranking of resources by their net energy return per unit of time spent in pursuit and handling. Energy value typically is determined by the edible mass captured. But if that mass is subject to tolerated theft, the **realized value** derived by the forager may be less than would be inferred from the size of the resource. The loss to tolerated theft will lower the ranking of the resource, perhaps sufficiently that it drops from the optimal diet. The half of a hare remaining after tolerated theft may not be worth the effort of capturing the whole animal. By contrast, if a forager expects a realized value that is enhanced through reciprocity, he or she may well find it optimal to harvest a resource that otherwise would be ignored. The individual use value of a wildebeest may not justify its pursuit unless there are delayed returns to be realized through **exchange**.

Models of food transfers among social foragers reveal the linkages be-

tween resource selection and distribution.^{8,14-16} They should change the way in which we apply and evaluate long-standing models of production, such as for **encounter-contingent foraging**.¹⁷ Because behavioral ecology hypotheses often turn on small differences in a balance of costs and benefits, marginal accounting may be critical in a wide variety of circumstances.

Producers, Scroungers, and Opportunists

Social foragers that harvest one or more resources in packets have the option of obtaining food by producing it or by **scrounging** from the production of others. The rewards of active foraging are diminished by scrounging; the advantages of scrounging are heightened by the chance of obtaining a meal with minimal effort. In a population of **producers**, the pure **scrounger** has a significant advantage. Easy taking diminishes the attractiveness and the fitness advantages of procuring one's own food. Because the costs and benefits of these tactics are frequency-dependent—as long as there are a few of them, scroungers do well relative to producers, but do poorly if they become too common, so that more and more of them compete for a smaller harvest—the goal of analysis is to describe the **evolutionarily stable strategy** or combination of strategies.

Among the several recent models of this situation,^{18,19} I will summarize one developed by Vickery et al.²⁰ There are three tactics: Producers expend energy to locate resource packets; scroungers avoid search costs by appropriating portions of a producer's packet; and **opportunists** produce or scrounge as the occasion presents. By definition, producers and scroungers adopt pure tactics. The equilibrium mix of these behavioral options is determined by group size, producer priority, and the opportunist's detection opportunities.

Producer priority measures the degree to which the finder of a packet is able to monopolize its consumption, thus lowering the **scroungers' share**. Producer priority will be high if a packet can be quickly consumed or if the scroungers are slow to detect and reach it. **Detection opportunity**

Box 2. The Producer-Opportunist-Scrounger Game

Across a wide variety of species, social foragers are afflicted by scrounging (tolerated theft). Individuals having the fortune (and paying the costs) to locate a food patch or packet may inadvertently signal the discovery to group members who hasten to appropriate part of it. This tolerated theft has consequences for social tactics, foraging strategies, and subsistence viability.

Consider three tactics. Producers actively seek to procure food. Scroungers avoid search and pursuit costs by feeding only from the finds of producers. Opportunists do both, producing and scrounging as the chance arises. Vickery et al. (Table 1, p. 854)²⁰ have derived the evolutionarily stable strategy (ESS) proportions of these tactics as a function of three variables: the relative frequency of the feeding opportunities available to the opportunists, the percentage of a packet or patch that scroungers seize, and group size. ESS analysis of this situation is necessary because the payoffs to scrounging and alternative tactics are frequency-dependent. Relative to producers, scroungers do very well when they are few and opportunities to parasitize producers are abundant. Scroungers do poorly when they become common. Not only are there fewer chances to cadge, but more scroungers compete for each item.

The chance that an opportunist will feed depends on the

compromises that individual must make in order both to produce and to scrounge. Detection opportunity can range from 0 to 2. At a value of 0, the opportunist, in trying to detect both types of feeding situations, succeeds at locating neither. At a value of 2, the opportunist detects all of the opportunities garnered by either producers or scroungers, thus doubling its chances of feeding relative to either of the pure tactics. Finally, if a producer consumes a large portion of a patch before being joined by scroungers (high producer priority), the scroungers' share is diminished.

Figure 2 depicts an outcome of this game. There are 10 foragers and 20 food items per patch. A/F , the scroungers' share, varies from 0 (the producer gets all 20 items; complete producer priority) to 1 (scroungers arrive before the producer can consume even 1 item; no producer priority). The variable c is the relative ability of an opportunist to detect feeding situations that would be found by a specialist producer. The variable h is the same for the opportunist relative to a scrounger. For simplicity, we assume that opportunists' abilities are symmetrical ($c=h$). Then $0 \leq c+h \leq 2$ measures the relative frequency with which the opportunist detects feeding opportunities. The five graphs show a range of values for $c+h < 1$.

Several things can be observed here. For $c+h$ there are no opportunists. If the scroungers' share (A/F) is less than $1/N$ (0.1 in this example), the population is composed entirely of producers. Put differently, producer priority must be greater than 0.9 to exclude scroungers from the equilibrium. Otherwise, there is a two-tactic mix of producers and scroungers, with the former decreasing in frequency as A/F increases.

Above $c+h=1$, opportunists prevail, either alone (to increasing degree as $c+h$ approaches 2), in combination with producers (low-to-moderate A/F), or in combination with scroungers (high A/F). A population composed only of producers continues to be restricted to $A/F < 1/N$, but it is progressively squeezed out as detection opportunities approach 2.

In virtually all circumstances, the equilibrium is composed of only one or two of the options. Scrounging, whether by scroungers or opportunists, is present over most combinations of scroungers' share and detection opportunity. It is likely to be absent only from small groups (low N) in which $c+h < 1$ and producer priority is very high. In general, increasing the group size (N) shifts the boundaries between tactics to the left. Thus, larger groups allow increased likelihood and frequency of scroungers.

Three cautions are germane. First, this is only one set of transition thresholds and frequencies. Others are possible with changes in N and the other fixed parameters (F , c , and h). Second, because opportunists both produce and scrounge, this chart gives only a rough sense of the total amount of production and scrounging in the economy. Finally, it cannot be inferred that all of these combinations represent viable populations. At high scroungers' share (A/F), the ESS approach can produce an equilibrium that leaves everyone with too little food to survive.

will be low if the opportunist, by dividing his or her attention, fails to find as many feeding opportunities as does either a producer or scrounger. Detection opportunities will be high if opportunists freely can avail themselves of the feeding situations available to both producers and scroungers. This effectively doubles their encounters with feeding opportunities relative to the opportunities provided by either of the pure tactics.

Box 2 shows a typical outcome of this kind of analysis. Opportunists are excluded from the evolutionary equilibrium if they detect fewer feeding events than are available to either producers or scroungers (detection opportunities < 1). The equilibrium most likely is a mix of producers and scroungers. It will be limited to producers if the scroungers' share falls below the reciprocal of group size. By contrast, if opportunists have a detection advantage (detection opportunities > 1), then the most likely outcome is opportunists either alone or in combination with producers and scroungers.

The producer-scrounger model hints at the complex behavioral dynamics affecting social foragers whose diet includes resources that are subject to tolerated theft. These dynamics might appear to require tactical skills that are too complex for nonhuman species. However, work with spice finches has shown that these birds alter their foraging behaviors in the ways predicted.²¹

Group living usually is analyzed for its advantages in, for example, locating food or detecting and deterring predators, but scrounging draws attention to its costs. Under a wide range of conditions we should expect groups of social foragers to experience tolerated theft, whether practiced by scroungers or opportunists (but not both) amongst producers, scroungers amongst opportunists, or opportunists amongst themselves (Box 2). Self-interest pushes the mix of tactics to an equilibrium at which no tactic garners more than another. Among other consequences, this can strongly depress the average rate of food harvest in such groups. In simulation models, it can jeopardize survival.¹⁹ Faced with scrounging, self-interested foragers come to underproduce.

Trade

Analyses of **trade** appear infrequently in the literature on foraging perhaps because it is rare in extant hunter-gatherer societies. Exceptions are those cases in which foragers trade regularly with horticultural neighbors.^{22,23} Relevant models are available from micro-economics,²⁴ but they rarely have been applied formally.

The productivity of hominid scavenging may have depended on quickly locating and then cooperatively defending a feeding site. The hominid discovering a freshly killed carcass would enhance the value he or she was able to derive from it by sharing the opportunity — and particularly its appropriation and defense — with others.

Because trade implies incommensurate goods or services, it is difficult to measure the relative costs and benefits of such exchange.

Two empirical examples are notable for their similar proposals, although the data in both cases are quite limited. Kaplan and Hill²⁵ suggested that more productive Aché hunters trade foodstuffs for reproductive advantages such as mating opportunities and better treatment of their offspring. Stanford²⁶ believes that chimpanzees capture game — primarily colobus monkeys — both for its nutritional significance and because it can be exchanged for sexual access and political support. He observes that most hunting occurs during the food-scarce dry season. Hunts also are

more likely if a female in estrus is present. The hunting group grows larger and is more likely to be successful as the number of estrous females increases. Further, males favor their allies and exclude their political rivals from such distributions, suggesting trade for political support.

By-Product Cooperation

Transfers may also result from evolutionary mutualism. In **by-product cooperation**, an organism undertakes an action with a personal benefit that will be augmented if it is performed cooperatively, whether actively or inadvertently.^{27,28} Conversely, noncooperators pay a cost if they opt to avoid joint action. By-product cooperation may be common in nature.²⁹ Like tolerated theft, it generates conditions that could prime the evolution of reciprocity cooperation.

Social foraging provides an example. Assume the optimal diet of a forager includes a medium-sized packet, highly ranked by its realized value. In seeking the advantages of high foraging efficiency, group members inadvertently cooperate in providing one another scrounging opportunities. Foragers can fail to cooperate, passing by the resource in question, only at their own expense. Hominid scavenging presents a second case. Ethnoarchaeological work suggests that the productivity of hominid scavenging may have depended on quickly locating and then cooperatively defending a feeding site.³⁰ The hominid discovering a freshly killed carcass would enhance the value he or she was able to derive from it by sharing the opportunity — and particularly its appropriation and defense — with others.

Risk and Reciprocity Cooperation

Tolerated theft occurs among foragers whose diet depends significantly on relatively large resource packets or on patches that are encountered sporadically and asynchronously by individual foragers. Because these encounters are also likely to be unpredictable, subsistence **risk** is likely to affect the evolution of resource transfers.

Ethnographers routinely report that food sharing ensures band mem-

Box 3. The Ambivalence of Sharing

How are we to understand generosity that must be evoked by a firmly tendered request? This question is at the heart of an essay by Nicolas Peterson, titled "Demand Sharing: Reciprocity and the pressure for generosity among foragers."³⁴

Using Australian and other ethnographic materials, Peterson corrects a widespread mis-impression: although ethnographers and secondary sources often gloss hunter-gatherer sharing in an idiom of unsolicited and beneficent giving, the record more often speaks of demands and claims, and occasional resistance to these claims:

"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, in Hiatt's view, 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 ..." (p. 860).

Peterson explains the discrepancy between anthropological representation and native practice by the positive value that Western culture and Western anthropologists place on altruistic giving. A secondary explanation is the tendency in ethnographic interpretation to rely on idealized, normative statements rather than on behavioral practices in specific situations.

Peterson also considers the advantages of what he calls "inertial sharing," in which the burden of reciprocity is put onto the taker rather than the giver. An uninvited offer can appear rude if refusal to accept is ruder yet, and if the potential recipient does not wish the obligation to reciprocate. Further, faced with highly complicated socio-economic bookkeeping of past transactions among kin and camp mates, the holder of a resource might be tempted to simplify and just respond to demands as they are made: "Difficult decisions are avoided; the onus is placed on others; discrepancies in the evaluation of relationships are not laid bare; and an excellent excuse is provided for not meeting some obligations within the context of behaving generously" (p. 864). Faced with awkward calculations of giving, the victim of tolerated theft may have reason to appreciate being taken.

It is tempting to speculate that the overly romanticized interpretations of sharing in contemporary foraging societies have influenced the recent rejection of exchange as an element in accounts of hominid origins. Such interpretations invite a reaction in which the paleoanthropologist plays Hobbes to the ethnographers' Rousseau. By contrast, Peterson's review couches the ethnographic record in terms that are consistent with predictions of the accompanying text. The multiple origins and motives for food transfers conflate self-interest and benevolence, giving the practice its ambivalent quality. They also help to explain how foragers committed to sharing might nonetheless go out of their way to avoid a situation in which it would be expected.

The Yolngu (of Arnhem Land) chastise supplicants who overhear talk of food with the line, "Your ears have fingers" (p. 862). A similar rebuke must have occurred many times among the early hominids.

bers a more regular day-to-day diet. Behavioral ecology models have refined this empirical generality by identifying more precisely the ecological contexts in which sharing is effective in reducing risk and by drawing our attention to the varying forces that may motivate it.

Food sharing pools the yield from spatially separated foraging expeditions, allocating shares to the partici-

pants more evenly than they initially were acquired. Most models assume that each participant gets an equal share. This is formally analogous to the risk reduction achieved by the farmer who plants multiple, dispersed agricultural plots.³¹ Three variables determine its effectiveness: the number of foragers who participate, the day-to-day variation in their individual foraging success, and the degree of

synchrony in their short-term success rates. High day-to-day variation of success in hunting and gathering of course elevates the individual's risk of periodic shortfalls. But with even modest degrees of asynchrony in the yield among foragers, pooling is quite effective in mitigating the likelihood of harmful shortfalls. Further, most of the benefit of sharing can be achieved in small groups of six to eight foragers.³²

We now have good quantitative evidence of this phenomenon. For instance, based on their field work with Aché forager-horticulturists, Kaplan and Hill⁶ have calculated the improvements in nutritional status of individuals achieved through food sharing: 20% with the sharing of honey alone, 40% with the sharing of meat alone, and 80% with the sharing of all foods.

Food sharing among hunter-gatherers typically has been explained by its seemingly obvious group benefits. Behavioral ecologists prefer an explanation in terms of individual self-interest and mechanisms that are consistent with neo-Darwinism. In by-product cooperation, an individual advances its own interest while incidentally providing a common good. In reciprocity cooperation, an individual provides a common good at some cost, expecting that in the future similar behavior by others will more than compensate for that cost. Because the delay carries a chance of cheating, analysis of reciprocity cooperation requires tit-for-tat and related game theory models.³³

If foraging groups, whether of early hominids, nonhuman primates, or modern hunter-gatherers, are composed of small bands with relatively stable membership, they provide the context needed to make reciprocity-based food sharing an evolutionarily stable tactic.^{12,13} Food sharing may be routine, providing an indefinite prospect for future transactions. Because such sharing is a highly visible activity of most adults, cheating can be monitored and sanctioned. Resource capture is fortuitous, ensuring regular role reversals. Marginal valuation shows the fitness gains of regular sharing; risk adds to those benefits by enhancing the marginal value of food that unpredictably is in short supply.

Although tolerated theft may have preceded and catalyzed sharing, it apparently has remained a factor in hunter-gatherer transactions. Although generalized discussions of sharing stress social obligation and personal generosity, close scrutiny of first-hand ethnographic accounts reveals transactions fraught with ambivalence. Peterson³⁴ characterizes the Australian materials with terms like "demand sharing" and "mutual taking," descriptions that ring true for non-Australian cases as well (Box 3). As recorded in ethnographies, sharing encompasses diverse practices mixing generosity, tit-for-tat reciprocity, and barely disguised social extortion. Behavioral ecology models couched in terms of tolerated theft, marginal valuation, scrounging, and reciprocity lead us to expect such variation in the form and motives of this behavior.

Showing Off

Ethnographies record that men typically are the hunters, and that hunting often is a risky, high-variance activity, especially if it is for large game. Hawkes¹⁶ believes that these men are providing a "public good," a service costly to them and valuable to others. Transfers of large game are uncompensated by reciprocity or trade, leaving a lower realized benefit to such hunters than they might gain from alternative subsistence pursuits. Because this appears to defy the assumption that individuals act from self-interest, Hawkes seeks to explain hunting in terms of the less tangible benefits it might garner. Primarily, these are the attention, potential social influence, and, perhaps, the mating opportunities these men might receive from their conspicuous displays of food sharing largess. In the show-off hypothesis, men seek large game not to eat or to feed their families, but in order to cultivate support from a coterie of allies and paramours.

The evolutionary mechanism here is sexual selection. Females will prefer a mate who is intent on regularly provisioning her children, but should be willing to encourage any males who sporadically provide a windfall of resources. Males have two options: the low-variance but relatively constrained fitness option of provisioning

a family or the high-variance, potentially high-reward option of showing off before the whole community. By this hypothesis, women are advised to marry the town grocer but flirt with a generous buccaneer, and men to consider carefully which role represents their best opportunity.

Foragers often pursue large game; when they do so, it is the men who do the hunting; and when these men are successful, their harvest is distributed widely, benefiting group members beyond themselves and their families. The show-off proposal is attractive because it neatly explains these three correlated observations with one idea.

In the show-off hypothesis, men seek large game not to eat or to feed their families, but in order to cultivate support from a coterie of allies and paramours.

Nonetheless, this hypothesis has had a mostly critical reception and has generated lengthy debate.³⁵⁻³⁷ It has been difficult to show that large game are public goods. For instance, if the sharing of large game is a matter of by-product cooperation, then there is no need to invoke intangible benefits to explain the pursuit of such game. Hawkes¹⁶ argues that the alternative risk-minimization (or sharing) hypothesis is weakened by the difficulty of enforcing reciprocity. The show-off proposal not only entails the same difficulty, but also recreates the public goods problem by supposing that delayed and somewhat diffuse social attention is the hunter's reward.³⁸ If everyone collects, why should anyone bother to repay? Finally, in practice it may be difficult to separate this hypothesis from that of trade, in which sexual selection alters the value males and females assign to the elements in the transaction.

DISCUSSION

Mechanisms and Lacunae

At their best, studies of behavioral ecology combine **models of circumstance** and **models of mechanism**.³⁹ The former models show how specific environmental conditions constitute adaptive costs and benefits; the latter identify which of these costs and benefits are potentially consequential within neo-Darwinian and related mechanisms of evolutionary change. Tolerated theft and scrounging, marginal valuation, trade, and by-product cooperation can be matched to simple, individual-level selection. Risk minimization and reciprocity-based sharing require selection for reciprocal cooperation.^{40,41} The show-off hypothesis invokes the mechanism of sexual selection.⁴²

Kin selection^{43,44} has not been linked with particular models of circumstance, perhaps because it has seemed self-evident that food would be shared to advantage among related individuals. Here the most interesting evidence is negative. Although good data are rare, there does not appear to be a strong kin bias in band- or community-level sharing.^{6,45,46} In fact, the marginal advantages of widespread distribution within a group that includes individuals who are not kin may swamp the direct fitness benefits to be achieved by exchange that is limited to relatives. "Reciprocal aid giving ... can generate a substantial selective force independent of kin selection even when performed among related animals."⁴⁷

Unfortunately, we lack models of circumstance that are specifically linked to two additional kinds of selection, interdemic (or group) selection⁴⁸ and dual inheritance approaches.⁴⁹ Because interdemic selection and dual inheritance appear more congenial to the evolution of group-level, cooperative behaviors, they may be especially promising venues for investigating exchange.

Despite these lacunae, half a dozen models of circumstance already have been more or less matched to an equal number of evolutionary mechanisms. Each model is peculiar to different environmental or evolutionary conditions. Taken together in combinations

set by the environment and history of a population, they predict diversity and considerable flexibility in the expression of intragroup exchange behaviors. Whereas ethnographic summaries have tended to stress broad generalizations (e.g., band-level sharing⁵⁰), behavioral ecology theory would have us attend to the variants.

Hunter-Gatherers, Primates, and the Hominids

Hunter-Gatherers

A common generalization from hunter-gatherer ethnographies is that of band-level organization involving radial foraging from a base camp by individuals or small groups. Food often is consumed as it is procured, with the surplus, and especially the bulk of medium-to large packets, carried back to camp to be shared at the end of the day.⁵¹ Recast in the variables of the producer-scronger model, this scenario reveals links to other features of the foraging mode of production. Partial consumption of foodstuffs as they are gathered ensures a high degree of producer priority. Concurrently, end-of-day sharing sharply reduces any conflict between the detection of producing and scrounging opportunities. By ensuring that the individuals benefit first from their own production and that producers will miss few opportunities to scrounge, this arrangement eliminates pure scroungers from the evolutionarily stable mix of tactics. Producers and opportunists will dominate, an observation that is consistent with the ethnographic record. Central place sharing may be a group's best defense against parasitism by pure scroungers.

Routine scrounging by opportunists in a mix of producers and opportunists also provides a sufficient explanation for the "underproduction" observed in foraging societies.⁵² ⁵⁴ The self-interest of each forager generates an equilibrium mix of tactics in which the average production of all is constrained. Further, because scrounging increases in frequency in larger groups, we perhaps should include it among the list of factors influencing band size.⁵¹ Small groups diminish the frequency of scrounging, moderating

the degree to which it depresses average food harvests.

Primates

The chimpanzee food transfers described by Stanford²⁶ might be explained by some combination of scrounging, trade, and showing-off. Stanford's observations are of a population infrequently and incompletely dependent on medium-sized packets. Because meat supplements a diet otherwise low in risk, these chimpanzees may be an instance of social foragers whose transfers lack the ecological conditions necessary to establish the regular, reciprocity-based exchange of

...primate studies show reciprocity-based sharing to be a widespread capacity in the order, when evoked by appropriate evolutionary circumstances.

ethnographic hunter-gatherers. The "fission-fusion"²⁶ reworking of group membership also may impede the development of reciprocal cooperation.

By contrast, experimental studies based on the provisioning of nine adult, corral-living chimpanzees give clearer evidence of reciprocity in food sharing.⁹ Observation of 4,653 food interactions showed that exchanges are balanced among dyads, although not in a tit-for-tat manner. Instead, prior grooming and aggression are linked to food transfers in a turn-taking pattern that helps maintain equivalence in the general exchange of social benefits. An individual that had been groomed was more likely, later, to transfer food to its benefactor. Individuals that hoarded food were more likely to receive an aggressive response when they sought food. Chimps rarely offered food, but they often relinquished it selectively to animals seeking a portion of a bundle. On balance, de Waal⁹ described his

data as better supporting an interpretation of reciprocity than one of tolerated theft or social enhancement. By strict definition, this is reciprocity in trade. The counter-flows entail unlike commodities and services.

In other cases, the practice of primate reciprocity has been securely established in more naturalistic settings. Some species— rhesus macaques living at Cayo Santiago are an example^{55,56}— separate to forage, with individuals giving food calls that signal to their fellows the discovery of a rich patch. Hauser and Marler⁵⁶ describe these calls as "honest" signals reflecting food possession, noting that "Those who fail to signal and are caught with food are apparently punished." Because of this aggressive punishment, non calling females that were detected by conspecifics ate less food from their discoveries than did those that gave calls (the sample of males was not large enough to make this comparison). The temptation to remain quiet upon discovery of a patch and the attempt by conspecifics to enforce signaling suggests that this is reciprocity rather than by-product cooperation. Females call more than males, and their call rate is positively correlated with the number of female kin in the vicinity,⁵⁵ suggesting an element of kin selection. Although not explicitly analyzed in terms of the transfer models presented here, the general form, and especially the carefully documented nuances of rhesus macaque food calls, might well reward such an effort.

Hominids

In the 1970s, Plio-Pleistocene hominids were described as hunter-scavengers who transported portions of medium-to-large herbivores to central camps to be shared among the members of a small band. This home base provided selection pressures for language and complex social skills; hominids were considered to be unique primates because they shared food in this context.⁵⁷⁻⁵⁹ By the mid-1980s, however, this "consensus scenario" had been rejected.⁶⁰ In the new view, early hominid scavengers found only morsels too small to share, gleaned from carcasses abandoned by other carnivores. Only "just prior to the appearance of fully modern man"⁶¹ (p.

321; italics in original) did *Homo sapiens* begin hunting from a camp, transporting back to it large packets for redistribution. Sharing was very late and did not influence hominid divergence from other primates.

These debates about hominid origins are debates about behavioral ecology. When and with what effects did protohumans take up scavenging or hunting, the pursuit of intermediate and larger packets, and passive or active transfers of food?

Studies of the Hazda³⁰ showed that scavenging can intermittently but significantly contribute to the diet of savanna woodland hunter-gatherers if the foragers are able to locate fresh kills quickly and cooperatively displace larger carnivores such as lions. Scavenging opportunities are eagerly sought by the Hazda, presumably because of their high return rates. Blumenschine et al.⁶² have identified a variety of contexts in which carcasses still bearing flesh would be available to hominids without competition from other carnivorous scavengers. In a prehistoric setting, radial foraging by early hominids in search of a variety of resources would multiply their opportunities for finding fresh kills. The base camp population could be readily mobilized for their collective seizure, whether it involved active displacement of other species or stealthy, passive appropriation. Winter-scavenging ravens,⁶³ as well as the Hazda, may be an apt model of this process.

Resource items gain a place in the encounter-contingent diet if they have a sufficiently high net value (the value after pursuit and handling costs). A partially consumed carcass, even one that has been reduced to morsels by a prior carnivore, may still be valuable if its cost is slight. Small or easily captured game may also be profitable for a hominid. But intermediate and large game are costly to capture and may offer the hunter a realized value that is much less than their bulk suggests. By these observations, we would predict hominid scavenging prior to active hunting, and active hunting of small game prior to that of intermediate-sized game.

Larger game present a particular difficulty. If pursuits were costly, ac-

tive hunting of intermediate and large game may have become profitable only after the realized value of such prey to the hunter could be enhanced through reciprocity-based exchange. The difficulty is one of two linked preconditions. Intermediate or large packets are a condition for the evolution of exchange, but they are more likely to enter the diet when they have exchange value. As noted, radial foraging with scavenging offers one solution to this evolutionary dilemma. We need only envision that, once secured, such low-cost but larger packets were reallocated through tolerated theft and by-product cooperation, thereby catalyzing the evolution of reciprocity-based sharing. Once reciprocity was active, encounter-contingent hunting of medium and large game became profitable because the forager was more certain of recouping the costs of pursuit and handling.

It commonly is posited that technological developments were necessary precursors to large game hunting. It is also possible that social developments in the form of stabilized reciprocity and exchange relationships were preconditions of this activity.

This scenario illustrates one possible application of behavioral ecology models to questions of hominid origins. In practice, local production and resource transfers would reflect a balance of by-product and reciprocity cooperation, scrounging, nepotism (kin selection), and sex-linked exchange tactics. Nonetheless, the scenario described is consistent with the apparent overlap in the feeding patterns of hominids and carnivores.^{59,64} Bone fragments from multiple hearths that can be refit and reliably inferred to be from a single animal provide us one means of gaining insight into prehistoric sharing.⁶⁵

The sharing hypothesis of the early 1970s faded, in part, because it became tainted by charges of romanticism.⁵⁸ Early hominid foragers seemed too nice and too much like their modern counterparts, extant hunter-gatherers. However, evolutionary ecology offers a supportive account of sharing that is grounded in unsentimental self-interest. Further, primate studies show reciprocity-based sharing to be a widespread ca-

capacity in the order, when evoked by appropriate evolutionary circumstances.

CONCLUSIONS

Intragroup resource transfers are much more common than has been thought and may have a variety of causes. They take diverse forms. Stable roosting groups of related and unrelated vampire bats share food, the supplicant signaling need by grooming the distended abdomen of an individual that was successful during the previous night's foraging. This behavior, which forestalls starvation in the otherwise high-risk food quest of these animals, is explained by reciprocity-based cooperation.^{47,66} Common ravens use aggregation at roosting sites to share information about the location of infrequent but rich scavenging opportunities, which then are cooperatively defended.⁶³ By-product cooperation is a good candidate for the origin of this behavior. Social carnivores hunt cooperatively and engage in varying forms of resource transfers.⁶⁷

Each of the cases cited here — band-organized foragers, hunting chimps, and hominid scavengers, as well as bats, ravens, finches, rhesus macaques, and social carnivores — draws on a somewhat different combination of circumstances and mechanisms. However, all of these cases have in common the asynchronous harvest of medium-sized or large packets by social foragers. Behavioral ecology not only tells us to expect diversity, it gives us a means of predicting the variants. This capacity and the empirical work it has stimulated have three broad implications for hunter-gatherer studies. I will use paleoanthropology as an example, for it is here that inferences must be developed most directly from theory and comparative materials. Analyses by Winterhalder,³⁹ O'Connell,⁶⁸ and Blumenschine et al.⁶² develop implications for ethnography, ethnoarchaeology, and paleoanthropology, respectively.

Behavioral ecology establishes a theoretical basis for wide ranging comparative studies of behavior. Models of hominid behavior have been derived from phylogenetic analogies (chimpanzees, baboons) or ecological

analogies (social carnivores). Ethnographic analogy once flourished, but now has declined. Behavioral ecology both broadens the range of such comparative possibilities and gives us theoretical rationales for selecting particular comparisons. By clear theoretical orientation, it collapses the distinction between "conceptual" and "referential" models.⁶⁹ In principle, ravens may tell us much about hominid scavengers as will chimpanzees, wild dogs, or even modern foragers. When this type of comparative analysis is routine in paleoanthropology, the field will have advanced significantly as an evolutionary science.⁷⁰

Behavioral ecology provides an alternative to unilinear evolutionism. Key issues in paleoanthropology have centered on the acquisition of traits that occur regularly in extant foraging societies but presumably were absent in our last common ancestor with the great apes. The issues have been those of ordination; sequence and timing motivate the central debates. Was sharing (or for that matter, hunting, base camps, pair bonding, etc.) a capacity that was acquired early or late, and with what consequences? Current thinking, leery of the tyranny of the ethnographic record,⁷¹ holds that these "advanced traits" were extremely late. Thus, they were not formative influences on the divergence from the pongids or panids, as was believed in the 1970s.

To a behavioral ecologist, this all looks uncomfortably like old debates in social theory over the stages of **unilinear evolutionism**. Our models and field work tell us that it is ecological circumstance and evolutionary mechanism that allow us to explain the presence and form of exchange and other complicated behaviors. Taxonomic line or grade appear to have weak predictive power in this realm. This observation will be as true of hominid species as it is of the broader comparative materials that stimulate it. Any or all of the types of resource transfers defined or exemplified here might have characterized any or all populations of hominids. Forms of transfer presumably were locally specific. They may have appeared, developed, changed, and disappeared many times in many

taxonomic lines throughout hominid history, depending on ecological circumstances. Fearful of projecting contemporary ethnographic observations onto early hominids, we inadvertently have robbed them of the capacities of bats.

Behavioral ecology shows the importance of theory-driven studies. Recent field and laboratory observations of flexible, highly tactical behaviors in a variety of species generally have been theory-driven. Behavioral ecology models often have predicted the evolution of sophisticated means of self-interest prior to the empirical work revealing their presence. Risk-averse foraging choices⁷² and facultative shifts in scrounging behavior²¹ are examples. In like fashion, paleoanthropology surely will benefit from greater attention to behavioral ecology theory and observations. We might take a cue from Darwin himself and try to imagine the *Descent of Man*, had it been written with full awareness of these new models and studies.

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REFERENCES

- 1 Borgerhoff Mulder M (1991) Human behavioural ecology. In Krebs, JR, Davies NB (eds), *Behavioural Ecology: An Evolutionary Approach*, 3rd ed. Pp 69–98. Oxford: Blackwell.
- 2 Cronk L (1991) Human behavioral ecology. *Ann Rev Anthropol* 20:25–53.
- 3 Smith EA (1992) Human behavioral ecology: I. *Evol Anthropol* 1:20–25.
- 4 Smith EA (1992) Human behavioral ecology: II. *Evol Anthropol* 1:50–55.
- 5 Smith EA, Winterhalder B (1992) *Evolutionary Ecology and Human Behavior*. New York: Aldine de Gruyter.
- 6 Kaplan H, Hill K (1985) Food sharing among Aché foragers: Tests of explanatory hypotheses. *Curr Anthropol* 26:223–246.
- 7 Smith EA (1988) Risk and uncertainty in the 'original affluent society': Evolutionary ecology of resource-sharing and land tenure. In Ingold T, Riches D, Woodburn J (eds), *Hunter-Gatherers, Vol I: History, Evolution and Social Change*, pp 222–251. New York: Berg.
- 8 Hawkes K (1992) Sharing and collective action. In Smith EA, Winterhalder B (ed), *Evolutionary Ecology and Human Behavior*, pp 269–300. Hawthorne, NY: Aldine de Gruyter.
- 9 de Waal FBM (1989) Food sharing and reciprocal obligations among chimpanzees. *J Hum Evol* 18:433–459.
- 10 Blurton Jones NG (1984) A selfish origin for human food sharing: Tolerated theft. *Ethol Sociobiol* 5:1–3.
- 11 Blurton Jones NG (1987) Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Soc Sci Inf* 26:31–54.
- 12 Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 211: 1390–1396.
- 13 Axelrod R, Dion D (1988) The further evolution of cooperation. *Science* 242:1385–1390.
- 14 Winterhalder B (1996) A marginal model of tolerated theft. *Ethol Sociobiol* 17:37–53.
- 15 Hawkes K (1992) On sharing and work. *Curr Anthropol* 33:404–407.
- 16 Hawkes K (1993) Why hunter-gatherers work: An ancient version of the problem of public goods. *Curr Anthropol* 34:341–361.
- 17 Stephens DW, Krebs JR (1986) *Foraging Theory*. Princeton: Princeton University Press.
- 18 Giraldeau Luc-A, Hogan JA, Clinchy MJ (1990) The payoffs to producing and scrounging: What happens when patches are divisible? *Ethology* 85:132–146.
- 19 Caraco T, Giraldeau Luc-A (1991) Social foraging: Producing and scrounging in a stochastic environment. *J Theor Biol* 153:559–583.
- 20 Vickery WL, Giraldeau Luc-A, Templeton JJ, Kramer DL, Chapman CA (1991) Producers, scroungers, and group foraging. *Am Nat* 137:847–863.
- 21 Giraldeau Luc-A, Soos C, Beauchamp G (1994) A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behav Ecol Sociobiol* 34:251–256.
- 22 Hart TB, Hart JA (1993) The ecological basis of hunter-gatherer subsistence in African rain forests: The Mbuti of eastern Zaire. In Pulford MH (ed), *Peoples of the Ituri*, pp 36–61. Fort Worth: Harcourt Brace.
- 23 Bailey RC, Peacock NR (1993) Efe Pygmies of northeast Zaire: Subsistence strategies in the Ituri Forest. In Pulford MH (ed), *Peoples of the Ituri*, pp 102–129. Fort Worth: Harcourt Brace.
- 24 Hill K (1988) Macronutrient modifications of optimal foraging theory: An approach using indifference curves applied to some modern foragers. *Hum Ecol* 16:157–197.
- 25 Kaplan H, Hill K (1985) Hunting ability and reproductive success among male Aché foragers: Preliminary results. *Curr Anthropol* 26:131–33.
- 26 Stanford CB (1995) Chimpanzee hunting behavior and human evolution. *Am Sci* 83:256–261.
- 27 Mesterton-Gibbons M, Dugatkin LA (1992) Cooperation among unrelated individuals: Evolutionary factors. *Q. Rev Biol* 67:267–281.
- 28 Connor RC (1995) Altruism among non-relatives: Alternatives to the 'prisoner's dilemma.' *TREE* 10:84–86.
- 29 Brown JL (1983) Cooperation—A biologist's dilemma. *Adv Stud Behav* 13:1–37.
- 30 O'Connell JF, Hawkes K, Blurton Jones N (1988) Hadza scavenging: Implications for Plio/Pleistocene hominid subsistence. *Curr Anthropol* 29:356–363.
- 31 Winterhalder B (1990) Open field, common pot: Harvest variability and risk avoidance in agricultural and foraging societies. In Cashdan E (ed), *Risk and Uncertainty in Tribal and Peasant Economies*, pp. 67–87. Boulder, CO, Westview Press.
- 32 Winterhalder B (1986) Diet choice, risk and food sharing in a stochastic environment. *J Anthropol Archaeol* 5:369–392.
- 33 Sigmund K (1993) *Games of Life: Explorations in Ecology, Evolution and Behaviour*. London: Penguin.
- 34 Peterson N (1993) Demand sharing: Reci-

- procity and the pressure for generosity among foragers. *Am Anthropol* 95:860-874.
- 35 Hill K, Kaplan H (1993) On why male foragers hunt and share food. *Curr Anthropol* 34:701-710.
- 36 Dwyer PD, Minnegal M (1993) Are Kubo hunters 'show offs'? *Ethol Sociobiol* 14:53-70.
- 37 Hawkes K (1993) Reply. *Curr Anthropol* 34:706-710.
- 38 Smith EA (1993) Comment. *Curr Anthropol* 34:356.
- 39 Winterhalder B (1997) Gifts given, gifts taken: The behavioral ecology of intra-group, non-market exchange. *J Archaeol Res*, in press.
- 40 Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35-57.
- 41 Boyd R (1988) Is the repeated prisoner's dilemma a good model of reciprocal altruism? *Ethol Sociobiol* 9:211-222.
- 42 Trivers RL (1972) Parental investment and sexual selection. In Campbell B (ed), *Sexual Selection and the Descent of Man*, pp 136-179. Chicago: Aldine.
- 43 Hamilton WD (1964) The genetical evolution of social behaviour. I. *J Theor Biol* 7:17-51.
- 44 Hamilton WD (1964) The genetical evolution of social behaviour. II. *J Theor Biol* 7:17-51.
- 45 Feinman S (1979) An evolutionary theory of food sharing. *Soc Sci Inf* 18:695-726.
- 46 Bliege Bird RL, Bird DW (1996) Delayed reciprocity and tolerated theft: The behavioral ecology of food-sharing. *Curr Anthropol*, in press.
- 47 Wilkinson GS (1988) Reciprocal altruism in bats and other mammals. *Ethol Sociobiol* 9:85-100.
- 48 Wilson DS, Sober E (1994) Reintroducing group selection to the human behavioral sciences. *Brain Behav Sci* 17:585-654.
- 49 Soltis J, Boyd R, Richerson PJ (1995) Can group-functional behaviors evolve by cultural group selection? An empirical test. *Curr Anthropol* 36:473-494.
- 50 Bird-David N (1990) The giving environment: Another perspective on the economic system of hunter-gatherers. *Curr Anthropol* 31:189-196.
- 51 Kelly RL (1995) *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington: Smithsonian Institution Press.
- 52 Sahlins M (1972) *Stone Age Economics*. Chicago: Aldine de Gruyter.
- 53 Lee RB (1979) *The !Kung San: Men, Women, and Work in a Foraging Society*. Cambridge: Cambridge University Press.
- 54 Winterhalder B (1993) Work, resources and population in foraging societies. *Man* 28:321-340.
- 55 Hauser MD, Marler P (1993) Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behav Ecol* 4:194-205.
- 56 Hauser MD, Marler P (1993) Food-associated calls in rhesus macaques *Macaca mulatta*: II. Costs and benefits of call production and suppression. *Behav Ecol* 4:206-212.
- 57 Cartmill M, Pilbeam D, Isaac G (1986) One hundred years of paleoanthropology. *Am Sci* 74:410-420.
- 58 Isaac GL (1984) The archaeology of human origins: Studies of the lower Pleistocene in East Africa 1971-1981. *Adv World Archaeol* 3:1-87.
- 59 Toth N, Schick KD (1986) The first million years: The archaeology of protohuman culture. *Adv Archaeol Method Theory* 9:1-96.
- 60 Blumenshine RJ (1991) Breakfast at Olorogaislie: The natural history approach to Early Stone Age archaeology. *J Hum Evol* 21:307-327.
- 61 Binford LR (1985) Human ancestors: Changing views of their behavior. *J Anthropol Archaeol* 4:292-327.
- 62 Blumenshine RJ, Cavallo JA, Capaldo SD (1994) Competition for carcasses and early hominid behavioral ecology: A case study and conceptual framework. *J Hum Evol* 27:197-213.
- 63 Heinrich B, Marzluff J (1995) Why ravens share. *Am Sci* 83:342-349.
- 64 Stiner MC (1993) Modern human origins — faunal perspectives. *Ann Rev Anthropol* 22:55-82.
- 65 Enloe JG, David F (1992) Food sharing in the paleolithic: Carcass refitting at Pincevent. In Hofman JL, Enloe JG (ed), *Piecing Together the Past: Applications of Refitting Studies in Archaeology*, pp 296-315. Oxford: Tempus Reparatum.
- 66 Wilkinson GS (1990) Food sharing in vampire bats. *Sci Am* 262:76-82.
- 67 Packer C, Rutten L (1988) The evolution of cooperative hunting. *Am Nat* 132: 159-198.
- 68 O'Connell JF (1995) Ethnoarchaeology needs a general theory of behavior. *J Archaeol Res* 3:205-255.
- 69 Stanford CB, Allen JS (1991) On strategic storytelling: Current Models of Human Behavioral Evolution. *Curr Anthropol* 32: 58-61.
- 70 Cartmill M (1990) Human uniqueness and theoretical content in paleoanthropology. *Int J Primatol* 11:173-192.
- 71 Wobst HM (1978) The archaeo-ethnology of hunter-gatherers or the tyranny of the ethnographic record in archaeology. *Am Antiquity* 43:303-309.
- 72 Caraco T, Martindale S, Whittam TS (1980) An empirical demonstration of risk-sensitive foraging preferences. *Anim Behav* 28:820-830.

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Books Received

- Byrne R (1995) *The Thinking Ape: Evolutionary Origins of Intelligence*. New York: Oxford University Press. ix + 266 pp. ISBN 019852188X. \$52.50 (cloth).
- Primack RB, Lovejoy TE (eds) (1995) *Ecology, Conservation, and Management of Southeast Asian Rainforests*. New Haven: Yale University Press. vii + 304 pp. ISBN 0-300-06234-6. \$35.00 (cloth).
- Walker A, Shipman P (1996) *The Wisdom of Bones: In Search of Human Origins*. New York: Alfred A. Knopf, Inc. x + 338 pp. ISBN 0-679-42624-8. \$26.00 (cloth).
- Shore B (1996) *Culture in Mind: Cognition, Culture, and the Problem of Meaning*. New York: Oxford University Press. xvii + 428 pp. ISBN 0-19-509597-9 (cloth).
- Williams GC (1996) *Adaptation and Natural Selection*. Princeton: Princeton University Press. xv + 307 pp. ISBN 0-691-02615-7. \$14.95 (paper).
- Bonner JT (1996) *Sixty Years of Biology: Essays on Evolution and Development*. Princeton: Princeton University Press. x + 143 pp. ISBN 0-691-02130-9. \$24.95 (cloth).
- Markova I, Graumann CF, and K Foppa (eds) (1995) *Mutualities in Dialogue*. New York: Cambridge University Press. xvii + 282 pp. ISBN 0-521-49595-4. \$54.95 (cloth).
- Buss DM, Malamuth NM (1996) *Sex, Power, Conflict: Evolutionary and Feminist Perspectives*. New York: Oxford University Press. vi + 339 pp. ISBN 0-19-509581-2. \$24.95 (paper).
- Hersey GL (1996) *The Evolution of Allure: Sexual Selection from the Medici Venus to the Incredible Hulk*. Cambridge: The MIT Press. xvi + 219 pp. ISBN 0-262-08244-6. \$30.00 (cloth).
- Hauser MD (1996) *The Evolution of Communication*. Cambridge: The MIT Press. xii + 592 pp. 0-262-08250-0. \$55.00 (cloth).
- Vrba ES, Denton GH, Partridge TC, Burckle LH (eds) (1995) *Paleoclimate and Evolution with Emphasis on Human Origins*. New Haven: Yale University Press. v + 547 pp. ISBN 0-300-06348-2. \$85.00 (cloth).