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# Hunting, Sharing, and Multilevel Selection

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## The Tolerated-Theft Model Revisited<sup>1</sup>

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by David Sloan Wilson

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Natural selection is potentially a hierarchical process that can produce adaptive groups in addition to adaptive individuals. The possibility of group selection was largely rejected in the 1960s and replaced with a number of theoretical frameworks that appear to rely exclusively on self-interest. More recently, it has emerged that these frameworks merely view the process of multilevel selection from different perspectives and do not constitute arguments against group selection. The confusion between process and perspective is illustrated with a detailed case study from the anthropological literature. Food is often shared in hunter-gatherer societies, which appears to benefit the group at the expense of the individual provider. The tolerated-theft model attempts to explain food acquisition and sharing as a form of self-interest. I show that the tolerated-theft model is virtually identical to one of the first group-selection models and that the appearance of self-interest is based on the redefinition of terms. I then show how additional insight can be gained by modeling the evolution of hunting and sharing as a multilevel selection process. This detailed case study is intended to contribute to a legitimate scientific pluralism and to a general reassessment of human social groups as adaptive units.

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Evolutionary theories of social behavior suffer from a massive confusion between process and perspective. Theories that invoke different processes count as alternative hypotheses, such that one can be right and the other wrong. However, a single complex process can often be viewed from different perspectives. Multiple perspectives are like the proverbial group of people feeling an elephant in a dark room. One person describes the shape of a trunk, another the shape of an ear, and another the shape of a leg. Together they can piece together the shape of the elephant, as long as none of them argue that they are right and the others are wrong.

This is exactly the problem that has beset the study of social behavior in evolutionary biology. Group-selection theory claims that behaviors sometime evolve because they benefit whole groups even though they are selectively disadvantageous within groups. A consensus emerged during the 1960s that group selection was theoretically possible but so unlikely to occur in nature that it could be ignored (Williams 1966). The rejection of group selection was treated as a major event, allowing evolutionary biologists to focus on self-interest as a grand principle to explain the evolution of social behavior. A number of theoretical frameworks were developed as alternatives to group selection, including inclusive-fitness theory (Hamilton 1964a, b), evolutionary game theory (Trivers 1971, Maynard Smith 1982), and selfish-gene theory (Dawkins 1976, 1982). These theories are correctly viewed as different ways of viewing the same evolutionary process. Few would claim that selfish-gene theory is "right" and inclusive-fitness theory is "wrong"; they merely calculate gene frequency change in different ways and deserve to coexist to the extent that each leads to new insights. The only theory that is excluded from this happy family is group selection. The consensus reached during the 1960s was that group-selection theory invoked a different *process* (natural selection at the group level) that had proven to be insignificant. Group-selection theory was not merely a different perspective but an alternative hypothesis that could be and had been falsified. What has emerged during the past three decades is that this conclusion is false. Group-selection theory is another person in the dark room, feeling the shape of the same elephant.

This article describes the anatomy of the confusion between process and perspective in detail for a single subject. Food is often shared in hunter-gatherer societies, and this appears to benefit the group at the expense of the individual provider (Blurton Jones 1984, 1987; Boehm 1993; Hawkes 1993; Hawkes, O'Connell, and Rogers 1997; Kaplan and Hill 1985a, b; Kaplan, Hill, and Hurtado 1984; Winterhalder 1997). The sharing of large game can be so fair that even when the different portions are weighed with portable scales over a period of months, the hunters who expend the effort receive no more than anyone else (Kaplan, Hill, and Hurtado 1984). A group selectionist would explain these behaviors by saying that groups that hunt and share outcompete other groups. Those who reject group selection are challenged to find explanations based on selective forces

that operate within groups. The tolerated-theft model (Blurton Jones 1984, 1987) is one effort that seems to change the status of hunters from "altruists" to "forager-thieves." However, this change is entirely a matter of perspective and not process. The tolerated-theft model is virtually identical to one of the first models of group selection, proposed by Sewall Wright in 1945.

This article is intended to be read at three levels. First, it advances the study of a single subject, the evolution of food acquisition and sharing in hunter-gatherer societies. Second, it helps to resolve the more general confusion between process and perspective that exists for many other subjects. Third, it serves as a tutorial for how to build a multilevel selection model. Any perspective in science must ultimately prove its worth by producing fresh insights. If the multilevel perspective merely redescribed the results of the tolerated-theft model, it would not merit much interest. As we shall see, however, new insights emerge from multilevel selection theory that easily justify admittance into the dark room.

### Sewall Wright's Model of Group Selection

Because natural selection is based on relative fitness, adaptation at the individual level does not necessarily lead to adaptive groups (Wright 1945, 1961 [1948]; Williams 1966). The classic example is altruism, which benefits the group as a whole but reduces the relative fitness of the altruist within the group. Darwin (1871) was aware of this problem and proposed group selection as a solution. Nonaltruists may outcompete altruists within single groups, but groups of altruists would outcompete groups of nonaltruists within a larger metapopulation. Darwin relied on group selection to explain the suicidal sting of the honey bee and the more virtuous aspects of human behavior (1871:500): "It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and advancement in the standard of morality will certainly give an immense advantage to one tribe over another."

Fisher (1930), Haldane (1932), and Wright (1945) considered group selection as part of their more general effort to place evolutionary theory on a mathematical foundation. Their specific models differed in detail, but all defined individual selection as natural selection within groups and group selection as natural selection based on differences in the survival and reproduction of groups.

Wright spent most of his career studying nonsocial traits such as coat color in guinea pigs (Provine 1986). He became convinced that most traits had a complex genetic basis that impeded natural selection in large randomly mating populations. However, if a large population consisted of many semi-isolated groups, different

genetic combinations might become prominent in different groups and the best of these might ultimately spread through the metapopulation. This conception of evolution became known as the shifting-balance theory, which is still being debated by evolutionary biologists (e.g., Goodnight 1995, Moore and Tonsor 1994). For our purposes, we need to distinguish the evolution of individual traits with a complex genetic basis from the evolution of social behaviors that are selectively disadvantageous in all groups.

Wright considered the problem of altruism only briefly, in a review of George Gaylord Simpson's *Tempo and Mode in Evolution* (Wright 1945). He imagined a trait that benefited the entire group, including the individuals expressing the trait. In addition, the trait had an individual cost that was not shared. He made this idea mathematically precise with the following one-locus model, in which  $p$  is the frequency of the altruistic allele (A),  $b$  represents group benefit, and  $s$  represents individual cost:

$$W_{AA} = (1 + bp)(1 - 2s) \quad (1)$$

$$W_{Aa} = (1 + bp)(1 - s) \quad (2)$$

$$W_{aa} = (1 + bp) \quad (3)$$

It is easy to see that the "selfish" aa genotype has the highest relative fitness because it receives all the benefits of having altruists in the group without paying the cost of being altruistic. Natural selection within groups is totally insensitive to the group benefit because it does not affect *relative* fitness. Mathematically, the  $(1 + bp)$  term cancels out of the equations when fitnesses are compared, leaving the  $s$  term as the only relevant factor. The A allele can easily increase the *absolute* fitness of the AA and Aa genotypes if  $b$  is sufficiently large and  $s$  sufficiently small. Nevertheless, the A allele still cannot evolve because it decreases the *relative* fitness of AA and Aa whenever  $s > 0$ . Natural selection within groups sees only the size of the slice, not the size of the pie. Wright's model accurately captures the basic dilemma that group-selection theory is intended to solve: Natural selection within groups is completely insensitive to the welfare of the group.

Equations 1–3 describe the disadvantage of altruism within groups but do not describe the process of group selection that favors altruism. Wright (1945) did not provide an explicit model of group selection but merely speculated verbally about how it might operate. He imagined that groups were spatially isolated units connected by a trickle of dispersers. If the altruistic gene became established in some of the groups by genetic drift, these might outcompete the selfish groups by persisting longer and producing more dispersers that founded new groups. Unfortunately, subsequent efforts to model Wright's scenario have not been very successful (reviewed by Wade 1978, Wilson 1983). The groups must be very isolated for altruism to drift to fixation, but if they are *that* isolated it is difficult to see how they can compete in the formation of new groups. Even if the model can be fine-tuned to work, it fails to describe the

majority of groups that exist in nature. Wright himself may have had little faith in his own scenario, since he ended his discussion with the following tepid statement: "It is indeed difficult to see how socially advantageous but individually disadvantageous mutations can be fixed without some form of intergroup selection" (p. 417). *Something* like this must be going on, he seemed to be saying, even if this particular version is unconvincing.

Williams and Williams (1957) used Wright's model to show that group selection could be effective in a different kind of metapopulation. They considered a single large randomly mating population in which every female produced a clutch of offspring that interacted only with each other during a period of their life cycle. A good example would be the interactions among baby birds in their nests. Williams and Williams realized that the sibling groups were completely isolated from each other as far as the behaviors expressed among siblings were concerned. The single randomly mating population was not only a population of individuals but also a population of isolated groups that formed and dissolved every generation. In their words (p. 32), "we also use favorable between-group selection to balance unfavorable within-group selection, but our groups are sibships, not mendelian populations."

The Williams and Williams (1957) model was a precursor to a more general conception of groups as relatively ephemeral units that periodically form and dissolve (Maynard Smith 1964; Hamilton 1967, 1975; Wilson 1975). Gene frequency change in the global population can be influenced by fitness differences among individuals within groups and by fitness differences among groups within the metapopulation. Mathematical models, laboratory experiments, and field studies based on this multilevel view show that group selection can be a significant evolutionary force (reviewed by Sober and Wilson 1998, Wilson 1997*b*, Wilson and Sober 1994).

In summary, Wright's model of group selection described the disadvantage of altruism within groups but did not include the process of group selection that favors altruism. His verbal speculations about group selection assumed that groups were spatially isolated units connected by a trickle of dispersers, but groups can also be envisioned as relatively ephemeral units that periodically form and dissolve. Subsequent research has shown that group selection can be effective in the latter kind of metapopulation. It is therefore reasonable to expect the evolution of behaviors that benefit whole groups (represented by *b* in Wright's model) despite a selective disadvantage within groups (represented by *s* in Wright's model).

## The Tolerated-Theft Model

Blurton Jones (1984, 1987) advanced the provocative thesis that hunters share large food items with members of their group because it would be more costly for

them not to share. His argument consists of two parts. First, why should hunters share? Blurton Jones argues that the have-nots are more willing to fight for a piece of the carcass than the haves are willing to defend it, an imbalance that exists until the carcass is evenly divided. Second, if hunters must share, why should anyone bother to hunt? Blurton Jones argues that hunting can be individually advantageous despite the fact that the benefits will be shared by others who do not pay the cost.

It will be helpful to consider these arguments in reverse order. Blurton Jones (1987) illustrates his second argument with a numerical example shown in table 1. A group of ten individuals is divided into *x* hunters and (10 - *x*) scroungers. All hunters must share their catch equally. However, hunters are away from the group 25% of the time and miss the opportunity to share during these periods. This specific assumption may not be realistic, since food is often reserved for absent hunters and their families are present in any case (Hawkes 1993). Nevertheless, the 25% disadvantage can be interpreted more generally as the cost in time, energy, and risk associated with hunting. It should be obvious that hunters increase the fitness of everyone in the group but have the lowest relative fitness within the group. Blurton Jones acknowledges these facts but nevertheless describes hunting as a form of self-interest (p. 445):

It can be seen . . . that under these conditions foragers always do worse than scroungers. We can also see that the bigger the proportion of foragers there are in the group, the better everyone does. But if we

TABLE 1  
*The Tolerated-Theft Model of Blurton Jones (1987)*

Hunters	Scrounger's Share	Hunter's Share	Total Catch
1	205.1	153.8	2,000
2	421.0	315.7	4,000
3	648.6	486.5	6,000
4	888.9	666.7	8,000
5	1,142.8	857.1	10,000
6	1,411.7	1,058.8	12,000
7	1,696.9	1,272.7	14,000
8	2,000.0	1,500.0	16,000
9	2,322.6	1,741.9	18,000
10	-	2,000.0	20,000

NOTE: Each group contains *x* hunters and 10 - *x* scroungers. Each hunter contributes 2,000 g of food which is shared equally among all members of the group who are present. Scroungers are present all the time, but hunters are absent 25% of the time. By comparing the hunter's share with the scrounger's share for any row, the hunters can be seen to have the lowest relative fitness within groups, regardless of the number of hunters in the group. For the egoist, the comparison is between being a scrounger in a group of *x* hunters or a hunter in a group of *x* + 1 hunters (including himself). This comparison is given by the diagonal lines, which indicate that the egoist should become a hunter if there are fewer than four hunters in the group.

consider the outcome for an individual deciding whether to become a forager (and as a result change the composition of the group), we see that only at a quite low frequency of foragers is there a gain for a scrounger in becoming a forager (row 3 to row 4). At high frequencies of foragers we see that there is a gain for a forager in becoming a scrounger (row 5 to row 4). Consequently, there is an equilibrium mixture of forager-thieves and full-time scroungers.

The first part of this passage makes it clear that Blurton Jones's model is virtually identical to Wright's model, in which individuals provide benefits for the whole group (including themselves, represented by  $b$  in Wright's model) at a cost that is not shared (represented by  $s$  in Wright's model). Indeed, a 25% fitness disadvantage within groups is an exceptionally strong selection pressure (Endler 1986). Nevertheless, hunting is classified as a form of self-interest by appealing to an individual decision-making process. To follow the logic of this argument, consider the ruminations of a scrounger in a group with one hunter (first line of table 1): "As a scrounger, I am currently getting 205.1 grams of meat from the single hunter in my group. If I become a hunter, I will be in a group with two hunters and will get 315.7 grams of meat. Therefore I will become a hunter." The comparison between hunters and scroungers is not being made within a single group (horizontally in table 1) but rather diagonally between a scrounger in a group of  $x$  hunters and a hunter in a group of  $x + 1$  hunters. Now consider the same scrounger in a group with four hunters: "As a scrounger, I am currently getting 888.9 grams of meat from the four hunters in my group. If I become a hunter, I will be in a group with five hunters and will get 857.1 grams of meat. Therefore I will remain a scrounger." On the basis of this *psychological reasoning process*, Blurton Jones concludes that the *evolutionary process* will produce an equilibrium mix of hunters and scroungers at a frequency of approximately 0.4. He also concludes that hunting is a form of self-interest that can be explained without any reference to group-level benefits.

### The Confusion between Process and Perspective

One purpose of this article is to use the tolerated-theft model to illustrate the general confusion between process and perspective in the study of social behavior. Blurton Jones (1987) began his paper with two standard cautions: First, explanations of social behavior must "rely only on individual interests and not on the long range benefits to the group" (p. 32). Second, the proximate psychological mechanisms that motivate behavior "are irrelevant to the task of assessing the costs and benefits of behavior and calculating what would be an adaptive response to particular circumstances" (p. 34). Nevertheless, these cautions did not prevent him from

reinventing Wright's model of group selection and explaining it in terms of a psychological decision-making process. Furthermore, his analysis was warmly received without anyone's noticing that something was amiss.

In my opinion, this bizarre state of affairs can be attributed to the fact that most evolutionary biologists rejected group selection so strongly that they stopped reading the primary literature. As knowledge of group-selection models faded, the term "individual selection" took on a broader range of meanings than "natural selection within single groups." According to Blurton Jones (personal communication), it never even crossed his mind to think of his model in the context of group selection. Like many who think they have rejected group selection, Blurton Jones employed the following rule of thumb to predict which of two alternative behaviors will evolve by natural selection: If an individual performs  $x$ , then he will have a fitness of  $W_x$ . If the individual performs  $y$ , then he will have a fitness of  $W_y$ . Behavior  $x$  will evolve when  $W_x > W_y$ , and of course it evolves by "individual selection." This rule of thumb is tantamount to assuming that natural selection maximizes the absolute fitness of individuals. It also resembles the ruminations of a psychological egoist, who cares only about his own welfare without regard to others.

Unfortunately, this rule of thumb says nothing whatsoever about *relative* fitness, which, as Williams (1966) stressed, is the criterion for all evolution by natural selection. We must therefore confirm the rule of thumb with a proper model that is based on relative fitness. If a behavior increases *only* the fitness of the actor, without any effects on other members of the group, then increasing absolute individual fitness also increases relative fitness within the group. Group selection is not required to explain these behaviors. However, hunting in the tolerated-theft model extends beyond the individual to benefit the entire group. In this case, increasing absolute fitness reduces relative fitness within the group. Unfortunately, this nuance is lost on those who regard group selection as a dead issue and rely on thinking like an egoist to predict what evolves by natural selection.

To summarize, the tolerated-theft model claims that the evolution of hunting can be explained without invoking group selection. In addition, the rule of thumb "Maximize absolute fitness" is used to predict an equilibrium frequency of approximately 40% hunters in the population. The first claim is false. Hunting in the tolerated-theft model would be classified as a group-level adaptation by Wright (1945), Williams and Williams (1957), and more recent approaches to multilevel selection theory such as the Price equation (Price 1970, 1972; Hamilton 1975; Frank 1995) and contextual analysis (Heisler and Damuth 1987; Goodnight, Schwartz, and Stevens 1987; Goodnight and Stevens 1997). To evaluate the second claim, we must go beyond rules of thumb and build a proper model of natural selection within and between groups.

## A Multilevel Selection Model of Food Sharing

Following Blurton Jones (1987), consider a metapopulation that is divided into a large number of groups of size  $N = 10$ . Let  $P$  equal the proportion of hunters in the metapopulation and  $p_i$  equal the proportion of hunters in any single group ( $i$ ). We assume that hunting is not the only source of food so that it is possible for a group of 10 scroungers to survive. Hunting increases a baseline fitness that can be ignored because it is the same for all individuals. Every hunter contributes 2,000 g of meat, which is divided equally among members of the group who are present. Scroungers are always present, but hunters are absent 25% of the time. For the moment, assume that fitness is directly proportional to the amount of meat that is obtained. The fitness of hunters in any single group ( $i$ ) is then proportional to

$$W_h(p_i) = 1,500p_i/(1 - .25p_i) \quad (4)$$

and the fitness of scroungers to

$$W_s(p_i) = 2,000p_i/(1 - .25p_i). \quad (5)$$

These are the equations that Blurton Jones used to generate table 1, which are shown graphically in figure 1. Any vertical slice of this graph shows the fitness of hunters and scroungers ( $y$ -axis) in a particular group with  $10p_i$  hunters ( $x$ -axis). The fact that the lines do not

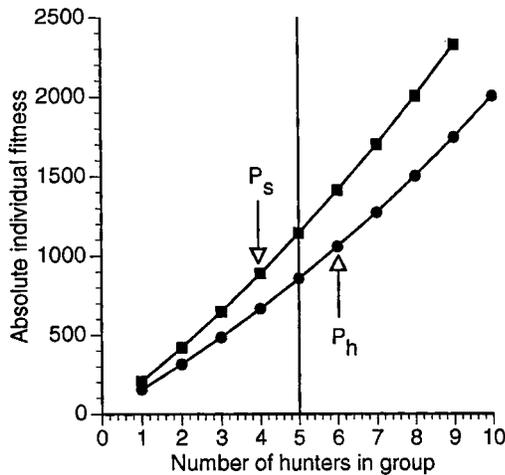


FIG. 1. The fitness of hunters (circles) and scroungers (squares) as a function of the number of hunters in the group ( $x$ -axis). Hunters increase the fitness of the group (positive slopes) but have the lowest relative fitness within groups. The vertical line indicates the number of hunters in the average group, while the arrows indicate the number of hunters experienced by the average hunter ( $p_h$ ) and the average scrounger ( $p_s$ ). The points identified by the arrows indicate the relative fitnesses of hunters and scroungers in the metapopulation (as opposed to a single group).

cross means that hunters always have the lowest relative fitness within single groups. The fact that the lines have a positive slope means that everyone benefits from the presence of hunters in the group. These are the essential features of Wright's model, even though the details of the equations are slightly different. Two ascending lines that do not cross represent the standard model of altruism and selfishness (e.g., Wilson 1977, 1980).

If the metapopulation consisted of only one group, the hunting behavior would quickly become extinct. Something more is required to explain the evolution of hunting. That "something" is the differential productivity of groups. To paraphrase Darwin, although hunting gives but a slight or no advantage to each hunter over the other men of the same group, an increase in the number of hunters will certainly give an advantage to one group over another.

In qualitative terms, selection within groups *always* favors the scroungers, and selection among groups *always* favors the hunters. However, a number of details about the metapopulation must be specified before we can evaluate the relative importance of these opposing forces. Blurton Jones (1987) was even less explicit about the nature of groups than Wright (1945). We will assume that the groups are relatively ephemeral units, lasting from a fraction of a generation to a few generations. Groups are isolated units with respect to sharing; a hunter shares only with members of his group while it exists. However, groups periodically dissolve as individuals or their progeny leave to form new groups. This conception of groups is consistent with the fluid nature of hunter-gatherer societies.

Now that we have specified the nature of groups, natural selection in the metapopulation can be determined by first calculating natural selection within groups and then taking a weighted average across all groups in the metapopulation. We artificially assume haploid reproduction because the genetic details are not specified in the tolerated-theft model or in most game-theory models. In a single group of size  $N_i$  that starts with a frequency of  $p_i$  hunters, the frequency of hunters after selection is

$$p'_i = p_i W_h(p_i) / [p_i W_h(p_i) + (1 - p_i) W_s(p_i)] \quad (6)$$

and the group size is

$$N'_i = 10 [p_i W_h(p_i) + (1 - p_i) W_s(p_i)]. \quad (7)$$

Because scroungers are always more fit than hunters within groups ( $W_s(p_i) > W_h(p_i)$ ), the frequency of hunters always declines within each group ( $p'_i < p_i$ ). However, the size of the group after selection increases in direct proportion to the number of hunters. The frequency of hunters in the global population after selection ( $P'$ ) is the weighted average of frequencies within each group multiplied by the size of the group:

$$P' = \sum p'_i N'_i / \sum N'_i. \quad (8)$$

The summation is across all groups in the metapopulation. The frequency of hunters can actually increase in the global population ( $P' > P$ ) despite the fact that hunters decline in frequency within each group ( $p'_i < p_i$ ), because the frequency of hunters correlates positively with group size after selection (Price 1970, 1972). When this happens, the balance tips in favor of group selection and the hunting trait evolves.

One way to visualize the balance between levels of selection is to calculate the frequency of hunters experienced by the average hunter ( $p_h$ ) and by the average scrounger ( $p_s$ ). Consider the extreme situation in which every group has exactly the same frequency of hunters and scroungers. In this case, both types experience exactly the same frequency of hunters ( $p_h = p_s = P$ ). Now consider the opposite extreme, in which any single group consists entirely of hunters or entirely of scroungers. In this case, the average hunter experiences a frequency of  $p_h = 1$  hunters and the average scrounger experiences a frequency of  $p_s = 0$  hunters. In general, the frequency of hunters in the metapopulation ( $P$ ) does not tell us what is experienced by hunters and scroungers. We must also know how the hunters and scroungers are distributed among the groups. Wilson (1977, 1980) showed that these subjectively experienced frequencies (or "subjective frequencies," for short) can be related to the variance in  $p_i$  among groups ( $\sigma^2$ ) as follows:

$$p_h = P + \sigma^2/P \quad (9)$$

and

$$p_s = P - \sigma^2/(1 - P). \quad (10)$$

When there is no variance among groups ( $\sigma^2 = 0$ ), the subjective frequencies equal the average frequency of hunters in the metapopulation. When there is maximum variance among groups ( $\sigma^2 = P[1 - P]$ ), then  $p_h = 1$  and  $p_s = 0$ , as described informally above. When hunters and scroungers are randomly distributed among groups, variance is given by the binomial distribution ( $\sigma^2 = P[1 - P]/N$ ) and

$$p_h = P + (1 - P)/N \quad (11)$$

and

$$p_s = P - P/N. \quad (12)$$

With binomial variation, the difference between  $p_h$  and  $p_s$  is always  $1/N$ . In other words, when hunters and scroungers are randomly distributed among groups, the average hunter experiences exactly one more hunter in its group than the average scrounger (Eshel 1972; Matessi and Jayakar 1973, 1976; Nunney 1985). As we shall see, this gives the absolute fitness criterion a limited validity.

The effect of group selection can now be calculated by using the subjective frequencies in equations 4 and 5:

$$W_h(p_h) = 1,500p_h/(1 - .25p_h) \quad (13)$$

and

$$W_s(p_s) = 2,000p_s/(1 - .25p_s). \quad (14)$$

Whereas equations 4 and 5 give relative fitnesses within a single group with  $p_i$  hunters, equations 13 and 14 give relative fitnesses over the entire metapopulation and therefore include both within- and among-group selection. Equations 13 and 14 are exactly correct when  $W_h(p_i)$  and  $W_s(p_i)$  are linear functions but only approximately correct when they are nonlinear functions. To obtain the exact solution for nonlinear functions, equations 6–8 must be used.

Subjective frequencies are useful because they allow multilevel selection to be explored graphically, as shown in figure 1. The frequency of hunters in the metapopulation (= frequency in the average group) is given by the vertical line. When groups vary in the frequency of hunters, the subjective frequencies diverge from the average frequency ( $p_s < P < p_h$ ), as shown by the arrows. The points identified by the arrows give the fitness of the average hunter and the average scrounger in the metapopulation. The difference between the relative fitnesses given by the arrows and the relative fitnesses given by the vertical slice is (approximately) the effect of group selection. The diverging arrows have the effect of increasing the fitness of hunters and reducing the fitness of scroungers in the metapopulation. If the arrows diverge enough, then the relative fitness of hunters will be greater in the metapopulation, despite the fact that it is lower within each and every group that contains both types.

Figure 2 shows that group selection can become a significant evolutionary force in three different ways (see also Wilson 1977, 1980). First, increasing variation among groups increases the divergence between  $p_s$  and  $p_h$ . Graphically, as the distance between the arrows widens, it becomes easier to overcome the gap between the fitness functions (fig. 2, left). Second, if we increase the slope of the fitness functions, it becomes easier to overcome a gap between the two lines (fig. 2, center). Third, if we reduce fitness differences within groups, the gap between the two lines narrows. At the extreme of no fitness differences within groups, the lines are superimposed on each other and any amount of variation among groups will be sufficient for the trait to evolve by group selection (fig. 2, right).

These basic principles allow us to draw a number of conclusions about the tolerated-theft model. The gap between the two fitness functions in figure 1 widens with the number of hunters in the group. A greater divergence in subjective frequencies is therefore required to counterbalance within-group selection when hunters are common than when they are rare. Blurton Jones implicitly assumes that the hunters are randomly distributed among groups. Given the numerical values that he uses in his table, random variation among groups is sufficient to select for hunters at a low frequency but not at a high frequency, resulting in a stable equilibrium. The equilibrium point can be found by setting  $W_h(p_h) = W_s(p_s)$ , letting  $\sigma^2 = P[1 - P]/N$  and solving for  $P$ . The (approximate) equilibrium value of  $P = 0.374$  agrees with Blurton Jones's result based on the ruminations of a psychological egoist. The egoist was compar-

ing his fitness as a scrounger in a group of  $x$  hunters with his fitness as a hunter in a group of  $x + 1$  hunters; this comparison is identical to the difference in the subjective frequencies of hunters and scroungers in randomly composed groups (equations 13 and 14). Thus, the rule of thumb “maximize absolute fitness” can be a valid heuristic for predicting what evolves but only if the groups are ephemeral and variation among groups is random. These assumptions should be made explicit because they are often violated in nature. In addition, the rule of thumb correctly predicts what evolves in the metapopulation, not what evolves within single groups. The multilevel selection model makes it obvious that hunting always requires group selection to evolve and that random variation among groups leads to a particular balance between levels of selection.

So far we have merely duplicated Blurton Jones’s original prediction of a polymorphism with hunters at a frequency of approximately 40%. However, the multilevel selection model can be used to derive additional insights that were not forthcoming from the original model. From figure 1 it is obvious that the diverging gap between the fitness functions is important for a stable polymorphism to evolve. Blurton Jones assumed that the cost of hunting is a proportion of kills that are not shared because the hunter is physically absent. The hunter’s family is present, however, and at least some ethnographic accounts suggest that food sharing is extended to members of the group who are not physically present when the food is divided (reviewed by Hawkes 1993). It may therefore be more plausible to assume that hunting involves a fixed energetic cost, in which case

the two fitness functions will be parallel ascending lines, as shown in figure 2. In this case, hunting will either evolve to fixation or not evolve at all, because the variation among groups required to evolve hunting at a low frequency also suffices at a high frequency. Since a polymorphism is one of the most interesting features of the tolerated-theft model, it is important to realize that it depends on the diverging gap between fitness functions, which may be a questionable assumption.

So far we have assumed that fitness is directly proportional to the amount of meat obtained by hunters. It is more reasonable to expect diminishing returns, such that the first kilogram of meat has a larger effect on fitness than the second kilogram, and so on (diminishing returns figure importantly in the question of why hunters share, which will be discussed below). If we incorporate diminishing returns into the fitness functions, they become asymptotic (as shown in figure 1*b* of Blurton Jones 1987), causing the lines not only to diverge (increasing within-group selection) but to flatten (reducing among-group selection). With two factors reducing the relative importance of group selection, we would expect the equilibrium to shift in favor of scroungers.

Our analysis so far is based on the assumption that hunters and scroungers are randomly distributed into groups. Nonrandom distributions can arise in a number of ways. If groups are composed of genetic relatives they will be nonrandom samples of the global population. In the extreme case of clonal reproduction, each group will consist of all hunters or all scroungers and the arrows will extend to the edges of the graph. Hamilton (1975) was among the first to recognize that the entire theory

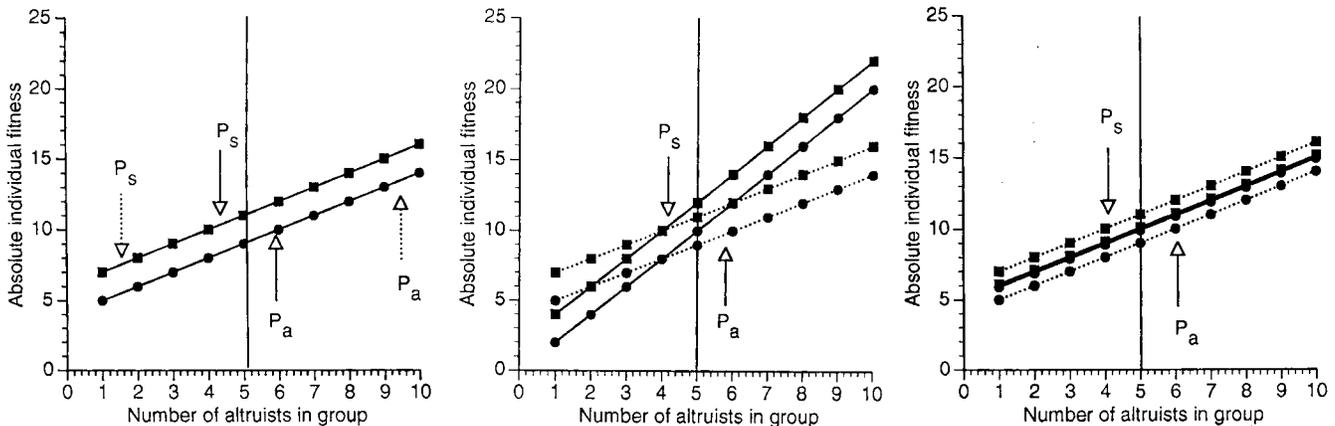


FIG. 2. Three factors that increase the relative importance of group selection. The fitness of altruists (= hunters in the tolerated-theft model) and of nonaltruists (= scroungers in the tolerated-theft model) is indicated by the circles and squares respectively. The vertical line indicates the number of hunters in the average group, while the arrows indicate the number of hunters experienced by the average altruist ( $p_a$ ) and the average scrounger ( $p_s$ ). Left, increasing variation among groups increases the difference between  $p_a$  and  $p_s$  (compare dotted arrows with solid arrows). Center, increasing the slope of the fitness functions makes it easier for the fitness of altruists to exceed the fitness of nonaltruists (compare dotted fitness functions with solid fitness functions). Right, decreasing the gap between fitness functions makes it easier for the fitness of altruists to exceed the fitness of nonaltruists (compare dotted fitness functions with solid fitness functions).

of kin selection can be understood in terms of multi-level selection theory (see Hamilton 1996 for an autobiographical account). Assortative interactions among nonrelatives provide another way for nonrandom groupings to form (Wilson and Dugatkin 1997). Since hunting and scrounging are observable behaviors, hunters might form groups of their own and leave the scroungers to fend for themselves. At the extreme, groups will consist of all hunters or all scroungers and within-group selection will be eliminated, just as for clonal reproduction. Assortative interactions are often discussed under the heading of reciprocal altruism (Trivers 1971, Alexander 1987), which is regarded as an alternative to group selection, but it should be obvious that they fit naturally into the multilevel selection framework.

The usual effect of genetic relatedness and assortative interactions is to increase genetic and phenotypic variation among groups, facilitating the evolution of altruism (= hunting in the tolerated-theft model). Blurton Jones discusses these effects but does not attempt to incorporate them into his model, nor is it obvious how he would have done so. They are easily incorporated into the multilevel selection model by determining how a given degree of relatedness or pattern of assortative interactions influences the distribution of hunters and scroungers among groups.

So far we have assumed that the metapopulation consists of pure hunters and pure scroungers. Of course, real people are expected to employ conditional strategies that allow them to hunt in some situations and scrounge in others (Winterhalder 1997). This is an important part of the tolerated-theft model, in which the

decision to hunt is based on the number of other hunters in the group.

To incorporate conditional strategies into our multi-level selection model, consider 11 strategies of the form "Become a hunter if there are fewer than  $x$  other hunters in the group," where  $x$  is an integer from 0 to 10. Type  $x = 0$  is a pure scrounger, type  $x = 10$  is a pure hunter, type  $x = 4$  hunts only if there are fewer than four other hunters in the group, and so on. These strategies were pitted against each other in a computer simulation that included the following steps:

1. The metapopulation initially consists of all 11 strategies in equal proportions.
2. Five hundred groups of size  $N = 10$  are formed by sampling at random from the metapopulation.
3. Within each group, individuals become hunters or scroungers depending on their strategies and the composition of the group. There is a unique solution for every group that satisfies the strategies of all group members, as shown for two groups in table 2. For both groups, the types with the largest  $x$ -values become hunters, down to a threshold below which everyone is a scrounger. In the second group, seven hunters would exist if all  $x = 5$  types became hunters and four hunters would exist if all  $x = 5$  types became scroungers. Both of these violate the  $x = 5$  strategy, so the unique solution involves one  $x = 5$  type becoming a hunter and the other two becoming scroungers. Each group ends up with five hunters, despite the fact that they differ in their composition of types.
4. Within each group, the fitness of each type is determined from table 1 on the basis of the number of hunt-

TABLE 2  
*Conditional Strategies*

Type ( $x$ )	Group 1			Group 2		
	Number	Hunters	Scroungers	Number	Hunters	Scroungers
0	3	—	3	0	—	—
1	0	—	—	1	—	1
2	0	—	—	1	—	1
3	2	—	2	1	—	1
4	0	—	—	0	—	—
5	1	1	—	3	1	2
6	1	1	—	0	—	—
7	1	1	—	1	1	—
8	2	2	—	0	—	—
9	0	—	—	2	2	—
10	0	—	—	1	1	—

NOTE: Here two groups of 10 individuals follow the conditional strategy "hunt if there are fewer than  $x$  other hunters in the group," where  $x$  can vary from 0 to 10. For each group, there is a unique solution in which the strategies of all individuals are satisfied, which involves the highest values of  $x$  becoming hunters down to threshold, below which everyone is a scrounger. In group 2, the threshold exists within the  $x = 5$  category, causing one individual within this category to become a hunter and the other two to become scroungers. The groups are phenotypically identical (with 5 hunters) despite the fact that they are genetically different.

ers in the group and whether the type has become a hunter or a scrounger (or both).

5. The progeny of all groups combine to form a new metapopulation. Each group returns a lower fraction of types that became hunters than entered the group, but groups with more hunters contribute more than groups with fewer hunters. The balance between these opposing forces determines the new frequency of types in the metapopulation, from which a new set of groups is randomly drawn.

6. Steps *b–e* are repeated until the relative frequencies of the strategies in the metapopulation reach an equilibrium.

The results of the simulation are surprising. As we have seen, a metapopulation of pure hunters and pure scroungers reaches a stable equilibrium in which the average group has 3.8 hunters. When the full range of conditional strategies—including the original pure types—is added, only types  $x = 0, 1,$  and  $2$  persist in the metapopulation, and the average group has approximately 1.5 hunters. How can we explain this counterintuitive result?

The answer involves the effect of conditional strategies on phenotypic variation among groups. When the metapopulation consists of pure hunters and pure scroungers, phenotypic variation among groups is linked directly to genetic variation: Both the frequency of  $x = 10$  types and the frequency of hunters follow a binomial distribution with a mean of  $P$  and a variance of  $P(1 - P)/N$ , as shown by the line with square symbols in figure 3. Conditional strategies make the rela-

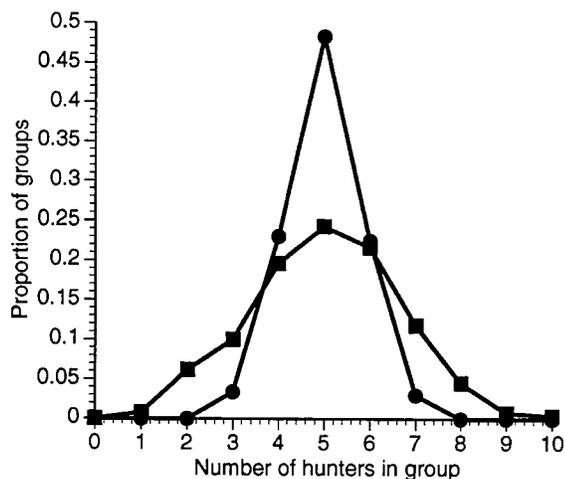


FIG. 3. The proportion of groups in the metapopulation (y-axis) with  $x$  hunters (x-axis). Hunters are binomially distributed among groups when the metapopulation consists of pure hunters and pure scroungers (squares), but variance among groups is lower (circles) when the metapopulation consists of conditional strategies of the form “hunt only if there are  $y$  other hunters in the group,” where  $y$  varies from 0 to 10.

tionship between genetic variation and phenotypic variation more complicated. As illustrated by the two groups in table 2, groups can be genetically different but phenotypically identical. The line with circles shows the variation in the frequency of hunters among groups when all 11 strategies are present at equal frequencies in the metapopulation. Even though *genetic* variation among groups is random, the *phenotypic* variance in the frequency of hunters among groups is less than a third of the binomial variance. Since natural selection at any level requires phenotypic variation in fitness that correlates with genetic variation, conditional strategies weaken group selection, shifting the balance in favor of the scroungers.

Another surprising result is shown in tables 3 and 4. All coexisting genotypes must have the same fitness at equilibrium in an asexual model or else their frequencies would change. In the case of the pure strategies, the genotype-phenotype relationship is direct, so fitness also equilibrates at the phenotypic level (table 3). In other words, when averaged across all groups, the fitness of hunters equals the fitness of scroungers at equilibrium. With conditional strategies, the equilibration of fitness at the genotypic level does *not* result in equilibration at the phenotypic level (table 4). To understand why, consider the fitnesses of types 0, 1, and 2 as hunters and as scroungers in table 4. Type  $x = 0$  is always a scrounger regardless of the number of hunters in its group. Its fitness as a scrounger is therefore averaged over all groups in which it exists. Type  $x = 1$  is a scrounger only in groups that contain one or more hunters. Its fitness as a scrounger is therefore higher than the fitness of type  $x = 0$  because it is averaged over a subset of groups that are more fit than the entire set of groups. The fitness of type  $x = 2$  as a scrounger is even higher because it only becomes a scrounger when there are two or more hunters, and so on. Since the coexisting types have unequal fitnesses as *scroungers*, they must also have unequal fitnesses as *hunters* to have equal fitnesses as *genotypes*. Thus, hunting appears less successful than scrounging when we focus on any single conditional strategy, but no individual can improve its fitness by changing its behavior. The entire logic of comparing alternative behaviors fails because the behaviors are expressed under different background conditions. Even more surprising (and disturbing for game theory), when we ignore the genotypes and calculate the average fitness of hunters and scroungers at the phenotypic level, scroungers appear to be more fit even when the system has reached its genetic equilibrium.

Conditional strategies have a dramatic effect on multilevel selection because they change one of its most fundamental parameters—phenotypic variation among groups. Genetic and phenotypic variation among groups is usually thought to range from random to highly above-random, depending on factors such as the degree of relatedness and assortative interactions. *Below-random* variation among groups has not been seriously considered for lack of a plausible general mechanism. Conditional strategies appear to provide a mechanism

TABLE 3  
*Stable Equilibrium with Pure Strategies*

Type ( $x$ )	Proportion of Hunters	Fitness of Hunters	Proportion of Scroungers	Fitness of Scroungers	Total Fitness
0	0.000	—	1.000	7.693	7.693
10	1.000	7.732	0.000	—	7.732

NOTE: Fitness of average hunter = 7.732; fitness of average scrounger = 7.693. When the metapopulation consists of pure scroungers ( $x = 0$ ) and pure hunters ( $x = 10$ ), the average group has approximately 0.35 hunters at equilibrium, which is the same as the frequency of type  $x = 10$  in the metapopulation. Since the  $x = 0$  and  $x = 10$  genotypes code directly for scrounger and hunter phenotypes respectively, equilibration of fitness occurs at both the genotypic and the phenotypic level. The fitnesses of the genotypes in the last column are not exactly equal because of sampling error caused by a finite number of groups and the use of a random-number generator to determine the composition of each group in the computer simulations.

that leads to highly below-random phenotypic variation among groups, even when genetic variation is random or above-random. The effect is to diminish the importance of group selection, favoring traits that would appear spiteful according to the absolute-fitness criterion. In addition, by complicating the relationship between the genetic and phenotypic composition of groups, fitness does not necessarily equilibrate at the phenotypic level, challenging a fundamental tenet of game theory.

If we want to make these results intuitive by stating them in the form of a psychological reasoning process, it might be as follows: "If I am a scrounger in a group of  $x$  hunters, I will get a certain fitness. If I change my behavior, I *may* become a hunter in a group of  $x + 1$  hunters, but one of the other hunters may turn into a scrounger, leaving me as a hunter in a group of  $x$  hunters and worse off than before." This exercise may help us grasp the results, but it does not substitute for the explicit model that gave us the results, nor does it con-

stitute an argument against hunting as a group-level adaptation.

### Why Share?

Our attempt to answer the question "Why hunt?" is predicated on the assumption that hunters must share. According to Blurton Jones (1987), people should be willing to fight for a resource in direct proportion to its fitness value. A hunter in possession of an entire carcass will be less willing to defend a portion than a scrounger with nothing will be willing to fight for it. In general, if all members of the group have equal fighting ability and if the effect of food on fitness is subject to diminishing returns, willingness to fight for the resource will equilibrate when all group members have equal shares.

Blurton Jones claims that this is a well-established result from game theory (citing Parker 1974 and others),

TABLE 4  
*Stable Equilibrium with Conditional Strategies*

Type ( $x$ )	Proportion of Hunters	Fitness as Hunters	Proportion of Scroungers	Fitness as Scroungers	Total Fitness
0	0.000	—	1.000	3.052	3.052
1	0.056	1.538	0.944	3.155	3.064
2	0.785	2.796	0.215	4.210	3.100

NOTE: Fitness of average hunter = 2.679; fitness of average scrounger = 3.133. When the metapopulation consists of the full range of conditional strategies, the average group has approximately 1.5 hunters at equilibrium and the frequencies of the surviving genotypes in the metapopulation are 0.59, 0.26, and 0.15 for types  $x = 0$ ,  $x = 1$ , and  $x = 2$  respectively. Equilibration of fitness occurs at the genotypic but not at the phenotypic level. Each genotype is more fit as a scrounger than as a hunter, and the fitness of the average scrounger exceeds the fitness of the average hunter. Nevertheless, no individual can increase its fitness by changing its strategy. The fitnesses of the genotypes in the last column are not exactly equal because of sampling error caused by a finite number of groups and the use of a random-number generator to determine the composition of each group in the computer simulations.

but there is an important class of exceptions. The “bourgeois” strategy (Maynard Smith and Parker 1976), in which firstcomers fight harder for a resource than latecomers, succeeds precisely when the cost of fighting exceeds the value of the resource. Similarly, Hirshleifer (1987) and Frank (1988) have argued that revenge and other seemingly costly and irrational emotions have a hidden logic in deterring threat. We need only to contemplate our response to a thief breaking into our home, who probably has much more to gain from the stolen items than we have to lose, to realize that the law of diminishing returns does not always result in equal sharing.

To relate these ideas to the tolerated-theft model, consider the strategy “As a successful hunter, fight to the death for your kill. Do not claim a share of others’ kills.” A population that employs this strategy cannot be invaded by a mutant that attempts to extract a share, despite the law of diminishing returns. The strategy may not be very adaptive at the group level, but that does not affect its internal stability. Now consider the strategy “As a successful hunter, share with others who are also trying to provide public goods to the best of their ability, but fight to the death against scroungers and hunters who do not share their kills.” This strategy is more adaptive at the group level and also cannot be invaded by mutant types that fail to provide public goods. In general, when social incentives are used to reward some behaviors and punish others, an infinite number of internally stable social conventions is possible, ranging from highly adaptive to highly maladaptive at the group level. Boyd and Richerson (1992) explore this topic in a paper provocatively entitled “Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups.”

If an infinite number of internally stable social conventions is possible, how can we predict which will evolve in natural populations? Although all are favored by within-group selection when in the majority, they differ in fitness at the group level. Groups with social conventions that discourage hunting and/or sharing will contribute less to the global population than groups with social conventions that promote hunting and sharing. This process is explored in another paper by Boyd and Richerson (1990) entitled “Group Selection among Alternative Evolutionarily Stable Strategies” that should be required reading for everyone interested in game theoretic approaches to human behavior. To the extent that selection operates among alternative internally stable social conventions, it results in the best of both worlds: a set of traits that is adaptive at the group level *and* favored within groups.

## Discussion

Complex subjects in science are often best studied from a number of different perspectives. A perspective that “sees” the subject in a unique way can achieve insights that are hidden from other perspectives. Alternative

perspectives often make different predictions that cannot both be right. However, the wrong answer can be discarded without rejecting the perspective, which merely “saw” the problem the wrong way in this particular case and can easily be made to “see” the right answer in retrospect. A good example is inclusive-fitness theory (Hamilton 1964*a, b*; Maynard Smith 1964), which initially appeared to predict that altruism should be confined to genealogical relatives. Hamilton (1975) later viewed the same subject from a different perspective (Price 1970, 1972), finding that the coefficient of relatedness ( $r$ ) can be interpreted more broadly and that altruism may not be confined to genealogical relatives after all. The initial prediction of inclusive-fitness theory was wrong but could be corrected without rejecting the entire theory. The advantages of multiple perspectives lead to a legitimate form of scientific pluralism, in which different ways of seeing the world deserve to coexist. However, some theories invoke processes that turn out to be just plain wrong. These theories deserve to be rejected in the way that is usually associated with the falsification of hypotheses. A legitimate scientific pluralism therefore requires the ability to distinguish alternative perspectives from alternative processes.

Group selection is a theory that invokes a certain process to explain the evolution of behaviors that benefit whole groups but are not favored by natural selection within groups. Darwin stated the essential idea when he proposed that groups of morally virtuous people would outcompete other groups even if morally virtuous people did not have the highest fitness within groups. Williams (1966) and others accepted this theoretical framework but questioned whether group selection was a significant force in nature. According to them, behaviors that *appeared* to require group selection could be explained as selectively advantageous within single groups. If this claim were true, then group-selection theory would deserve to be thrown in the dustbin of history. However, it is not true. Modern evolutionary theories of social behavior frequently assume the existence of many groups, and the behaviors that are predicted to evolve frequently do not have the highest relative fitness within groups. These theories may offer a different *perspective* on multilevel evolution, but they do not explain the evolution of social behaviors purely on the basis of natural selection within groups.

It would be hard to overestimate the magnitude of this confusion. *All* of the major evolutionary theories that currently form the foundation for the study of social behavior (inclusive-fitness theory, evolutionary game theory, and selfish-gene theory) were originally proposed as alternatives to group selection. If the differences are merely a matter of perspective, we must return to the basic issues that endowed the controversy with such importance and that seemed to be settled in the 1960s. The question is not whether inclusive-fitness theory, evolutionary game theory, and selfish-gene theory deserve to exist as *perspectives*—even though they fail to provide an alternative to group selec-

tion, they have proven their worth many times over by correctly predicting behaviors that evolve by natural selection. We need to question and reject some major conclusions that have appeared to emerge from these perspectives rather than rejecting the perspectives.

At the most fundamental level, the issue is whether the concept of adaptation can be applied to higher-level units such as social groups (at a variety of scales), species, and multispecies communities. Thinking of higher-level units in functional terms is an ancient intellectual tradition that exists in all branches of science and in everyday thought. Many biologists prior to the 1960s (and a few today) naively operated from within this tradition, assuming that it was consistent with Darwin's theory of evolution. Darwin realized that adaptation at the group level required a corresponding process of natural selection at the group level. His insight was refined by Fisher, Haldane, Wright, Williams, and others and finally came into sharp focus in the 1960s. A philosophical question of the first rank had actually been clarified to the point where it could be scientifically tested: Group-level functionalism is warranted to the degree that natural selection operates at the group level. The rejection of group selection in the 1960s robbed group-level functionalism of all authority in evolutionary biology, an event that has been spreading outward as evolutionary biology gains authority in other scientific disciplines and in popular culture.

This is the conclusion that can be regarded as dead wrong in the light of subsequent developments. When behaviors evolve by increasing the relative fitness of groups, then groups acquire the properties of functional organization that we normally associate with individuals. Thinking of groups as adaptive units is warranted precisely to the degree that natural selection operates at the group level. If inclusive-fitness theory, evolutionary game theory, and selfish-gene theory cannot explain the evolution of social behaviors in terms of the selective forces that operate within single groups, they cannot deny the interpretation of groups as adaptive units.

The original tolerated-theft model makes a number of specific claims about the evolution of hunting and sharing. For example, hunters are predicted to exist at an intermediate frequency that depends on parameters such as group size and the shape of the gain curve relating food to fitness. In addition, the entire analysis is suffused with the language of self-interest, culminating in the following parting words (Blurton Jones 1987:52): "The model suggests we look again at sharing in simple societies. Is it really so altruistic? Or really so reciprocal? Although hunter-gatherers all appear to support the sharing ethic, is there really an undercurrent of threat, appeasement, and personal power behind it?"

Blurton Jones obviously thought that his model was as important for demonstrating the need to think in terms of self-interest as for its specific predictions. Yet, he was *not* claiming that people necessarily think like psychological egoists. Evolutionary theories of altruism and selfishness are based on fitness effects, not the proximate psychological mechanisms that motivate behav-

ior. Blurton Jones would presumably agree with Alexander (1974, 1975, 1979, 1987) that psychological altruism can evolve in a number of ways that are evolutionarily selfish; it is only evolutionary altruism that must be rejected because it requires group selection. I have shown that this interpretation is based on a profound ignorance of the primary literature (see also Sober and Wilson 1998, Wilson n.d.). If Wright's (1945) model doesn't count as an example of group-selection theory, what does?

I do not mean to single out Blurton Jones here; group-selection theory was so thoroughly rejected that even good scholars such as Blurton Jones and his entire audience were no more tempted to read the primary literature on group selection than the primary literature on Lamarckism. Nevertheless, rectifying the situation requires reassessing the concept of self-interest in evolutionary biology. If it doesn't mean psychological egoism, and it doesn't mean the outcome of within-group selection, what does it mean? The answer is that self-interest is defined in a hodgepodge of ways that are seldom distinguished from each other. Self-interest can refer to maximizing relative fitness within groups, absolute individual fitness, inclusive fitness, fitness averaged across all situations, or fitness calculated at the gene level (Wilson and Dugatkin 1992). In each case, the mathematical concept of utility maximization is made intuitive by imagining an agent that "selfishly" strives to increase the utility without regard to anything else. Unfortunately, particular behaviors can appear selfish or altruistic depending on the perspective. Hunting in the tolerated-theft model is altruistic when defined in terms of relative fitness within groups but selfish when defined in terms of absolute fitness. Helping relatives is altruistic when defined in terms of classical fitness but selfish when defined in terms of inclusive fitness. Everything that evolves is selfish according to selfish-gene theory, which averages the fitness of genes across all contexts. There is no single language of self-interest in evolutionary biology. It is a Tower of Babel.

It is pointless to try to confine the use of terms such as "altruism" and "self-interest" to a single perspective. The best we can do is define the terms precisely to facilitate translating between perspectives. In addition, many problems can be avoided by focusing on the concepts of adaptation and natural selection rather than altruism and selfishness (Sober and Wilson 1998). Most evolutionary biologists would agree with the statement "Group-level adaptations require a process of group selection." Once they reeducate themselves on the subject of group selection, they can agree that hunting in the tolerated-theft model is a group-level adaptation, regardless of whether they want to call it altruistic.

These general issues are discussed in more detail elsewhere (Dugatkin and Reeve 1994; Sober and Wilson 1998; Wilson 1990, 1992, 1997a-c, n.d.; Wilson and Dugatkin 1992). In addition, it is important to evaluate the merits of multilevel selection theory at a more technical level. My version of the tolerated-theft model may seem cumbersome compared with the original version,

which uses the rule of thumb “Maximize absolute fitness” as an intuitive guide for predicting what evolves. If both versions produced exactly the same insights, simplicity might be a reason to prefer one over the other. As we have seen, however, the multilevel selection model has produced insights that were not forthcoming from the original model. Evolution in metapopulations is a complicated process. The multilevel selection model is cumbersome precisely because it retains the complexity. The original model achieves its simplicity only by restricting itself to a narrow region of the parameter space with assumptions that are largely unstated, creating an illusion of generality that is unwarranted.

Furthermore, multilevel selection theory has an appealing simplicity of its own, once its elements are understood. Like an exploded diagram of a machine, it allows one to identify the component parts of evolution in metapopulations and to see how they fit together. Natural selection within groups, variation among groups, and the way in which groups contribute to the formation of new groups are all fairly easy to understand as separate processes, after which they can be put together to determine what evolves.

Two results of the model presented here were so surprising to me that I initially attributed them to programming errors. First, it was surprising that hunting evolved to a frequency of .38 with pure strategies (as predicted by Blurton Jones) but a frequency of only .15 with conditional strategies. The reason was eventually easy to understand in terms of multilevel selection theory. Conditional strategies create *below*-random phenotypic variation among groups, even though genetic variation is random. This result has important implications for all models of conditional social interactions, which seldom consider the possibility of below-random variation among groups. It is also ironic that multilevel selection theory was required to identify an important new factor that *reduces* the importance of group selection. The purpose of multilevel selection theory is not to show that group selection is everywhere but merely to identify it where it exists. Second, it was surprising that the average scrounger in the metapopulation was more fit than the average hunter, even though each conditional strategy had the *same* fitness at equilibrium. Work was required to understand the complex interaction between the composition of the group and the decision of each strategy to become a hunter or a scrounger. This result also has important implications for all models of conditional social interactions, which typically assume that the equilibration of fitness at the genetic level will result in the equilibration of fitness at the phenotypic level. Both results were invisible to the perspective that employs the rule of thumb “Maximize absolute fitness” to predict what evolves by natural selection. They required a perspective comprehensive enough to keep track of the various components of evolution in metapopulations.

It remains to evaluate whether multilevel selection theory has shed any new light on the specific topic of

hunting and sharing in human social groups. The original model emphasized the importance of thinking about hunting and sharing as a form of self-interest. Perhaps this provided a needed antidote to previous explanations that naively invoked the good of the group, but now the pendulum needs to swing the other way. Group-level functionalism is a legitimate part of evolutionary biology, and multilevel selection theory provides the tools for determining whether hunting and sharing count as examples of group-level adaptations. In addition, simple rules of thumb that involve thinking like an egoist do not substitute for a proper model of natural selection in metapopulations.

At a more technical level, the tolerated-theft model emphasizes freeloading as a problem in hunter-gatherer society. Multilevel selection theory reveals that this problem may be even worse than Blurton Jones realized, at least given the specific assumptions of his model. However, the second step of his argument (why hunt?) is predicated on a first step (why share?) that can be questioned. Individuals are not always prepared to fight in direct proportion to the value of the resource. A multitude of internally stable social conventions may change the face of the problem. In the future it will be interesting to apply Boyd and Richerson’s model of group selection among alternative stable strategies to the specific topic of hunting and sharing.

The tolerated-theft model has stimulated a number of papers that share an emphasis on self-interest but alter a variety of specific assumptions (Bliege Bird and Bird 1997; Hawkes 1993; Winterhalder 1996, 1997; Hawkes, O’Connell, and Rogers 1997). For example, Hawkes (1993) suggests that men hunt and share as much for social status and sexual access to females as for food per se. This is an important insight, but it does not constitute an argument against group selection. If hunters provide meat as a public good to obtain social rewards, we must explain the evolution of the social rewards, which itself is a multilevel selection problem. If a man defers to a hunter who provides food for the entire group, has he increased his fitness relative to a man in the same group who does not defer? If a woman mates with a hunter who provides food for the entire group, has she increased her fitness relative to a woman in the same group who does not mate? Economists have known for a long time that causing others to provide a public good is itself a public good. When we focus on relative fitness within groups, the role of group selection in the evolution of social incentives becomes clear (Boyd and Richerson 1985, 1990, 1992; Sober and Wilson 1998). Boehm (1997*b*) has recently analyzed the general ethic of egalitarianism from the standpoint of multilevel selection theory, and many of his insights can be applied to the more specific topics of hunting and sharing.

Broad issues in science are sometimes best revealed through detailed case studies. I have used the tolerated-theft model to discuss a number of broad issues, ranging from the legitimacy of group-level functionalism to pluralism in science to the advantages of a particular theo-

retical framework to the nature of hunting and sharing in human groups. I hope that my analysis will contribute to the restructuring of ideas that is necessary to reinstate multilevel selection as an important theoretical tool for understanding the evolution of social behavior.

## Comments

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This is a frustrating paper for anyone who has had a deep commitment to individual selection. Wilson's interpretation of Blurton Jones's model seems like one of those perceptual illusions used by psychologists—look at it one way and it is a picture of an old woman, look at it another way and it is a young girl. If Wilson's goal is to get researchers to look twice at multilevel selection models, he has succeeded. Here he uses an example from classic anthropological behavioral ecology to make an argument that he has been making for the past 20 years. He argues that group selection has been seriously mischaracterized in the past and, contrary to accepted thinking, is an important evolutionary force. He makes the claim that group-selection theory is a different perspective on, not an alternative to, the important tools of evolutionary social theory—inclusive-fitness theory, selfish-gene theory, and game theory. Indeed, viewed from this perspective these models *are* multilevel selection models. In fact, Wilson claims that the tolerated-theft model of Blurton-Jones is identical to a group selection model first proposed by Wright (1945).

This reexamination of group selection has received significant theoretical attention in recent years (see Wilson and Sober 1994) and comes at an important time within the field of evolutionary ecology. Increased attention is being focused on issues related to cooperation (Heinsohn and Packer 1995), alliance formation, and collective action (Harcourt and de Waal 1992) as well as conflict, social parasitism, and cheating (Wrangham and Peterson 1996). Multilevel selection models could provide useful insights into all these issues.

Wilson notes elsewhere (Wilson and Sober 1994) that there is a growing literature in mainstream evolutionary biology that uses multilevel selection models. A recent special edition of *The American Naturalist* was devoted to the topic. While certainly not a justification for a paradigm shift, the increased attention the new models are receiving in standard, well-respected, peer-reviewed journals suggests that a reexamination may be in order. By not taking a hard look at the new models, evolutionary anthropologists *could* risk theoretical stagnation.

Wilson does not restate the "naive" group selection envisioned by Wynne-Edwards (1964) and criticized by

Williams (1966). Rather, his models of multilevel selection are presented as more sophisticated and designed to address many of the problems correctly perceived in the old models. One of the most interesting aspects of the new group selection is that groups are envisioned very differently. Wilson's groups do not have a permanence to them. They are viewed as transitory, periodically dissolving as their component individuals disperse and regroup. As Williams (1966) and others pointed out long ago, selfishness will eventually replace altruism as individual selection drives down the frequency of altruists within groups. This occurs unless groups are ephemeral as Wilson argues. If this is the case, the frequency of altruism can increase in the metapopulation because of absolute fitness advantages. One point that could use some clarification is the time frame involved. Given enough time, individual selection will drive altruists to extinction. Do groups (human or otherwise) split and reform at a rate sufficient for these multilevel models to work?

Surprisingly, Wilson has only one sentence that acknowledges that the social systems of many hunter-gatherers match the assumptions of the multilevel selection model very closely. For example, a recent detailed description of precontact Aché hunter-gatherer social organization describes periodic gatherings of 10–15 small bands from the larger metapopulation. Hill and Hurtado (1996:66, 70–73) describe populationwide meetings in which many bands that had been traveling separately in the forest came together. Areas of the forest were cleared away and males engaged in club fights. After this period of fusion, fighting, and intense social behavior, smaller groups would again split off with compositions different from the initial ones.

The strength of group selection is related to the difference cooperation can make to the success of its members, as well as the benefits of cheating. Nobody disagrees that groups of cooperators have tremendous advantages relative to groups filled with selfish folks. The examples are endless—sports teams, businesses, whaling ship crews, unions, bands of cooperating hunters, baboon alliances. Neither is there any argument that cheaters have an advantage over cooperators within such groups. The real issue with the new perspective provided by Wilson is whether it provides insights not provided by simply assuming individual fitness within the global population as the selection criterion. He claims that it does. For example, the polymorphism (40% hunters, 60% scroungers) predicted by Blurton Jones's tolerated-theft model is maintained because of the divergence of the fitness functions of scroungers and hunters with respect to the number of hunters in each group. This insight could not have been readily obtained without the multilevel perspective.

The other crucial aspect of Wilson's model is how it partitions fitness into within- and between-group components (Reeve and Keller 1997). It seems counterintuitive that a gene or trait can decrease in frequency within each group of a metapopulation yet increase in frequency within the metapopulation as a whole. This

happens if there is a correlation between the frequency of altruists in the group and the success of the group. The individual cost of being an altruist within a group must be less than the absolute benefits of being part of the group, and in this way the multilevel model resembles classic individual selection models. The difference lies in the extra information provided by the partitioning analysis. This perspective has proved useful in some investigations, particularly those that look at within-group social dynamics. An example is Reeves and Keller's (1997) model of social repression of within-group selfishness.

Finally, Wilson also draws attention to some of the semantic confusion in the literature, particularly concerning the term "altruism." The hunters here are selfish when viewed from the perspective of the metapopulation but altruistic when viewed from the perspective of the group (Wilson 1992). Altruism and its evil twin selfishness are two sides of the same coin, it seems, and this, Wilson argues, contributes to much confusion. It implies to some that the altruism produced by group selection is not genuine altruism at all, but with this reasoning neither is the apparent altruism produced by kin selection or any other type of selection (Wilson 1980). If Wilson's work accomplishes nothing else, it will perhaps begin the process of standardizing terms within the field.

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Wilson's critique of Blurton Jones's provocative explanation of meat sharing provides a wider lesson for anthropologists interested in all levels of natural selection. Our long-standing habit has been to depend upon powerful inclusive-fitness arguments, with reciprocal altruism as the only residual explanatory device. The advantage has been parsimony and power. The problem is that in a group-living species noted for sharing and cooperation, it is very difficult to reduce complex webs of behavior that exhibit altruistic components to kin selection and selfishly exact reciprocity (see Alexander 1987). Wilson and Sober (1994) have convinced many scholars that a multilevel approach has greater explanatory power, and this article provides a very welcome technical illustration. There appears to be more to natural selection than inclusive fitness.

Aside from methodological individualism, there are other simplifying assumptions, made so regularly that anthropologists tend to take them for granted, which limit our power to explain. One is that one gene disposes to one behavior, whereas the complex behaviors of humans must be based on polygenes which have pleiotropic effects (Boehm 1981). A different assumption, one posing substantial difficulties (Boehm 1997b), is that genotype and phenotype can be treated as isomorphic. Such isomorphism is challenged by Wilson's convincing simulation, which demonstrates that condi-

tional strategies of individuals weaken otherwise noteworthy group-selection effects. However, in other contexts conditional strategies may actually reinforce the operation of between-group selection. When groups behave as moral communities that promulgate norms of sharing and punish those who deviate too greatly (see Boyd and Richerson 1992), the operation of conditional strategies becomes pronounced and highly patterned (Boehm 1997a). Indeed, social control among nomadic foragers predictably reduces male competition and suppresses dominance tendencies (Boehm 1993, 1997b). When males conform phenotypically to egalitarian social expectations they are pursuing a special kind of conditional strategy which decreases within-group selection but should not be decreasing between-group selection. This multilevel analysis of variation has obvious implications for explaining selection of the altruistic traits that have made so much trouble for inclusive-fitness theory.

Wilson's multilevel approach will not be needed to improve every anthropological argument based on maximization of individual inclusive-fitness, but many of the behaviors we try to explain are involved with social norms that influence group members to follow conditional strategies whatever their (varied) individual genes may be telling them. If groups tend to ostracize liars, thieves, and extravagant free-riders, it becomes apparent to most individual decision makers that the punishment is likely to outweigh the benefits, and at the level of phenotype most people condition their strategies accordingly.

With respect to Blurton Jones's argument, group opinion and responsiveness to it would appear to be an important, immediate explanatory factor in the distribution of large-game meat, as well as one that has important implications if one wishes to discern and account for the levels of selection that are operative. Effects of social control can be considered apart from the tolerated-theft model and apart from the variance-reduction (Winterhalder 1986) and prestige-acquisition (Hawkes 1993) models that also help to explain the evolution of sharing behavior.

For one who has often watched wild chimpanzees harassing one another over meat, Blurton Jones's model has intuitive merit for *Pan*, surely some applicability to foragers in general, and perhaps a special applicability to relatively cantankerous sharers like the Hadza. However, aside from the problems raised by Wilson with respect to levels of selection, this tolerated-theft model should be tempered by serious consideration of the moral nature of the species in question. Conflict over prized resources must be taken into account both by anthropological theorists and by politically sophisticated foragers who are developing and maintaining rules of conduct. And once these rules are in place, morality makes a major difference. Social control helps to make individual strategies conditional, and members of bands tend to behave uniformly. This reduces within-group variation at the level of phenotype and thereby empowers selection at the between-group level when it comes

to support of altruistic traits. Multilevel analysis can be carried farther, for conditional strategies also crop up in the consensual decision making of bands, which both suppresses phenotypic variation within groups and augments phenotypic variation between groups (Boehm 1997b), further assisting the selection of altruistic traits.

As Wilson has demonstrated in this technical exercise, a multilevel approach has important implications for anthropological explanation. He concludes by saying, "Group-selection theory is another person in the dark room, feeling the shape of the same elephant." Perhaps the metaphor could be extended. It is the multilevel selectionist who is in a position to discover that this room is larger than anyone imagined and that there are several *herds* of elephants in it. If anthropologists are interested in creating an adequate explanation of generically altruistic behavior, one that goes beyond mere nepotism, then it may be necessary to examine all of these elephants.

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Language is not a very good tool for doing science. We need verbal summaries of scientific models, but we don't do very well using language to manipulate and develop models. For example "things fall down, not up" is a useful summary of gravity, but it can fail badly (in space) and it doesn't lead to new testable predictions. "Things fall down" is not part of the toolkit of a physicist designing an experiment about gravity. In evaluating Wilson's paper it is important to separate the models from the summaries that Wilson proposes should guide our understanding of social evolution.

There are three themes in the paper: (1) the suggestion that we should incorporate a hierarchical perspective into our language and our thinking about evolution, (2) a description and analysis of his own (Wilson 1975) model of selection in small randomly formed social groups, and (3) the suggestion that meat-sharing among foragers is the result of a process that leads to adaptive groups.

I am not convinced about point 1, that we need a multilevel perspective to think about social evolution, but there may be exceptions. The right example to pursue would be something like the evolution of avirulence in pathogens, where we can only observe the outcome of group effects (i.e., the group of pathogens in an infected individual). Wilson is correct that there is no contradiction between the perspectives and that group selection has been wrongly demonized in the literature of evolutionary biology. At any rate, the whole domain of verbal summaries and perspectives is just not very important for workaday formulation and testing of hypotheses, so this is an issue of more interest to philosophers and journalists than to scientists.

Wilson's important model of group selection, his second point, deserves careful examination. It is technically correct, but the equations can be rewritten any number of ways. I don't think that his style is the simplest or the most useful for generating testable predictions. He shows that selection on social interactions in random groups of an encompassing metapopulation can favor indiscriminate group-beneficial behaviors even though there is some fitness cost to the beneficent actors because the total reproductive output of groups that happen to have more beneficent actors is greater. In his model the actor receives part of the group benefit, and the condition for it to work is just that the total benefit to the actor ( $1/N$  of the benefit to the group) be greater than the cost. This condition is just that the individual benefit to the beneficent actor be greater than the cost to the beneficent actor: the model can be recast into one of simple selection on individuals, and there is no need to account for within- and between-group fitnesses. A concrete example helps.

Imagine that I am one of ten in a group and that, at the cost of one-half a duck of fitness, I bring back ten ducks that are shared equally with the nine other members of my group. If groups are formed at random, then the ducks that I give away have no effect at all on gene frequency change, since the recipients are a random sample of the whole population. Beneficence changes absolute population fitness but has no effect on relative fitnesses. I get one duck in fitness at the cost of one-half duck expenditure, so it is to my advantage to go duck hunting. This is precisely the model that Wilson has described (Wilson 1975). The conditions of this model are very important: there are exactly two types in the population, scroungers and nine-duck-sharers. We are not considering any richer set of alternatives. Nine-duck-sharers evolve to fixation because they have higher relative fitnesses (by one-half duck) than scroungers. At the same time evolution has led to more adaptive groups, that is, to a higher population mean fitness.

But there is nothing in this mechanism that favors sharing over doing anything else with the other nine ducks. The fitnesses are precisely the same of (1) sharing nine ducks, (2) discarding nine ducks on the way home, or (3) poisoning nine ducks, sharing them, and doing away with the rest of my group. These traits would have very different effects on population mean fitness, but they are all equal in the metric of individual relative fitness. Furthermore, nine-duck-sharing would be rapidly replaced by better strategies such as eating all ten ducks myself, eating five and giving five to my brother, etc. In other words, there is nothing in Wilson's mechanism that favors adaptive groups over maladaptive groups. There is a suggestion in this paper and other of Wilson's papers that there is a pervasive pressure from this group-selection mechanism toward group adaptation, but I do not think that it is there.

Blurton Jones's model, Wilson's point 3, is slightly more complex than the original Wilson model, since the fitnesses of hunters and scroungers are frequency-dependent, while in Wilson's model mean absolute fit-

ness is frequency-dependent but relative fitnesses are not. In the Blurton Jones model my duck-hunting trip costs me my share of one-quarter of the net harvest of the group rather than the constant one-half duck cost of the simpler model, so the cost varies with the number of other hunters in the group: if there are many other hunters I lose more by going hunting. Blurton Jones's model is sensible, elegant, and leads to testable predictions. If group fitnesses were observable, then it would be useful to cast the model in terms of Wilson's formalism, but we typically cannot observe group fitnesses in any realistic way in foraging societies.

The simulation in this paper of a population with varying conditional strategies and with frequency-dependent fitnesses is very revealing. It is easiest for me to understand it as a group-selection model with reduced among-group variance, but I am not convinced that that is the only way to model it. It is especially important as a case in which genotypes have equal fitness at equilibrium but behaviors do not. The assumption that we can equate behaviors ("strategies") with genotypes is widespread and, as this model shows, not justifiable.

There are two major families of models in the literature that are usually called group selection. One describes extinction of whole groups and repopulation by emigrants from remaining groups. These models were studied intensively in the 1970s, but there are few good examples from nature of the process. The other family, due to Wright, envisions groups emitting a stream of emigrants into a migrant pool, some of whom then enter other groups. In a simple version of this process (Harpending and Rogers 1987) there is just the  $1/N$  advantage described by Wilson, no matter what the migration rate is. Wright suggested that low migration would lead to high variance among groups and that this might favor the evolution of the altruistic trait. Unfortunately, it turns out that the same low migration that leads to high among-group variance also impedes the spread of an altruistic trait, and the two effects almost exactly cancel (see Wilson, Pollock, and Dugatkin 1992 for a similar result). Later Rogers (1990) extended the analysis to more complex forms of migration, including kin-structured migration, in which relatives move together. Surprisingly, the basic findings were the same: there is essentially no group-selection effect. Wilson's model of transient random groups can be regarded as the high migration limit of the more general Wright model, and the more general model does not lead to any stronger selection for adaptive groups.

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We agree with Wilson that (a certain kind of) food sharing in hunter-gatherer societies is a classic public-goods problem. Others wouldn't, including some who have made especially important contributions to the topic

(Hill and Kaplan 1993). In fact, the counter view, that food sharing is a quid pro quo exchange of (necessarily) private goods and *as such* promoted the evolution of distinctively human cognitive capacities, is very influential in evolutionary psychology (Cosmides and Tooby 1992). While agreeing with Wilson about this very important point, we disagree with him about practically everything else. He assumes that because hunting (often) supplies a public good, it necessarily follows that hunting can only be explained as a group-level adaptation. As the extensive work on collective-action problems makes clear, this is a faulty syllogism.

Economists exploring formally identical issues have made headway by looking carefully at the actual costs and benefits to individual suppliers of public goods, finding that suppliers' own costs and benefits (often including "selective incentives," which are additional private benefits) give them an overall net *individual* gain. These social scientists have often assumed that the conflicts between individual and collective interests found in large-scale human societies are absent in small groups (e.g., Olson 1965). Evolutionary biologists (to say nothing of anyone who has ever lived in a family) should know better. More scrutiny of ancillary costs and benefits to individuals, not less, should be the order of the day.

Blurton Jones's tolerated-theft model (1984, 1987) was a landmark contribution to explanations of food sharing because it showed that simple economic defensibility could account for patterns widely assumed to require some longer-term benefit to compensate for the obvious costs of sharing. Cultural anthropologists had traditionally nominated group-level benefits (e.g., Service 1962, Fried 1967). This was unsatisfactory to analysts who saw that costs and benefits to individuals can (and usually do) lead to patterns of behavior that are favored whatever their longer-term effects on the good of the group. In place of a group-level "social function" to explain sharing, many hypothesized individual-level compensation to the sharer in the form of delayed reciprocal returns by recipients. But both the absence of market-like calculations of credit and debt around food and sustained one-way flows in communities of foragers presented major challenges to such hypotheses (Sahlins 1965, Bliege Bird and Bird 1997). Tolerated theft showed another way to view the problem. If foragers did not own the food they acquired, then they would have no right to its exclusive use. Without well-defined property rights potential users might have to defend any claim to a share. The costs of defense and the (individual) benefits to be gained vary with characteristics of the resource. Foods that come in large packages and are acquired unpredictably are especially likely to fail the test of economic defensibility.

Wilson mentions the cost-benefit model for explaining why men hunt developed in Hawkes (1993), claiming that it leaves public-goods problems unsolved and so would still require group-level adaptations to be complete. The argument in that paper depended on Blurton Jones's demonstration that the costs of not

sharing *some kinds* of resources can be too high to pay. If foragers have a choice between targeting foods they expect to keep more of and those of which they expect to keep less, why does anyone ever target the latter? The answer hypothesized in Hawkes (1993) took advantage of Olson's (1965) analysis of the problem of collective action, showing that individuals supply public goods because of selective incentives. These are themselves private goods, something only providers get—something in addition to the public good that all can consume. A satisfactory explanation, *as noted there*, could not leave unsolved collective-action problems around those incentives.

Common ethnographic generalizations suggested that the incentive to hunters might be social attention: Men usually specialize in widely shared resources, while women choose more economically defensible alternatives. Hunting (perhaps because it supplies public goods) is a matter of general interest and marked respect. The verbal model was this: Suppliers would get more attention from other members of the group and thereby have an edge in getting quick responses to their requests for assistance, sexual access, etc. Social attention was the private benefit for public-good providers. No second-order collective-action problem emerged because the model assumed that all individuals served their own interest (in reading cues to dangers or potential benefits) by paying attention to other members of the group. Given some fixed optimal attention budget, each could then adjust the distribution of attention differentially among other group members. Those who allocated more attention to the public-goods suppliers would *by doing so* be more likely to end up on his side of a dispute, in his company in case of a split, increasing the probability of access to future public goods. The analog would be paying attention to an array of renewing resource patches with differential attention to those expected to give higher returns. Men would be more likely to supply public goods because under persistent mating competition they would have more to gain from attracting allies, so social attention would be more valuable to them. Women, in contrast, having more fitness to gain or lose in the welfare of their families, would more likely target economically defensible resources to feed the children.

This public-goods model implies variation in who supplies public goods, when, and how much. More work is in order (and is currently under way) to test whether this model or an alternative which nominates other selective incentives provides better understanding of the costs and benefits individuals incur from resource choices and why those choices vary. Instead of advancing our understanding of the public-goods problem, Wilson has used Blurton Jones's illustration of it as a vehicle to make a formal point about the role that population structure can play in evolution. It is the wrong vehicle. In using it this way Wilson ignores the leverage that Blurton Jones provided for explaining striking features of the empirical variation in food

sharing and resource choice within as well as between hunting-and-gathering communities.

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Wilson's stated aim is to reveal "the anatomy of confusion between process and perspective" in Blurton Jones's (1987) analysis of foraging effort and food transfers. While much of what he has to say is interesting and instructive, ultimately Wilson adds more confusion than he uncovers. The chief reason for this, ironically, is that contrary to his own admonitions he conflates differences between analytical perspectives (structured-deme or multilevel selection versus behavioral ecology) with differences in the particular set of assumptions concerning behavioral and evolutionary mechanisms (his versus those found in Blurton Jones 1987). In other words, Wilson claims to be analyzing the same problem as Blurton Jones but using a different perspective, whereas I claim he is analyzing a quite different problem.

The key substantive issue treated by both Wilson and Blurton Jones is the evolutionary fate of scrounging versus hunting in a hypothetical population of group-living foragers. To analyze this issue, Blurton Jones assumed that selection has shaped conditional strategies (Maynard Smith 1982) or "decision rules" (Krebs 1978) of the form "Hunt if doing so will yield me a larger portion of food; otherwise scrounge from those who do hunt." Thus, his analysis assumes that individuals are strategists who monitor the local socioecological situation and adjust their behavior accordingly so as to maximize their fitness-correlated gains. He considers only a single local group of foragers (varying from 3 to 20 members) and determines the frequency of the hunting tactic under different ecological conditions if all members of this local group follow the aforementioned decision rule. The phenomena under analysis vary over behavioral (rather than evolutionary) time scales, and there is no explicit evolutionary dynamic at all. However, if fitness is a function of food intake and the cognitive mechanisms shaping decision rules have exhibited heritable variation in the past, then there is an evolutionary background to the behavioral story being told. In sum, Blurton Jones adopts the set of assumptions typical of behavioral ecology (Grafen 1984, Krebs and Davies 1991, Smith and Winterhalder 1992).

In contrast, Wilson's analysis is based on a very different set of assumptions. His model consists of multiple groups of ten foragers, forming a structured deme (Wilson 1977) or "metapopulation." Initially he assumes that hunting and scrounging are alternative heritable traits, with no phenotypic (behavioral) variation other than that specified by genotype. Later in the article, he relaxes this assumption and considers the effect of con-

ditional strategies, but of a very different form than found in Blurton Jones; instead of an outcome-based strategy, Wilson assumes that scrounging versus hunting is conditional on group composition: "Hunt if there are fewer than  $x$  others hunting, otherwise scrounge." The dynamic being analyzed takes place over evolutionary (not behavioral) time, and the analytical tools are those of evolutionary population genetics.

As noted, a central contrast between the two analyses concerns population structure and group dynamics. Given his population genetics perspective, it is quite understandable for Wilson to be concerned with population structure and the ways in which local groups sample the metapopulation. But it is incorrect for him to claim that Blurton Jones (1987) models a metapopulation of multiple groups and hence to assert that he "re-invented Wright's model of group selection" without realizing it. A careful reading of Blurton Jones shows that he considers only a single local group; the metapopulation extension is Wilson's alone. Of course, one could argue that Blurton Jones's model makes implicit assumptions about the relation between local groups and the larger population (e.g., that group membership samples the metapopulation randomly), but given the behavioral ecology framework of Blurton Jones's analysis its focus on individual action within a single local group is a reasonable way to frame the analysis. Wilson's model assumes that foraging groups dissolve every generation or so "as individuals or their progeny leave to form new groups" as is "consistent with the fluid nature of hunter-gatherer societies." Although it is ethnographically naive to suppose that hunter-gatherer social dynamics are of a single type (Kelly 1995), in those relatively small and nomadic populations that deserve the appellation "fluid" individuals and families move frequently and independently between local bands, and hence the membership of these groups is more or less constantly reshuffled. I suspect that this would weaken the efficacy of group selection by continually eroding between-group differences.

Thus, Wilson's and Blurton Jones's analyses are radically different in the *process* assumed to underlie the behavioral variation and in the attention paid to evolutionary dynamics. That they yield different answers concerning the expected frequencies of hunting versus scrounging (in the conditional-strategy version of Wilson's model) is due completely to the different assumptions about the processes of heritability and phenotypic variation producing these frequencies. Contra Wilson, it has nothing directly to do with multilevel versus individual selection, except insofar as these perspectives (or, in actuality, population genetics versus behavioral ecology) motivate very different models with divergent assumptions, time scales, and mechanisms. Wilson presents a very interesting model for understanding the evolution of foraging effort, but he misconstrues the fundamental approach as well as the analytical details of Blurton Jones's model. Given this, it is pointless to debate which of the models is correct; given their (dif-

ferent) assumptions, each is correct in a deductive sense. But we might be able to decide which is more plausible, realistic, or empirically testable—a point I return to below.

Wilson makes much of his unexpected result showing the nonequilibration of phenotypic fitness in his conditional-strategy model and claims that this demonstrates that "the entire logic of comparing alternative behaviors fails because the behaviors are expressed under different background conditions." I believe that Wilson is barking up the wrong tree, for the logic of behavioral ecology involves comparing alternative *strategies* (decision rules); when these strategies produce conditional behavior (as is the case with Blurton Jones's model, for example), the behaviors will of course be "expressed under different background conditions." Wilson's result here is an artifact of the way in which he has defined the conditional strategies; as explained in his table 2 and accompanying text, individuals with the same inherited decision rule may often find themselves expressing different phenotypes (e.g., "hunter" versus "scrounger"), while different rules may produce identical phenotypes. But there is no theoretical basis for expecting fitness equilibration of different phenotypes. Rather, evolutionarily stable strategy theory predicts fitness equilibration between *different strategies* that are maintained in a mixed equilibrium (Dawkins 1980).

On the matter of realism, the decision rules Wilson defines in his conditional strategy model strike me as requiring a curious combination of cognitive sophistication and genetic determinism. Instead of deciding whether to scrounge or hunt on the basis of ecologically variable fitness payoffs (Blurton Jones's approach), Wilson's foragers follow genetically determined rules specifying the threshold number of hunters they will tolerate in a group (requiring 11 different decision rules to specify the full range of possibilities in a group of 10 foragers!). In this sense Wilson is modeling rather stupid decision makers who (unlike those of Blurton Jones) are incapable of phenotypically tracking short-term ecological variation in the payoffs to hunting versus scrounging. Yet when (for example) three individuals with genotype "Hunt if there are fewer than five hunters" find themselves in a group with four other hunters, two of them must decide to scrounge while one hunts. The resulting arbitrary assignment of phenotypes would seem to require rather complex cognitive processes and from a game-theoretical viewpoint looks like a game of Chicken nesting within an  $n$ -person Prisoner's Dilemma (Taylor 1987).

In conclusion, I find contradictions between several of Wilson's general points, which I often agree with, and his specific application of these to the case at hand, which I often find faulty. Yes, "psychological egoism" is an unreliable shortcut to evolutionary explanation; but Blurton Jones's analysis is hardly reducible to that rubric. Yes, knee-jerk anti-group-selectionism is as inadequate a basis for evaluating evolutionary explanations as the naive group-selectionism it replaced; but

tolerated theft and the scrounger model (whatever their virtues or failings) were proposed as alternatives to reciprocal altruism, kin selection, and the variance-reduction explanations of sharing, not as alternatives to group-selection explanations. And yet, it is important to distinguish between perspectives and hypotheses; Wilson's article would have been much more successful had he followed his own admonition.

## Reply

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I thank the commentators for their thoughtful remarks. My reply will address the broad subject of multilevel selection and human evolution in addition to the case study of tolerated theft.

*A three-way perceptual illusion.* Alvard compares my article to a perceptual illusion that flips between two configurations—the individual-level perspective of Blurton Jones and the group-level perspective of Sewall Wright. Dawkins (1982) used a similar metaphor to compare selfish-gene theory with the more traditional view of individuals as adaptive units. It is worth combining the metaphors to show how all three perspectives—gene, individual, and group—can be related to each other in a way that avoids important fallacies of the past and present.

According to Dawkins, genes can evolve in two ways—by causing individuals to increase relative to other individuals in the population or by causing themselves to increase relative to other genes within the same individual. The first pathway leads to individual-level adaptations as we usually think of them. The second pathway often leads to the breakdown of individual-level adaptations (e.g., cancer). Both are examples of selfish genes. Thus the selfish-gene concept does not deny the existence of individual-level adaptations but merely shows that they are not inevitable. Individual-level adaptations are expected when the fitness differences are between individuals but not when the fitness differences are within individuals. The question of where fitness differences occur is addressed by the vehicle concept in selfish-gene theory. The traditional view of individuals as adaptive units is fully compatible with selfish-gene theory as long as individuals are the vehicle of selection (Dawkins 1982, Grafen 1984, Maynard Smith 1987).

It is easy to add the group-level perspective to this framework. Genes can evolve in a third way—by causing groups to increase relative to other groups in a metapopulation. When groups are vehicles of selection, they acquire the same properties of adaptation that we normally associate with individuals. Group-level adapta-

tions are just as compatible with selfish-gene theory as individual-level adaptations. It would be wrong to claim that groups invariably evolve into adaptive units (the position aptly termed “naive group selection”), but it would be equally wrong to claim that groups never evolve into adaptive units. The issue must be decided on the basis of where the fitness differences occur—between genes within individuals, between individuals within groups, or between groups within the metapopulation.

Individual selectionists and selfish-gene theorists have always acknowledged group selection as a theoretical possibility, but they have forgotten how to settle the issue empirically. In essence, they ignore the concept of vehicles at the group level (Wilson and Sober 1994, Wilson n.d.). Benefiting oneself by causing one's group to do well and benefiting oneself at the expense of one's group count equally as examples of self-interest, which in turn is used to argue against group selection. This is exactly as wrong as using the selfish-gene concept to argue against individual-level adaptations. Evolutionary biologists have become fully sensitized to naive group selection, but they are often oblivious to this form of naive individual selection.

One purpose of my article was to expose naive individual selection, using the tolerated-theft model as a case study. It is therefore disappointing to see the same error committed by Hawkes, Bliege Bird, and Bird, who state: “Cultural anthropologists had traditionally nominated group-level benefits (e.g., Service 1962, Fried 1967). This was unsatisfactory to analysts who saw that costs and benefits to individuals can (and usually do) lead to patterns of behavior that are favored whatever their longer-term effects on the good of the group.” Consider how this passage reads when we frameshift downward: “Individual selectionists had traditionally nominated individual-level benefits. This was unsatisfactory to analysts who saw that costs and benefits to genes can (and usually do) lead to patterns of behavior that are favored whatever their longer-term effects on the good of the individual.” Both passages fail as arguments against higher-level adaptation. To summarize: Any group-level adaptation can be described in terms of individual advantage by averaging the fitness of individuals across groups, and any individual-level adaptation can be described in terms of gene advantage by averaging the fitness of genes across individuals. To discover where adaptations evolve in the biological hierarchy, we must determine where the fitness differences occur, which is the essence of multilevel selection theory.

*Multilevel selection and social incentives.* Social incentives provide an excellent example of Alvard's perceptual illusion. Hawkes et al. and Smith see social incentives as examples of self-interest, while Boehm sees them as mechanisms that increase the importance of group selection in human evolution. My article focused on an aspect of the tolerated-theft model that ignores social incentives because individuals can freely decide whether to hunt or scrounge. Nevertheless, I have con-

sidered social incentives in more detail elsewhere (Sober and Wilson 1998, Wilson and Kniffin n.d.) and welcome the opportunity to address the issue here.

Fundamentally, social incentives are like any other trait; to see if they function as individual- or group-level adaptations, we must compare fitness differences within and between groups. Consider behavior  $x$  (such as hunting in the tolerated-theft model), which benefits the group at some individual cost. If  $x$  is performed voluntarily, it counts as altruistic in a multilevel selection model because  $x$  is less fit than not- $x$  within groups and groups of  $x$  are more fit than groups of not- $x$ . Now consider behavior  $y$  (such as providing a social incentive to hunt), which causes another individual to perform  $x$ . If  $y$  is performed voluntarily and involves any individual cost, it also counts as altruistic in a multilevel selection model because  $y$  is less fit than not- $y$  within single groups and groups of  $y$  are more fit than groups of not- $y$  (by virtue of causing  $x$ ). For example, if I accord status to a hunter and if according status has any personal cost, then I reduce my fitness compared with that of another member of my group who does not accord status to the hunter. It is true that  $x$  no longer counts as altruistic if its costs are outweighed by the private benefits provided by  $y$  (as pointed out by Hawkes et al.). However,  $y$  does not receive any private benefit for providing its public good and remains altruistic. All we have done is replace one public-goods problem with another.

There are two broad solutions to this problem. One is to focus on the cost of the altruistic behavior. It is only high-cost altruism that poses a problem for multilevel selection theory, requiring special solutions such as genetic relatedness. Random variation among groups is sufficient for low-cost altruism to evolve by group selection. Thus, a private benefit is not required to explain the evolution of  $y$  if the individual cost of providing  $y$  is sufficiently small.

The second solution is to find a private benefit for  $y$ . Hawkes et al. suggest that "those who allocated more attention to the public-goods suppliers would be more likely to end up on his side of a dispute, in his company in case of a split, increasing the probability of access to future public goods." This suggestion is plausible, but it is based on the formation of future groups and does not identify a relative fitness advantage within any single group. In fact, it affords another opportunity to show how multilevel selection theory can be used to explore interesting problems. Suppose that groups are initially created at random.  $Y$ -individuals encourage others to hunt and therefore decrease their fitness compared with that of not- $y$  individuals in the same group. At some point the groups dissolve (as suggested by Alvard's interesting description of the Aché), but the next cycle of group formation is not random. Hunters and their  $y$ -individual supporters stick together, leaving not- $y$  individuals to associate with nonhunters by default. The segregation of  $y$  and not- $y$  into separate groups and the positive correlation of  $y$  with hunters is probably not perfect, however, and not- $y$  has the fitness advantage in

every mixed group. This scenario favors  $y$ -individuals by altering the population structure, not by increasing the relative fitness of  $y$ -individuals within single groups. Furthermore, it is not required to explain the evolution of social incentives. Hawkes et al. imply that the public-goods problem can be solved only by finding a private benefit, ignoring the possibility that low-cost public goods can evolve without private benefits. It is enough for individuals to benefit the group that includes themselves, just as it is enough for genes to benefit the individual.

*Why does perspective matter?* At this point, I imagine Harpending heaving sighs of exasperation. Who cares which perspective we employ as long as we do the math right? One way to answer this question is by describing some of the recent developments in evolutionary biology alluded to by Alvard, which emphasize social control rather than genetic relatedness in the evolution of higher-level adaptive units. For example, the evolution of insect societies has traditionally been explained in terms of relatedness (Hamilton 1964a, b). However, the members of social insect colonies are often less related than previously thought because the colonies include more than one queen and the queens have mated with more than one male. It should often pay for the members of colonies to replicate their own genes, even at the expense of colony function. Examples of these behaviors have been discovered, but they are comparatively rare, in part because individuals who behave "selfishly" are punished by other members of the colony (Ratnieks 1988, Ratnieks and Visscher 1989, Seeley 1995). In short, there are evolutionary pressures to cheat in social insect colonies, but there are also evolutionary pressures to suppress cheating. Social control rather than genetic relatedness explains at least some aspects of insect sociality. Even individual organisms are becoming viewed as highly integrated communities of subunits that led a more free-living existence in the distant past and still have the potential for "selfishly" replicating themselves at the expense of their collective. Organisms have preserved their integrity by evolving a system of genetic and developmental controls that minimize the potential for exploitation from within (Buss 1987; Maynard Smith and Szathmary 1995). The entire lexicon of words describing conflict and control in human groups has been borrowed by evolutionary biologists to describe genetic interactions: "outlaws," "sheriffs," "police," "parliaments," "rules of fairness," and so on.

Comparing human social groups to beehives and single organisms may have appeared far-fetched on the basis of genetic relatedness, but it appears more reasonable on the basis of social control mechanisms (Sober and Wilson 1998). Indeed, the human capacity for social control in small face-to-face groups might easily compensate for an absence of genetic relatedness. The concept of human groups as superorganisms (or group-level vehicles of selection, to use the language of selfish-gene theory) has become reasonable from the evolutionary perspective. Of course, this is the very proposition that

individual selectionists have been denying for the past 30 years. In Harpending's duck example, he concludes that sharing the ducks is no different from keeping one duck and throwing the rest away. Both are inferior to keeping all the ducks or giving half to one's brother. In general, he concludes that "there is a suggestion in this paper and other of Wilson's papers that there is a pervasive pressure from this group-selection mechanism toward group adaptation, but I do not think that it is there." Harpending might be right in a world without social control—and he might also be a dispersed microbial soup rather than the integrated community of bacteria known as Henry. In a world that includes social control, raw selfishness (keeping all the ducks for oneself), nepotism (giving half to one's brother), and simple wastefulness (throwing the rest away) are often excluded. I am proposing that group selection has been a pervasive pressure leading to many group adaptations in our species. If I can convince Harpending of this claim, presumably he will agree that it is important to view human evolution from a multilevel perspective, even when it is possible to calculate gene frequency change in other ways.

*Returning to the fundamental ingredients of natural selection.* Acceptance of kin selection as a grand explanatory principle has far outstripped knowledge of the actual theory. One of kin selection's many unstated assumptions is that behaviors are coded directly by genes, which means that the only way to create a behaviorally uniform group is to have a genetically uniform group. If the evolution of altruism requires phenotypic variation among groups and phenotypic variation requires genetic variation, then the degree of altruism that evolves should be directly proportional to the amount of genetic variation among groups. This is Hamilton's rule (stated in terms of multilevel selection theory), and it has had a tremendous impact on the way we think about social behavior.

Nevertheless, only a moment's reflection should make it obvious that phenotypic and genetic variation are not so tightly coupled in real organisms. There are many ways to create a behaviorally uniform group even when the members are genetically diverse. It is therefore necessary to step back from kin selection theory and return to the fundamental ingredients of natural selection—phenotypic variation, heritability, and fitness consequences—at each level of the biological hierarchy (Sober and Wilson 1998). When we do this, genetic relatedness assumes its proper place as an element of multilevel selection theory, as one of several factors that influence the ingredients of natural selection. Boehm is one of the first to apply this broader perspective to the study of human groups (see also Boehm 1996, 1997). He argues that social norms, consensus decision making, and other processes impose uniformity upon groups, especially for the behaviors that are mostly likely to influence survival and reproduction. The same processes often cause groups to become different from each other, even when there is considerable migration between groups (e.g., when immigrants adopt the social norms

of their new group). In short, the partitioning of phenotypic variation within and among human groups could never be predicted from their genetic structure and is highly conducive to between-group selection. Phenotypic variation is the first ingredient of natural selection. If there are no behavioral differences within groups, there can be no within-group selection. Of course, phenotypic variation at the group level must be heritable to result in evolutionary change. It might seem that Boehm's kind of phenotypic variation is not heritable because it is not coded directly by genes, but this is a mistaken interpretation of the heritability concept. Heritability is a correlation between ancestral and descendant units that can be influenced by cultural processes and genetic factors that indirectly affect the expression of behaviors (Boyd and Richerson 1985, Sober and Wilson 1998, Wilson and Kniffin n.d.).

Returning to the fundamental ingredients of natural selection may promote a merging of evolutionary and cultural anthropology, which have become almost completely isolated from each other. It is impossible to think about either phenotypic variation or heritability (properly construed) in human groups without considering cultural processes. For example, the expansion of the Nuer at the expense of the Dinka and other neighboring tribes has been studied by cultural anthropologists for over 60 years (reviewed by Kelly 1985 and discussed from the perspective of multilevel selection theory by Sober and Wilson 1998). The Nuer were historically derived from the Dinka but differed in their social organization in a way that allowed them largely to replace their ancestral culture (their expansion was halted by the British in the late 1800s). The main functional difference between the two tribes was that the Nuer were able to field a larger and more coordinated fighting force. Behind the functional difference was a complex set of cultural mechanisms involving animal husbandry practices, bride-price customs, and lineage systems that allowed villages to remain coordinated with respect to fighting even after they had stopped interacting with respect to the daily commerce of life. The cultural differences remained stable despite a massive influx of Dinka into Nuer society.

The Nuer expansion includes all three ingredients of natural selection—phenotypic variation, heritability, and fitness differences—and therefore qualifies as an example of group selection in action even though there were probably no genetic differences between the two tribes. Cultural anthropology and multilevel selection theory have much to offer each other, and I hope that other cultural anthropologists will follow Boehm's lead by forging a connection.

*The evolution of behavioral strategies.* One problem with kin selection and evolutionary game theory is that they make assumptions about population structure but do not make the assumptions explicit. *N*-person game theory implicitly assumes that a very large population randomly sorts into groups of size *N* for purposes of social interaction, after which the groups dissolve back into the global population. The behavioral strategies

that evolve in this population structure are not necessarily favored in other population structures. For example, groups composed of siblings are nonrandom samples of the population at large, and this favors a different set of behaviors than random grouping. As another example, the plantlike deposition of offspring close to parents creates a population structure in which social interactions are not punctuated by a global dispersal stage. Hamilton (1964a, b) thought that this “viscous” population structure would favor the evolution of altruism because it increases the genetic relatedness of neighbors. Limited dispersal does indeed create patches of altruists and nonaltruists, but the many progeny produced by altruistic patches tend to fall back into the same patch and are not exported to other regions of the landscape. At the same time, the advantages of selfishness are local, allowing altruistic patches to be devoured by selfish invaders. Viscous populations are not favorable for the evolution of altruism, a fact that remained invisible to kin selection theory for almost 30 years before it was discovered with a multilevel selection approach (Wilson, Pollock, and Dugatkin 1992, Queller 1992, Taylor 1992). If Smith thinks that behavioral ecologists can ignore population structure, we have a major disagreement, and I don’t see how his argument can be sustained. My model and the original tolerated-theft model have the same purpose—to predict the behavioral strategies that are likely to evolve in a specified social environment. However, Smith may be on more solid ground when he criticizes the particular strategies that I included in my model. The strategy that he has in mind (based on the original tolerated-theft model) is “Hunt if doing so will yield me a larger portion of food; otherwise scrounge from those who hunt.” This strategy results in different decisions depending on parameters such as group size and the shape of the gain curves. The strategies in my model are of the form “Hunt if there are fewer than  $x$  other hunters in your group.” Taken literally, my strategies are too rigid (as Smith notes) because they lead to the same decision regardless of other parameter values. However, my model is confined to a single set of parameter values (shown in table 1), which causes Smith’s strategist to hunt whenever there are fewer than four other hunters in the group. Type  $x = 4$  accurately represents Smith’s strategy for these parameter values, which makes my model more reasonable than he implies.

The problem with the original tolerated-theft model is that it fails to consider the possibility that one individual’s decision to become a hunter might cause an existing hunter to become a scrounger. This possibility can be described in the form of a psychological reasoning process as follows: “If I am a scrounger in a group of  $x$  hunters and I become a hunter, I may be a hunter in a group with  $x + 1$  hunters (the original tolerated-theft model). However, my decision may cause one of the hunters to become a scrounger, leaving me as a hunter in a group of  $x$  hunters (not considered in the original tolerated-theft model).” Smith may be able to devise a strategy that avoids this new consideration, but

he needs to demonstrate it with an explicit model. Until then, I regard the results of my model as valid for the parameter values in table 1.

*Reviving the group-level perspective in anthropology.* Behind all the technical arguments, there is a fundamental issue at stake that can be stated simply: Adaptationism has its problems, but it is undeniably an important tool for understanding the properties of nature. Evolutionary biologists and evolutionary anthropologists have made tremendous progress by asking the simple question “What would individuals be like if they were well adapted by natural selection?” The answers to this question are not always correct, but they provide testable hypotheses that are often confirmed by empirical data. Unfortunately, the equally simple question “What would groups be like if they were well adapted by natural selection?” has been excluded from evolutionary thought on the basis of a consensus that is now over 30 years old and needs to be reexamined. Multilevel selection theory provides a disciplined way to ask the adaptationist question at all levels of the biological hierarchy and to determine the balance between levels of selection in specified social environments.

The group-level perspective has not always been excluded from biological and anthropological thought. Darwin was willing to speculate about group selection, and Wynne-Edwards (1962) was inspired by the anthropologist Carr-Saunders (1922). Most anthropologists during the first half of this century found it reasonable to think about human groups as adaptive units. This literature can be criticized as naive by modern standards, but it cannot be categorically rejected for employing the group-level perspective as Hawkes et al. appear to suggest. I don’t know how often human groups function as adaptive units, but I do know that multilevel selection theory is required to find out.

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